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# BEYOND POTENTIAL VEGETATION: COMBINING LIDAR DATA AND A HEIGHT-STRUCTURED MODEL FOR CARBON STUDIES

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*Abstract.* Carbon estimates from terrestrial ecosystem models are limited by large uncertainties in the current state of the land surface. Natural and anthropogenic disturbances have important and lasting influences on ecosystem structure and fluxes that can be difficult to detect or assess with conventional methods. In this study, we combined two recent advances in remote sensing and ecosystem modeling to improve model carbon stock and flux estimates at a tropical forest study site at La Selva, Costa Rica (10°25′ N, 84°00′ W). Airborne lidar remote sensing was used to measure spatial heterogeneity in the vertical structure of vegetation. The ecosystem demography model (ED) was used to estimate the consequences of this heterogeneity for regional estimates of carbon stocks and fluxes. Lidar data provided substantial constraints on model estimates of both carbon stocks and net carbon fluxes. Lidar-initialized ED estimates of aboveground biomass were within 1.2% of regression-based approaches, and corresponding model estimates of net carbon fluxes differed substantially from bracketing alternatives. The results of this study provide a promising illustration of the power of combining lidar data on vegetation height with a height-structured ecosystem model. Extending these analyses to larger scales will require the development of regional and global lidar data sets, and the continued development and application of height structured ecosystem models.

*Key words: aboveground biomass; carbon fluxes; Costa Rica; ecosystem demography; ecosystem modeling; La Selva; lidar; regional carbon stocks; remote sensing.*

## Introduction

Large-scale estimates of terrestrial carbon stocks and fluxes are uncertain, particularly over regions where measurements are sparse. Regional carbon stocks have been estimated primarily by extrapolating data obtained in soil surveys and ground-based measurements made on individual trees (Post et al. 1982, Olson et al. 1983). Uncertainties among such estimates can be as large as a factor of two or more in some regions (Houghton et al. 2001). Regional estimates of carbon fluxes have been made using various methods including repeatedly inventoried ground plots (Birdsey and Schreuder 1992, Phillips et al. 1998, Goodale et al. 2002), flux-tower measurements (Wofsy et al. 1993, Grace et al. 1995, Goulden et al. 1996, Baldocchi et al. 2001), and inversion of atmospheric tracer–transport models (Fan et al. 1998, Battle et al. 2000, Ciais et al. 2000, Gloor et al. 2000, Gurney et al. 2002). Even in the most intensively studied regions, the limited number of ground-based measurements, sparse nature of the flux tower network, and the coarse effective resolution of inversion methods make it difficult to resolve the spatial and temporal heterogeneity in stocks and fluxes required for more accurate estimates at regional scales. Improving the estimates of regional carbon stocks and fluxes in most areas will require more data from multiple scales and sources.

In addition to data, models are needed for synthesizing knowledge gained in local studies and for making projections. For models to be reliable tools, however, they must be thoroughly tested and initialized to reflect nonequilibrium conditions where they exist. Natural disturbance, land use, and regrowth, for example, are processes occurring at many spatial and temporal scales on the landscape that have traditionally been difficult to track empirically and in regional models. From blowdowns to fires, logging, agriculture, and abandoned agricultural plots, landscapes are generally composed of a heterogeneous mixture of patches of different successional ages. Both ecosystem structure and carbon fluxes vary strongly with successional age (e.g., Botkin et al. 1972, Shugart and West 1977, Shugart 1984), and without an accurate initialization of

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these conditions, even the best models are limited in their ability to make reliable projections on policy-relevant time scales.

There are three major approaches to obtaining initial land-surface conditions for ecosystem models. The most common is to assume that vegetation is in its ''potential'' state, i.e., for any land cover class (e.g., broadleaf evergreen) the vegetation is assumed to be in its final condition as determined by climate. This approach has been commonly used in studies that assess ecosystem dynamics in the absence of land use and other disturbance events (Melillo et al. 1993, Potter et al. 1998, Tian et al. 1999). However, without knowledge of land-use activities or the current successional status of lands recovering from prior land use and natural disturbances, carbon estimates for a given area assuming the potential state may be highly inaccurate. For example, a forest in early stages of secondary regrowth likely will have a very different carbon stock and net carbon flux than a mature forest in the same area.

A second approach to obtain initial conditions is to ''spin-up'' models to the present using land-use history information as input. Such an approach has recently been used to estimate the past and current state of U.S. ecosystems as a basis for projecting the future of the U.S. carbon sink (Hurtt et al. 2002). While efforts to construct relevant global land-use history products are needed and ongoing (Ramankutty and Foley 1999, Goldewijk 2001), adequate historical reconstructions are difficult to compile, have significant uncertainties, and are currently unavailable in many regions. In tropical regions, the needed information is typically sparse or nonexistent (Brown 1997).

A third route is to measure initial conditions directly. In principle, the effects of prior land use and disturbances are manifested in the current state of ecosystems. On forested lands, relevant metrics of forest structure include diameter at breast height (dbh), height, species identification, and other attributes. Direct measurements can be obtained on individual plants over plot-sized areas, and potentially over larger areas with statistical sampling approaches such as that used in the U.S. Forest Inventory (Birdsey and Schreuder 1992, Gillespie 1999). However, limited resources and access can make ground-based studies prohibitive in at least some areas. Standardizing field protocols between different regions present additional challenges.

