

Variation in carbon storage among tree species: Implications for the management of a small-scale carbon sink project

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Abstract

Despite growing evidence for an effect of species composition on carbon (C) storage and sequestration, few projects have examined the implications of such a relationship for forestry and agriculture-based climate change mitigation activities. We worked with a community in Eastern Panama to determine the average above- and below-ground C stocks of three land-use types in their territory: managed forest, agroforests and pasture. We examined evidence for a functional relationship between tree-species diversity and C storage in each land-use type, and also explored how the use of particular tree species by community members could affect C storage. We found that managed forests in this landscape stored an average of 335 Mg C ha⁻¹, traditional agroforests an average of 145 Mg C ha⁻¹, and pastures an average of 46 Mg C ha⁻¹ including all vegetation-based C stocks and soil C to 40 cm depth. We did not detect a relationship between diversity and C storage; however, the relative contributions of species to C storage per hectare in forests and agroforests were highly skewed and often were not proportional to species' relative abundances. We conclude that protecting forests from conversion to pasture would have the greatest positive impact on C stocks, even though the forests are managed by community members for timber and non-timber forest products. However, because several of the tree species that contribute the most to C storage in forests were identified by community members as preferred timber species, we suggest that species-level management will be important to avoiding C-impoverishment through selective logging in these forests. Our data also indicate that expanding agroforests into areas currently under pasture could sequester significant amounts of carbon while providing biodiversity and livelihood benefits that the most common reforestation systems in the region – monoculture teak plantations – do not provide.

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1. Introduction

Land cover changes, particularly tropical deforestation, contribute about 25% of anthropogenic carbon (C) emissions and are the leading cause of species extinctions (Sala et al., 2000; IPCC, 2001; Thomas et al., 2004). Atmospheric C concentrations are now estimated to be at 1.3 times pre-industrial levels and losses of biodiversity at up to 1000 times the background rate (IPCC, 2001; Houghton, 2005; CBD, 2006). The effects of these changes on ecosystem functioning and human well-being are driving the development of

mitigation initiatives at local to international levels (e.g., UNEP, 1992; UNFCCC, 1992; MEA, 2005).

A number of observers and a few pilot projects have highlighted the practical opportunities for optimizing both C storage (or C sequestration) and biodiversity conservation within a single project (Swingland, 2002; World Bank, 2002). Not only do vegetatively complex systems tend to store more C and support more species (Fujisaka et al., 1998; Hardner et al., 2000; Koziell and Swingland, 2002; Leader-Williams, 2002), but biodiversity is likely to play an important role in determining stakeholder support for C-sink initiatives (Bloomfield and Pearson, 2000; Smith and Scherr, 2003).

Ecologists have also become interested in potential functional relationships between diversity and C sequestration and storage (e.g., Chapin et al., 2000; Tilman et al., 2001; Spehn et al., 2005; see Schwartz et al., 2000; Srivastava and Vellend, 2005 for reviews). Several experiments in grassland systems

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have found linear increases in productivity with increasing species diversity (Tilman et al., 1996; Hooper and Vitousek, 1997; Hector et al., 1999). One explanation for these findings, the “niche-complementarity hypothesis,” holds that as a system includes more species (and therefore more resource uptake strategies), resources are used more fully and the system is more productive. However, some grassland experiments have found that increases in productivity disappear once a threshold of just a few species is reached (Loreau and Hector, 2001; Tilman et al., 2001). These findings provide support for the “sampling effect hypothesis,” which argues that it is the inclusion by chance of functionally important species in more diverse assemblages that results in any observed increases in productivity rather than increases in diversity per se. In forests, examples of the uneven contribution of species to C sequestration and storage include the higher rate of C sequestration by species that are fast- versus slow-growing and, in established systems, the greater storage of C in large, long-lived species and in species with dense versus light wood (Brown et al., 1997; Fearnside, 1997; Pinard and Cropper, 2000; Caspersen and Pacala, 2001; Baker et al., 2004; Balvanera et al., 2005; Bunker et al., 2005).

