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Ecology of Tropical Rain Forests

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Abstract

Occupying less than 7 percent of Earth's land surface, tropical rain forests harbor perhaps half of the species on Earth and are ecologically, economically, and culturally crucial for issues in global food security, climate change, biodiversity, and human health. Geographically located between the latitudes 10°N and 10°S of the equator, lowland tropical rain forest ecosystems share similar physical structure but vary in geology, species composition, and anthropogenic threats across the forests of Southeast Asia, Australia, Africa, Central and South America. Numerous evolutionary and ecological hypotheses to explain the origin and maintenance of high biological diversity in tropical forests have garnered support and include biogeographic history, evolutionary mechanisms of adaptation and speciation, range size and distribution constraints, and ecological mechanisms promoting species coexistence. Gradients in climate, parent material and soil age, topography and landscape stability, and atmospheric deposition result in strong heterogeneity in soil nutrient availability from local to regional scales. Tropical forests account for approximately 40 percent of terrestrial net primary productivity, store half of Earth's vegetative carbon stocks but less than 10 percent of its soil carbon stocks. Woody lianas are increasing in abundance and biomass in a number of tropical rain forests. The additive effects of an increase in liana biomass are correlated with a reduction in tropical forest carbon (C) storage, a value that is currently not considered in global vegetation models. The tropical biome is undergoing significant change. Stronger El Niño Southern Oscillation effects are increasing the frequency and severity of droughts, fires, hurricanes and cyclones, and flooding events. Recovery of aboveground biomass, species composition, and forest structure all depend on the type and severity of disturbance and its effect on soil fertility. Understanding the drivers and impacts of these changes will require sustained advances across multiple disciplines. Ultimately as a society, we are left asking what is the capacity of our remaining and re-growing tropical rain forests to adapt to long-term anthropogenic and climate change and what can we do to moderate these effects while nourishing a healthy human population?

Keywords

Biodiversity; Carbon; Deforestation; Janzen-Connell; 50 ha plot; Liana; Mycorrhiza; Net Primary Productivity (NPP); Nitrogen; Oil Palm; Phenology; Tropical Rain Forest

Introduction

Along with their extraordinary biodiversity and predominant influences on global carbon (C), nitrogen (N), and water cycles, tropical rain forests provide powerful inspiration that has driven

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biological inquiry for centuries. Theories in biogeography, ecology, and evolution by natural selection crystallized through the South America and Southeast Asian journeys of Alexander von Humboldt, Charles Darwin, Alfred Russel Wallace, and Johannes Eugenius Bülow Warming – considered by some to be the founder of tropical ecology. From the lowland rain forests of Venezuela into the Andes, von Humboldt recorded the change in vegetation with climate, drawing the first conclusions that laid the groundwork for the field of biogeography. Both Darwin and Wallace developed their ideas of evolution by natural selection through their observations of exceptional species diversity in South America and Southeast Asian rain forests. Current research questions in tropical rain forest plant ecology comprise determining the origins and maintenance of such extraordinary genetic, species, and habitat diversity; the factors that regulate net primary productivity (NPP) of intact and disturbed tropical forests; and the consequences of the loss and conversion of these forests on global biogeochemical cycles, water cycles, and ecosystem services.

Occupying less than 7 % of Earth's land surface, tropical rain forests harbor perhaps half of the species on Earth and are ecologically, economically, and culturally crucial for issues in global food security, climate change, biodiversity, and human health. Tropical rain forests share a particular combination of climate parameters, floristic composition, forest structure, and plant physiognomy. Though they differ in geology and climate patterns such as intensity of El Niño Southern Oscillation (ENSO) events, tropical rain forests face the common threats of deforestation, land use conversion, invasive species, and changing climate that require the same dedication to conservation and management practices that best suit the unique socioeconomic and cultural characteristics of each region. Current global, multi-institutional networks, such as the Center for Tropical Forest Science (ctfs.si.edu), monitor the growth and survival of approximately 4.5 million trees and 8,500 species in forests around the world to understand forest function, diversity, and sustainable management to inform natural resource policy and build capacity in the face of climate and land use change.

Biogeography and Climate

Geographically located between the latitudes 10°N and 10°S of the equator, lowland tropical rain forest ecosystems share similar physical structure but vary in geology, species composition, and anthropogenic threats across the forests of Southeast Asia, Australia, Africa, and Central and South America (Fig. 1). Approximately 50 % of tropical rain forests are found in the Neotropics, primarily in the Amazon and Orinoco basin with patches in Central America, the Caribbean, and along the Atlantic coast of Brazil. African rain forests are mainly located in the Congo basin extending to the west coast and remnant forests remain in Madagascar. The Australian tropical realm (Oceania) includes Australia, New Guinea, and the Pacific Islands. During his travels, Alfred Russel Wallace noted distinct faunal, though not necessarily floral, differences between Australia and Southeast Asia and the “Wallace line” denotes this boundary. The severely fragmented areas of South and Southeast Asian rain forests account for less than 30 % of rain forests worldwide and are found in India, Sri Lanka, mainland Southeast Asia, the Malay Peninsula, and Indonesia.

The climate of lowland tropical rain forests is warm, humid, and relatively stable. Tropical rain forests are characterized by mean annual temperatures ranging from 23 °C to 28 °C, with mean monthly temperatures no less than 18 °C and rarely exceeding 35 °C. Diurnal temperature fluctuations typically exceed mean monthly ranges, with annual temperature ranges of less than 5 °C. Tropical biomes do not generally experience frost, even at high elevations, and tropical plants and animals do not tolerate freezing. Local variation in rainfall is much higher than temperature variation. Mean monthly precipitation exceeds 60 mm, and annual precipitation can exceed 10 m in

aseasonal, evergreen rain forests such as the northwestern region of Colombia known as the Chocó. Peak rainfall typically correlates with the intertropical convergence, which lies over the equators during the two equinoxes. In semi-evergreen forests with seasonal variation in precipitation resulting in distinct rainy and dry seasons that drive plant phenological responses, mean annual rainfall is lower, with dry season months characterized by greater evaporative potential than precipitation. Average humidity in the forest understory is approximately 80 % with higher diurnal variation in the canopy.

Biomes within tropical latitudes are distinguished by differences in elevation and the seasonal patterns of rainfall that create a gradient of vegetation from wet, aseasonal rain forest at high and low latitude to seasonal forest, scrub, savanna, and desert. While there is phylogenetic overlap among the plants of tropical rainforests, tropical montane forests, and tropical deciduous forests, the environmental variables driving ecosystem processes and plant adaptations such as fog, in the case of montane forests, and fires and drought in seasonally dry tropical forest are sufficiently different from tropical rain forests and are beyond the scope of this chapter.

Vegetation Structure and Phenology

Vegetation characterization of tropical rain forests can be defined by structural and physiognomic properties that are strongly influenced by physicochemical edaphic factors. Mature tropical rain forests are stratified by multiple canopy and understory layers. The distinct vertical profile of tropical rain forests generally includes emergent trees that arise above the canopy, high upper canopy trees with average height of 30–40 m, low tree sub-canopy, shrub understory, and ground layer of herbaceous plants and ferns (Fig. 2a, b).