Remote sensing provides another approach for obtaining initial conditions over large areas. Optical remote sensing strategies have successfully been used to characterize land cover, land-cover change, phenology, and other important properties of ecosystems (Skole and Tucker 1993, Myneni et al. 1997, Belward et al. 1999). Optical information has also been used to infer biomass and successional status (Foody et al. 1996, Curran et al. 1997, Lucas et al. 2000, Nelson et al. 2000, Steininger 2000, Myneni et al. 2001). However, many optical metrics, such as those related to leaf area index (LAI), saturate much earlier in succession than biomass and other important structural properties. Passive radar techniques have also made strides in estimating biomass, but have similar challenges (Kasischke et al. 1997). Neither passive optical nor passive radar techniques directly measure the vertical components of the vegetation canopy. Even if such canopy data were available, say for example, a histogram of tree heights for an area, most ecosystem models are not structured such that they could easily assimilate these data.

There have been two recent developments, one in remote sensing technology, the other in ecosystem modeling, that offer the potential for improved carbon estimates based on more accurate representation of initial vegetation conditions. The first is the maturation of airborne and space-based lidar remote sensing of vegetation canopy height structure (Dubayah and Drake 2000, Dubayah et al. 2000, Lefsky et al. 2002). Recent studies have validated the ability of lidar to measure canopy height and vertical structure (e.g., Lefsky et al. 1999*a*, Peterson 2000, Harding et al. 2001, Drake et al. 2002*b*). It has also been shown that such data can be used to infer associated biophysical variables, such as aboveground biomass, with unprecedented accuracy and consistency, even in the most complex canopies, and over large areas (e.g., Lefsky et al. 1999*b*, Means et al. 1999, Lefsky et al. 2001, Drake et al. 2002*a*, *b*, Drake et al. 2003). The second is the development of a new height-structured terrestrial ecosystem model, the ecosystem demography (ED) model (Hurtt et al. 1998, 2002, Moorcroft et al. 2001). ED is particularly amenable to initialization and testing with field and remote sensing data because it is defined at the scale of individual plants. Furthermore, because ED is height structured, its use of canopy structure derived from lidar data is natural and immediate.

The goal of this study was to assess the potential for using lidar observations of tropical forest structure to initialize the ED model for improved estimates of carbon stocks and fluxes. Our approach focused on La Selva, Costa Rica, and used the simplest lidar metric, mean canopy height. First, we tested that ED accurately predicts biomass as a function of canopy height for this site. We next used lidar data to initialize ED to produce spatial estimates of aboveground carbon stocks and net fluxes. Comparisons of the ED-based estimates with field data and regression-based estimates served the dual purpose of enabling an assessment of the efficacy of our approach to model initialization, while providing a validation of important aspects of the ED model.

## New Developments

Lidar (light detecting and ranging) remote sensing is an active technology, analogous to radar, but using laser light (Dubayah and Drake 2000, Dubayah et al. 2000, Lefsky et al. 2002). Pulses of laser energy are

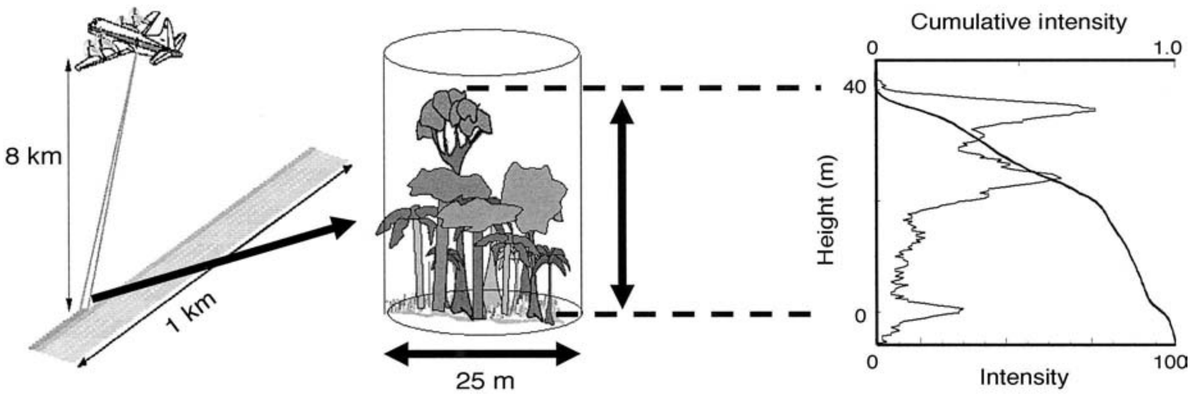


FIG. 1. Remote sensing of canopy vertical structure using the Laser Vegetation Imaging Sensor (LVIS). LVIS images a 1-km swath of 25-m footprints, as shown on left. Each return waveform within a footprint records the amount of nadir reflectance as a function of height, giving the vertical distribution of leaves and branches as shown on the graph at right. A greater amplitude (intensity) is indicative of more canopy material at that height. Canopy height is determined by subtracting the range to the ground from that to the first detectable return or some threshold above that return. Metrics derived from the waveform, such as the height of median energy and the cumulative return, also have been shown to be useful metrics for ecological applications.

fired towards the surface where they reflect off the various structural elements of the surface, such as leaves, branches, and ground. The incident pulse is extended in time (usually Gaussian in shape) so that the return signal is extended as well. The incident Gaussian waveform is returned as a reflected waveform that provides a record of the vertical structure of the surface. Lidar systems record the roundtrip time for these pulses of laser energy to travel between the instrument and the surface, enabling a distance or range measurement to be taken. Where the return signal also includes a return from the ground, the difference in range from the top of the canopy to ground provides a measurement of the height of the canopy. Similarly, by reference to the ground, the height of any element of vertical forest structure (e.g., the bottom of the canopy or midstory) may be estimated (see Fig. 1).

