Spatial and temporal variability of net ecosystem production in a tropical forest: testing the hypothesis of a significant carbon sink

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Abstract

Tropical forest ecosystems play an important role in the global carbon balance. Depending on age and land use, they can act as carbon sources, sinks, or be in approximate balance, but it is uncertain if global environmental changes are forcing these ecosystems outside their natural range of variation. We asked the question of whether or not the net carbon flux of a tropical primary forest, which should be in balance over the long term, is within the expected range of natural variation. A simple Bayesian hypothesis testing method was used to address this question for primary forests in the Porce region of Colombia. Net ecosystem production (NEP) was measured in this forest in a set of 33 permanent plots from 2000 to 2002 in 2, 1-year intervals. Our estimate of NEP ranged between -4.03 and $2.22 \, \mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ for the two intervals. This range was compared with *a priori* defined range of natural variation estimated from the ecosystem model STANDCARB, which estimated spatial and temporal variation due to gap dynamics. The prior range of variation was estimated between -1.5 and $1.5 \, \mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$. The observed data on NEP did not provide sufficient evidence to reject the null hypothesis that these forests are in C balance. We concluded that the ecosystem is likely behaving within its range of natural variation, but measurement uncertainties were a major limitation to finding evidence to reject the null hypothesis. A literature review of C flux studies in the tropics revealed that about half of the observations could be explained by gap dynamics alone, while significant C sinks have only been observed during La Niña years, with contrasting results in other tropical forests. In conclusion, observational data of carbon fluxes do not appear to provide direct evidence for a significant carbon sink in some sites in the tropics.

Keywords: Bayesian inference, biomass production, ENSO, heterotrophic respiration, litter decomposition, litterfall, Monte Carlo simulations, net carbon balance, net primary production, root production

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Introduction

The role of tropical forests as carbon sources or sinks has been a topic highly debated in the last decade. It has been hypothesized that primary tropical forests are acting as a significant carbon sink as a result of global atmospheric change (Grace *et al.*, 1995; Malhi *et al.*, 1998; Phillips *et al.*, 1998; Baker *et al.*, 2004). However, this hypothesis has been controversial (Clark, 2002, 2004; Saleska *et al.*, 2003; Rice *et al.*, 2004; Wright, 2005).

Measuring C fluxes in tropical forest ecosystems is a difficult task and all the studies reported so far had been constrained by technical difficulties which can limit interpretation of the results.

Studies developed using the eddy covariance technique (Baldocchi, 2003) have provided important information for the understanding of the dynamics and variability of CO_2 fluxes in tropical forests, however, the technique still has limitations for predicting

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reliable annual estimates of net ecosystem exchange (NEE) (Ometto *et al.*, 2005). Previous studies conducted in tropical forests have encountered problems in measuring fluxes at night and under still-air conditions (Araujo *et al.*, 2002; Loescher *et al.*, 2003; Kruijt *et al.*, 2004; Martens *et al.*, 2004; Miller *et al.*, 2004). Other studies that used this technique (Fan *et al.*, 1990; Grace *et al.*, 1995; Malhi *et al.*, 1998; Carswell *et al.*, 2002) directly measured NEE during time periods shorter than 1 year. This can bias the observations to either dry or wet seasons giving uncertain estimates of the annual C flux. As a consequence of these limitations, previously reported estimates of annual NEE in tropical forests have to be interpreted carefully.

Interpreting data from ground-based measurements using permanent plots can also be problematic (Clark, 2004). Using a large set of permanent plots over the tropics, Phillips *et al.* (1998) hypothesized that mature neotropical forests are acting as considerable carbon sinks. This hypothesis has been challenged (Clark, 2002) due to problems associated with the data set (however, see Phillips *et al.*, 2002). In a reanalysis of this data set that addressed problems raised by critics, Baker *et al.* (2004) reached similar conclusions as in their previous analysis (Phillips *et al.*, 1998), specifically they infer a net C uptake of the ecosystems solely from changes in aboveground biomass. From theory, the net accumulation of C in a forest ecosystem is accounted for by net ecosystem production (NEP) which includes inputs (gross primary production, GPP) and outputs (ecosystem respiration, ER) from the system (Landsberg & Gower, 1997; Sala & Austin, 2000; Chapin *et al.*, 2002, 2006; Randerson *et al.*, 2002). Unfortunately, the analysis of the neotropical plots only estimate the C balance of a single pool (aboveground biomass), and it is uncertain if the same conclusions apply at the ecosystem level. The magnitude of respiratory C losses from these plots is unknown. In partially addressing the problem of excluding heterotrophic respiration Rice *et al.* (2004) showed that the inclusion of losses due to decomposition of coarse woody debris (CWD) largely offset the fixation of C in the processes of growth and recruitment. However, the analysis of Rice *et al.* (2004) did not include losses from soil respiration which might be very important in the total C budget (Raich & Schlesinger, 1992; Chambers *et al.*, 2004).

Modeling experiments suggest that mature tropical forests can respond with high C fluxes to external forcing such as climate and atmospheric CO_2 (Tian *et al.*, 1998; Cramer *et al.*, 2001; Clark *et al.*, 2003). However, modeling results also appear to be highly uncertain and contradictory (Clark, 2004), and there is generally no experimental evidence that corroborates specific model predictions.

The debate of whether tropical forests are C sources or sinks has been limited in part by the lack of a common conceptual framework for hypothesis testing. Research published to date is not consistent about the type of flux that should be measured and the spatial and temporal scope of inference allowed by the data. Lovett *et al.* (2006) and Chapin *et al.* (2006) have proposed the concept of NEP as a common term for multi-scale comparison of measured fluxes. Under this framework, we propose a common set of hypotheses to test the role of mature forests in the ecosystem carbon balance using annual observations of NEP.

A null hypothesis to assess external forcing on carbon fluxes

Odum (1969) described the theoretical flows of energy in ecological systems during different stages of ecosystem development. In his model, a mature ecosystem reaches a stage in which production and respiration are balanced, (i.e. NEP=0). During previous successional stages production and respiratory fluxes are highly imbalanced. For this reason, mature ecosystems are a good model system to test hypotheses about external forces such as climate change that might disrupt this balance by increasing or decreasing GPP or ER.

Odum's model is probably our best theoretical understanding of how ecosystems should work at maturity without any changes in external forcing. Alternative models of ecosystem development (Bormann & Likens, 1979; Shugart, 1984), as well as observational studies (Campbell *et al.*, 2004) agree with Odum's predictions. A good candidate null hypothesis to test the effect of changes in external forcing on carbon fluxes would be that NEP=0. However, we know that processes such as mortality, recruitment, competition, as well as interannual climatic fluctuations, introduce spatial and temporal variations in carbon fluxes that are propagated to the net flux. We hypothesize that NEP in mature ecosystems fluctuates around zero with an associated probability distribution. For this reason, we propose the following null and alternative hypotheses to test the effects of external forcing on the net carbon flux of a mature ecosystem:

$$H_0 : \quad \text{NEP} \in \theta, \quad \theta = [-1.96\sigma, 1.96\sigma] \tag{1}$$
$$H_1 : \quad \text{NEP} \notin \theta$$

We hypothesize that the average NEP $\sim$ N $(0,\sigma^2)$ over the long-term (multiple years) according to the Central Limit Theorem (Mukhopadhyay, 2000). Note that these hypotheses are framed in Bayesian terms. Within this framework, we can test the null hypothesis that the net carbon flux of the ecosystem is within *a priori* defined range of variation (θ). This range can be subjective and

defined by specific mechanisms such as forest stand dynamics, long-term disturbances, or interannual climatic variations. Evidence against the null hypothesis would suggest that other factors such as climate change or anthropogenic disturbances are forcing the ecosystem outside its expected range of natural variation.

