Review TRENDS in Ecology and Evolution Vol.xxx No.x

Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests

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Ecological studies in tropical forests have long been plagued by difficulties associated with sampling the crowns of large canopy trees and large inaccessible regions, such as the Amazon basin. Recent advances in remote sensing have overcome some of these obstacles, enabling progress towards tackling difficult ecological problems. Breakthroughs have helped transform the dialog between ecology and remote sensing, generating new regional perspectives on key environmental gradients and species assemblages with ecologically relevant measures such as canopy nutrient and moisture content, crown area, leaf-level drought responses, woody tissue and surface litter abundance, phenological patterns, and land-cover transitions. Issues that we address here include forest response to altered precipitation regimes, regional disturbance and land-use patterns, invasive species and landscape carbon balance.

Introduction

Research addressing ecological questions has long been challenged by the spatial dimension and the complexity of ecosystems [1]. Ultimately, only a small portion of a landscape is amenable to field-based sampling, whereas many properties are distributed nonlinearly across environmental gradients. Temporal sampling is similarly restricted. Tropical ecology is particularly limited by logistical hurdles involved in studies of large and diverse regions such as the Amazon basin, and local-scale difficulties as simple as accessing the crowns of large trees. Here, we highlight how recent advances in remote sensing of tropical forests can help overcome some of these obstacles, shedding light on important ecological processes at spatial scales ranging from leaf-level chemistry to regional forest functioning.

Overview

Remote-sensing methods are rapidly advancing an expanding portfolio of resources with which to better understand tropical forest structure and function. Current advances center on new sensors, image-processing techniques (Boxes 1–3) and comparison and integration with field data. These advances can be clustered into four themes by the spatial and temporal resolution of both ecological processes and remote-sensing observations (Figure 1). First, new sensors at hyperspatial and hyperspectral resolution provide ecological measurements directly from remotely sensed imagery [2–4]. Recent studies have derived field-quality estimates of canopy nutrient and moisture content, crown area, and leaf-level responses to drought conditions directly from image data [5–8]. Second, high spatial resolution analysis has shifted from discreet classes of vegetation types to continuous field metrics, largely driven by sub-pixel spectral mixture analysis (SMA), enabling more ecologically relevant remote-sensing measurements and more direct linkages with field investigations [9]. For example, sub-pixel fractional abundances of green vegetation (GV), non-photosynthetic vegetation (NPV; woody tissues and litter), and soil, and temporal changes in these features, can be directly evaluated in both remote-sensing and field studies [10,11]. Next, daily observations of tropical forests at moderate resolution enable cloud-free coverage for large-scale land-cover change products (e.g. deforestation rates), the detection of phenological patterns, and the timing and nature of land-cover transitions to be determined [12–15]. These new satellite sensors have opened the temporal domain of ecological processes for regional study. Finally, advances have also enabled a more thorough integration of field data, remote-sensing analyses and simulation modeling to provide a more comprehensive view of ecosystem processes at regional to global scales [16–18].

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Within and among these four themes, we highlight remote-sensing investigations that have resulted in new ecological insights for tropical forests that would not otherwise have been possible, and focus on three major research areas: (i) ecosystem processes and forest function; (ii) forest structure and species composition; and (iii) land-use and land-cover change. We emphasize the role of recent findings that successfully leverage the unique spatial, spectral and temporal resolution of remote-sensing data to investigate ecological processes. Many of the advances stem from research conducted under the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) project [19], with additional key insights from other regions. Given the paucity of comparable paleotropical research, we focus on neotropical studies, taking a positive approach to what can be achieved with existing technology and research capacity.

Ecosystem processes and forest function

Phenological cycles

Patterns of phenology in tropical forests are highly diverse, although environmental triggers for leaf flush and other cyclical changes are still poorly understood [20]. Deciduousness is a key functional trait of many tropical trees, and often provides a main axis for vegetation classification. Shifts in canopy leaf area exert strong control over atmospheric carbon dioxide exchange rates, and could be a sensitive indicator of climate change. Tropical forests of Southeast Asia, for example, exhibited a burst of leaf shedding and subsequent leaf flushing in response to severe drought associated with the 1997–1998 El Niño event [21]. Tropical tree phenology also impacts foraging behavior, species interactions and community structure [22]. Although detailed phenologies for a few individual tree species are relatively common, quantitative measures of the fraction of canopy lost during seasonal leaf fall are rare [20].

Recent investigations using remote sensing enable regional mapping of phenological events and aid in developing relationships between environmental stressors and changes in canopy structure. Using Moderate Resolution Imaging Spectroradiometer (MODIS) imagery, Huete *et al.* [15] found that Amazon forests experience an increase in leaf area during the late dry season, in contrast to most ecosystem models, which predict that dry-season water

Box 1. Hyper remote sensing

The term ‘hyper’ in remote sensing refers to a condition where the question of interest is fully determined in spectral resolution (hyperspectral), in the spatial dimension (hyperspatial), or in time (hypertemporal). In each case, new sensors provide greater detail than is possible with previously available technology.

Hyperspectral remote sensing

Results from hyperspectral remote sensing (or imaging spectroscopy) indicated that spectroscopic canopy reflectance signatures were correlated with canopy nitrogen and lignin concentrations [69], which are ecosystem chemical ‘features’ linked to ecological processes, including leaf turnover and plant decomposition. Despite initial success, scientific growth was slow owing to (i) limited capabilities of available instrumentation; (ii) insufficient data and theories to address interactive effects of canopy structure and chemistry; and (iii) inadequate physical–chemical canopy models. In recent years, instrumentation and theories have improved and, what was once a search for subtle canopy reflectance and absorption features in a sea of instrument noise, has now become a spectroscopic signature of nearly the quality expected from laboratory instruments. Theories and supporting data have also advanced to provide more quantitative approaches to canopy chemistry research, and newer statistical and physical models enable a more quantitative determination of canopy chemical properties. Most of these advances required the integration of detailed ecological and biophysical knowledge from field research.