Numerous studies have validated the ability of lidar to measure canopy height and canopy vertical structure in a variety of forest ecosystems (e.g., Nelson et al. 1988, Naesset 1997, Magnussen et al. 1999, Lefsky et al. 1999*a*, Drake and Weishampel 2000, Peterson 2000, Harding et al. 2001, Parker et al. 2001, Drake et al. 2002*b*). Lidar may also be used to infer associated biophysical variables, such as aboveground biomass, with high accuracy and consistency (e.g., Lefsky et al. 1999*b*, 2001, Means et al. 1999, Harding 2001, Drake et al. 2002*a*, *b*). Recent results from the Vegetation Canopy Lidar (Dubayah et al. 1997) calibration/validation campaign over dense tropical forests surrounding La Selva Biological Station have confirmed that lidar data may be used to accurately retrieve canopy heights, basal area, mean stem diameter, and aboveground carbon across a spectrum of successional conditions (Peterson 2000, Drake et al. 2002*a*). As such, lidar instruments provide a suite of important land surface characteristics (Dubayah and Drake 2000) that can be used to initialize terrestrial ecosystem models (see Lefsky et al. 2002 for a review of lidar applications in terrestrial ecology).

A second development is an individual-based terrestrial ecosystem model, ED (ecosystem demography), that addresses the challenges of scaling up local heterogeneity in studies of regional ecosystem dynamics (Hurtt et al. 1998, 2002, Moorcroft et al. 2001). ED is a stochastic simulator of vegetation dynamics with integrated submodels of plant growth, mortality, phenology, biodiversity, disturbance, hydrology, and soil biogeochemistry. Individual plants of different functional types compete mechanistically in ED under local environmental conditions for light, water, and nutrients. ED differs from most other terrestrial models by formally scaling up physiological processes through vegetation dynamics to ecosystem scales, while simultaneously modeling natural disturbances, land use, and the dynamics of recovering lands. ED has recently been implemented in South and Central America (Moorcroft et al. 2001), the United States (Hurtt et al. 2002), and is under development as a global model. Of particular relevance to this study is the fact that all plants in ED have an explicit height, a property that creates the potential for direct connection to lidar remote sensing.

## STUDY AREA AND DATA

La Selva Biological Station is located in the Atlantic lowlands of northeastern Costa Rica at 35–150 m elevation near the town of Puerto Veijo de Sarapiqui. The area is classified as Tropical Wet Forest (Holdridge et al. 1971, Hartshorn and Hammel 1994) and receives a mean rainfall of 4000 mm per year (Sanford et al. 1994, Matlock and Hartshorn 1999).[9] La Selva has been well characterized in terms of forest demography and