Aside from bamboos, grasses are uncommon in most tropical rain forest understories. Epiphytes and woody vines called lianas that rely on trees for structural support to reach the forest canopy are conspicuous, as are tree buttresses that support trees by providing stability in shallow tropical soils (Fig. 3a, b). Approximately three quarters of the world's fern species and half of the world's bryophytes (mosses, liverworts, and hornworts) are found in tropical forests. Physiognomic properties include evergreen broadleaf tree species, a preponderance of species with large leaves to aid with sunlight capture in the light-limited understory, and leaf properties such as entire margins and drip tips that channel water efficiently from the leaf surface. Cauliflory, the development of flowers on tree trunks and main branches, is common in aseasonal tropical understory trees and facilitates pollination by non-volant insects or animals. Not surprisingly, the percentage of deciduous tree species increases with increasing seasonality. Across the strong precipitation gradient along the Isthmus of Panama, deciduous trees account for less than 5 % in more aseasonal forests on the Atlantic to a quarter of tree species in the forest communities on the Pacific side.

Competition for light, water, and nutrients varying over heterogeneous landscapes generate and shape ecophysiological adaptations in plants. Equatorial solar radiation levels are high, and canopy leaves and leaves exposed to direct sunlight experience very different irradiance and humidity than understory leaves. Greater than 99 % of sunlight is absorbed and reflected as the light passes through the forest canopy, resulting in low light intensity and quality in the forest understory where competition for light is high and certain plants can rapidly respond to the patchworks of light created by sunflecks. Life history strategies across the light demanding to shade tolerant spectrum include, at the one end, pioneer species with high photosynthesis and respiration rates and low wood density to slow growing, well-defended, high wood density species that can persist in the understory until a gap forms overhead. Species are aligned across a competition–colonization continuum along a multitude

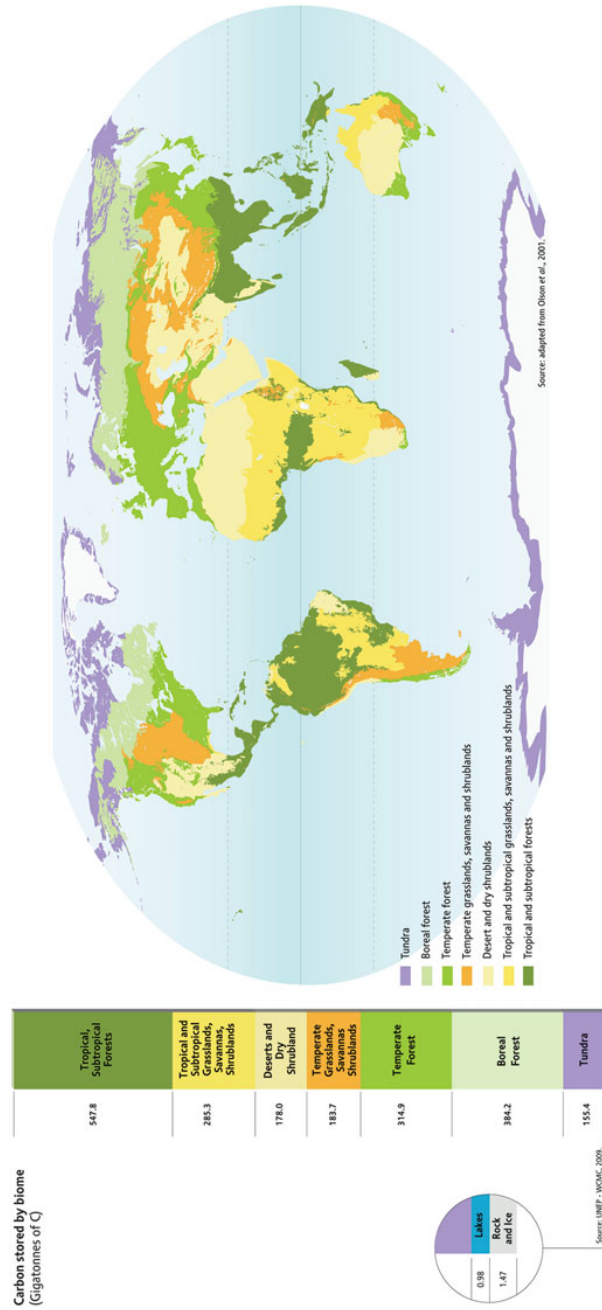


Fig. 1 Tropical forest distributions and carbon stored by biome (in gigatonnes). Tropical and subtropical forests store more C than any other biome (Reprinted with permission (Riccardo Pravettoni, UNEP/GRID-Arendal, http://www.grida.no/graphicslib/detail/carbon-stored-by-biome_9082))

of axes including seed size and dispersal, leaf lifespan, and population turnover that together highlight tradeoffs in resource allocation and reproductive strategies. Water limitation controls transpiration and photosynthesis, and tropical trees can transpire several hundred liters of water a day, which emphasizes the importance of reducing cavitation risks during low water availability. Of course environmental tolerances to temperature and water availability drive global patterns of plant distributions, and within tropical forests interspecific differences in drought tolerance have been shown to determine plant species distributions at local scales and across the strong rainfall gradient of the Isthmus of Panama. Among the soil nutrients that affect plant productivity, phosphorous (P), which is rapidly mobilized by chemical and microbial activity, is often limiting in highly weathered tropical soils. A more detailed discussion of biogeochemistry and plant productivity can be found in section “[Productivity and Nutrient Cycling in Tropical Rain Forests](#)”.

While lianas are found in temperate rain forests, their predominance and diversity in tropical rain forests are notable, as is the trend that they are increasing in abundance and biomass in a number of tropical rain forests. Contributing up to 45 % of woody stems and 35 % of species richness in a tropical forest community, lianas significantly reduce tree growth rates through direct competition, more than double tree mortality risks, and increase gap size and severity through canopy connectivity, and the capacity for lianas to alter successional pathways in tropical rain forests is only beginning to be understood (van der Heijden et al. 2013). An increase in liana biomass has serious implications for tree community diversity, gap dynamics and forest structure, and tropical forest nutrient cycling. For example, lianas reduce tree growth and survival in the slower-growing, higher wood density trees that support them, which, along with changing gap regimes, shift species composition towards faster-growing trees with lower wood density. While accurate predictions require more data, the additive effects of an increase in liana biomass are correlated with a reduction in tropical forest C storage, a value that is currently not considered in global vegetation models.