Hyperspectral advances now enable measurements of canopy biochemistry, physiology and even species diversity, in both temperate and tropical forests [5,28]. In tropical forests, there is increasing knowledge of the use of hyperspectral remote sensing to determine canopy chemistry. Chemical components of vegetation differentially absorb optical and non-thermal infrared (IR) radiation, and these absorption features can be diagnostic. In some cases, differences in targets of interest are large enough that simple multispectral data provide enough information to distinguish features of interest (i.e. endmembers). In cases where absorption features are similar or multispectral data do not provide adequate information to distinguish among endmembers, mapping individual species or differences in canopy chemistry can be possible with hyperspectral data (Figure I). Hyperspectral data sample more regions of the electromagnetic spectrum with higher fidelity than do multispectral sensors, such that important absorption features from leaf pigments, canopy structure, or leaf water content can be distinguishable.

Hyperspatial imagery

Hyperspatial imagery ($\leq$1 m) has become available through satellite platforms such as Quickbird and IKONOS, facilitating new avenues of ecological research, particularly in tropical forests [70]. The imagery is considered hyperspatial when many pixels comprise a single tree crown, enabling forest structure investigations on individual trees. Manual interpretation of tropical forest crowns has been conducted with some promising results [2,3,8]. However, owing to user biases and the amount of resources required for manual interpretation, automated crown delineation algorithms are desirable, and can be replicated and easily modified. Automated detection of crown structure in forests with high-resolution imagery has mainly used two algorithms: (i) local maximum filtering; and (ii) local minima value finding. The first delineates crowns using the assumption that the brighter local pixel is the apex of the local crown [71]. Local minima functions by delineating a crown using the assumption that dark pixels are associated with valleys or shadows between crowns, or between canopy apexes and, thus, can be used to differentiate individual trees.

Hypertemporal imagery

Hypertemporal imagery (repeat coverage $\leq$1 day) is one technological solution to the major limitation for remote sensing of tropical forests: persistent cloud cover. Despite repeat satellite coverage every 16 days, cloud-free Landsat observations for central and northern regions of the Amazon basin can be restricted to one image per year. Ecological investigations that require frequent canopy observations or coverage during specific periods have therefore been restricted to dry-season phenomena in southern and eastern regions of the basin during months with low rainfall and corresponding cloud-free skies. The crucial tradeoff in remote sensing with current technology is the ability to have either hyperspatial or hypertemporal coverage, but not both. Moderate spatial resolution (250 m–1 km) sensors with daily temporal coverage, such as MODIS, are a compromise between the need for modest definition of land-surface features and high-frequency observations to minimize cloud interference. By compositing daily imagery at eight, 16, or 32-day intervals, recent results from MODIS data over tropical forests provide both better cloud-free spatial coverage, and the ability to better investigate the temporal domain of ecological processes. Hypertemporal observations have fundamentally changed our understanding of canopy phenology [15] and the timing of land-use changes [46], and open the possibility to explore other spatial–temporal gradients in tropical forests.

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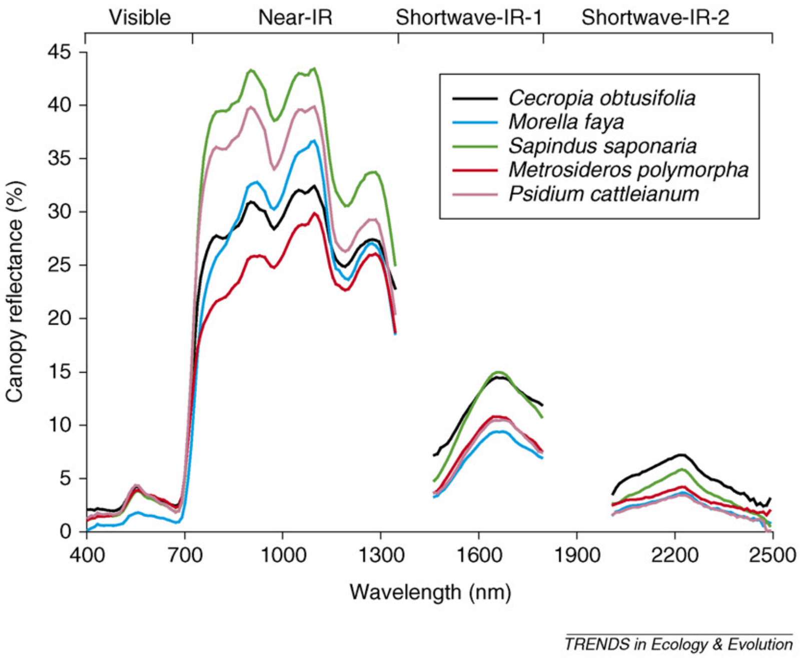

Figure I. Distinguishing tropical tree species using hyperspectral reflectance features. Hyperspectral reflectance signatures, such as these collected using an airborne imaging spectrometer over Hawaiian lowland rainforests [90], express differences in leaf and canopy biochemical properties that can inform regional ecological studies. The visible (400–700 nm) region of the spectrum is dominated by top-of-canopy leaf pigments; the near-IR (700–1300 nm) region expresses canopy water content; and the shortwave-IR (1300–2500 nm) regions are influenced by leaf water, nitrogen and carbon (e.g. lignin and cellulose) constituents. Together, these spectral regions indicate both biophysical and functional attributes that can be used to distinguish among individual species. Data from Ref. [90].