In this study, we evaluated NEP in a mature tropical forest of the Porce region in Colombia, using the hypotheses described above. We used an ecosystem carbon model to define a hypothetical range of natural variation of the net carbon flux caused by processes such as recruitment, growth, mortality, and decomposition. This range was compared against our observational data and different carbon flux studies in the tropics.

Methods

Data for this analysis were collected at the Porce region in Colombia (6°45′37″N, 75°06′28″W). Mean annual precipitation for this site was 2078 mm between 1990 and 2002, and mean annual temperature was 23.0 °C, with a monthly minimum of 21.2 °C and maximum of 25.1 °C (Fig. 1). Altitude ranges from 900 to 1500 m in the transition from lowland to premontane tropical rain forests. Soils are derived from granitic rocks, have low fertility, and high acidity. Entisols and ultisols are the main soil orders found in the area (Jaramillo, 1989). In a previous study (Sierra *et al.*, 2007) we estimated total aboveground biomass (trees >1 cm diameter plus palms and vines) as $111.6 \pm 17.3\,\mathrm{Mg\,C\,ha^{-1}}$, total belowground biomass (coarse and fine roots) as $37.6 \pm 7.6\,\mathrm{Mg\,C\,ha^{-1}}$, total necromass (fine and coarse standing litter) as $6.6 \pm 0.7\,\mathrm{Mg\,C\,ha^{-1}}$, and soil organic carbon to 4 m depth as $227.9 \pm 38.3\,\mathrm{Mg\,C\,ha^{-1}}$.

Thirty-three permanent plots (20 m × 50 m) were established in this forest. Plot locations were determined by random selection on a map and then located in the field using a GPS unit. All trees, lianas and palms ≥10 cm in D (diameter at breast height or above irregularities) were measured in these primary forest plots. Additionally, plants ≥1 cm in D were measured in one subplot (10 m × 10 m) per plot. The total sampling area was 3.3 ha, from a total study area of 694 ha. Diameters were initially measured using aluminum tree calipers (0.05 mm in accuracy) for plants ≥10 cm, and digital calipers (0.01 mm in accuracy) for plants $10 > D \geq 1$ cm. For buttressed trees its D was measured above the highest buttress. As stems are not perfectly circular in shape the points to measure D with the calipers at each tree were randomly selected; using this procedure for all trees (>11 000 individuals) we expect to avoid bias at the ecosystem scale. The two points where the jaws of the caliper were supported against the bark were marked with yellow crosses. Radial increments were
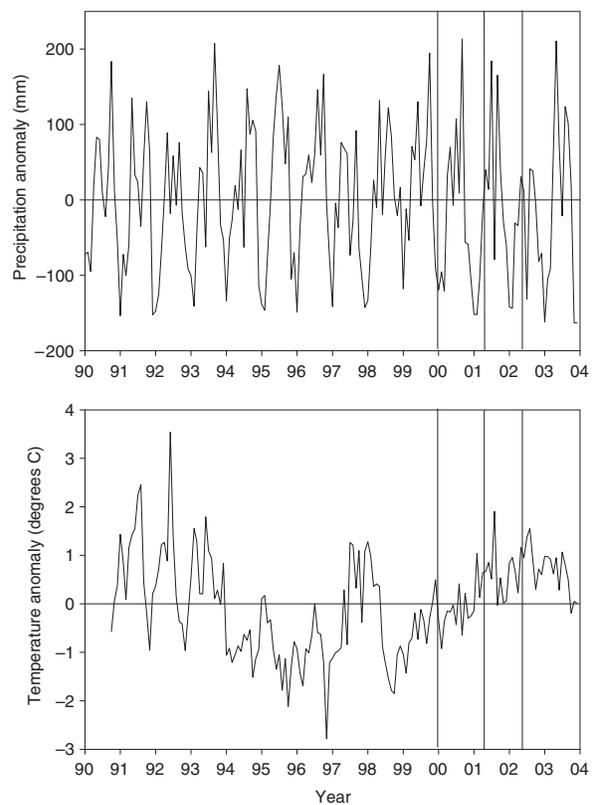

Fig. 1 Temperature and precipitation anomalies for the study site from 1990 to 2003. The two intervals of study are enclosed between vertical bars.

measured to each tree >10 cm D using dial-gauge microdendrometers (0.01 mm in accuracy) (Daubenmire, 1945). Three 3 in. galvanized nails were installed below one of the yellow crosses in each tree to provide support for the microdendrometer. Trees $1 < D < 10$ cm were remeasured using digital calipers and supporting the jaws of the calipers on the center of the two opposite crosses previously painted in the stems. Plots establishment and initial measurements were conducted between November 1999 and August 2000. All plots were remeasured at approximately 1-year interval between November 2000 and May 2001. Between November 2001 and November 2002 all plots were measured again, thus, completing a second 1-year interval.

Biweekly observations of fine litterfall (leaves, reproductive parts, fine woody debris <2 cm diameter) were conducted in two sampling plots. Twenty-eight litterfall traps (0.5 m²) were installed in these plots (14 traps each) in December 1999. Twenty additional traps were installed in February 2001. The complete measurement period extended from December 1999 to November 2003. Coarse litterfall (debris >2 cm diameter) was sampled in subplots (10 m × 10 m) within each plot for the same time period and same frequency

(M. A. Herrera 2000, unpublished data) (Agudelo & Aristizábal, 2003; Moreno, 2004).

Fine root (<5 mm diameter) production was measured using the ingrowth core method (Fahey *et al.*, 1999). Two plots were used to install seven ingrowth core sets (0–15, 15–30 cm depth) per plot for two 6-month periods. This experiment was conducted between January 2000 and January 2001. A second experiment was installed from September 2001 to May 2003. In the second experiment, ingrowth cores were sampled every 2 months, approximately (Sierra, 2004).

The litterbag method (Harmon *et al.*, 1999) was used to estimate decomposition rates of fine litter in two of the sampling plots. Two experiments were performed. The first experiment was conducted between January 2000 and January 2001 and the second between February 2001 and May 2002 (Berrouet & Loaiza, 2003). A simple exponential decomposition model (Olson, 1963) was fit to the data to estimate the decomposition rate (k'). Decomposition rate of coarse woody debris was estimated using a time-series approach (Harmon *et al.*, 1999) for 1 year. A set of 400 preweighted pieces of wood of different sizes (2–23 cm diameter) from three different species [*Jacaranda copaia* (Aubl.) D. Don, *Vismia baccifera* (L.) Triana & Planch, and *Virola sebifera* (Aubl.)] were placed on the ground and collected at regular intervals. Decomposition rate constants were calculated as the proportion of weight lost.

Soil respiration was measured in three plots using a LI-COR soil respiration chamber (Li-6000-09, LI-COR Inc., Lincoln, NE, USA) connected to a LI-COR portable photosynthesis system (Li-6200). Within each plot, paired subplots (2 m × 2 m) were established to measure total soil respiration and heterotrophic respiration separately. The trenching-plot technique (Hanson *et al.*, 2000) was used to measure heterotrophic respiration by excluding the growth of any living plant within the subplot. Five 10.5 cm diameter and 4.5 cm height PVC collars were inserted 1.5 cm into the soil surface in each subplot. Measurements were conducted from October 2001 to June 2002. We extrapolated soil respiration to our first sampling campaign (approximately between January 2000 and May 2001) using the relationships between soil respiration and temperature and soil moisture developed by Moreno (2004) for this site.