A functional relationship of either form between diversity and C storage and sequestration could have important implications for the management of C-sink projects, not only for reforestation and afforestation type projects, which are currently supported under international agreements such as the Kyoto Protocol’s clean development mechanism, but also for emissions reductions projects that focus on forest conservation and management (UNFCCC, 1997, 2005). In the former case, the relationship of tree-species diversity to C sequestration is likely to be of greatest concern for managers interested in sequestering the maximum amount of C over the short term, though in some cases long-term C storage may also be of concern. In the latter case, understanding the relationship of tree-species diversity to carbon storage will be critical to maintaining C stocks of protected forests over the long term. To our knowledge, the importance of species-level management has only been explored in model landscapes to date (Balvanera et al., 2005; Bunker et al., 2005).

In this study we explore variation in carbon storage among tree-species in a landscape of Eastern Panama that is actively managed by local people. Specifically, we worked with the community of Ipetí-Emberá, whose members are exploring the possibility of establishing a C-sink project on their 3145 ha *tierra colectiva* or “collective lands”. We examined the relationships between C-storage, species composition and land use in three land-use types: managed forest, agroforest, and pasture. We first use inventory data to estimate above- and below-ground carbon stocks and tree species diversity for each land-use type. We then examine evidence for a species diversity or species composition effect on above- and below-ground carbon storage. Finally, we explore the use of tree species by community members and discuss the implications of these uses to the design of a C-sink project in this landscape.

2. Methods

2.1. Study area

The study was carried out in the *tierra colectiva* (TC) of Ipetí-Emberá in eastern Panama Province, Panama (N08°58′15.34″, W078°31′00.65″). The TC of Ipetí-Emberá encompasses 3145 ha of land in the Bayano watershed, and is framed by the Ipetí river to the east, the Curtí river to the west, and the Pan-American highway to the north (Dalle and Potvin, 2004). The TC is in the foothills (50–300 m elevation) of the Serranía de Maje which rises to the south of the TC and forms a barrier to the Pacific Ocean (Instituto Geográfico Nacional, 1988).

The mean annual temperature is 26 °C, and mean annual rainfall is 2500 mm with a pronounced dry season from December to April (Instituto Geográfico Nacional, 1988; Dalle and Potvin, 2004). The primary vegetation is tropical moist forest according to the Holdridge lifezone system, and common forest tree species include *Matayba glaberrima*, *Castilla elastica*, *Gustavia fosteri* and *Quararibea asterolepis*. The bedrock geology of the TC consists of massive conglomerate with basalt boulders and cobbles in a sand matrix of Oligocene age. The highlands to the south of the TC are comprised of older, pre-Tertiary metamorphic and igneous rocks (Stewart, 1966). Soils in eastern Panama are variable and range from inceptisols to vertisols (Dames and Moore, 2001). Soils at our study sites were clay-rich and had an average pH of 6.4 (range 5.3–7.8).

The TC was designated by the Panamanian government in 1970 for Emberá families whose lands were to be flooded during the construction of the Bayano Dam, which is approximately 25 km to the northwest of the TC (Wali, 1993; Dalle and Potvin, 2004). The majority of relocated families arrived in Ipetí in 1975, and since then the community has grown from approximately 12 households to 71 households and ca. 550 people (Tschakert et al., 2007). Prior to the flooding of the Bayano Dam and associated resettlement, the landscape of the TC was largely old-growth forest (McKay, 1984). The landscape surrounding the TC has been settled by colonists from central Panama over the last three decades and is now largely dominated by cattle pasture.

In this paper we examine the carbon stocks and tree-species diversity of three common land-use types in the TC: (1) managed forest (primary forest from which timber and non-timber forest products are selectively harvested), (2) traditional agroforests (home and outfield gardens, which consist of perennial tree crops that include fruit, timber and medicinal species) and (3) pasture. A participatory mapping exercise carried out in 2004 revealed that these land-use types occupy 47%, 2% and 18% of the land base, respectively (Potvin et al., 2006).