availability should limit canopy photosynthesis. This observed greening is probably caused by changes in leaf pigments associated with the production of new foliage, after old foliage is shed from canopies. Using a different approach, high-resolution satellite studies demonstrate that canopy-scale effects of drought can be observed as pigment changes in leaves found at the top of the canopy, rather than as a change in total canopy leaf volume (leaf area index; LAI) [5]. In extremely dry years, such as during El Niño events, a time-series of satellite observations demonstrated that foliage in Amazon forest canopies declines [23]. Vina and Henebry [24] showed that remotely sensed vegetation indices were useful in quantifying the impacts of El Niño/Southern Oscillation (ENSO) events on phenological cycles of tropical vegetation in South America.

Although we still lack details about when and how drought and phenology are expressed in tropical forest canopies, the past five years have demonstrated that evergreen forests are far from static canopies. We now know that tropical forest canopies are highly dynamic, responding to climatic and anthropogenic factors over time. These technical and scientific advances provide new opportunities for regional mapping of climate impacts on ecosystem processes, and aid in determining which forests are particularly sensitive to drought. Maps of forest phenology are valuable in directing field investigations toward environmental response gradients and investigating ecological mechanisms operating at regional scales. These tools are currently being applied to questions related to the strong 2005 Amazon drought, and are likely to lead to new and novel contributions to tropical forest response to dramatic changes in water supply.

Canopy chemistry

Knowledge of the structure and chemistry of a tropical forest canopy would provide key insights into ecosystem function and ecological processes, although canopy access is often an insurmountable hurdle. A forest canopy is an important site of carbon, nutrient and water interactions, and canopy structure and chemistry both reflect and affect those interactions.

The hyperspectral remote-sensing reflectance signatures (Box 1) of deciduous and coniferous canopies are determined by a combination of structural (e.g. architecture and LAI) and biochemical properties [25]. In densely foliated, closed-canopy tropical forests, spectral signatures are dominated by leaf biochemical properties such as nitrogen and moisture content, and less so by variation in total LAI [5]. Early applications of hyperspectral data provided basic regional insight into the chemical variability of tropical forests. Recently, Asner *et al.* [6,26] used the Earth Observing-1 (EO-1) Hyperion satellite sensor to estimate spatial variation in upper-canopy pigments across substrate age and precipitation gradients, and among native and invasive tree species, in Hawaiian forests. Airborne hyperspectral observations have also been used in Hawaiian rainforests to highlight the location of nitrogen-fixing trees and invasive species in the understorey based on measurements of upper-canopy nitrogen concentrations and total canopy water content [27].

Remote measurement of canopy nitrogen and, indirectly, phosphorus, has opened the possibility to map localized fertility gradients from airborne and satellite data [7]. Carlson *et al.* [28] used airborne imaging spectroscopy to map tree species richness in lowland wet tropical Hawaiian forests. Hyperspectral signatures provided metrics of

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Box 2. Spectral mixture analysis

The goal of SMA is to determine the fraction of the reflected signal that comprises a target (endmember) of interest. These endmembers can be selected directly from the image or chosen from a spectral library based on data collected using hand-held field spectrometers. For questions relating to vegetation, a common technique is to use GV, NPV, soil and sometimes shade as endmembers, and assume that every pixel is a linear combination of these targets.

Another SMA approach utilizes the pure spectra of a single target, again either derived directly from the image or from a hand-held spectrometer. In this case, SMA provides the fraction of per-pixel reflectance that is accounted for by the selected target. Results from SMA can be directly evaluated in field campaigns, including endmember abundance change over time. For example, an NPV value of 0.50 from SMA indicates that woody tissues, surface litter and other dead vegetation occupy 50% of the surface area of the pixel. The temporal or spatial change in the NPV fraction can provide a quantitative measure of disturbance. For example, Souza *et al.* [11] use GV, NPV, soil and shade fraction to calculate an normalized difference fraction index (NDFI), which provides a single scale to evaluate disturbance intensity from bare soil (−1.0) to pure green vegetation (+1.0).

Box 3. Radar and LiDAR

LiDAR and radar sensors provide complementary information about forest structure, because LiDAR is sensitive to leaf material and radar to structural features, which can be combined to increase accuracy of biomass and the forest structure estimates. Radar measurements can penetrate into the forest canopy, where the radio waves are returned through various scattering mechanisms. The main scattering components are the crown surface and volume, tree stems and interactions with the ground, with precise reflectance patterns dependent on wavelength, polarization and incidence angle. At L (~1 GHz) and P (~400 MHz) band wavelengths, penetration is deeper and the scattering is primarily from woody biomass components (stems and branches). The incidence angle determines the amount of vegetation illuminated by the radar beam, and the polarization determines the type of interaction with the forest structural components and their orientations [72]. The sensitivity of backscatter to structure and moisture has enabled several unique applications in forests, such as mapping vegetation types and measuring forest biomass components [16,73,74]. One limitation of L-band radar for measuring the biomass of old growth forests was partially overcome with the use of P-band airborne sensors [36]. Additionally, recent innovations in radar interferometry (InSAR) enable measurements of forest height and other vertical dimensions for accurately resolving the vegetation biomass over a variety of old growth and regenerating tropical forests [17,41]. However, in the absence of satellite radar sensors at P-band or with interferometric capability, direct measurements of forest biomass have been limited [40].