Annual estimates of NEP* were obtained by processing the information collected from the sampling plots. The following conceptual model was used to estimate net ecosystem production (after Chapin *et al.*, 2006)

$$NEP = GPP - ER = (NPP + Ra) - (Ra + Rh)$$
$$NEP = NPP - Rh, \qquad (2)$$

where Ra is autotrophic respiration, NPP net primary production, and Rh heterotrophic respiration. Net pri-

mary production was calculated using the approach proposed by Landsberg & Gower (1997):

$$NPP^* = \Delta W + w_{det} + w_{herb}, \qquad (3)$$

where ΔW is total biomass increment, w_{det} is total detritus production, and w_{herb} is herbivore consumption. In this study, we distinguish between the conceptual and the measured flux using an asterisk sign (*) for the latter. Data to estimate w_{herb} was not directly measured in the plots. However, entomological studies conducted by J. C. Giraldo and R. A. Bedoya (unpublished data) in the area present a rough estimate of leaf herbivory by ants. These authors estimated annual herbivory rates as 16% of leaf standing biomass. We used this rate to calculate herbivory consumption by ants during the two intervals studied.

Biomass increment (ΔW) was calculated using the procedure proposed by Clark *et al.* (2001a):

$$\Delta W = \left(\sum \text{Increments of surviving trees} \right)$$
$$+ \left(\sum \text{Increments of ingrowth} \right), \qquad (4)$$

where ΔW includes biomass change above- and belowground. Local biomass equations reported in (Sierra *et al.*, 2007) were used to calculate biomass of each individual. Biomass change was the difference of the estimated biomass for two consecutive measurements. Fine root biomass increments were added to plot biomass increments. Detritus production was calculated as annual fine litterfall measured in the plots.

Heterotrophic respiration associated with soil organic matter (SOM) was separated from respiration of the litter layer ($Rh^* = R_{SOM} + R_{det}$). Our estimations of heterotrophic respiration obtained from the trenched plots were used as R_{SOM}. Heterotrophic respiration from litter was calculated as

$$Rh_{litter} = SL \times (1 - \exp(-k')), \qquad (5)$$

where k' is the decomposition rate constant from an exponential decomposition model and SL is standing litter. Alternatively, we used our litterfall data to compute decomposition rates assuming that the system is in steady state ($k = $ fine litterfall/SL) (Olson, 1963):

$$Rh_{litter} = k \times SL. \qquad (6)$$

Estimates of standing litter for three main pools, fine litter, coarse woody debris, and standing dead trees (snags) were extracted from Sierra *et al.* (2007).

Uncertainty analysis

The uncertainty in our estimations was assessed by performing a Monte Carlo procedure. In this procedure, we defined prior probabilities for each component of NPP* and Rh* based on the results from our measure-

ments. These *a priori* probabilities include uncertainty associated with measurement errors and spatial variation. Measurement errors are associated with the sampling procedure used. Uncertainty associated with spatial variation is obtained by differences in topography and soils over the landscape, as well as heterogeneity in canopy cover introduced by gap dynamics. Multiple estimations (10 000) of NPP* and Rh* were computed by randomly sampling the distribution of the *a priori* probabilities. *A posteriori* probabilities (frequency distributions) from the outcomes were obtained and their SD was used as a measure of uncertainty. The 95% confidence intervals for NPP*, Rh*, and NEP* were calculated using these SD.

We tested the effect of correlation between production and respiratory fluxes in our uncertainty analysis. According to statistical theory, the variance (σ^2) of two random variables A and B is propagated to a third variable $C = A + B$ by the expression $\sigma_C^2 = \sigma_A^2 + \sigma_B^2 + 2\text{cov}_{AB}$. We used the Monte Carlo procedure to model the effect of correlation between variables. Two extreme scenarios were tested: complete correlation and complete randomness between all fluxes. Neither of these scenarios is very realistic but they provide boundaries to constrain our estimation of variances. A third and more realistic scenario was tested, partial correlation between production and respiratory fluxes assuming a correlation of 50% between them. The coefficient of variation (CV) of the net flux was estimated for the ratio NPP* : Rh* instead of NEP* because the closer the average NEP* is to zero the larger the estimate of the CV. We avoided this shortcoming by estimating the CV on the NPP* : Rh* ratio which should be close to 1 for mature ecosystems (Odum, 1969).

Calibration of the carbon model STANDCARB

We used the ecosystem carbon model STANDCARB version 2 (Harmon & Domingo, 2001; Harmon & Marks, 2002) to assess the range of variation θ of NEP due to stand dynamics for this forest. Specifically, we expect that the dynamic nature of mortality and regrowth will produce short-term variation in the carbon balance at the ecosystem scale. STANDCARB 2 is a simulation model of living and dead C pools of forest stands. This is a hybrid model that incorporates features of a gap model with an ecological process model. The effects that tree species, succession, and regeneration have on carbon dynamics can be examined with this model. The spatial scale is restricted to the stand and stochastic processes such as mortality and recruitment are included.

STANDCARB was calibrated for the study site using parameters from the literature and local information. Five different groups of species were simulated simul-

taneously: early successional, late successional, legumes, palms, and gap species. Predictions of carbon stocks with this model were compared against our estimations for primary and secondary forests (Sierra *et al.*, 2007). Details about model parameterization for this study site are given in (Sierra and Harmon, 2007).

The model was run five times to obtain a representation of variation in carbon dynamics given the stochastic framework of the model. NEP was calculated from the output of total carbon stores for the interval 500–1000 years. During this interval, the modeled ecosystem reached a steady state in all simulations where carbon stores plateau. The variance of NEP was calculated from the five simulations for this 500 year period ($n = 2500$ observations).

Hypothesis testing

To test the hypothesis posed in Eqn (1), we estimated the posterior probability of NEP given the observed NEP* data. This posterior probability distribution was estimated applying the Bayes' theorem (Gelman *et al.*, 2000):

$$P(\text{NEP}|\text{NEP}^*) = \frac{P(\text{NEP}^*|\text{NEP})P(\text{NEP})}{\int P(\text{NEP}^*|\text{NEP})P(\text{NEP})d\text{NEP}}. \quad (7)$$

The prior probability distribution of NEP was estimated from STANDCARB's output. The likelihood function of the observed data given the null hypothesis ($P(\text{NEP}^*|\text{NEP})$), as well as the integral in a possible range of NEP between -5 and $5\,\text{Mg C ha}^{-1}\,\text{yr}^{-1}$, was estimated using the statistical software R 2.1.1 (Ihaka & Gentleman, 1996).

The posterior probability was evaluated over the space of the null and alternative hypotheses (Mukhopadhyay, 2000):

$$\alpha_0 = \int_{\text{NEP}\in\theta} P(\text{NEP}|\text{NEP}^*)d\text{NEP},$$

$$\alpha_1 = \int_{\text{NEP}\notin\theta} P(\text{NEP}|\text{NEP}^*)d\text{NEP}.$$

We consider α_0 and α_1 posterior evidence in favor of H_0 or H_1, respectively. Specifically, if $\alpha_0 < \alpha_1$ the null hypothesis will be rejected (Mukhopadhyay, 2000).

C flux data from other primary tropical forests

We compiled data from C flux studies developed in other primary tropical forests. As criteria, we only used data that integrated production and respiratory fluxes. All eddy covariance studies developed in primary tropical forests and available in the scientific literature were included in our data set. We did not include

permanent-plot data that only provide estimates of aboveground biomass change, as the respiratory component is absent from these studies. Oceanic Niño Index data was gathered from the Climate Prediction Center of the National Oceanic & Atmospheric Administration's web page, and used as indicator of large-scale climatic variations in the tropics.

Results

NPP*

The major components of NPP* measured during the two intervals were biomass increments of surviving trees (Table 1) and fine litterfall (Fig. 2). For the first interval the increment of survivors was $5.25 \pm 0.44 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$, and for the second interval $5.89 \pm 0.74 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$. Fine litterfall was $4.83 \pm 0.28 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$ for the first interval, and $4.6 \pm 0.23 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$ for the second interval. Biomass increments due to ingrowth were relatively small compared with increments of surviving trees. During the second interval, a reduction in biomass increments of ingrowing trees was observed. Increments of ingrowth were 1.09 ± 0.29 and $0.05 \pm 0.02 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$ for the first and second interval, respectively. Larger biomass increments were observed for trees rather than for other life forms such as palms and lianas (Table 1).