Little is known about cambial phenology – the seasonality of stem growth – in tropical rain forest trees. Our lack of understanding of the triggering factors of cambial dormancy in tropical rain forest trees has led to the long-standing assumption that tropical trees do not form annual growth rings (Jacoby 1989; Worbes 2002). Furthermore, the complex wood anatomy characteristic of the

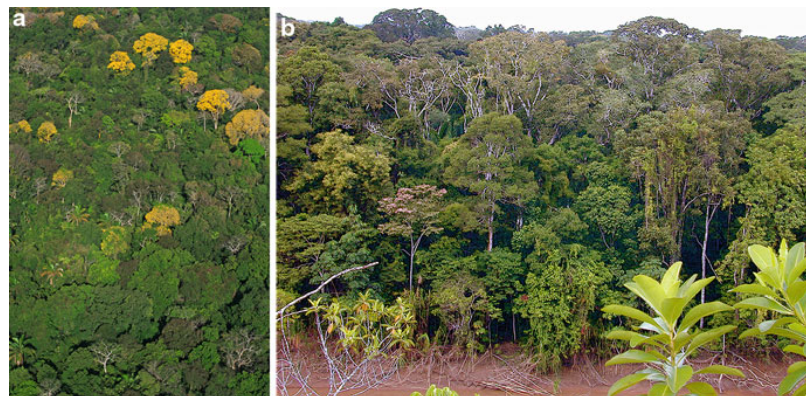


Fig. 2 (a) Aerial photo of a Neotropical rain forest canopy. The brilliant *yellow crowns* display the synchronous flowering of *Tabebuia guayacan* (Bignoniaceae) trees. Emergent trees rise above the forest canopy and palm trees and various tree architectures are apparent. The range in hue of individual crowns depicts variation in foliar chemistry and water content (Photo credit Christian Ziegler). (b) Cross section of a lowland Amazon rain forest in Manu National Park, Peru, shows a distinct vertical profile from understory shrubs to emergent trees. River erosion exposes roots (Photo credit Kyle Dexter)



Fig. 3 (a) The buttress of this *Ficus* (Moraceae) tree in Corcovado National Park, Costa Rica, provides support and stability in shallow tropical forest soils (Photo credit Andrea Vincent). (b) Woody lianas rely on trees for structural support to reach the forest canopy. Liana abundance and biomass are increasing in a number of tropical rain forests, including the La Selva Biological Station, Costa Rica, where this photo was taken, with significant implications for tree community diversity, gap dynamics and forest structure, and tropical forest nutrient cycling (Photo credit Eloisa Lasso)

majority of tropical tree species has long steered dendrochronologists away from tropical regions. In recent decades, however, distinct annual growth ring boundaries, often consisting of marginal parenchyma bands and induced by cambial dormancy, have been detected in multiple lowland tropical rain forest species. As a result, an increasing number of reliable, climate-sensitive tree-ring chronologies are now available based on trees from various tropical biomes across Asia, the Amazon region, and Africa. These chronologies reflect seasonally fluctuating climatic conditions that typically consist of distinct dry seasons but can also consist of periodical flooding (Schongart et al. 2004). In regions with a bimodal rainfall distribution (e.g., eastern Africa), trees can exhibit a bimodal pattern of cambial activity, and two growth rings can be found per year. Water availability is a major driver of phenological periodicity in seasonal tropical rain forests, and leaf phenology is generally synchronized with the seasonality of soil water content and tree water status. In deciduous trees, leaf fall typically occurs at the end of the dry season and leaf flushing in the wet season. Deciduousness, however, is species and site specific and can be a function of tree canopy status, with canopy and emergent trees generally showing a more distinct phenological seasonality and deciduousness than understory trees (see Fig. 2a). There is plasticity in this trait; some species have seasonal leaf fall at dry sites but are evergreen at sites with less moisture stress.

Though the climate of tropical rain forests has more tempered seasonality relative to other ecosystems, most rain forest tree species do not grow, flower, or fruit year-round. Periods of leaf flush, bud burst, flowering, fruiting, and senescence that are related to climate conditions and day length (photoperiod) are considered phenological responses, the proximate and ultimate causes of which have been studied from individual variation within populations to community and guild-level patterns. In seasonal tropical rain forests, peaks in leaf flushing, flowering (see Fig. 2a), and fruiting coincide with the high irradiance and low water stress associated with the onset of the wet season. This synchrony of events is common within communities and largely driven by resource availability,

though biotic explanations for synchrony include selection to attract pollinators or seed dispersers and to avoid herbivory and seed predation (van Schaik et al. 1993). The synchronous flowering of canopy emergent tree species such as *Dipteryx panamensis* (Fabaceae) is visible in high-resolution satellite images, which enable individual tracking and have revolutionized the study of remote and large tracks of forests. Synchronous supra-annual flowering and mast fruiting that may lead to seed predator satiation are defining features of the Dipterocarp forests of Southeast Asia, with Borneo housing the greatest diversity of Dipterocarpaceae that are increasingly threatened by extensive logging and land conversion. Bamboos also wait decades between synchronized flowering before dying back. Monocarpic or semelparous trees that reproduce only once are uncommon, though examples can be found in the Neotropical genera *Tachigali* (Fabaceae) and *Spathelia* (Rutaceae) and the genus *Harmsioplanax* (Araliaceae) in tropical Asia. Wind pollination is relatively rare in tropical rain forests and many coevolutionary pollination, and seed dispersal relationships have developed between plants and insects, birds, bats, fish, and mammals.

In this chapter on tropical rain forest plant ecology, I would be remiss not to highlight a few of the archetypal associations between tropical plants and the organisms that rely on them for food and habitat. Each of the examples detailed below are pantropical and emphasize the extraordinary complexity of ecological systems. They also demonstrate the coevolution of symbiotic relationships between plants, insects, and fungi for protection, nutrient acquisition, and pollination.

Ant-plant (myrmecophytic) symbioses are a pantropical phenomenon involving greater than 100 plant genera and 40 ant genera, whereby ants living within specialized structures of the plant – called domatia – defend the plant against herbivory and pathogen attack (Fig. 4; reviewed in Heil and McKey 2003). These often-obligate symbioses are incredibly effective with ants receiving food – namely, Beltian bodies and nectar – and habitat and plants receiving a full-time security force. Whereas herbivores and pathogens have counter adapted many strategies for overcoming plant chemical defenses, the resident ants of myrmecophytes earn their keep by effectually defending plants from their pests.

Generally considered keystone species in tropical forests, figs of the genus *Ficus* (Moraceae), (Fig. 3a) range in growth form from small shrubs to climbers to canopy trees and epiphytic parasites (e.g., strangler figs). Fig fruits are a reliable year-round and nutritious food source for numerous frugivores, and the fig keystone status stems from their role in sustaining frugivore communities when other food resources are limiting. Most notable is the intimate mutualism between figs and their tiny, obligate wasp pollinators (Agaonidae, Chalcidoidea). Phylogenetic evidence supports the hypothesis that this mutualism arose once approximately 87 million years ago. The long-standing view of a unique one-to-one species-specific pollination syndrome, however, has been challenged by recent progress in phylogenetic studies of figs and their pollinating wasps (reviewed in Herre et al. 2008). Fig species pollinated by two or more wasp species suggest that fig and pollinator speciation are not always tightly linked. Non-pollinating fig wasps are common and these parasites exploit this mutualism in diverse ways that might also drive fig adaptations. Finally, figs have some of the most effective long-distance dispersal of any tropical tree species, with dispersal ranges of hundreds of square kilometers driven by fig wasp-mediated gene flow and seed dispersal via the numerous fig frugivores.