LiDAR systems incorporate a laser altimeter to measure accurately the distance from the sensor to the canopy top and bottom elevations. The energy returned from distances between the canopy and ground provides evidence of the vertical distribution of subcanopy strata. One application of LiDAR technology has been to map variations in canopy height with meter-level accuracy [38]. Canopy heights can then be translated into estimates of aboveground biomass based on the allometric relationships between height, basal area and biomass [18,37]. Recent results from the analysis of data from the GLAS laser aboard the ICESAT satellite over the Amazon basin demonstrate the potential of spaceborne LiDAR for sampling the vertical structure of tropical forests and measuring aboveground biomass [39].

canopy biochemical variability, which was directly linked to species richness. Although few tropical forest studies have proven the validity of remote chemical mapping, these early studies highlight the potential application of hyperspectral observations for determining the chemical composition of tropical forest canopies.

Forest structure and species composition

Crown detection and species identification

The size distribution of trees in a tropical forest conveys much information about site-to-site differences in growth and mortality rates, stem density, canopy architecture and forest structure. An ability to track these structural properties over time enables assessments of directional changes in forest dynamics. Processes impacting the largest trees are particularly important as large trees comprise most of the biomass in many tropical forests, serve as a focal point for biological activity and create large canopy gaps at death. Until recently, the ability to measure attributes of individual trees was limited to a few field-based forest inventory plots. Now, high spatial resolution data (Box 1) and other active remote-sensing methods (Box 3) are advancing our ability to monitor and map forest structure at the scale of individual trees over large areas.

High-resolution imagery (≤4 m) is necessary to quantify key canopy structural attributes. New high-resolution satellite sensors have augmented existing forest inventory plots by sampling canopy characteristics over large areas, where field access to remote locations is difficult and expensive. Satellite-based measurements of crown area and width correlated well with field data on forest size structure from forest inventories [3]. Maps of individual trees from 10-cm resolution aerial imagery have also been used to estimate carbon stocks in a tropical forest in Belize [29]. High-resolution satellite data provide a means for estimating rare events, such as large tree mortality, across areas larger than traditional field plots, based on maps of individual tree crowns over time [2].

The ability to map structural attributes for individual trees over large areas opens several new questions [30] including: (i) how does the density of canopy-emergent trees vary across tropical forest landscapes? (ii) Does the size distribution of trees vary with environmental factors, such as dry-season length or forest productivity rates? And (iii) how does large tree mortality vary across landscapes and regions in response to intense drought? Future development of new crown delineation algorithms, in combination with new field-based allometric equations, will offer additional benefits in understanding tropical canopy structure at the landscape scale. In ecological terms, major limitations in using high-resolution data for canopy mapping include the relationship between image spatial resolution and the smallest trees that can be detected, and the paucity of field data with which to validate remotely sensed information. The high cost and limited spatial coverage of high-resolution data and persistent cloud cover over the Amazon also prohibit the widespread use of these techniques.

Moving from the delineation of individual tree crowns in high-resolution imagery to mapping individual tropical tree species at regional scales would provide new research opportunities in conservation, evolutionary biology and community ecology. Estimates of tropical tree species

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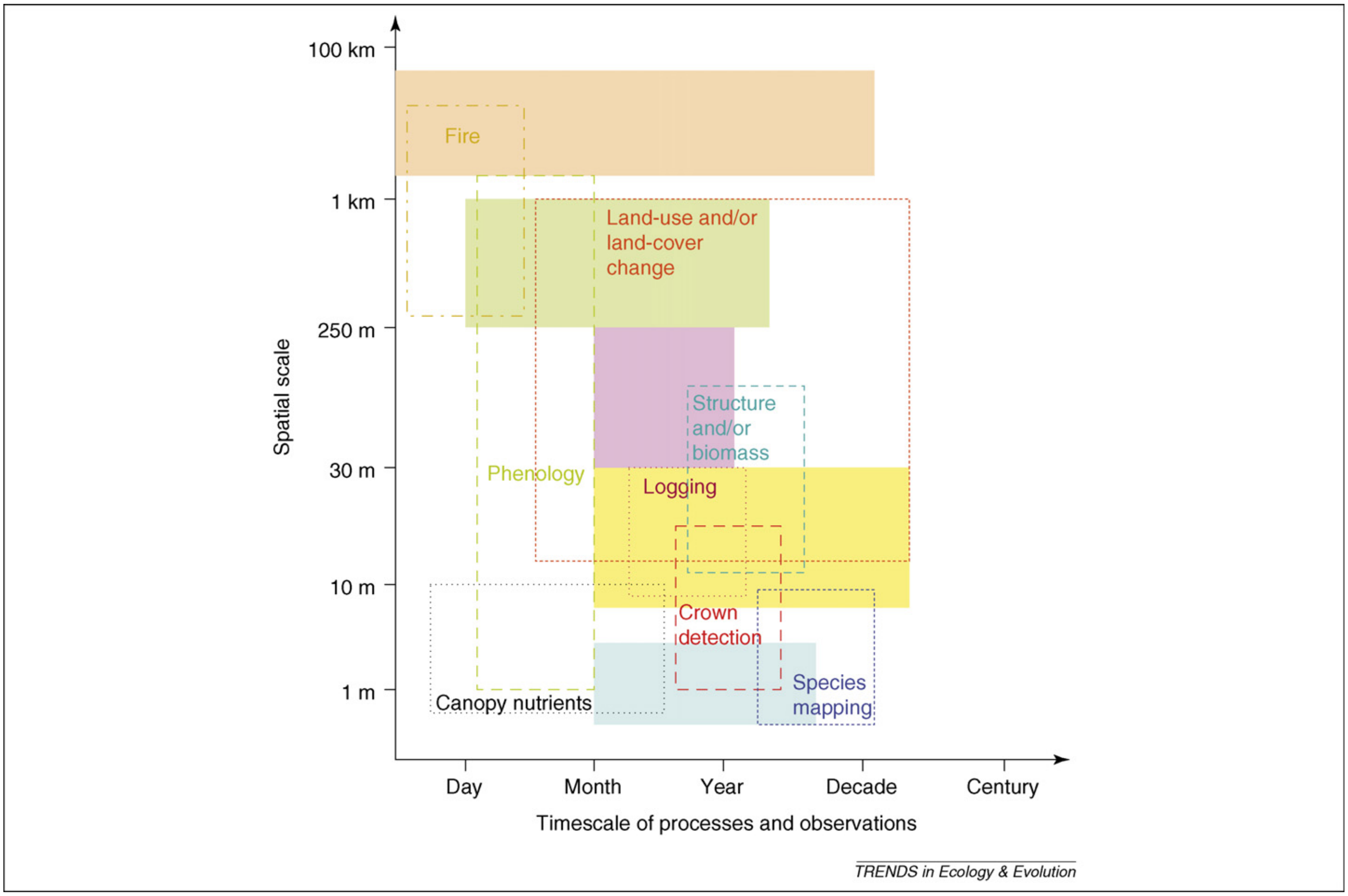