[9] URL: ⟨http://www.ots.duke.edu/en/laselva/⟩

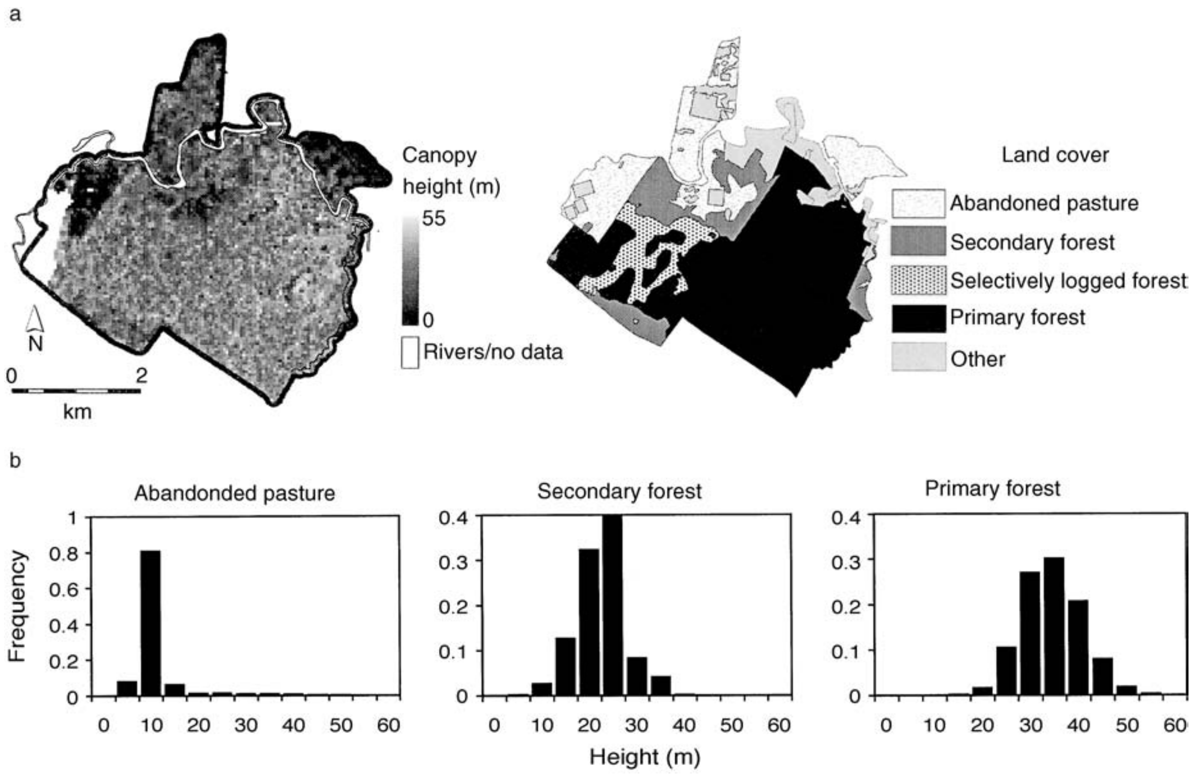


FIG. 2. (a) Map of canopy heights measured by Laser Vegetation Imaging Sensor (LVIS) and a corresponding land cover map of La Selva Biological Station in Costa Rica. (b) Distribution of mean canopy heights measured by LVIS from areas with three different land-use histories. The spatial patterns of canopy heights illustrate the utility for using lidar to distinguish among forests in various stages of succession.

structure (e.g., Guariguata et al. 1997, Clark and Clark 2000), land-use history (Pierce 1992, Read et al. 2001), edaphic conditions (Clark et al. 1999) and many other biotic and abiotic characteristics (McDade et al. 1994). In addition, a $50 \times 100$ m grid system with permanent monuments has been precisely surveyed and installed over a large portion of the landscape enabling the georeferencing of the landscape with remote sensing and other ancillary data (e.g., see Rocchio 2000, Hofton et al. 2002).

La Selva has an important history of land use that is still evident in the structure of the vegetation and the functioning of the ecosystems found there (McDade et al. 1994). The landscape is comprised of a mixture of plantations and agroforestry patches, secondary forests of various ages, selectively logged forests, and old-growth tropical wet forests. In addition, the soil types at La Selva are found in ~52% of the lowland tropics. Field measurements from areas with different land-use histories were used to derive plot-level mean canopy heights and aboveground biomass estimates.

In March of 1998, the laser vegetation imaging sensor (LVIS; Blair et al. 1999, Dubayah et al. 2000) collected lidar data over areas of Costa Rica including La Selva. LVIS was flown at an altitude of ~8 km with a nominal footprint size of 25 m diameter. LVIS footprints were spaced every ~9 m across track, for a total swath width of 1 km, and were spaced ~27 m along track for approximately contiguous coverage. The return waveform was digitized at 60 cm vertical increments giving a detailed description of canopy vertical structure. Several flights were conducted over La Selva to provide nearly complete coverage (Fig. 2).

## METHODS AND RESULTS

Our goal was to combine lidar data and a height-structured ecosystem model to take advantage of the relationships that exist between vegetation height and ecosystem structure and dynamics. These relationships are expected to exist because as forests grow during succession, plants get larger and taller, and stand level biomass tends to accumulate at a decelerating rate (Botkin et al. 1972, Shugart and West 1977, Shugart 1984, Saldarriaga et al. 1988, Moorcroft et al. 2001). Therefore, information on vegetation height should be a powerful indicator of important ecosystem properties. To illustrate this idea, we ran ED (ecosystem demography) under climatological conditions to produce projections of how forest structure can be expected to change through succession at La Selva. ED estimates were calculated using the version of ED described in Moorcroft et al. (2001), and following that study, used the mean

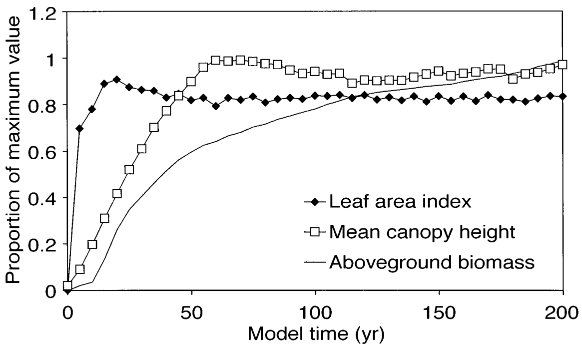


FIG. 3. Normalized (fraction of maximum value) estimates from the ED (ecosystem demography) model of leaf area index (LAI), mean canopy height, and aboveground biomass through time for La Selva, Costa Rica. To produce these estimates, ED was run from an initial condition of seedlings of all functional types as specified in Moorcroft et al. (2001). LAI saturates relatively quickly as a function of stand age. In contrast, mean canopy height and biomass saturate over longer time periods. This implies that conventional remote sensing approaches may not easily be able to distinguish primary from secondary forests, while lidar-derived height data should provide more information on successional status.

values of 1987 and 1988 climate data from NASA-ISLSCP (International Satellite Land Surface Climatology Project) Initiative I (Meeson et al. 1995, Sellers et al. 1995). Normalized model output for three important variables: aboveground biomass, mean canopy height, and LAI are shown in Fig. 3. Note that biomass is projected to take more than 200 years to equilibrate. LAI, in contrast, is expected to saturate in only 10–15 years at ~12% of the final biomass. Mean canopy height saturates more slowly than LAI and is therefore expected to be an informative indicator of biomass later into succession. Mean canopy height is also retrievable by lidar.

Given these expected relationships between canopy height and ecosystem structure, we assessed the efficacy of using lidar data with the ED model at La Selva. We first produced a map of aboveground carbon stocks for validation by applying an empirical relationship between field-based estimates of carbon and the height of median energy derived by lidar (described later in the *Methods and results*). We then produced a comparable map of ED estimates of aboveground carbon stocks using lidar estimates of canopy height to initialize the ED model. Thus initialized, ED was used to produce corresponding estimates of the spatial distribution of mean aboveground net carbon fluxes over the region. This methodology is summarized in Fig. 4. Before implementing this methodology, we first validated ED estimates of biomass as a function of canopy height.