Mycorrhizal associations between plant roots and symbiotic fungi are pervasive and not unique to tropical rain forests; greater than 90 % of plant families form mycorrhizal associations. While ectomycorrhizal tree species are less common, both endo- and ectomycorrhizal fungi are found in tropical forests worldwide, and trees can host both groups of symbionts simultaneously. Arbuscular mycorrhizas (AM; Glomeromycota) are endomycorrhiza whose hyphae enter plant cells and produce vesicles or arbuscules that increase the surface area of contact between the plant root and



Fig. 4 Ant-plant (myrmecophytic) symbioses are a pantropical phenomenon involving greater than 100 plant genera and 40 ant genera. In this photo taken in Santa Rosa National Park, Costa Rica, the *Acacia* (Fabaceae) species form mutualistic associations with ants in the genus *Pseudomyrmex* (Formicidae) (Photo credit Andrea Vincent)

fungus to facilitate nutrient transfer. AM fungi are cosmopolitan with broad host ranges though different plant species responses to mycorrhiza communities can influence the competitive outcome among seedlings. Ectomycorrhizas (EM) are found across fungal phyla (Basidiomycota, Ascomycota, Zygomycota) and their species number in the thousands compared to only hundreds of arbuscular mycorrhizal species. EM hyphae sheath the root and an extensive hyphal network, called a Hartig net, runs between plant cells within the root cortex. Tree species with EM are less common than those with AM, but all species of Dipterocarpaceae form EM associations, as do species in the Fagaceae and Fabaceae subfamily Caesalpinioideae. In both types of association, carbon fixed from the plant is transferred to the heterotrophic fungus. In return both ecto- and endomycorrhizas increase root surface area, thereby improving plant nutrient acquisition of P, N, calcium, potassium and other ions that tend to be limiting in tropical soils. There is evidence that these associations also improve plant resistance to root pathogens and tolerance to drought. The host-specific effect of different mycorrhizal communities on plant growth has been proposed as a potential mechanism reducing plant community richness. Tree species hosting particular suites of mycorrhizal communities could create a positive feedback for conspecific over heterospecific juvenile recruitment. Furthermore, in certain low diversity forests the dominant tree species tends to form EM associations and it has been hypothesized that an EM network may provide recruitment advantages to EM plant species over non-EM plant species through positive feedbacks. This hypothesis requires further testing.

Tropical Rain Forest Biodiversity

With few exceptions, species richness across the tree of life is highest in equatorial tropical regions and decreases towards the poles. Numerous evolutionary and ecological hypotheses to explain the origin and maintenance of the latitudinal gradient in biodiversity have garnered support and include biogeographic history, evolutionary mechanisms of adaptation and speciation, range size and distribution constraints, and ecological mechanisms promoting species coexistence. After decades of research on this topic it is evident that no individual explanation is sufficient to explain this conspicuous biogeographic pattern.

The current diversity and distribution of modern plant lineages has been shaped by numerous extinction (e.g., Devonian, Permian, Cretaceous) and radiation events throughout Earth's history. The retraction of tropical rain forests during the cooler, drier Pleistocene glacial periods (ca. 100,000 year per cycle) and expansion of tropical rain forests during warmer, wetter interglacial periods (ca. 10–20,000 year per cycle) created fragmented refugia in African and Australian, though recent evidence suggests not Neotropical, forests, that may have promoted lineage differentiation and allopatric speciation that contribute to the extant high tropical plant diversity. Different scales over which diversity is measured include alpha diversity (local, habitat scale), beta diversity (species turnover at landscape to regional scales), and gamma diversity (total regional species richness). Since regional diversity reflects a balance between speciation and extinction, it should be higher in larger, older areas that offer more opportunities for isolation and divergence through environmental heterogeneity as well as lower extinction probabilities through species-area relationships and millennia without major climatic shifts, in other words, in tropical rain forest biomes.

Continental drift, climate constraints, and long-distance dispersal are responsible for some of the similarities and differences in species across tropical regions. Dipterocarpaceae are dominant only in Southeast Asia, and palms (Arecaceae) and legume species in the Fabaceae are abundant in South American tropical rain forests (e.g., Fig. 2a), but not in African ones. There are, however, a number of plant families shared between South America, Africa, and Southeast Asia (from 27 to 44 in a recent global analysis of 4 ha plots by Ricklefs and Renner 2012). In contrast, independent diversification and species radiation mean that much fewer genera are shared across regions. Between 58 % and 68 % of plant families (44 families) are shared between Yasuni, Ecuador, (65 families) and Pasoh, Malaysia, (76 families), whereas only approximately 12 % (35 genera) of their 296 (Yasuni) and 259 (Pasoh) genera overlap. Some species are widely distributed with pantropical ranges, for example, *Ceiba pentandra* (Malvaceae), a canopy pioneer tree, whose range encompasses Central and South America, the Caribbean, and eastern Africa. Interestingly, the low nucleotide divergence in microsatellite chloroplast and nuclear ribosomal DNA data among Neotropical and African populations supports long-distance dispersal, and not vicariance, as the explanation for this species' range (Dick et al. 2007). Population genetic data provide a means of inferring the dispersal and historical biogeography of species. See Kraft and Ackerly (this volume; ► [The Assembly of Plant Communities](#)) for an excellent description of phylogenetic analysis and structure within and among communities.

Tropical rain forests harbor approximately two thirds of the estimated 350,000–500,000 extant flowering plant species on Earth. Floristic endemism, whose cause may be attributed to young species age, is high – especially in island systems such as Indonesia where greater than 50 % of the indigenous vascular plant taxa do not occur anywhere else. Although tropical rain forests are generally considered synonymous with diversity, within these systems tree alpha diversity varies considerably and is broadly correlated with mean annual temperature (MAT) and mean annual precipitation (MAP). Numerous studies using the CTFS forest inventory plots reveal that patterns of alpha diversity and species or familial dominance vary across African, American, and Asian tropical rain forests from a mean of 22 species of tree ≥ 10 cm dbh per ha in southern India to 254 species per ha in Ecuadorian Amazon (Table 1; Condit et al. 2005). Similarly, the number of plant families represented in forest communities varies from 47 in Korup, Cameroon, to 76 in Lambir, Malaysia (Ricklefs and Renner 2012).

Local dominance by one or a few species is found in primary rain forests throughout the tropics. In the Asian tropics, the family Dipterocarpaceae (e.g., *Dryobalanops aromatica*) dominates, while many species in the leguminous family Caesalpiniaceae dominate in the African and Neotropics (e.g., *Gilbertiodendron dewevrei* in Congo, *Mora excelsa* in Trinidad, and *Peltogyne gracilipes* in

Brazil). A comprehensive assessment by Ter Steege et al. (2013) of the composition and biogeography of tree communities from 1,170 inventory plots throughout Amazonia yielded the stunning discovery that a mere 227 of the roughly 16,000 tree species in this region account for half of the trees. Species of palm trees in the Arecaceae are predominant, as well as species in the Myristicaceae, Lecythidaceae, and commonly cultivated trees. Most of these so-called hyperdominant species forming “predictable oligarchies” are only dominant in certain forest types and, while they demonstrate large geographic ranges, show strong evidence of habitat specialization though a broad range of shade tolerance is represented. It is the rare species, with average abundances of ≤ 1 individual per hectare that drive species richness of tropical communities (Table 2). The striking discovery that a small suite of species largely drives Amazonia’s biogeochemical cycling opens areas of inquiry into the implications of species-specific effects of climate change on productivity and phenology in this region. Elucidating mechanisms that promote dominance and monodominance also provide important conceptual contrast to those explaining high species diversity.