2.2. Field inventory

The community selected six men to make up a carbon inventory team, including two men considered by the

community to be experts of the taxonomy of local forest trees. Based on team members' knowledge of land uses in the TC and a participatory map of land use that was developed in the community in 1998 (Potvin et al., 2006), we identified all landholdings in the TC containing primary forest, agroforest, and/or pasture. For each land-use type, 16 landholdings containing that land-use type were randomly selected, stratifying by sub-watershed to distribute the sampling sites throughout the 3145 ha of the TC as much as possible. Although this scheme was successful in distributing forest sites, most of the randomly selected agroforest and pasture sites are concentrated near the village and along the highway, reflecting development patterns within the TC. Overall, forest sites were more likely to be located on hillsides than were agroforests or pastures. However, there were no significant differences in soil characteristics among land-use types (pH, Munsell colour, percent nitrogen content), suggesting that the site types underlying forests, agroforests and pastures were not significantly different. At each site we established a pair of circular plots with radii of 15 m in which we measured all above- and below-ground carbon pools (pair of plots = site). In forest and pasture the centre of the paired plots were separated by 40 m, leaving 10 m between the outside edge of each plot. In agroforests, this method was followed except when the shape of the agroforest prevented it, in which case the two circular plots were placed wherever they fit within the agroforest as long as they did not overlap. In using paired plots of 15 m radius we were able to use the same sampling method in all land-use types, as larger plots would not have fit in agroforests. Other studies of C storage in both managed and natural landscapes have used a similar sampling design (Kotto-Same et al., 1997; Fujisaka et al., 1998; Brown, 2002).

In each 15 m-radius plot we measured the diameter at breast height (DBH) of all trees, palms and lianas ≥ 10 cm DBH to the nearest millimeter. When buttresses were present, we measured 50 cm above the buttresses (Condit, 1998). In the few cases where this was not possible we measured as high as could be reached without a ladder; the number of trees measured in this way was less than 1 per site. In the centre of each plot we established a sub-plot with a 6 m radius in which we measured all trees, palms and lianas 5–10 cm DBH. We estimated the height of standing trees that had snapped below the crown. Lianas were measured 1.3 m along the stem from the point where they entered the ground (hereafter referred to as liana DBH). From the centre of each 15 m radius plot we laid a 15 m transect in each of the South and East cardinal directions. The diameter of all pieces of downed woody debris (≥ 1 cm diameter) along the 15 m transects was recorded. At the point where each transect intersected the plot perimeter (15 m), we established a 3 m \times 3 m quadrat in which we used calipers to measure the basal diameter (BD; diameter at 10 cm above the ground) of all saplings and small palms (< 5 cm DBH, BD ≥ 1 cm) and the diameter of all lianas 1–5 cm DBH. In one randomly selected corner of each 3 m \times 3 m quadrat we established a 1 m \times 1 m quadrat in which we harvested all woody vegetation with BD < 1 cm.

We then established a 50 cm \times 50 cm plot in this quadrat in which we harvested all herbaceous plants and collected the leaf litter. In each 50 cm \times 50 cm quadrat, we also took a vertical soil core at the soil surface (0 cm) and at a depth of 30 cm. The soil cores were 3.0 cm in diameter and 10 cm in height. With two soil cores per quadrat (one at each depth), two quadrats per plot, and two plots per site, we collected eight soil cores per site.

At each site we recorded latitude and longitude using a GPS at the centre of each 15 m-radius plot. We later uploaded these data to Arcview version 3.2 and calculated direct distances between each site and the village. We also asked landowners a series of questions about the history and management of their site. Forest owners were asked if they had ever harvested timber from their landholdings and, if so, when they had last harvested trees, how many individuals of each species had been harvested, and the monetary value of the harvested timber. Agroforest and pasture owners were asked when the original forest on their site had been cleared, when the agroforest or pasture had been established, what management practices they currently employed, how they used the products from their agroforests (source of income, home consumption), and if their pasture was currently being grazed and/or rented to another cattle owner.