Figure 1. Scales and sensors. Recent advances in remote sensing of tropical forests have improved our understanding of a range of ecological processes that operate at varying spatial and temporal scales. Colored boxes show the spatial and temporal range of coverage from different satellite and airborne sensors (red, GOES; green, MODIS; pink, LiDAR, Radar; yellow, Landsat, EO-1; blue, IKONOS, Quickbird, Airborne). Suitable overlap between the scales of ecological processes, human actions and remote-sensing technology is denoted by dash and dot boxes.

diversity are uncertain, driven primarily by a lack of comprehensive field inventories. In tropical forests, the use of environmental variation as a proxy for variation in species composition is rare [31], although the identification of key species-habitat interactions is a fundamental requirement for effective conservation planning. In this regard, remote-sensing data are a promising source of information, which is often correlated with floristic and environmental variation [32]. Recently, high spatial resolution imagery from cameras, videography, and multispectral airborne and spaceborne sensors has stimulated the development of techniques for individual species detection and floristic measurements. Such capabilities in the tropics will improve multiscale and systematic monitoring of forest types, tree floristic composition, species richness, habitat type and disturbance history [4]. Given methodological issues, studies are currently limited to emergent trees or species with clear canopy architectural traits that facilitate detection. The ability to detect and map individual species will be advanced with the integration of high spatial resolution imagery with hyperspectral data, validated against field data. Improved scaling methods from high to moderate resolution imagery are also needed.

Forest biomass and structural attributes

Trees constitute one of the major stocks of carbon in tropical forests and have an important role in the cycling of carbon at regional and global scales (Box 4). Overall, regional variation in forest biomass is the result of differences in tree stem density, growth and mortality rates, and other species-specific attributes, such as wood density. However, lack of spatially explicit maps of biomass over the Amazon basin is one of the largest sources of error in estimates of carbon emissions from tropical forest conversion [33,34].

Remote-sensing techniques offer the most practical approach to estimating forest biomass and monitoring changes in forest structure over large heterogeneous areas. Radar sensors (Box 3) enable direct measurements of live aboveground woody biomass (carbon stocks) and structural attributes such as volume, basal area and crown mass [35,36]. Light Detection and Ranging (LiDAR) measurements provide the most direct estimates of canopy height and the vertical structure of canopy foliage [37–39]. Together, these measurements enable ecologists to quantify the 3D distribution of vegetation at a landscape scale; to understand processes of carbon accumulation and forest succession; and to improve the state of ecosystem models. Several studies have also used synthetic methods for mapping tropical forest biomass [8,40,41]. Saatchi *et al.* [40], for example, combined forest inventory plot data with optical and radar remote-sensing data to map biomass distribution of the Amazon basin at 1-km resolution in ranges extending up to 400 Mg ha^{-1} (Figure 2). This map provides the first information about how basin-wide gra-

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Box 4. Amazon forest carbon balance

Remote sensing has improved our ability to provide spatially explicit and consistent estimates of the extent of tropical deforestation [43,45]. Although conversion of forest clearing rates into an associated carbon flux is problematic [33,75], there is substantial evidence that Amazon deforestation is a source of ~2 Pg carbon yr^{-1} to the atmosphere [33,44]. Although carbon in recovering anthropogenic secondary forests could partially offset the deforestation source, remote-sensing studies of these transitional ecosystems show that this offset is small [9,48,63]. Additional investigations based on satellite imagery have quantified the carbon flux associated with processes that are subtle and more difficult to detect, such as selective logging [10,11] and understorey fires [53]. Advances in remote sensing will continue to improve our understanding of the land-use carbon source from tropical forests through future refinement of methods to develop spatially explicit maps of aboveground biomass [40]. New sensors, such as the Orbiting Carbon Observatory (OCO), scheduled to be launched in 2008, will open the possibility to monitor directly atmospheric concentrations of CO_2 over tropical forests.