Why Are There so Many Tree Species in Tropical Forests?

What processes underlie the diversity and assembly of communities and, to paraphrase Egbert Leigh et al. (2004), why are there so many tree species in certain tropical forests? A combination of factors (historical biogeography, environmental tolerances, demographic stochasticity, and limitations to propagule dispersal) leading to neutral ecological drift (Hubbell 2001) have been proposed as the main influences over the composition and relative abundance of species in a regional species pool. Environmental heterogeneity and dispersal limitation influence species turnover among communities (beta diversity), which can be low even when alpha diversity is high. In contrast, alpha diversity may be more strongly controlled by stochastic and biological processes such as disturbance and especially pressure and specialization of pests on locally abundant hosts. Instead of dichotomous either-or explanations, it is likely that high sympatric species coexistence results from “The Ecological Theater and The Evolutionary Play,” (Hutchinson 1965) – a combination of ecological filtering and biotic interactions operating over ecological (short-term selective processes in a fixed gene pool) and evolutionary (long-term process acting on a variable gene pool) timescales.

When intraspecific interactions are more negative than interspecific interactions, species are at a relative advantage when rare and disadvantage when common. This has a stabilizing effect on species diversity. Interspecific trade-offs in species dispersal and competitive abilities result in niche partitioning along the competition–colonization continuum of traits. Niche partitioning and compensatory mortality (e.g., Janzen–Connell negative density-dependent effects and low recruitment near conspecifics) are therefore among the significant factors that favor the sympatric coexistence of tree species by preventing species dominance and competitive exclusion of species from the community. They maintain alpha diversity within communities by reducing interspecific competition or through density-dependent pest regulation of plant populations. Pervasive dispersal and recruitment limitation, whereby a species does not successfully establish in all sites it is capable of occupying, further reduce the extirpation of less competitive species in a community.

Forest disturbances such as tree fall gaps create light and nutrient heterogeneity that generate niche opportunities allowing tree species coexistence across the continuum of light-demanding “pioneer” to longer lived, better defended shade-tolerant species. Tree fall gaps are colonized in a number of ways that can alter regeneration or successional pathways. Light-demanding pioneer species germinate readily from soil seed banks when the high light quality and temperature

Table 1 Forest diversity by region from large tropical forest plots associated with the Center for Tropical Forest Science (CTFS). Lines in the table denote Southeast Asian, Neotropical, and African regions. Annual precipitation for each forest is shown in millimeters (mm), and the number of dry season months is in parentheses. Two different size classes are shown for the full plot and per hectare. Sites marked with an asterisk were < 25 ha, and data for those sites are based on the full 16 or 20 ha. Main references for each plot are footnoted (Redrawn with permission Condit et al. 2005)

	Plot size (ha)	mm annual precipitation (dry season in mo.)	Species per ha ≥ 10 cm dbh	Species in full plot ≥ 10 cm dbh	Species per ha ≥ 1 cm dbh	Species in full plot ≥ 1 cm dbh
Lambia, Borneo, Malaysia ^a	52	2,664 (0)	245.7	1,008	618.1	1,179
Huai Kha Khaeng, Thailand ^b	50	1,476 (6)	65.6	217	101.8	259
Mudumalai, India ^c	50	1,206 (6)	22.0	63	25.6	72
Pasoh, Peninsular Malaysia ^d	50	1,788 (0)	207.3	678	496.5	814
Sinharaja, Sri Lanka	25	5,074 (0)	71.2	167	142.7	205
Palanan, Philippines*	16	3,218 (4)	98.9	262	201.6	335
Barro Colorado, Panama ^e	50	2,551 (3)	90.7	227	168.0	301
La Planada, Colombia	25	4,087 (0)	85.0	172	150.1	219
Yasuni, Ecuador ^f	25	3,081 (0)	253.6	820	665.2	1,104
Luquillo, Puerto Rico ^{g*}	16	3,548 (0)	42.2	87	77.6	140
Korup, Cameroon	50	5,272 (3)	85.4	307	235.1	494
Ituri, D.R. Congo ^h :						
Lenda (monodominant)	20	1,674 (2)	49.1	211	166.0	365
Edoro (mixed)	20	1,785 (2)	67.0	212	172.2	380

^aLee et al. (2002)

^bBunyavejchewin et al. (2001)

^cSukumar et al. (1992)

^dManokaran et al. (1992), Condit et al. (1996b, 1999)

^eHubbell and Foster (1983), Condit et al. (1996a, 1999)

^fRomoleroux et al. (1997), Valencia et al. (2004)

^gZimmerman et al. (1994), Thompson et al. (2002)

^hMakana et al. (1998)

conditions from gaps arise. The rapid growth rate of these species results in a developing understory that leads to favorable microsites for other species to recruit. Recruitment from the seedling bank is equally common. Shade-tolerant seedlings and saplings persisting in the understory for decades are also able to exploit the high light environment of gaps and respond with rapid growth rates. Vegetative propagation, clonal shoots, and lateral growth from vines and lianas are also pathways

Table 2 Species rarity and dominance by region. Percent of rare species (those with ≤ 0.3 individuals per ha) at each of the plots and relative abundance of the dominant species. Both are given as mean \pm 95 % confidence limits, based on replicate 20-ha subquadrats. Confidence limits for Congo sites could not be calculated, since the plots were only 20 ha; for sites marked with an asterisk, the estimates are based on the full 16 ha and also lack confidence limits. Dominant species for each site is listed along with authority and family (Redrawn with permission Condit et al. 2005)