Estimated fine root production increased between the two intervals. The average fine-root biomass production was estimated as $1.21 \pm 0.62 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$ during the first interval, and $2.19 \pm 0.52 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$ during the second interval. This change in increment of fine root production was not associated with a similar change in the increment of leaf production.

Herbivory was the smallest flux estimated and only accounted for 1.5% of total NPP*. Our estimate of herbivory for the two intervals was $0.19 \pm 0.09 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$. This estimate was nearly constant for the two intervals because standing leaf mass also remained relatively constant; changing from $1.22 \, \mathrm{Mg \, C \, ha^{-1}}$ during the first interval to $1.21 \, \mathrm{Mg \, C \, ha^{-1}}$ during the second interval.

Uncertainty bounds were higher for fine roots and increments of suriviors than for the other NPP* components (Fig. 2, Table 1). Small sample size was the main factor contributing to the observed uncertainty for fine roots. The uncertainty observed for the increment of surviving trees was probably the combination of spatial variation and the size of the pool. Larger pools showed larger absolute variation.

Net primary productivity was estimated as $12.59 \pm 0.90 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$ for the first interval and $12.93 \pm 0.96 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$ for the second interval. There was not a significant difference between these two estimates (P-value = 0.80 from a t-test).

Heterotrophic respiration

Decomposition rates estimated using the litterbag method were different between the two intervals. For the first interval, k' was $0.89 \pm 0.03 \, \mathrm{yr^{-1}}$ and for the second interval it was $0.34 \pm 0.08 \, \mathrm{yr^{-1}}$. Using the steady-state method, decomposition rates (k) for the first and second

Table 1 Changes in biomass of surviving and recruited individuals to the plots for the two intervals of study

	Survivors		Ingrowth	
	Average ± SE	% of total	Average ± SE	% of total
2000–2001				
AGB of trees >1 cm D	8.75 ± 0.87	75.0	1.43 ± 0.60	59.1
CRB of trees >1 cm D	2.31 ± 0.40	19.8	0.30 ± 0.14	12.4
AGB of Lianas	0.19 ± 0.06	1.6	0.08 ± 0.05	3.3
AGB *Oenocarpus bataua*	0.10 ± 0.03	0.9	0.28 ± 0.16	11.6
AGB of other palms	0.32 ± 0.10	2.7	0.33 ± 0.17	13.6
Total increment	11.67 ± 0.96	100	2.42 ± 0.65	100
2001–2002				
AGB of trees >1 cm D	9.87 ± 1.56	75.5	0.07 ± 0.06	63.6
CRB of trees >1 cm D	2.70 ± 0.44	20.6	0.01 ± 0.001	9.1
AGB of Lianas	0.25 ± 0.06	1.9	0.001 ± 0.001	0.9
AGB *Oenocarpus bataua*	0.22 ± 0.01	1.7	0	0
AGB of other palms	0.05 ± 0.02	0.4	0.02 ± 0.02	18.2
Total increment	13.08 ± 1.60	100	0.11 ± 0.05	100

Numbers are giving in $\mathrm{Mg \, OM \, ha^{-1} \, yr^{-1}}$ to reduce the number of decimal places. To convert to $\mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$ multiply by 0.45
AGB, Aboveground biomass; CRB, Coarse root biomass.
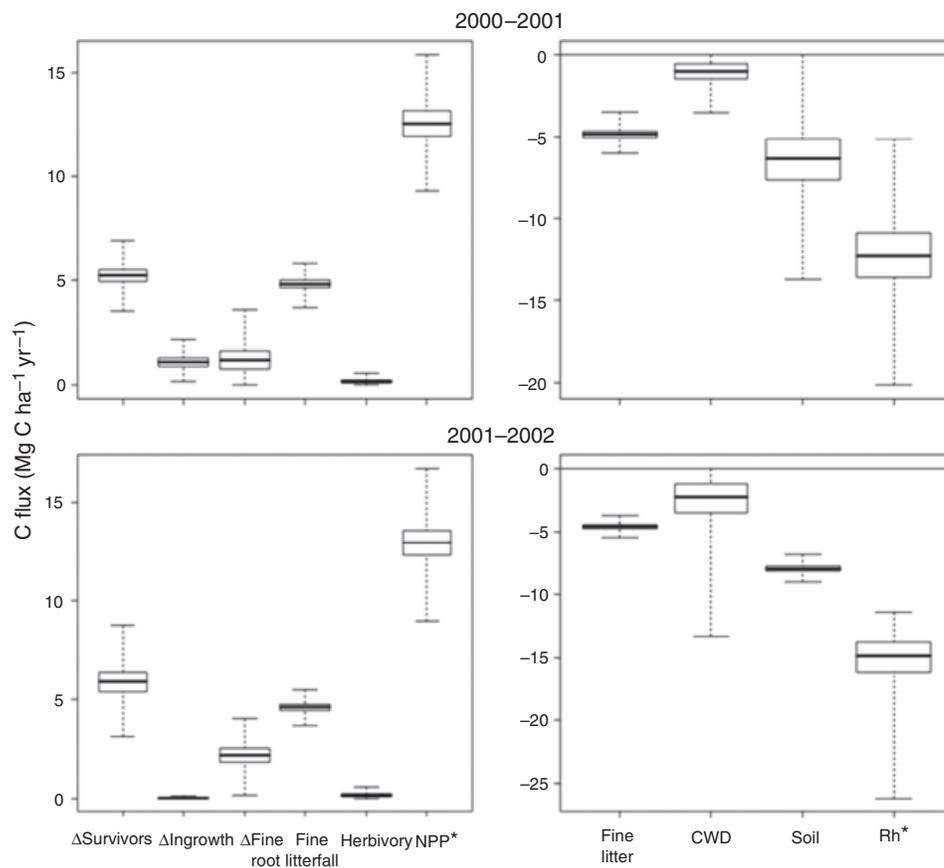
2000–2001

2001–2002

Fig. 2 Box plots of each component of net primary production and heterotrophic respiration for the two measurement intervals (2000–2001 and 2001–2002). The plot was constructed with the outputs from the Monte Carlo simulations (10 000 observations). Boxes contain values between the 25 and 75 percentiles. Whiskers extend to the maximum and minimum values obtained from the simulation.

Table 2 Effect of correlation in the estimate of uncertainty for each mayor flux

Scenario	NPP SD	Rh SD	NEP SD	CV of mean NPP/Rh (%)
Complete randomness	0.90	2.05	2.21	19.7
Complete correlation	2.19	2.89	0.70	8.3
Partial correlation	1.57	2.44	1.15	10.5

Results only for the first interval of study. Units in $Mg\,C\,ha^{-1}\,yr^{-1}$.

intervals were 1.79 ± 0.17 and $1.68 \pm 0.30\,yr^{-1}$, respectively. Decomposition rates are more consistent between intervals using the steady-state method because litter fall rates are almost the same between the two intervals (Fig. 2) and fine litter mass also remained relatively constant during the two intervals. Standing fine-litter mass in this forest was estimated as $6.03 \pm 0.45\,Mg\,ha^{-1}$ for the first interval and $6.23 \pm 0.99\,Mg\,ha^{-1}$ for the second interval. Owing to the fact that litterfall and standing litter remained relatively constant, it is very likely that decomposition rates also remained constant. Differences between litterbag materials between the two intervals may have been associated with the differences observed in decomposition rates. For this reason, we used decomposition rates estimated with the steady-state method in further calculations. Consequently, fine litter respiration was equal to fine litterfall for the two intervals (see Eqn (6)).