By contrast, the carbon balance of primary forest that is not directly impacted by human activity is contentious [76–78]. Based on the average biomass accumulation from investigations carried out on permanent forest inventory plots across the Amazon basin, a basin-wide old-growth forest carbon sink of 0.5–1 Pg carbon yr^{-1} has been suggested [79], apparently of sufficient size to offset the land-use source. Several studies have questioned these estimates on methodological grounds [80,81], and these potential artifacts have been contested by the targeted investigators [82–84]. Another potential source of error is spatial sampling error. If forest carbon source and sink patches are distributed nonlinearly across the landscape, addressing the large-scale carbon balance could require a sampling scheme that is different from that offered by the network of Amazon forest inventory plots [76]. Remote-sensing techniques have much to offer this debate by improving our ability to map canopy gaps, tree mortality events and phenological patterns across the landscape.

For most Amazon trees, the rate of carbon release from dead trees is more rapid than the rate at which it is accumulated in live trees. For example, in the Central Amazon, average age (time accumulating carbon) for trees ≥10 cm trunk diameter is ~175 years [85,86], whereas a dead tree is, on average, completely consumed by decomposition in ~15 years [87]. Thus, areas that have been recently impacted by a high mortality event will be strong carbon sources, but most forest patches could be accumulating carbon in response to historical disturbances. How variability in disturbance history plays out at the landscape scale to influence forest carbon balance remains to be adequately investigated.

Forest inventory plots provide little information about catastrophic mortality events, including gaps >0.10 ha and intensity >5% dead stems per event. For example, of 1284 gaps (in a 50-ha plot) investigated in Panama, only nine were >0.04 ha, with the largest gap occupying just 0.11 ha (1100 m^2) [88]. At the other extreme, large natural blowdown gaps >30 ha in size (produced by high-velocity downburst winds) have been detected across the Amazon using spectral reflectance features in Landsat TM images, with the largest event occupying 3000 ha [89]. Although the recurrence interval for events >30 ha is probably on a millennial timescale, inclusion of smaller gaps down to 5 ha decreased the return interval by an order of magnitude [89]. In the gap size range between tree mortality investigations on forest inventory plots, and events impacting large tracts of forests, little is known about return intervals for mortality events of ~0.1–5 ha, and this scale might be crucial for determining landscape carbon balance.

Remote-sensing investigations have much to offer the debate about whether Amazon forest inventory plots provide an unbiased estimate of landscape carbon balance. SMA (Box 2) on multispectral and hyperspectral imagery appears particularly promising for mapping tree mortality events at the landscape scale. Similar to subtle disturbance signals associated with selective logging [10,11], natural mortality events also result in an ephemeral increase in the NPV signal. The magnitude of the increase in this woody signal (ΔNPV) is likely to be correlated with the intensity of the disturbance event. A 2005 Hyperion image from the Central Amazon demonstrates how blowdown gaps can be distributed at the landscape scale, and application of SMA tools to this image will enable forest inventory plots to be established along the entire disturbance gradient (Figure I).

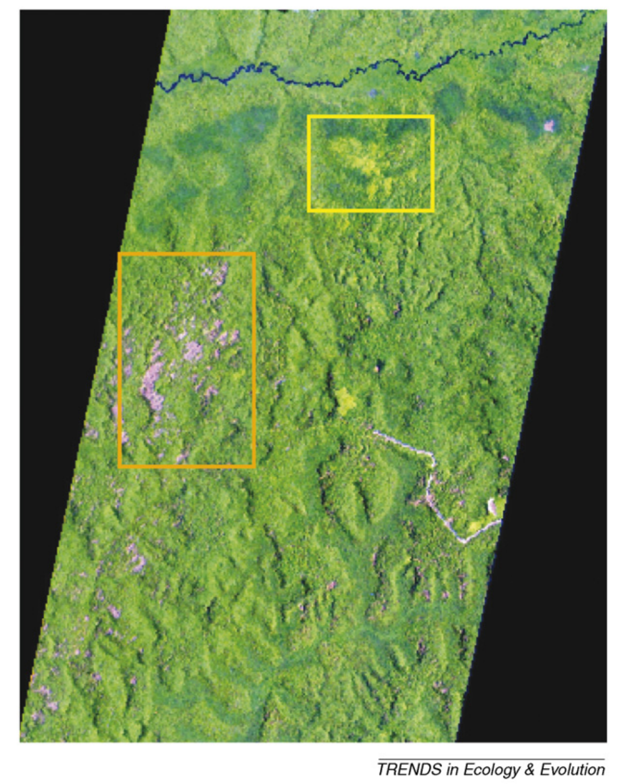

Figure I. Blowdown gap distribution in the Central Amazon. This 2005 Hyperion image (available from the NASA LBA-ECO Project Office) shows blowdown gaps distributed across a landscape north of Manaus, Brazil, at the end of the ZF-2 road (entering from below-middle right) with shortwave-IR (1709 nm) as red, near-IR (1053 nm) as green, and visible red (650 nm) as blue. Owing to spectral reflectance differences in exposed wood and surface litter in blowdown gaps, these patches show up as red–blue (orange box). An old blowdown, with regrowing vegetation showing strong reflectance in the near-IR, shows up as bright green (yellow box), but with the clear blowdown pattern characterized by Nelson *et al.* [89]. Quantitative disturbance maps can be developed from this image by applying SMA methods similar to those used to detect logging [10,11]. In contrast to existing forest inventory methods, stratified random sampling across this entire disturbance gradient will enable researchers to address important questions regarding controls over species distribution and abundance, and landscape carbon balance. [ED: please move figure to Box 4].

dients, such as total precipitation and dry season length, drive regional biomass distribution, and significantly improves our ability to estimate the carbon flux resulting from land-use change. The fusion of LiDAR and radar data could offer even more promise for accurate measurement of biomass distribution in forests worldwide [42].