### *Biomass estimates as a function of canopy height*

Before lidar data may be used to initialize ED, it is important to verify that there is close agreement be-

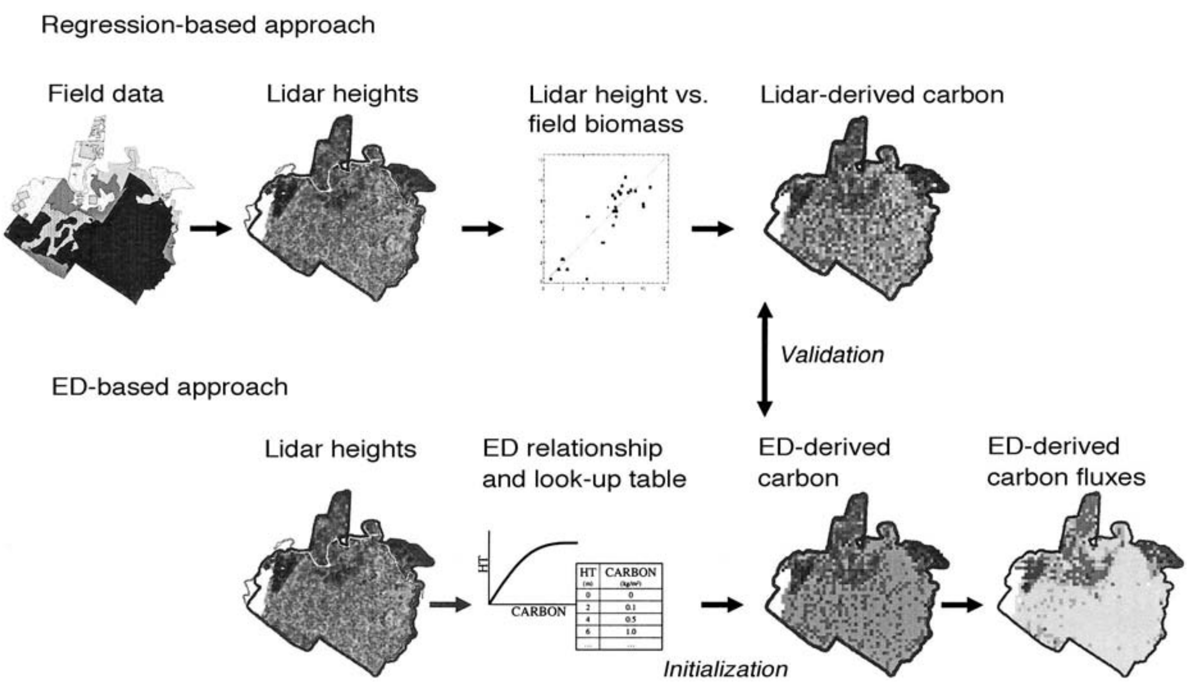


FIG. 4. Summary of the methodology for the regression-based and ED (ecosystem demography)-based approaches. The top row illustrates the regression-based approach in which field data and lidar data are statistically related and used to produce mapped estimates of carbon stocks. The bottom row illustrates the use of lidar data to initialize the ED model to produce mapped estimates of carbon stocks and net fluxes. Regression-based and ED-based estimates of carbon stocks are compared for validation.

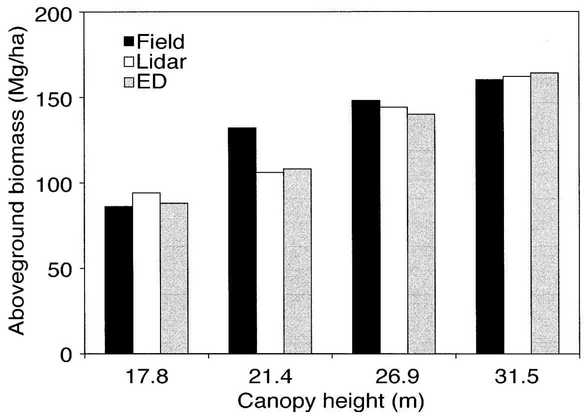


FIG. 5. Estimates of aboveground biomass at La Selva from field-based, regression-based, and ED (ecosystem demography)-based methods in stands of different mean canopy height (representing different canopy ages).

tween field-based and model-based estimates of biomass as a function of vegetation height. If this is not the case, then initialization of ED using stand height would lead to an inaccurate initialization of biomass. To investigate this, we compared ED estimates of aboveground biomass (AGB) with estimates from field-based and regression-based techniques at four key plots in the domain (Fig. 5). These plots differ in successional age, and are 14, 22, 33 years old, and ''old growth,'' respectively. Field-based estimates of plot-level AGB were estimated by applying a tropical wet forest equation (Brown 1997) to all stem diameters (≥10 cm at breast height or above buttressing) in 18 old-growth forest plots (0.5 ha per plot), three secondary forest plots (0.5 ha per plot), and three agroforestry plots (0.25 ha per plot) (see Drake et al. 2002*a*, 2003).

Regression-based estimates were produced using the lidar height of median energy metric and applying a plot-level linear regression equation between this statistic and the field-estimated AGB after Drake et al. (2002*a*). The height of median energy and mean canopy height were shown to be highly correlated with each other and both are strong predictors of biomass (Drake et al. 2002*a*). However, because the former produced significantly better results, it is the metric we use here. Note that because the relationships between lidar and field-based estimates of AGB have already been developed and validated (Drake et al. 2002*a*), either could have been used for plot-level comparisons with ED. We have presented both for clarity and to illustrate the strength of the relationship between lidar and field-based estimates of AGB. ED-based estimates of AGB were obtained using lidar estimates of mean canopy height as an index to the set of ED model estimates representing 0–200 years of succession at the site.