Respiration of CWD increased from $1.04 \pm 0.62\,Mg\,C\,ha^{-1}\,yr^{-1}$ in the first interval to $2.52 \pm 1.69\,Mg\,C\,ha^{-1}\,yr^{-1}$ during the second interval (Fig. 2). Average dead coarse-wood mass changed dramatically between the two intervals due to an increase in mortality, especially of large trees. For the first interval, CWD mass was $8.74 \pm 1.55\,Mg\,ha^{-1}$ and for the second interval it increased to $20.86 \pm 6.72\,Mg\,ha^{-1}$. The decomposition rate for coarse wood was estimated as $0.27 \pm 0.30\,yr^{-1}$. Although this rate was only measured during the

second interval, we used it in our calculations for both intervals (notice the high variation of this decomposition rate which is due to the small sample size and the averaging effect of different coarse wood sizes).

Our estimates of soil respiration were associated with large uncertainties mainly due to the small sample size used. During the first interval soil respiration was $-6.36\pm1.94\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ and for the second interval it was $-7.98\pm0.29\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$. Uncertainty bounds for soil respiration in the first interval were higher because this flux was predicted in part from measurements taken during the second interval.

Carbon losses due to heterotrophic respiration were estimated as -12.26 ± 2.05 and $-15.07\pm1.70\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ for the first and second intervals, respectively. The major component of heterotrophic respiration was soil organic matter respiration (approximately 52% on average), which is also the major driver of the final uncertainty during the first interval. For the second interval, an important source of uncertainty was introduced by the observed mortality of large trees, which was propagated from the coarse wood pool to our estimate of heterotrophic respiration.

NEP*

Correlation between fluxes has an important effect on the estimate of uncertainty in net carbon flux (Table 2). Assuming complete randomness the uncertainty of the average NPP*:Rh* ratio was as high as 19.7%, while assuming complete positive correlation this uncertainty dropped to 8.3%. Assuming positive correlation of 0.5 between production and respiration the uncertainty of the net flux was estimated as 10.5%. We used the estimate of uncertainty from the partial correlation scenario in our subsequent examination of uncertainty for the first and second intervals, given that much of the forest production replaces litterfall and mortality.

Net ecosystem production was estimated as $0.34 \pm 1.15\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ for the first interval. The uncertainty analysis showed that NEP* for the first interval may have ranged between -1.88 and $2.59\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ (95% confidence limits). NEP* for the second interval was estimated as $-2.15 \pm 0.76\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ with 95% confidence limits between -3.75 and $-0.61\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ (Fig. 3).

Combining the results from the first and second interval, we found a possible range of variation of NEP* between -4.03 and $2.22\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ (Fig. 4), which
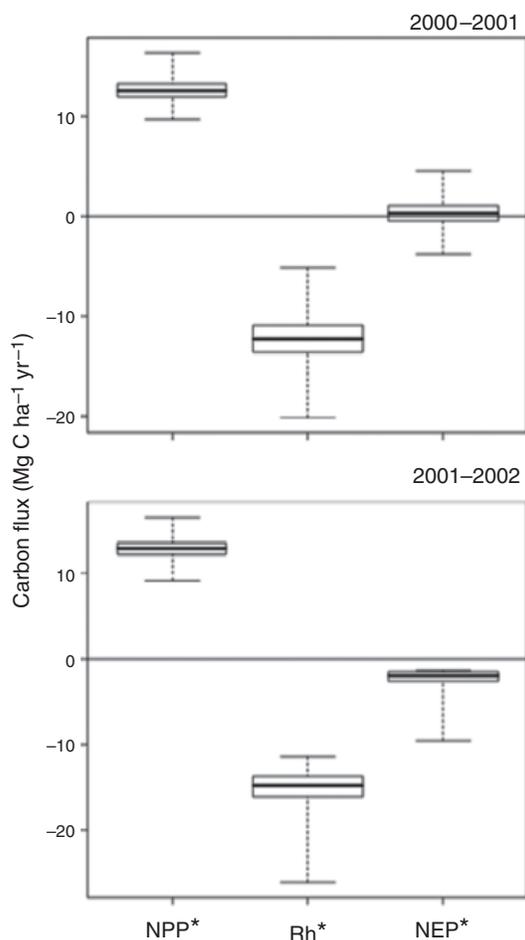

Fig. 3 Box plots of each component of net ecosystem production for the two measurement intervals (2000–2001 and 2001–2002). The plot was constructed with the outputs from the Monte Carlo simulations (10 000 observations). The horizontal line is the median, and the box includes 25 and 75 percentiles. Whiskers extend to the maximum and minimum values obtained from the simulation.
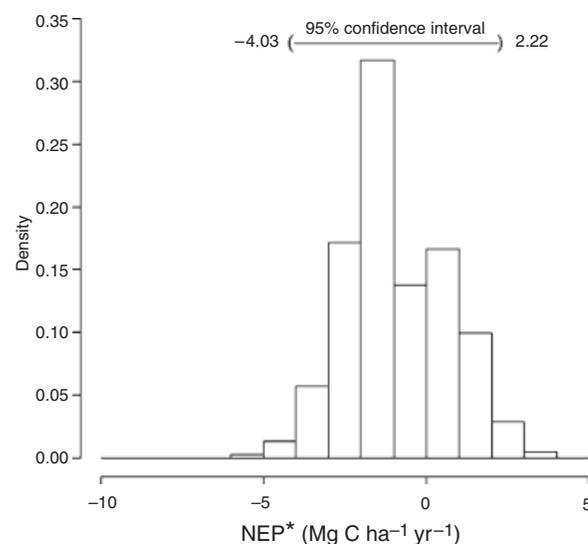

Fig. 4 Histogram and 95% confidence interval of net ecosystem production for the two intervals from the observed data and the Monte Carlo simulations.

includes uncertainty in the estimates, as well as spatial and temporal variation.

Simulations of carbon fluxes from STANDCARB

Our simulations of NEP from STANDCARB (Fig. 5a) followed the theoretical pattern for ecosystem development (Odum, 1969). The minimum and maximum values of NEP for mature forests predicted by the model were -4.36 and $1.24\,Mg\,C\,ha^{-1}\,yr^{-1}$, respectively. This range includes larger negative than positive values but the probability of large emissions was low (Fig. 5b). Large negative pulses are due to mortality events and subsequent decomposition, which is in general faster than biomass recovery. The mean and median NEP estimated from these simulations were -0.015 and $0.14\,Mg\,C\,ha^{-1}\,yr^{-1}$, respectively. The expected (and subjective) natural variation ($\hat{\sigma}^2$) of NEP was estimated as $0.60\,Mg\,C\,ha^{-1}\,yr^{-1}$. This variation is basically the result of the interaction of ecosystem processes such as

recruitment, growth, mortality, and decomposition of the five species groups simulated. The effects of climatic variations were not included in these simulations, but would have increased the degree of natural variation.

From these results, we hypothesize that $\theta/N(0, 0.60)$. The assumption of normality implies that the expectancies of NEP are made over long-term averages. We hypothesize a mean of zero because it is the theoretically expected value for NEP in any mature ecosystem (Odum, 1969) and close to STANDCARB predictions.

Testing the null hypothesis

The prior probability interval (95% probability) for NEP calculated from STANDCARB outputs was -1.51 to $1.51\,Mg\,C\,ha^{-1}\,yr^{-1}$. Our posterior probability for NEP given the observed data NEP* was estimated within the prior range (Fig. 6), therefore, our estimate of $\alpha_0 = 1$. From this analysis no evidence against our posed null hypothesis was found.