Anthropogenic impacts

Land-use and land-cover change

Given the rapid decline in tropical forest cover as a result of deforestation, spatially explicit and consistent information about changes in forest cover is perhaps the most successful ecological role of remote sensing [43–45]. The regional-scale

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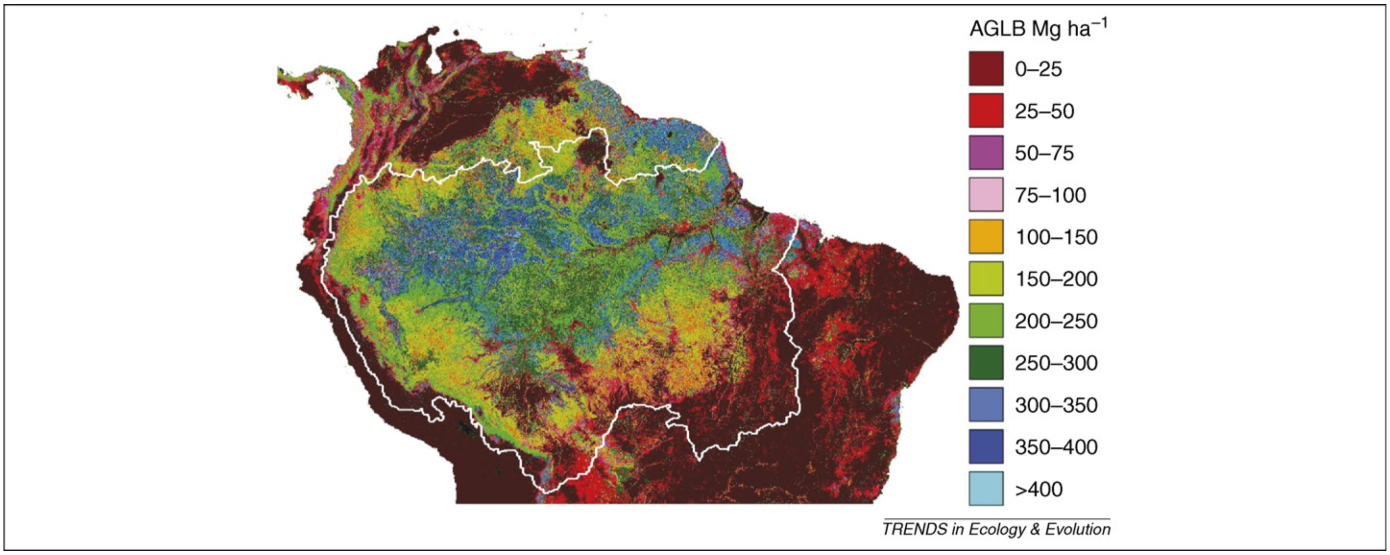

Figure 2. Amazon basin-wide biomass distribution. The aboveground live biomass (AGLB) classification was derived from the fusion of moderate resolution (1 km) optical and microwave remote-sensing data [40]. The distribution was produced by a hybrid algorithm of direct estimation and the decision rule approach from seasonal MODIS LAI and NDVI (Normalized Difference Vegetation Index), QSCAT scatterometer data representing canopy moisture and roughness, percent tree cover from MODIS the continuous fields product, JERS-1 radar backscatter measuring low-density vegetation biomass, and the landscape topography from SRTM (Shuttle Radar Topography Mission). The figure demonstrates strong gradients in biomass distribution at both large and small spatial scales. Few of these gradients have been explored, and this map will serve as the basis for new ecological field investigations.

perspective on land-cover change from satellite data provides an overview of carbon dynamics and defines the surrounding matrix conditions on deforested lands that form the basis of studies in conservation biology and community ecology. Regional maps of land-cover change are also a common scale for interactions between ecology and other disciplines, such as Earth system science and land–atmosphere modeling. Recent advances in remote sensing of land-use and land-cover change have taken one of two approaches. First, daily observations of the entire Amazon basin (Box 1) from new moderate resolution (250 m–1 km) satellite sensors enable the temporal dynamics of various land-cover transitions and vegetation phenology to be studied. Second, given improvements in computing power and data storage capacities, detailed analyses of higher resolution data can now be applied at regional scales.

New satellite sensors that provide daily coverage of the Amazon basin have led to advances in remote sensing of land-cover change at regional scales and improved temporal resolution of change processes. Since 2000, daily coverage from MODIS has been composited at eight-day and 16-day intervals to provide cloud-free observations of the entire basin, enabling for near real-time monitoring of the temporal patterns of forest clearing across the Amazon [13,14,46]. Consistent satellite time series have also led to phenology-based classifications of land-cover change in cerrado [47] and tropical forest [48]. Greater continuity of high- and moderate-resolution satellite observations define the trajectory of land-cover changes over time, from intact forest through logging, deforestation, and subsequent conversion to pasture and cropland [26,48]. The fate of cleared lands ultimately determines important aspects of regional carbon balance (Box 4), forest fragmentation and the strength of feedbacks from the land surface to atmosphere. For example, conversion of pasture to cropland in the Amazon [49] changes the carbon pathway from C4 grasslands to C3 soybeans, thereby altering land-surface water and energy balance [50] and the matrix of non-forest land-cover types that influence species dispersal, habitat quality and conservation objectives. New information from remote sensing about the timing and trends in regional land-cover change highlights the importance of field research and process-level modeling to link our understanding of ecosystem functioning at a common scale.