For each tree, palm and liana we measured, the local name, either Spanish or Emberá, was recorded by one of the two team members who had been selected by the community as an expert of local plants. We recorded 129 different tree morphospecies (hereafter also referred to as species). The Chiefs of the Congress of the Comarca Emberá-Wounaan asked that we not create biological voucher specimens for the species we encountered as they are concerned that any such specimens could open the door to biopiracy on Emberá-Wounaan lands. We therefore related local names to scientific names for each of the 129 morphospecies using a combination of (1) discussions with botanists at the Smithsonian Tropical Research Institute who are familiar with the flora of Eastern Panama, (2) available databases (Duke and Porter, 1970; CTFS, 2004) or (3) photographs of the trunk, leaves, and/or fruits as identification aids.

In addition to recording the name of each tree in the field, crew members also recorded if and how that tree was used by community members. At the conclusion of the inventory the uses that had been attributed to the trees in the inventory included: food, medicine, timber (for construction or resale), construction material (palms and lianas only), firewood, materials for making "motetes" (carrying baskets), rubber, fencing material, and artisanal material. Because we were particularly interested in the effects of timber harvesting on carbon stocks, the species that landowners identified in interviews as most recently having harvested from their landholdings were assigned to the use category "preferred timber"; in all cases, these species would otherwise have been classified as "timber". Similarly, because we were interested in identifying agroforest species that provided a source of income for their owners we assigned species that produced fruits that are currently sold by community members to the category "food for market".

2.3. Estimating biomass and carbon stocks

Diameter measures of trees, palms, lianas and woody debris were individually converted to measures of above-ground biomass (AGB), and then summed by plot. Results were then scaled from Mg plot⁻¹ to Mg ha⁻¹ after plot size or transect length was corrected for steepness of slope.

We estimated the AGB of trees ≥ 5 cm DBH using the allometric model of Chave et al. (2005) (Table 1; see Appendix A for estimates using alternative models). The model of Chave et al. (2005) is based on trees harvested from moist tropical forest sites around the world and requires data on DBH and wood density for each tree. We obtained wood densities for our trees by linking the species or genus names of the trees we inventoried with species- and genus-specific average wood densities (H. Muller-Landau, J. Chave and colleagues, unpublished data). When we could not identify the species or genus of a tree, or when no wood density was available for a species or genus, we assigned a value of 0.54 g cm⁻³ – the average wood density of trees ≥ 10 cm in a plot on Barro Colorado Island, Panama – to the tree (Muller-Landau, 2004).

We grouped palms with trees for AGB estimates. In contrast to tree AGB, palm AGB is argued to be more reliably predicted by height than DBH, as palms increase biomass through apical growth with little growth in diameter (Brown, 1997, 2002). However, here we follow arguments that hold that the tendency for DBH-only models to underestimate palm stem biomass will be offset by their tendency to overestimate palm ‘crown’ biomass (Malhi et al., 2004). On average palms contributed only 8%, 10% and 1% of the total basal area of trees and palms ≥ 10 cm in our forest, agroforest, and pasture plots, respectively.

AGB of dead trees and palms was estimated as for live trees and palms, with values reduced by 10% to account for the loss of leaves, twigs, and small branches (Delaney et al., 1998; Table 1). For dead trees that had snapped below the crown, we applied a taper function multiplied by average wood density (Graça et al., 1999 in Nascimento and Laurance, 2002; Table 1). AGB for dead trees and snags was added to live tree AGB for calculations of tree AGB at the plot level.