ED-based and regression-based estimates of AGB agree well with field estimates at all four plots (Fig. 5). This suggests that ED produces a reasonable relationship between biomass and mean canopy height and serves as a partial validation of model structure and parameterization. To investigate this further, we plotted regression-based and ED-based estimates of aboveground biomass as a continuous function of mean canopy height. To convert biomass to carbon units, we assumed a carbon to biomass ratio of 0.5. Regression-based and ED-based estimates are in close agreement up to a mean canopy height of ~29 m (Fig. 6). This result provides the basis for using lidar measurements to produce a reliable initialization of the aboveground biomass within ED. Above 29 m, the comparison degrades because the mean canopy height in ED asymptotes earlier than observed. The consequences of this property of the model are evaluated below.

### *Spatial distribution of aboveground carbon stocks*

Given that there was close agreement between regression-based and ED-based techniques, we next initialized ED with lidar data to produce a map of estimated carbon stocks that can be compared to a map of carbon stocks produced using a regression-based approach. To produce the regression-based map, we created a spatial grid of lidar height of median energy at 1.0 ha resolution, and used these values as input to the regression equation (Drake et al. 2002*a*). The map of ED estimates was created by first producing a spatial grid of lidar mean canopy heights at 1.0 ha. The values in this grid were then used to index a set of ED model

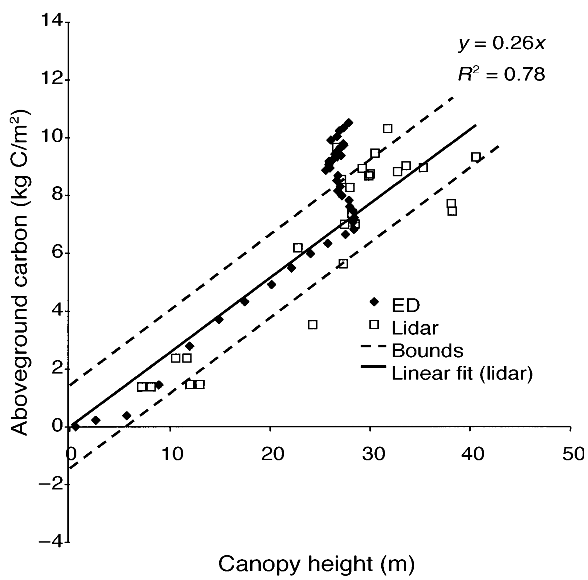


FIG. 6. Aboveground carbon estimates from regression-based (lidar) and ED (ecosystem demography)-based methods as a function of mean canopy height. The solid line gives the relationship between carbon stocks and lidar height, with dashed lines showing the 95% confidence bounds (assuming a zero intercept). Note that the ED model estimates of carbon as a function of height are within the confidence bounds across most of the height range. Above 29 m, ED estimates asymptote earlier than observed in the field.

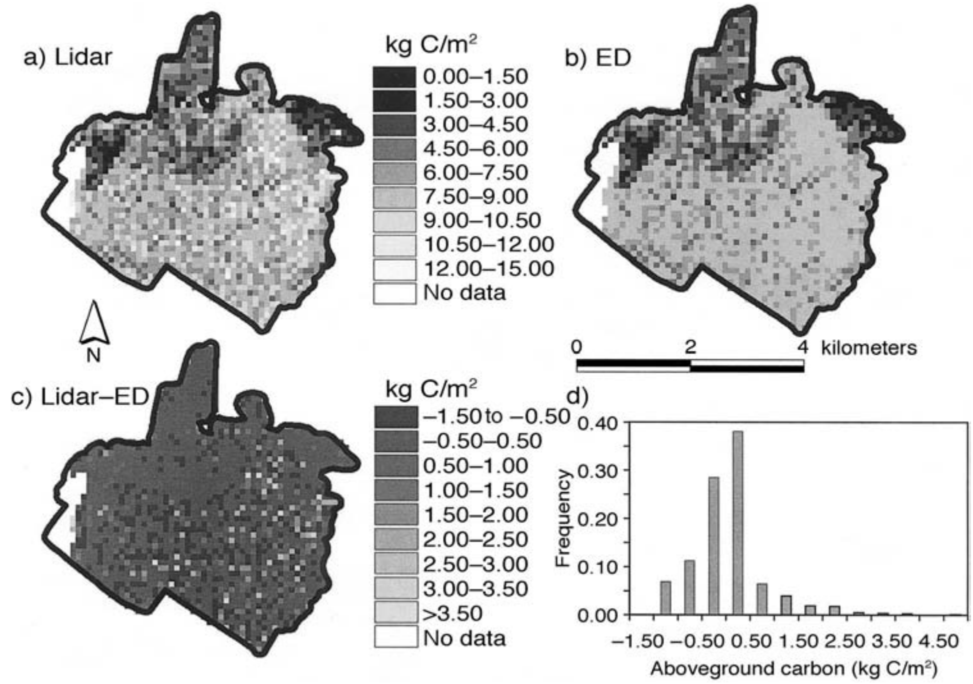


FIG. 7. Estimates of aboveground carbon stocks using lidar data as input to (a) regression-based (lidar), and (b) ED (ecosystem demography)-based methods. (c) Map of the differences between the regression-based and ED-based estimates (lidar–ED). (d) Histogram of the differences mapped in panel c.

results that relate aboveground carbon stocks to canopy height.