Advances in remote detection of fire [51], burned area [52] and biomass-burning aerosols have also changed our understanding of forest functioning. Alencar *et al.* [53] highlight the regional importance of understorey fires on forest structure and estimate carbon emissions from the 1997–1998 ENSO event. In combination with fires for land clearing and management [54], the carbon emissions from the arc of deforestation are globally significant [55]. The feedback between biomass burning and forest net primary productivity has been explored by using new models that track atmospheric transport of smoke from observations of active fires [56]. Smoke from deforestation fires impacts large areas of the southern and central Amazon basin, with the potential to influence net incoming solar radiation, nutrient deposition and rainfall patterns [57,58]. Oliveira *et al.* [59] suggest that atmospheric aerosols can enhance the daytime forest carbon dioxide sink over large regions by providing more diffuse radiation than under clear-sky conditions.

Many human activities do not result in a change of land-cover (e.g. forest to pasture). Selective logging is the most common of these diffuse [60] tropical forest disturbances, altering forest functioning for years after the selective harvest of trees. Until recently, little was known about the spatial extent and intensity of selective logging in tropical forests. This remains largely true except for the Brazilian Amazon. Rapid advances in remote-sensing algorithms and methods have opened doors for the large-scale geographical mapping of diffuse forest disturbances in Brazil [10,11,26,61,62]. Souza *et al.* [11,62] used

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SMA (Box 2) to map forest disturbances caused by logging and fire, demonstrating a tight geographical link between logging and subsequent forest degradation via fire for years following timber harvest. Asner *et al*. [10,26] showed that the geographical extent of logging ranged from ~12 000 to 20 000 km^2 yr^{-1}, more than doubling previous estimates of the total forest impacted by human activity. Detailed disturbance maps were also valuable in determining where boundaries, such as national parks and protected indigenous areas, were functioning as an effective deterrence. Comparison of high-resolution logging and deforestation maps [45] demonstrated that previously logged forests have a higher probability of being clear-cut than do intact forests [26]. In combination, these forest disturbance studies show that logging operations have not been treated as a sustainable alternative to deforestation in the Brazilian Amazon.

Despite recent advances in remote sensing of land-cover change, gaps remain in our understanding of forest disturbance in tropical forests and related ecological processes. First, consistent satellite observations are necessary to evaluate the forest response to variable climate conditions. The short duration of the MODIS time series limits more detailed analyses of vegetation phenology or land-cover changes, and Landsat-resolution data that are necessary for canopy damage studies have an uncertain future following the failure in May 2003 of a key component of the Landsat 7 satellite. Maps of regenerating vegetation and forest structural characteristics are also limited by the use of coarse-resolution optical data. Secondary forests have been identified by using time series of MODIS [63] and Multi-angle Imaging Spectroradiometer (MISR) multi-angle optical data [64] but high-resolution radar or LiDAR data are needed for more detailed understanding of forest structure, especially in continuously cloudy regions of the Amazon Basin. Additionally, changes in land-cover do not easily scale to carbon equivalents because of unknown variation in forest biomass [33] and subtle, but important, forest disturbances that are not yet detectable with remotely sensed data [60]. Recent remote-sensing studies have provided the framework to assess the impacts of tropical forest conversion under a changing climate [65], in forest fragmentation [66], for biodiversity loss [67] and for conservation objectives [68]; the next step is to integrate remote sensing of land-cover change and forest disturbance with ecological research on forest recovery, dispersal, community dynamics and other regional-scale ecosystem processes.

Conclusions

Recent contributions from remote sensing to the field of tropical forest ecology stem largely from an improved capacity to sample canopy-level processes across large areas. New sensors and image-processing techniques that enable direct measurement of ecological properties from remote-sensing platforms have generated novel understanding of canopy chemistry, crown detection and forest phenology, and hold the promise for mapping individual species and estimating forest biomass over expansive areas. Advances in remote-sensing methods over large areas also provide regional estimates of diffuse land-cover changes such as selective logging. Remote-sensing data can generate information about tropical forest ecology that is not practical or possible from ground-based studies. The timing and extent of land-cover change and the relationship between climate and forest phenology highlight unique information that is available only from satellite and airborne sensors.

These advances in remote sensing have also altered the dialog between ecology and remote sensing. High-resolution satellite data have expanded the scope of analysis from small field plots to regional understanding across landscapes that are costly and impractical to sample directly. These measurements provide robust estimates of rare events, such as large tree mortality [2], that cannot be easily achieved at the landscape-scale using forest inventory data. Remote-sensing studies are generating new perspectives on regional-scale ecology, offering direction for future field studies based on the location of key environmental gradients or unique species assemblages. The emphasis on ecologically relevant measures from satellite data has created common currencies between field and remote-sensing metrics, enabling the development of process models that link directly to both scales of observation.

In addressing ecological questions with remote-sensing technology, it is important not to be constrained by the observational capacity from currently available airborne and spaceborne sensors. Although we emphasize here the role of new technology for improving our understanding of tropical forests, we also present novel uses of established capacity based on insights from field experiments and other disciplines. The most effective use of remote-sensing data is through its fusion with appropriate ecological field investigations, while effectively leveraging the unique capacity of remote sensing to overcome spatial, temporal, and logistical challenges toward developing novel understanding of tropical forest structure and dynamics.

Acknowledgements

We thank the participants of the NASA LBA-ECO Forest Disturbance and Recovery Synthesis Workshop held at Tulane University in June 2006: Luiz Aragao, Vilany Carneiro, Elise Chapman, Marcos Costa, Ruth DeFries, Jeremy Fisher, Niro Higuchi, George Hurtt, Michael Keller, Steve Klooster, Mark Kramer, Paul Moorcroft, Lucie Plourde, Amanda Robertson, Sami Rifai, Marie-Louise Smith, Liliane Teixiera and Yadvinder Malhi. This work was funded by NASA LBA-ECO grant CD-34.

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