Discussion

In an extensive literature review of NPP* data in tropical primary forests, Clark *et al.* (2001b) found that past studies were usually limited to one or two components of aboveground NPP. In our study, we included changes in biomass above- and belowground as well as litterfall, herbivory, and fine root production. For this reason, our estimates of NPP* are among the highest reported for tropical forests. In forests with relatively similar biomass to our study site, total NPP* can be
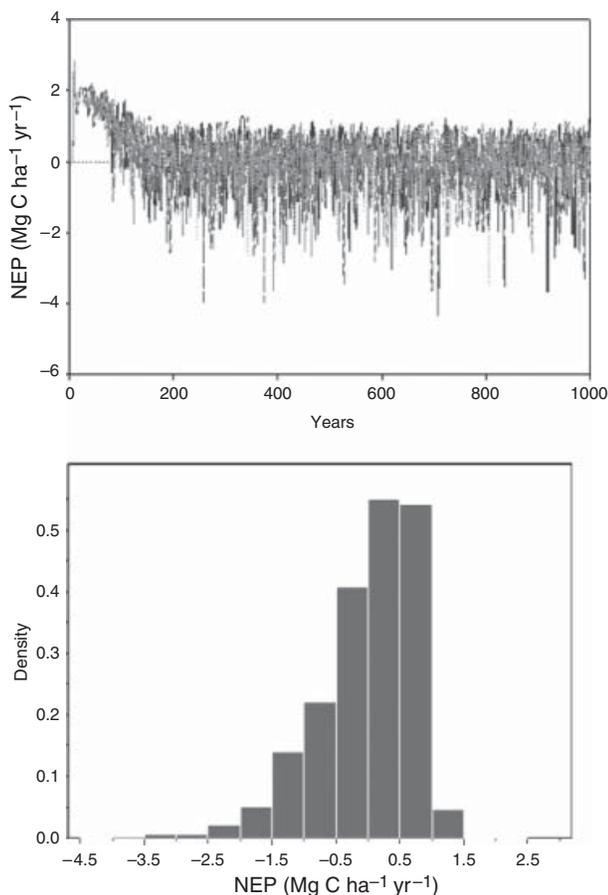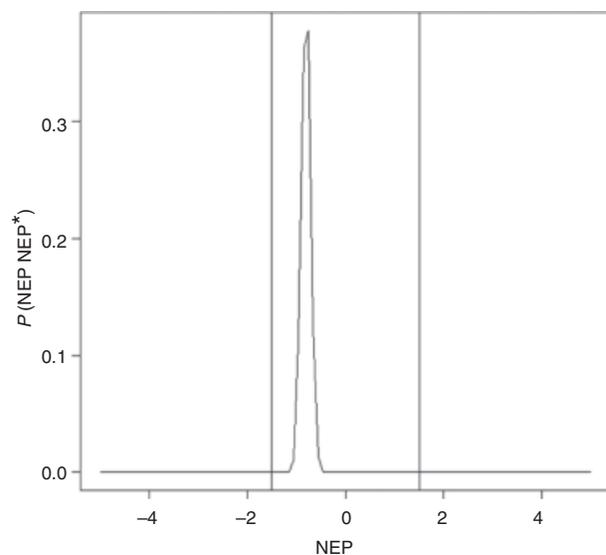
Fig. 5 Results from STANDCARB simulations of net ecosystem production plotted against time (upper) and as histogram (lower). Lines in the upper panel represent different simulations. The histogram only includes results from years 500 to 1000.

Fig. 6 Posterior probability of NEP given the data NEP*. Vertical lines represent the 95% confidence interval of the prior distribution of NEP.

found between 6.0 and 21.7 Mg C ha^{-1} yr^{-1} according to Clark *et al.* (2001b). The range for NPP* in our site was between 10.9 and 14.6 Mg C ha^{-1} yr^{-1} suggesting that this site has intermediate productivity compared with other tropical forests with the same biomass. Comparing our results with the temperature–productivity relationship reported by Clark *et al.* (2001b) these forests are in the upper range of productivity relative to other forests with the same temperature.

Uncertainty of measured fluxes

Changes in biomass were the most important components of total uncertainty in NPP* (Fig. 2). Although ecosystem models of succession predict little variation in biomass change for mature forests, other factors such as soil characteristics and species composition, are important drivers of spatial variation in biomass accumulation. We observed large variations of changes in biomass across the landscape, larger than the variations between observational periods. Although we did not observe an important change in the average NPP* during the two intervals, changes in the relative importance of some components were observed. For example, in the second interval we observed a decrease in the average biomass change of the ingrowth and an increase in the average fine root production.

The large uncertainties observed in soil respiration were probably a consequence of the small sample size used and the large size of the flux. Larger fluxes are generally more variable and also often more difficult to measure. We estimated that it would be necessary to measure soil respiration on at least 10 plots to decrease the coefficient of variation of the average below 20%.

The mortality events observed during the second interval were very important in causing an additional source of uncertainty in the respiratory flux. During the first interval, we were unable to capture that uncertainty in our measurements. It is likely that other temporal processes such as pest outbreaks or prolonged droughts were not captured in our observational timeframe. This study was mainly designed to capture the spatial variations over the landscape, thus the temporal variations remain relatively unexplored (although as in chronosequence studies, spatial variation may partially represent temporal variation introduced by gap dynamics).

Uncertainty of non-measured fluxes

We recognize that not all components of primary productivity as in Clark *et al.* (2001a) were measured in this study. Specifically, we did not measure volatile and leached organics as well as other components of her-bivory such as sap-sucking, frugivory, and herbivory of species other than ants. We found that leaf herbivory by ants only accounted for 1.5% of total NPP*, although Clark *et al.* (2001b) report larger proportions. It is likely that we have underestimated total herbivory; however, we do not have a good representation of the magnitude of the total of this flux in the study site. Our personal observations, though, are consistent with the idea that ant herbivory is the major consumer flux in this forest. It is also likely that more herbivory only means higher Rh, so it is unlikely to impact estimates of NEP.

A likely range of VOC emissions in tropical forests has been reported as 0.15 to 0.31 Mg C ha^{-1} yr^{-1} by Clark *et al.* (2001b), based on modeling results reported by Guenther *et al.* (1995), who found maximum VOC emissions of 4% of annual NPP. However, this range is highly uncertain (Guenther *et al.*, 1995; Clark *et al.*, 2001b). Recent research has shown that VOC emissions in tropical forests are highly seasonal (Andreae *et al.*, 2001; Kuhn *et al.*, 2004) as opposed to constant annual emissions assumed in previous modeling studies. Additionally, Kuhn *et al.* (2002) and Andreae *et al.* (2002) have found that the exchange of VOCs is bi-directional (i.e. that canopies in tropical forests can act as sinks (via reuptake) of some organic compounds such as short-chain volatile organic acids). Andreae *et al.* (2002) found consistent emission trends only for isoprene and mono-terpenes at different sites in the Amazon. Monoterpenes contributed no more than 10–15% of the total isoprenoid flux. These results suggest that emissions of VOC are lower than previously thought, although they are highly dependent on variations of community composition over the landscape (Greenberg *et al.*, 2004). Geron *et al.* (2002) found isoprene emissions ranging from 0.078 to 0.083 Mg C ha^{-1} yr^{-1} at La Selva, Costa Rica, and total VOC emissions probably did not exceed 0.1 Mg C ha^{-1} yr^{-1}. We believe that by not including VOC emissions in our calculations we underestimated NPP* by <1%.

Our budget did not include coarse root growth of palms and lianas. We only used root biomass equations for trees, but were unable to develop this type of equations for other life forms. This flux is probably not very large. The coarse root: shoot growth ratio of trees was about 0.27 for the first interval. Applying this ratio to the aboveground growth of palms and lianas, we found a possible underestimation of total growth of 0.31 Mg C ha^{-1} yr^{-1} for this interval.