Fig. 7 illustrates the close agreement between the regression-based and ED-based maps of carbon stocks. Using a map of land cover as a reference (Fig. 2), areas of abandoned pastures, secondary forest, and old-growth forest are all clearly distinguishable by their different carbon densities in both the ED-based and the regression-based maps. Areas of secondary forest in the northwestern portion of La Selva were estimated to have lower carbon densities than adjacent patches of old-growth forest. The map of differences between the two techniques (Fig. 7c) showed little spatial coherence in the differences, and the histogram of differences (Fig. 7d) had a mean close to zero, suggesting little if any systematic error or bias. In addition to this spatial similarity, there was also close agreement between the estimates of area totals using both techniques. The total aboveground carbon stock within the La Selva boundary was estimated to be 118 658 Mg using ED and 119 988 Mg using the regression-based approach. These estimates translated to a domain mean of 6.92 kg C/m² and 7.0 kg C/m², respectively, a difference of 1.2%.

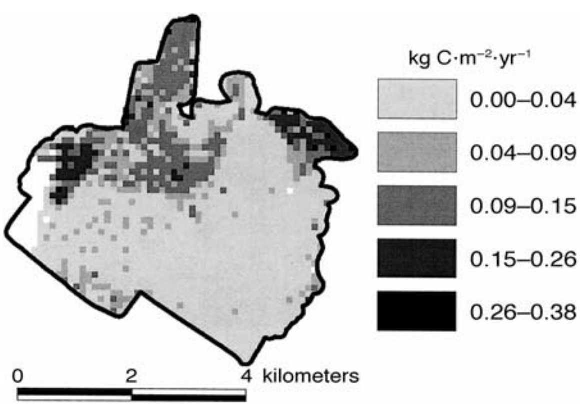


FIG. 8. ED (ecosystem demography)-based estimates of mean aboveground net flux (kg C·m$^{-2}$·yr$^{-1}$) using lidar mean canopy height for input. To produce these results, ED was run with the means of 1987 and 1998 climate data from NASA-ISLSCP Initiative I, as described in Moorcroft et al. (2001).

*Spatial distribution of aboveground carbon fluxes*

We next used lidar data and ED to produce spatially resolved estimates of mean aboveground net carbon flux. This involved using the same grid of canopy heights used above to index ED estimates of mean aboveground net carbon flux. These estimates are generally a decreasing function of mean canopy height, because as stands get taller and accumulate more biomass during succession, they tend to approach an equilibrium state when growth equals mortality (in constant environmental conditions). The specific set of estimates produced are for ''average'' climate conditions as defined by the two-year mean climate data used as model input (Moorcroft et al. 2001).

Fig. 8 shows the spatial estimates of average aboveground net carbon flux from ED. Areas of abandoned pastures, secondary forest and old-growth forest are all clearly distinguishable by their estimated fluxes. Areas of relatively low mean canopy height (e.g., secondary regrowth) were estimated to be accumulating carbon relatively quickly, whereas areas of relatively high mean canopy height (e.g., older growth) were estimated to have lower net carbon fluxes. The total mean aboveground net carbon flux within the La Selva boundary was estimated to be 991 Mg C/y or 0.058 kg $C \cdot m^{-2} \cdot yr^{-1}$.

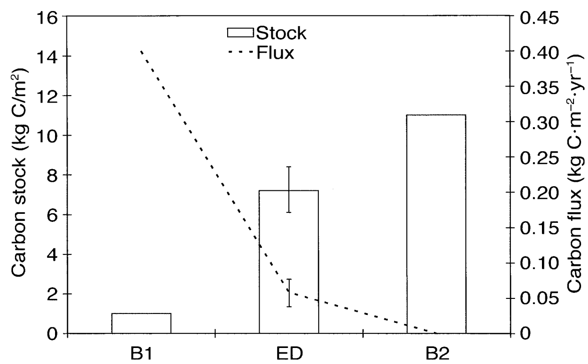


FIG. 9. Estimates of domain mean aboveground carbon stocks (bars) and net carbon fluxes (dashed line). ED-based estimates use lidar canopy height data for initialization, and range bars indicate the range of uncertainty in stocks and fluxes. For comparison, B1 and B2 are ''bracketing'' scenarios that do not use lidar data for model initialization. The entire domain is assumed to be early in succession in B1 and late in succession in B2.

## DISCUSSION

Data on vegetation canopy height collected from an airborne large-footprint lidar instrument were effectively used to initialize a height-structured ecosystem dynamics (ED) model. The ability to obtain these initial conditions from remotely sensed observations is a major step forward in carbon modeling because it ultimately allows for carbon flux predictions based not on potential vegetation, but the actual vegetation structure present. In so far as the structure is representative of the actual successional state of forest, vis a vis land-use history and disturbance, the resulting estimated stocks and fluxes should be more accurate. Other remote sensing techniques may not be as well suited to initialize terrestrial ecosystem models because the metrics they provide may reach an asymptote early in the process of regrowth. In contrast, lidar remote sensing measures vertical forest structure. The vertical structural properties of forests contain more information that can be used to initialize the aboveground state of terrestrial ecosystem models.