Liana diameter was first converted to basal area (BA = $\pi \times \text{DBH}^2/4$) and then to AGB using an allometric model developed in a wet tropical forest in Venezuela (Putz, 1983; Table 1). AGB of saplings (trees < 5 cm DBH, ≥ 1 cm BD) for forest and agroforest sites was estimated from BD using a regression model developed for 30 saplings (representing 20 morphospecies) that were harvested from a forest understorey ($r^2 = 0.886$, $p < 0.0001$, $n = 30$; Table 1), following Brown (1997). For saplings in pasture sites we estimated AGB using a model developed for saplings growing in a central Panama pasture ($r^2 = 0.856$, $p < 0.0001$, $n = 31$; C. Potvin, unpublished data; Table 1). We classified the young palms we encountered in the 3 m \times 3 m sapling quadrats in all land-use types into one of two groups. The first group included individuals with tree-like stems (e.g., most *Cryosophila warscewiczii* and *Bactris* spp.); we estimated their AGB using the allometric models for saplings. The second group included young palms that did not have an obvious stem but had fronds growing from their base (e.g., most individuals of the genera *Attalea* and *Astrocaryum*); individuals in this group were not measured but were destructively sampled as part of the ‘woody vegetation’ component when they fell in the 1 m \times 1 m quadrats.

We indirectly estimated the total root biomass for our sites as 24% of the above-ground biomass of trees > 1 cm BD (Cairns et al., 1997; Jobbagy and Jackson, 2000). We could not locate any published estimates of root-to-shoot ratios for lianas, and therefore also apply this relationship to lianas.

AGB of woody debris was estimated using the planar-intersect method (Van Wagner, 1968; Brown and Roussopoulos, 1974; Table 1). Debris was classified according to diameter (fine debris 1.0–7.6 cm and coarse debris > 7.6 cm); and coarse debris was further classified as either sound or rotten. Wood densities for the different classes were assigned as follows: 0.319 g cm⁻³ for rotting coarse debris (mean of “partially decomposed” and “fully decomposed” in Clark et al., 2002) and 0.453 g cm⁻³ for sound coarse woody debris and fine debris (Clark et al., 2002). Most pieces of debris lay directly on the forest floor and we therefore consider the error in transect biomass due to tilt of individual pieces to be negligible (Van Wagner, 1968).

Table 1
Allometric models used to convert measures of vegetation and woody debris to AGB

Above ground component	Land-use type	Model	Source
Trees and palms > 5 cm DBH	All	$\rho_i \times \exp(-1.499 + 2.148 \ln(\text{DBH}) + 0.207(\ln(\text{DBH}))^2 - 0.0281(\ln(\text{DBH}))^3)$	Chave et al. (2005)
Lianas ≥ 1 cm	All	$10^{(0.12+0.91 \log(\text{BA}))}$	Putz (1983)
Saplings ≥ 1 cm BD, < 5 cm DBH	Forest, agroforest	$\exp[3.965 + 2.383 \ln(\text{BD})]$	This study
Saplings ≥ 1 cm BD, < 5 cm DBH	Pasture	$\exp[3.790 + 2.476 \ln(\text{BD})]$	Potvin (unpublished data)
Tree snags ≥ 5 cm DBH	All	$\rho_i[\pi(\text{DBH}/2)^2 \times (\text{height}) \times 0.78]$	Nascimento and Laurance (2002)
Dead trees ≥ 5 cm DBH	All	90% of total AGB of live tree	Delaney et al. (1998)
Root biomass	All	24% of AGB of trees, palms, lianas ≥ 1 cm DBH	Cairns et al. (1997)
Downed woody debris	All	$\rho_{\text{dwd_class}}[\pi^2 \Sigma(d^2)/8L] \times C_s$	Brown and Roussopoulos (1974)

DBH = diameter at breast height (cm); BD = basal diameter (diameter at 10 cm above ground level; cm); BA = basal area (cm²); ρ_i = species specific wood density value (g cm⁻³) of tree {i}, or 0.54 when wood density of species or species unknown; $\rho_{\text{dwd_class}}$ = wood density of downed wood debris class (g cm⁻³); $\rho_{\text{sound_cwd}} = 0.453$; $\rho_{\text{rotting_cwd}} = 0.319$; $\rho_{\text{fwd}} = 0.453$; C_s = slope correction factor; L = transect length (cm).