Other belowground components of total NPP* that were not measured are the production of root exudates, exports to mycorrhizae, and root herbivory. We are not certain about the magnitude of these fluxes, but we measured the respiratory fluxes associated with these processes as part of soil heterotrophic respiration. Thus,

our budget might be biased towards the respiratory component, although not all the C losses were accounted in the heterotrophic respiration flux. For example, from the respiratory losses, we did not account for decomposition of litter intercepted in the overstory. This flux is especially important for dead branches and mid-sized coarse woody debris that are being consumed by decomposers. Decomposition of intercepted fine litter does not affect the total budget because it is not being measured in the litterfall component.

Lateral carbon fluxes such as erosion and leaching were also omitted in our calculations. Leached organic compounds have been measured in other forests and small fluxes have been detected. At La Selva, Schwendenmann & Veldkamp (2005) found a DOC flux of $0.28 \, \mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ in the litter leachate. Similarly, a small flux of $0.58 \, \mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ was measured in a temperate rain forest in Western Oregon, USA (Lajtha *et al.*, 2005).

Our omission of different components of the production and respiratory fluxes introduced uncertainty in our estimations of NPP* and Rh*, however, most of these fluxes cancel out in the estimation of NEP*. We used the Monte Carlo procedure to estimate the uncertainty introduced by the exclusion of the fluxes mentioned above. Using the ranges reported in Table 3, we estimated an average underestimation of NPP* of the order of $0.77 \pm 0.22 \, \mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$. Similarly, the underestimation of Rh* is of the order of $-0.47 \pm 0.18 \, \mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$. For NEP*, we predict an average underestimation of $0.30 \, \mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$ ranging from -0.26 to $0.85 \, \mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$. This uncertainty is lower than the uncertainty associated with spatial and temporal variation observed during the two intervals studied.

This analysis showed that the estimation of NPP* and Rh* is consistent with the 'complexity paradox' (Oreskes, 2003) in ecological modeling. Recent models of NPP, Rh, and NEP (Clark *et al.*, 2001a; Chapin *et al.*, 2002;

Randerson *et al.*, 2002) stress the importance of including all carbon fluxes in the estimation of carbon budgets. This approach leads to a better description of complex processes. However, as more processes are included in the models, more uncertainty occurs as measurement and estimation errors are propagated in to the final estimates (Fig. 7). Some of the processes reviewed in this study that were not measured, added more uncertainty to the final estimates of NPP* and Rh* than the reduction of bias accomplished by their inclusion. Interestingly, most of these uncertainties and biases cancel out in the estimation of NEP*.

Possible overestimation of Rh

The calculations we used to estimate Rh may contribute to overestimate this flux by an unknown amount. In our calculation method, we assumed that the respiration chambers in the trenched plots accounted only for the respiration of organic matter in the mineral soil. However, litter was not removed from the respiration chambers at the beginning of the experiment nor during the intervals in which measurements took place. In practice, this implies that the respiration chambers accounted for both respiration of organic matter in the mineral soil and the litter layer. The litter present at the time of installing the chambers in the field was legacy litter from previous years and does not account for the respiration of new litter reaching the soil during the measurement interval. The amount of new litter reaching the ground in this forest is high (almost twice the amount of litter stored in the litter layer) and needs to be accounted for as well in the respiratory component. Although an unknown proportion of litter probably fell into the chambers, it is very unlikely that the chambers completely captured the amount of litterfall measured with our litter traps given the small size and number of collars. Our calculations assumed that all fresh input litter was respired. This means that the fraction of new

Table 3 Hypothetical uncertainty bounds and their distribution for non-measured fluxes

| Pool	Distribution	Spread	Units
Production			
Herbivory	Uniform	Min = 0, max = 5.5	% of NPP
VOC	Uniform	Min = 0.5, max = 1.5	% of NPP
CR increment of survivors of other life forms	Normal	Average = 0.07, SD = 0.01	$\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$
CR increment of ingrowth of other life forms	Normal	Average = 0.06, SD = 0.02	$\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$
Root exports	Uniform	Min = 0.5, max = 2.0	% of NPP
Losses			
CW mass intercepted undergoing decomposition	Uniform	Min = 5, max = 15	% of standing mass on the forest floor
DOC	Uniform	Min = 0.1, max = 0.7	$\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$

Max, maximum; min, minimum.
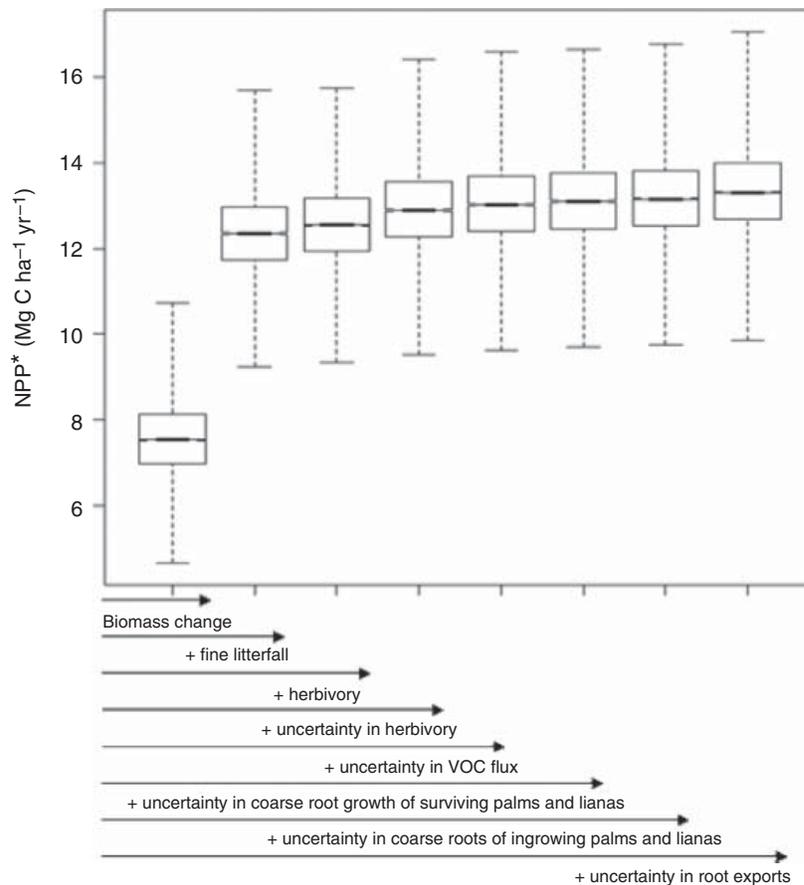
Fig. 7 Effect of the addition of different fluxes in the estimation of NPP*. Uncertainties calculated from Table 3.

and old litter that was incorporated into the soil during the two intervals was assumed to be zero. This assumption may not be valid over the long term, but we did not have data to estimate this fraction.

We evaluated the effect of assuming that 100% of new litter decomposes in a year on the overall conclusions presented below. A sensitivity analysis was performed on the calculation of heterotrophic respiration changing the proportion of new litter that would be respired for the two measurement intervals. This analysis indicated that our conclusions are robust even assuming that 85% of litterfall was not respired during the intervals. Assuming that only 15% of the new litter was respired during the intervals the 95% confidence interval for NEP would be -0.2 to $6.3 \, \mathrm{Mg \, C \, ha^{-1} \, yr^{-1}}$, which includes the value of zero and still does not provide evidence to reject the null hypothesis.

Evidence for a local C sink

Given the large uncertainties observed we did not find sufficient evidence to reject the null hypothesis that this ecosystem is outside the *a priori* defined natural range of

variation. Although the observed uncertainty range includes values well outside the theoretical range of variation it also covers the complete range of possible theoretical values of NEP for a mature ecosystem. The observed uncertainty range is obviously higher than the *a priori* natural variation because uncertainties in measurements and estimates are included. Variations due to climate or long-term disturbance cycles were not included in our *a priori* defined range. For this reason, this hypothetical range of natural variation is likely underestimated.