In general, it is exceptionally difficult to validate terrestrial ecosystem models over large spatial scales given the sparse plot network from which in situ observations of important diagnostic variables, such as biomass, may be derived. It long has been a goal of remote sensing to provide the ground truth required to validate such models over large scales. The work presented here takes a significant step forward in that direction. By statistically linking spatially continuous lidar data with sparse plot data, we were able to produce spatially continuous fields of biomass and carbon that could be compared with those from ED across the entire landscape of La Selva. Even though lidar heights were used to initialize ED, the overall agreement between estimates from ED and those derived from field-based and regression-based approaches nonetheless served as validation of many aspects of the ED model.

The aboveground carbon content of terrestrial ecosystems is the result of many factors including climate, ecosystem dynamics, land use, disturbance, and others. Even for a given canopy height, the ability of ED to estimate reasonable values of biomass is a partial validation of the model. To produce estimates of biomass, ED must predict a reasonable combination of underlying plant density and size structure. The individual-based plant allometry within ED is important to this, but the estimates also depend on rates of plant growth, recruitment, and mortality.

The ability to compare the spatial distribution of carbon stocks obtained from lidar using the regression-based approach with comparable estimates from ED provided opportunities to analyze model estimates in ways not otherwise possible. The map of the differences between the two shows that in most cases there was excellent agreement between ED and regression-based estimates. Those areas where there are discrepancies are easily identifiable spatially and provide the basis for investigating model estimates further in a geographic context. For example, large differences occurred in some isolated old-growth areas of La Selva where regression-based estimates of carbon were greater than ED estimates. These errors occur because trees in ED were parameterized to have a maximum height that is shorter than observed at La Selva. Without this methodology, identifying and understanding these differences would be difficult.

The use of lidar data provided an important constraint on model estimates of carbon stocks and fluxes beyond the assumption of potential vegetation. To illustrate this, we estimated the range of uncertainty in carbon stocks and fluxes assuming that no information on vegetation height or successional status was available. In this case we have two ''bracketing'' scenarios. In the first scenario, the entire domain is assumed to be low biomass (''young'') and rapidly regrowing. In the second scenario, the domain is assumed to be high biomass (''old growth'') and in approximate carbon balance. In these cases, mean aboveground carbon stocks and aboveground net carbon fluxes were estimated to be in the range of 1.0–11 kg $C/m^2$ and 0.4–0.0 kg $C \cdot m^{-2} \cdot yr$, respectively (Fig. 9). These ranges included the range of relevant estimates from ED, as well as the regression-based estimates of plot level biomass. For comparison, using lidar canopy height for initialization of ED gave domain mean values of 6.1–8.4 kg C/m$^2$ and 0.04–0.08 kg C·m$^{-2}$·yr$^{-1}$. To compute these narrower ranges, we applied upper and lower bounds for the biomass and associated carbon fluxes to the plots with a height greater than or equal to the maximum mean canopy height in ED. Specifically, for one bound we assumed these plots all had the maximum biomass estimated by ED after 200 years of simulation and were in carbon balance (i.e., 10.5 kg C/m$^2$, and 0.0 kg C·m$^{-2}$·yr$^{-1}$). For the other bound, we assumed these plots all had the biomass and associated net carbon flux of sites when they first reach the maximum canopy height during succession (i.e., 6.7 kg C/m$^2$ and 0.06 kg C·m$^{-2}$·yr$^{-1}$).

In extending the analyses using lidar data and ED to estimate aboveground net fluxes, forest patches with low canopy heights were effectively assumed to be younger in recovery from past disturbance, and hence accumulating carbon faster than taller patches. However, some forest patches may contain relatively short vegetation for other reasons, such as limitations caused by fine-scale topography or edaphic factors. Detailed information on two potential variables, slope and soil type, were used to explore the importance of these factors at La Selva. We first examined the potential effects of slope on canopy heights within old-growth plots. We did not find a significant relationship between slope and lidar canopy height within the old-growth areas ($R^2 = 0.032$). We next looked for potential effects of soil type on canopy height. We used five broad soil types that were defined by Clark et al. (1999): recent alluvium, old alluvium, stream associated, swamp associated, and residual soils (from former lava flows). An ANOVA test for differences in lidar canopy height within each soil category showed that there were significant differences in canopy heights across soil categories ($P < 0.01$). A Bonferroni multiple comparison test revealed that canopy heights in the residual soil class were significantly different ($P < 0.05$) from all other soil classes. The mean lidar canopy height in the residual soil areas was 30.8 m, whereas the mean height from the remaining soil classes was 33.6 m, a difference of 2.8 m. This difference was near the limit of our lidar height sensitivity at La Selva (Peterson 2000) and was thus difficult to evaluate in terms of importance. In the future, it is expected that ED will need to be extended to track the consequences of these forms of fine-scale environmental heterogeneity to yield improved estimates of net carbon fluxes.

The approach presented here focused on the simplest lidar metric, mean canopy height. Additional information on ecosystem structure may be obtainable by using other lidar metrics. For example, the subgrid scale distribution of canopy heights and the vertical foliar profiles may allow for improved description of ecosystem state. There is a potential wealth of information in lidar profiles and their spatial distributions that is at this stage largely unexplored.

The results of this study provide a promising illustration of the power of combining lidar data on vegetation height with a height-structured ecosystem model. Extending these analyses to larger scales will require the development of regional and global lidar data sets, and continued model development. The data used in this study have been acquired as part of the VCL calibration and validation program for various biomes, but have very limited spatial extents. The first global lidar observations will come from the ICESat mission (Zwally et al. 2002) and should prove useful for extending the approaches described here to large-scale estimates of carbon stocks and fluxes.

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