Plot	% Rare species	% Dominance	Dominant species
Lambia, Borneo, Malaysia	14.9 \pm 3.7	2.6 \pm 1.0	<i>Dryobalanops aromatica</i> Gaertner (Dipterocarp-)
Huai Kha Khaeng, Thailand	44.8 \pm 1.5	10.0 \pm 5.2	<i>Croton oblongifolius</i> Roxb. (Euphorbi-)
Mudumalai, India	41.7 \pm 4.8	22.8 \pm 6.5	<i>Kydia calycina</i> Roxb. (Malv-)
Pasoh, Peninsular Malaysia	19.2 \pm 3.5	2.7 \pm 0.3	<i>Xerospermum noronhianum</i> Blume (Sapind-)
Sinharaja, Sri Lanka	16.6 \pm 0.9	12.1 \pm 0.4	<i>Humboldtia laurifolia</i> M. Vahl (Fab-)
Palanan, Philippines*	37.9	5.6	<i>Nephelium lappaceum</i> Poiret (Sapind-)
Barro Colorado, Panama	25.6 \pm 2.7	15.7 \pm 1.9	<i>Hybanthus prunifolius</i> Schulze-Menz (Viol-)
La Planada, Colombia	24.2 \pm 2.9	15.6 \pm 0.1	<i>Faramea coffeoides</i> C.M. Taylor (Rubi-)
Yasuni, Ecuador	31.1 \pm 0.6	3.1 \pm 0.1	<i>Matisia oblongifolia</i> Poeppig & Endl. (Malv-)
Luquillo, Puerto Rico*	40.7	19.6	<i>Palicourea riparia</i> Benth. (Rubi-)
Korup, Cameroon	29.2 \pm 2.6	8.3 \pm 1.5	<i>Phyllobotryum spathulatum</i> Müll. Arg. (Salic-)
Ituri, D.R. Congo:			
Lenda (monodominant)	48.4	45.0	<i>Scaphopetalum dewevrei</i> Wildem. & Th. Dur. (Malv-)
Edoro (mixed)	52.2	41.8	<i>Scaphopetalum dewevrei</i>

for gap colonization, and plant recruitment and growth rates thin and slow as competition for light increases. Despite the importance of forest gaps, there is little evidence that variations in adaptation to disturbance account for the high alpha tree species diversity of tropical rain forests. Disturbance is nevertheless one of several factors that add to seemingly unpredictable microclimatic conditions within tropical forests.

Case Study: Plant Pests Maintain Tree Species Diversity

As mentioned above, plant–pest interactions are considered one of the predominant mechanisms allowing high species diversity to be maintained in tropical tree communities. The long-standing Janzen–Connell hypothesis suggests that specialized pests such as insects and pathogens maintain high plant diversity by causing increased mortality in areas of high conspecific plant density (negative density dependence), thereby preventing species dominance. A recent experimental test

of this hypothesis shows that fungal plant pathogens, but not insects, have a community-wide role in maintaining seedling diversity in a Neotropical forest (Bagchi et al. 2014). In a 17-month experiment, researchers compared the diversity of the seed rain to the diversity of seedlings germinating in adjacent control, fungicide, and insecticide-treated plots. The diversity of germinating seedlings was higher than that of the seed rain, suggesting an important recruitment filter at the seed-to-seedling stage. Among plots, plant species richness was reduced by 16 % in plots treated with fungicide. There was no change in species richness in plots treated with insecticide though a change in relative abundance of plant species indicates a disproportionate effect of insects on certain plant species. The original assumption of specialized pests driving the negatively density-dependent mortality thought to regulate populations (see Janzen 1970; Connell 1971), however, does not seem to hold either for plant–phytophage or plant–pathogen interactions in tropical forests. Polyphagy in insects (Novotny et al. 2002) and fungi (Gilbert and Webb 2007) is the more common strategy in species-rich communities with high numbers of locally rare species. Nevertheless, plant preferences of pests and the variation in plant responses to common pests appear to be sufficient to facilitate coexistence among plants as described in the Janzen–Connell hypothesis.

Productivity and Nutrient Cycling in Tropical Rain Forests

Gradients in climate, parent material and soil age, topography and landscape stability, and atmospheric deposition result in strong heterogeneity in soil nutrient availability from local to regional scales. Tropical rain forests encompass a gradient of soils ranging from young, N-poor Alfisols whose nutrients are primarily derived from parent material to older, highly chemically weathered Ultisols and Oxisols (Townsend et al. 2008). Widespread Ultisols, or “red clay soils” due to their accumulated clay minerals in the B-horizon, are acidic with low fertility and cation exchange capacity; however, their clay content gives them greater nutrient-holding capacity than Oxisols. The highly weathered, nutrient poor, acidic Oxisols are dominated by aluminum and iron oxides and have low humus and clay content. Less common are volcanic Andisols, found in areas such as Hawaii and the infertile white sand Spodosols of Amazonia.

Tropical forests are typically characterized by rapid recycling of nutrients through the action of ants, termites, fungi, and other soil microbes, with dead organic matter decomposing over the scale of weeks compared to years in more temperate zones. Productivity and decomposition of necromass are tightly coupled in tropical forests and can be controlled by a number of different limiting nutrients. For example, denitrification often exceeds N fixation resulting in significant N losses. A meta-analysis of 81 lowland tropical rain forest sites showed soil order, which is generally correlated with soil fertility, to be a strong predictor of aboveground NPP. Through this analysis, Cleveland et al. (2011) found that soil P availability controls the tropical C cycle directly and indirectly through constraints on N turnover and N availability and the subsequent effects on photosynthetic rates. NPP can be limited by temperature, moisture, or nutrient availability, and higher elevation forests are generally less productive than lowland forests because of a combination of these limiting factors. Although Hawaiian forests show a strong increasing trend in NPP with increasing rainfall, the controls of NPP are not simple or linear. The relationships between rainfall, temperature, and NPP estimated from 39 different tropical forests were complex; both low and high MAT were associated with high NPP, and therefore the ratio of MAP to MAT was a better predictor of NPP (Fig. 5; Clark et al. 2001).

Tropical forests store approximately half of Earth’s vegetation carbon stocks but less than 10 % of Earth’s soil carbon stocks (see Fig. 1). In tropical forests there is as much carbon stored in live

biomass as there is in soils, in contrast to other biomes where soils are the dominant C store. Although there are seasonal patterns of plant growth in the tropics, high solar radiation and a relatively stable warm, wet climate provide more consistently suitable conditions for growth than drier and colder regions. Consequently, tropical forests account for approximately 40 % of NPP. An estimated 60 % of tropical forests are classified as secondary or degraded forests (Chazdon 2003), meaning tropical deforestation has considerable implications for Earth's carbon cycle.

There is evidence that aboveground biomass production is increasing in the forests of South America, Africa, and Asia, though notably not Australia. The primary mechanisms driving this trend are thought to include increased resource availability through the effect of rising atmospheric CO₂, air temperature, and solar radiation on NPP, and forest recovery from past disturbances. The contrasting pattern in Australian tropical rain forests is linked to the magnitude, frequency, and scale of natural disturbances such as cyclones and strong droughts from El Niño events. Intact tropical forests are net C sinks, but the uptake of C ($1.1 \pm 0.3 \text{ Pg C year}^{-1}$) in intact tropical forests is counteracted by the emissions from tropical biome conversion – a net C source to the atmosphere of $1.3 \pm 0.2 \text{ Pg C year}^{-1}$ that results in a tropical biome net C balance of approximately zero (Malhi 2010). However, there are few studies under ambient or elevated CO₂ conditions where the net C uptake of tropical forests has been quantified, and the role of tropical forests in Earth's C cycle, while critical, is far from understood.