Climate records from the study site showed that our measurements were conducted during a period of consistent warming (Fig. 1). Precipitation records did not show consistent trends during the past decade, but our measurements were conducted during one La Niña event in which unprecedented rain was recorded during September 2001, followed by a prolonged dry period until April 2001. The combination of drought and increasing temperatures might be associated with the large values of heterotrophic respiration observed during the second interval. However, other factors may confound the direct effects of climate on the observed

carbon fluxes. Indirect climatic effects can also play an important role in the variation of carbon fluxes (Shaver et al., 2000), as well as processes associated with stand dynamics (Shugart, 1984).

The evidence obtained in this study is not sufficient to infer effects of systematic changes in external forcing on the carbon flux of this ecosystem, but this does not mean that there is no effect of anthropogenic disturbances. These forests are highly fragmented and processes such as community dynamics or microclimate are likely to be altered (Laurance, 2004). Over the landscape, it would seem that fragmentation is not affecting the overall carbon flux, but it is also possible that the effects of fragmentation are masked by the uncertainties in our estimates. Effects of other important global processes such as increases in temperature and atmospheric CO_2 concentration are not possible to infer from this study.

The methodological framework for hypothesis testing proposed in this study can be very helpful to address the effect of global change on carbon dynamics as long-term observations are not strictly needed. Using a prior probability distribution it is possible to ask the question of whether or not the observed data are within an expected range of variation. This study shows that, a distribution of estimates is more important than the average NEP* for a given ecosystem, because it provides a range of variation that can be compared with a hypothetical range. If observational evidence against the null hypothesis is found, we can be more certain whether an external factor is driving the ecosystem outside its expected range. Models are an important tool to set prior distributions of NEP because they are our best integrated representation of physiological and ecological processes that affect carbon dynamics.

Evidence for a significant C sink in primary tropical forests

Our results agree with recent studies of carbon dynamics in mature tropical forests (Saleska et al., 2003; Rice et al., 2004) that also found a neutral balance of these ecosystems with respect to the atmosphere. The estimates of carbon fluxes from Grace et al. (1995), Saleska et al. (2003), Rice et al. (2004), and partially Loescher et al. (2003) are within the prior probability range that we assumed for our study site (Fig. 8). Only three studies were well outside this range (Fig. 8). Fan et al. (1990) study was conducted over a very narrow period of time so the interpretation of this datum on an interannual basis is problematic. The highest measurements of NEE ever reported in tropical forests (Malhi et al., 1998; Loescher et al., 2003), were conducted during La Niña events of 1995–1996 and 1998–2000, respec-
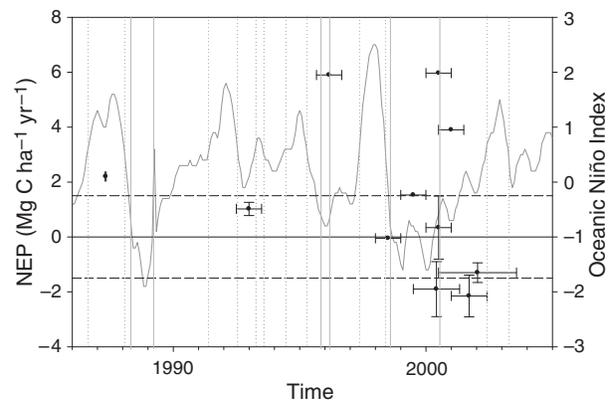

Fig. 8 Previous carbon flux studies in mature tropical forests. Positive numbers refer to C sinks and negative numbers as carbon sources. Reported NEE data were transformed to NEP multiplying by −1. The two periods measured from this study are included. Horizontal lines for each observation represent the duration of each study, and vertical lines error bars when reported. The area between the two thick dotted lines is the *a priori* defined range from this study. Temporal trends of the Oceanic Niño Index are presented in a continuous line. Thin dotted vertical lines represent El Niño years, and thin continuous vertical lines La Niña years. NEP data from (Fan et al., 1990; Grace et al., 1995; Malhi et al., 1998; Loescher et al., 2003; Saleska et al., 2003; Miller et al., 2004; Rice et al., 2004) and this study.

tively. However, the study reported by Rice et al. (2004) and our study were also conducted during the 1998–2000 La Niña and no large net fluxes were observed, suggesting that the effects of large-scale climatic variations differ geographically. The effect of ENSO on climatic variables such as temperature varies considerably over tropical regions (Malhi & Wright, 2004), which may also explain spatial differences in carbon fluxes (Rolim et al., 2005). However, reported large fluxes may also be explained by methodological issues such as uncorrected u^* filtering (Araujo et al., 2002; Saleska et al., 2003), especially in the case of Malhi et al.'s (1998) study.

If methodological issues in reported C fluxes are disregarded, it is clear from Fig. 8 that large deviations of carbon fluxes from the expected mean of mature forests in the tropics have been associated with extreme large-scale climatic effects. Figure 8 also suggest that fluctuations in C fluxes associated with stand dynamics are in the same order of magnitude as fluctuations in C fluxes associated with normal climatic fluctuations. This two-factor explanation of sources of variation remains little explored but could be tested by integrating models that only consider stand dynamics with models that consider climatic fluctuations. Our assessment of variation due to stand dynamics suggests that previously studied mature tropical forests might be oscillating

within their expected range of natural variation. The studies used for this analysis do not show any consistent trend of NEP that would support the hypothesis of an overall carbon sink in primary tropical forests.

Data from census plots in the neo-tropics suggest the aboveground biomass of undisturbed tropical forests has been increasing during the last decades (Phillips *et al.*, 1998; Baker *et al.*, 2004). These changes in aboveground biomass suggest that the productivity in primary tropical forests might be increasing. However, the behavior of Rh during the last decades in those plots is uncertain. Moreover, it is uncertain if consistent and systematic changes in NEP have been occurring, which would provide strong evidence for either a C source or sink in primary tropical forests.

Scope of inference and limitations

The random procedure used in this study for the location of sampling plots allows us to make inferences for a total study area of 694 ha (Welsh, 1996). Inferences beyond this area cannot be made from these results. Our analysis showed that there is not enough evidence in favor of the hypothesis of a significant carbon sink at this particular location for these particular time intervals.

Taken together, previous studies in the tropics estimating annual carbon fluxes at the ecosystem level did not provide evidence in favor of this hypothesis either. However, because the compilation of these studies was not strictly a random sample of sites from the Neotropics we cannot make inferences beyond this set of sites. Differences in the methodologies used in those studies also limit the scope of inference to the studied sites and not beyond larger areas. Our analysis did show, however, that the majority of estimates of annual carbon fluxes in primary tropical forests are within an expected range of variation, consistent with the hypothesis that these forests are in a state of dynamic equilibrium.

Conclusions

In this study, we did not find evidence to reject the hypothesis that tropical primary forests of the Porce region of Colombia were in carbon balance with the atmosphere between 2000 and 2002. At a larger scale, we conclude that observations of C fluxes in primary tropical forests are highly variable spatially and temporally, but an important fraction of this variation could be explained by natural processes of ecosystem dynamics. There is some evidence that the net carbon flux of these ecosystems has responded to global climatic signals such as La Niña. However, there is not sufficient and strong evidence to support the hypothesis that previously studied primary tropical forests are acting as a consistent major C sink as an effect of global change.

A number of studies have hypothesized several effects of global change on different components of tropical forest ecosystems. Giving that the available observations do not provide definite evidence for important effects on the net carbon flux, three non-mutually exclusive hypothesis are plausible: (1) Responses of production and respiratory fluxes to atmospheric change counterbalance in the net carbon flux, (2) the response of tropical forests to global change is lagged and we have not been able to observe it yet, and (3) our current measurements are inadequate to identify such an effect.

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