To convert AGB to C, AGB was multiplied by the %C content of the component in question. C content was assumed to be: 45% for litter, 43% for seedlings, 41% for grass, and 50% for downed woody debris (Hughes et al., 1999). For trees, palms and lianas (including roots) we assume a C content of 47%. This was the mean C content for palms in a wet forest in Mexico (Hughes et al., 1999), and is intermediate to the mean C content for trees of two neotropical studies (46% in Elias and Potvin (2003) and 48% in Hughes et al. (1999)).

The organic carbon content of all soil samples was assessed using the loss-on-ignition (LOI) method (Ball, 1964). Because water and other inorganic constituents of soil may also be lost upon ignition and result in inflated estimates of organic carbon (Nelson and Sommers, 1982), the cores from one quadrat at each site were also analyzed for total organic carbon using a high temperature combustion method (GEOTOP Laboratories, Université de Québec à Montréal). Once eight outlying samples suspected to contain carbonates (pH > 7 or outlying C:N ratio) were removed from the high temperature combustion dataset, regression analysis was used to relate % organic carbon (%C) to weight lost on ignition, where $\%C = -1.0260 + 0.363(\text{LOI})$ ($r^2 = 0.83$, $p < 0.0001$, $n = 88$). This relationship was used to predict %C for plots in which no cores had been analyzed by

high temperature combustion. Bulk density was also determined for every soil core. Finally, soil organic carbon (SOC) per hectare per layer (0–10 cm or 30–40 cm) was determined according to the following formula: $[\%C] \times [\text{bulk density}] \times [\text{depth of layer}]$, with bulk density measured in g cm^{-3} and depth of layer in cm. As an estimate of SOC in the 10–30 cm layer we took the mean SOC value for the 0–10 cm and 30–40 cm layers, and applied it to each of the 10–20 cm and 20–30 cm layers. We found that this method produced summed values for the 0–20 cm and 20–40 cm layers in forest sites that were consistent with previous accounts of the relative distribution of SOC with depth in tropical deciduous forests (Jobbagy and Jackson, 2000), with the 20–40 cm layer in our forest sites making up 41.1% of the 0–40 cm layer.

Table 2 summarizes the methods we used to convert biomass estimates to C stocks and to combine estimates from all quantified C pools to produce an estimate of total above- and below-ground C stocks for each land-use type.

2.4. Analysis

Above- and below-ground carbon pools were contrasted among forest, agroforest, and pasture sites using nested

Table 2
Summary by land-use type of the above- and below-ground biomass and/or carbon stocks of all vegetation pools and for each soil layer. The final row of the table represents the total carbon stocks of each land-use type (including all above ground pools, tree roots, and soil organic carbon to 40 cm depth). The units for all values are Mg ha^{-1} and are presented $\pm 1\text{S.E.}$ Post hoc means comparisons show significant differences among land use types (F = forest; A = agroforest; P = pasture; NS = not significant). We did not test for differences in root biomass or SOC in the 10–30 cm layer as these values were extrapolated from values for above-ground vegetation and surrounding soil layers, respectively