Threats to Tropical Rain Forests

Population growth in tropical developing countries, large-scale agriculture for food and biofuels, industrial logging, construction of roads and dams, and oil and gas development are among the most significant anthropogenic threats to tropical old growth rain forests and the biodiversity they contain. Current estimates put global tropical deforestation rates at greater than 15 million hectares per year with the highest contemporary deforestation rates recorded in Southeast Asia (Laurance et al. 2011). In 1988, Norman Myers introduced the biodiversity hotspot concept in an effort to define regions of utmost importance for biological diversity conservation. Defined as threatened regions that harbor a high diversity of endemic species, the 34 biodiversity hotspots currently identified by Conservation International (expanded from 25 in Myers et al. 2000) contain over 50 % of the world's endemic plant species yet account for less than 3 % of Earth's terrestrial cover. The tropical hotspots in most urgent need of protection and sustainable management include forests of Madagascar, Philippines, Atlantic coastal forest of Brazil, the Caribbean, Indo-Burma, and Western Ghats/Sri Lanka (Sodhi et al. 2007), which will require economic incentives and feasible sustainable alternatives to deforestation.

The Millennium Ecosystem Assessment projects that 11–22 % of 2000 tropical forest cover will disappear by 2050 (Table 3; Asner et al. 2009). Forest fragmentation is arguably no less a threat to tropical forests than whole-scale deforestation. Harder to quantify, fragmented patches of forest within a matrix of anthropogenically manipulated landscapes are susceptible to small island effects such as the loss of species diversity through unsustainable coexistence in shrinking patches, loss of population genetic diversity through restricted migration and shrinking population size, and nonnative and disturbance-adapted species invasions that alter community diversity and successional pathways. Strong edge effects in forest patches increase tree mortality of drought-sensitive species and from physical exposure to increased winds that cause blow down. Deposition of dust and aerosols rich in N and P from surrounding agriculture and development alters plant growth rates. Increased evaporation, decreased soil moisture, and the accumulation of litter increase susceptibility

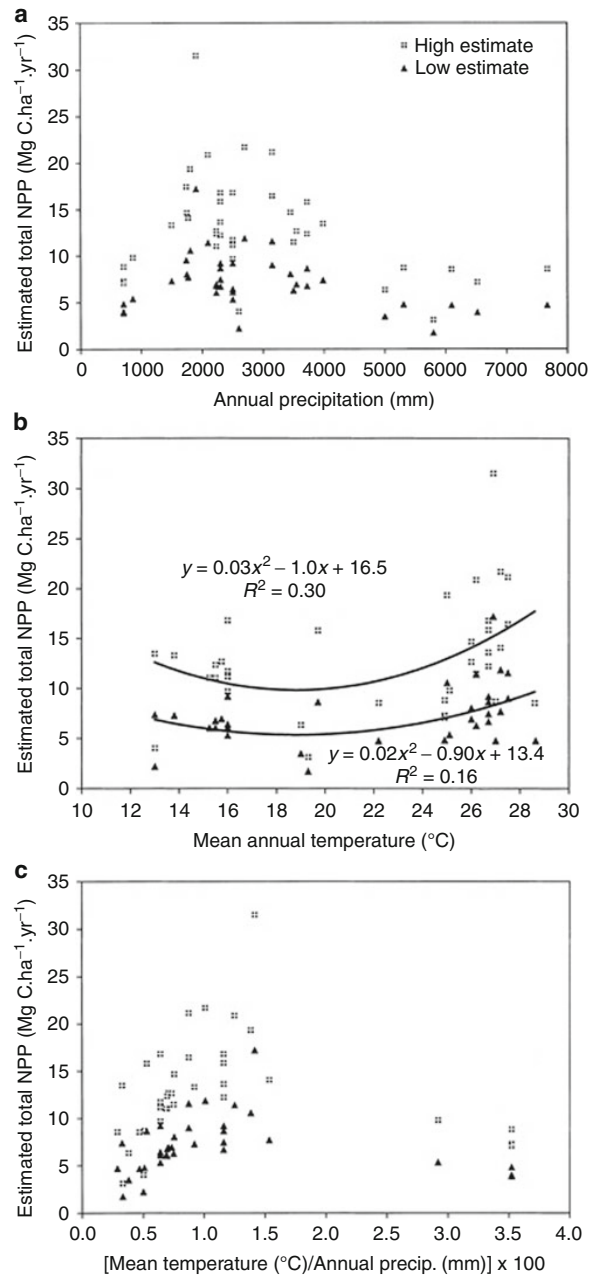


Fig. 5 The relationships between low and high estimates of NPP for 39 old-growth tropical forest sites around the world and (a) annual precipitation (P), (b) mean annual temperature (T), and (c) the ratio $T/P \times 100$ (Reprinted with permission Clark et al. 2001)

to fires, and, indeed, contemporary fire occurrence in tropical forests is largely associated with forest edges (Cochrane 2003). Nevertheless, these forest mosaics are the future of tropical regions, and thoughtful management can benefit agriculture as well as preserve forests and their ecosystem services that contribute to water quality and global food supply (e.g., pollinators).

Stronger ENSO effects are increasing the frequency and severity of droughts, fires, hurricanes and cyclones, and flooding events. Historical records and charcoal in soil profiles show that tropical forest fires, even in wetter forests, are not unprecedented. Fire is considered endemic but rare in most tropical rain forests, with return intervals of hundreds if not thousands of years (Cochrane 2003). Drought is a major driver of fires. The El Niño drought in the years of 1997–1998, for example, burned tens of thousands of kilometers of forest in Brazil and Borneo, and the projected drying of parts of the tropics will greatly increase forest susceptibility to fire. Recovery after hurricanes and other disturbances that primarily affect canopies is faster than recovery after disturbances that heavily disturb soils and vegetation such as bulldozing, overgrazing, and severe fires (Chazdon 2003). Recovery of aboveground biomass, species composition, and forest structure all depend on the type and severity of disturbance and its effect on soil fertility.

Case Study: Oil Palm

Agriculture expansion, while necessary for supporting a healthy growing world population, is currently occurring at the expense of tropical rain forests with catastrophic consequences for global biodiversity and carbon and water cycles. Oil palm (*Elaeis guineensis*), one of the world’s most rapidly expanding crop, is grown across more than 13.5 million ha in lowland tropical areas with Malaysia and Indonesia supplying greater than 80 % of global production (Fig. 6; Fitzherbert et al. 2008). With rising demand for vegetable oils and biofuels, there is no evidence that the

Table 3 Approximate geographic extent of contemporary forest cover, deforestation, and selective logging by region in the humid tropical forest biome. Values are in km², with percentage of biome extent also given^a (Redrawn with permission Asner et al. 2009)

Region	Total biome extent (km ²)	Area with 0–50 % forest cover, 2005 (km ²) ^b	Area with 50–100 % forest cover 2005 ^b (km ²)	Forest area cleared 2000–2005 ^c (km ²)	Selective logging ^d (2000s) (km ²)
Africa	2,918,511	1,085,941 (37.2 %)	1,832,569 (62.8 %)	14,972 (0.5 %)	561,153 (19.2 %)
Asia/Oceania	7,191,529	5,234,293 (72.8 %)	1,957,236 (27.2 %)	93,955 (1.3 %)	1,777,963 (27.2 %)
Central America/Caribbean	685,840	501,415 (73.1 %)	184,425 (26.9 %)	9,687 (1.4 %)	36,097 (5.3 %)
South America	8,826,966	3,194,632 (36.2 %)	5,632,334 (63.8 %)	156,001 (1.8 %)	1,603,166 (18.2 %)
Total	19,622,846	10,016,282 (51.0 %)	9,606,564 (49.0 %)	274,615 (1.4 %)	3,978,379 (20.3 %)

^aPercentage of regional biome extent is in parentheses, except in the column totals (last row), where percent refers to the global biome extent. Differences in the composition, spatial extent, temporal scale, and quality of the available data make it difficult to quantitatively compare rates of deforestation and selective logging. They are listed here to provide a general global perspective on the magnitude of reported or detected contemporary changes among these land-use processes

^bForest cover in 2005 calculated as 2000 forest cover minus losses from 2000 to 2005 with data from Hansen et al. (2008). Percent forest cover is based on percent within each 500 m grid cell, followed by conversion to vector format for global calculations

^cCalculated from Hansen et al. (2008)

^dLogging does not represent actual harvested trees, but rather regional forest areas in which timber operations occur

rapid trajectory of oil palm production will abate. With a 25-year rotation cycle, oil palm monocultures are defined by uniform tree structure, low canopy, and sparse understory that support a paucity of vertebrate and invertebrate diversity. In a literature review, Fitzherbert et al. (2008) found that only 15 % of species recorded in primary forest were also present in oil palm plantations. Presence does not equate with a sustainable population, and oil palm plantation features cannot support the tropical forest fauna that tend to be of highest conservation concern. Accordingly, the predominant species in oil palm plantations tended to include non-forest specialists and nonnative invasive species – especially ants and pests. Of equal concern are the long-standing consequences of monoculture plantations such as oil palm on reduction in soil fertility, reduction in soil microbial diversity and function, and the consequent reduction in potential for native plant community recovery. Figure 6 outlines current oil palm production areas as well as areas that are suitable for oil palm production expansion – at the expense of tropical deforestation or not. Increasing demand for certified sustainable oil palm that is not produced through forest conversion is but one strategy for mitigating the impacts of oil palm on tropical forests, but it is an action that each of us can take.

Future Directions

The tropical biome is undergoing significant change. Understanding the drivers and impacts of these changes will require sustained advances across multiple disciplines. Ultimately as a society, we are left asking what is the capacity of our remaining and regrowing tropical rain forests to adapt to long-term anthropogenic and climate change and what can we do to moderate these effects while nourishing a healthy human population? Below is an incomplete list of potential research emphases.

- Continued observation of tropical plant natural history is needed to inform ecology and taxonomy, advance phylogenetic hypotheses, and expand our database of described tropical species.
- Long-term, multifactorial experiments are needed to identify the mechanisms explaining high species coexistence and identify the relative importance of altered climate (temperature and precipitation), elevated CO₂, aerosol deposition, and land cover change on tropical NPP and C storage.
- Emphasis on tropical plant physiology measurements and scaling from leaf-level to stand-level processes will better constrain our estimates of NPP and tropical forest contributions to the global carbon cycle.
- Hypothesis-driven high-throughput sequencing surveys exploring metabolomic, transcriptomic, and proteomic pathways will provide insights into how tropical plants and microorganisms will respond to environmental change.
- Greater use of remote sensing imagery from satellites, airborne Light Detection and Ranging (LiDAR) data, and unmanned drones will improve monitoring of remote and large tracts of impenetrable forests. High-fidelity carbon maps such as the one generated for the entire country of Panama (Asner et al. 2013) will allow accurate tracking of disturbance and C stocks – a first step towards providing much-needed data to support economically driven climate change mitigation activities such as the United Nations Reducing Emissions from Deforestation and Forest Degradation (REDD) program.
- Expanded uses of these information-rich remote sensing datasets will improve tracking and monitoring of phenology, foliar canopy chemistry, individual species identification, and biodiversity estimates from local to regional scales. For example, spatially explicit phenological records can serve as a useful proxy for historic temperature and seasonality values.

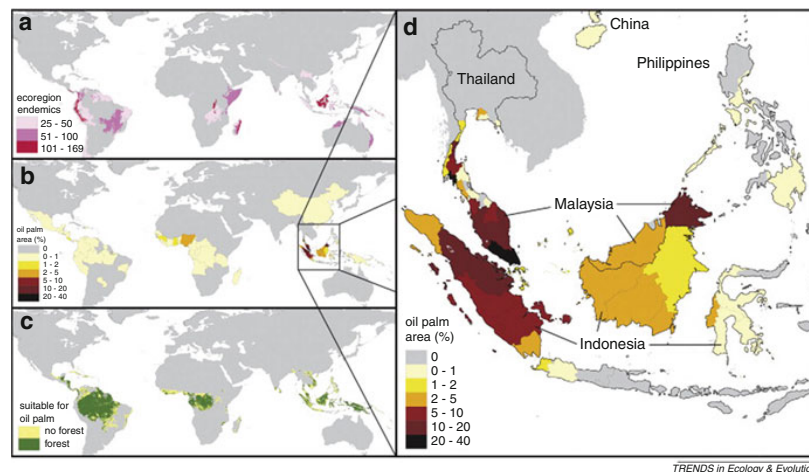


Fig. 6 Global distribution of oil palm and potential conflicts with biodiversity: (a) areas of highest terrestrial vertebrate endemism (ecoregions with 25 or more endemics are shown), (b) global distribution of oil palm cultivation (harvested area as percentage of country area), (c) agriculturally suitable areas for oil palm (with and without forest), and (d) oil palm-harvested area in Southeast Asia. In (b) and (d), Brazil, Indonesia, Malaysia, the Philippines, and Thailand are subdivided by province, but other countries are not. Data are for 2006, except for the Philippines and Thailand, where 2004 data are the most recent available (Sources: (a) World Wildlife Fund (2006) WildFinder: online database of species distributions, version Jan-06, <http://www.worldwildlife.org/wildfinder>; (b, d) world: <http://faostat.fao.org>; Brazil: <http://www.ibge.gov.br/estadosat>; Indonesia: <http://www.deptan.go.id>; Malaysia: <http://econ.mpob.gov.my/economy/annual/stat2006/Area1.7.htm>; Philippines: http://www.bas.gov.ph/downloads_view.php?id=127; Thailand: <http://www.oae.go.th/statistic/yearbook47/indexe.html>; (c) forest area: European Commission Joint Research Centre (2003) Global Land Cover 2000 database, <http://www-gem.jrc.it/glc2000>; oil palm suitability: updated map from G. Fischer, first published in Fischer, G. et al. (2002) Global Agro-Ecological Assessment for Agriculture in the 21st Century: Methodology and Results, International Institute for Applied Systems Analysis and Food and Agriculture Organization of the United Nations) (Reprinted with permission Fitzherbert et al. 2008)

- Fostering research synergies across disciplines and engaging stakeholders will lead to better understanding of the socioeconomic drivers of tropical deforestation and conversion, promote understanding of tropical forest ecosystem services, and put in place a framework for governance and regulation of sustainable forest product extraction and bioprospecting.

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Index Terms:

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