	Biomass			Proportion, biomass = carbon ^a	Carbon			Tukey's post hoc ^b
	Forest	Agroforest	Pasture		Forest	Agroforest	Pasture	
Above-ground pools								
Trees + palms (≥ 10 cm DBH)	464.3 \pm 58.8	153.0 \pm 14.1	4.6 \pm 2.5	0.47	218.2 \pm 27.6	71.9 \pm 6.6	2.2 \pm 1.2	F > A > P
Saplings (1–10 cm DBH)	13.1 \pm 1.2	6.6 \pm 1.6	0.6 \pm 0.2	0.47	6.2 \pm 0.6	3.1 \pm 0.8	0.3 \pm 0.1	F > A > P
Lianas (≥ 1 cm DBH)	8.8 \pm 2.1	0.4 \pm 0.2	0 \pm 0	0.47	4.1 \pm 1.0	0.19 \pm 0.09	0 \pm 0	F > A > P*
Seedlings	0.34 \pm 0.04	0.32 \pm 0.05	0.4 \pm 0.1	0.43	0.15 \pm 0.02	0.14 \pm 0.02	0.16 \pm 0.04	NS
Herbs	0.26 \pm 0.08	0.35 \pm 0.07	2.7 \pm 0.4	0.41	0.10 \pm 0.03	0.14 \pm 0.03	1.1 \pm 0.2	P > A, F
Litter	5.2 \pm 0.5	5.8 \pm 0.6	0.5 \pm 0.1	0.45	2.4 \pm 0.2	2.6 \pm 0.3	0.23 \pm 0.04	A, F > P
Woody debris	8.1 \pm 1.9	7.1 \pm 1.6	0.4 \pm 0.3	0.5	4.0 \pm 1.0	3.5 \pm 0.8	0.20 \pm 0.15	F > A > P*
Total above-ground C (Mg ha^{-1})	500.0 \pm 58.6	173.5 \pm 14.1	9.3 \pm 2.7		235.1 \pm 27.5	81.6 \pm 6.6	4.2 \pm 1.3	F > A > P
Roots								
Trees + palms (≥ 10 cm DBH) ^c	111.4 \pm 14.1	36.7 \pm 3.4	1.1 \pm 0.6	0.47	52.4 \pm 6.6	17.2 \pm 1.6	0.5 \pm 0.3	Not tested
Saplings (1–10 cm DBH) ^c	3.1 \pm 0.3	1.6 \pm 0.4	0.14 \pm 0.05	0.47	1.5 \pm 0.1	0.7 \pm 0.2	0.7 \pm 0.2	Not tested
Lianas (≥ 1 cm DBH) ^c	2.1 \pm 0.5	0.10 \pm 0.05	0 \pm 0	0.47	1.0 \pm 0.2	0.04 \pm 0.02	0 \pm 0	Not tested
Total C in roots (Mg ha^{-1})					54.8 \pm 6.6	18.0 \pm 1.6	0.6 \pm 0.3	Not tested
Soil								
SOC 0–10 cm					15.3 \pm 1.1	15.1 \pm 0.8	14.6 \pm 0.8	NS
SOC 30–40 cm					7.2 \pm 0.6	7.4 \pm 0.6	5.8 \pm 0.4	NS
SOC 10–30 cm ^d					22.5 \pm 0.9	22.5 \pm 0.7	20.5 \pm 0.6	Not tested
Total C in soil (0–40 cm depth) (Mg ha^{-1})					45.1 \pm 2.4	45.0 \pm 2.3	41.0 \pm 1.8	Not tested
Total estimated C by land use (Mg ha^{-1})					335.1 \pm 34.6	144.7 \pm 2.3	45.7 \pm 2.6	

^a C stocks of vegetation pools were estimated by multiplying biomass by the C content of the pool in question (Hughes et al., 1999; Elias and Potvin, 2003).

^b Or non-parametric means comparison (Mann–Whitney *U*-test), indicated by ‘*’.

^c Calculated as 24% of above-ground biomass (Jobbagy and Jackson, 2000).

^d Estimated using the mean of the SOC value for the 0–10 cm and 30–40 cm layers.

analyses of variance (ANOVAs) with plots nested within sites, or with a Kruskal–Wallis test when data could not be transformed to meet assumptions for parametric tests. Where the tests indicated significant differences among land-use types, means were contrasted with post hoc Tukey HSD tests ($\alpha = 0.05$) or, for non-parametric data, with two-way post hoc Mann–Whitney U -tests. Although previous studies have suggested that plots smaller than 0.25 ha in size can lead to a skewed distribution of AGB among plots because only a few of the plots will include a rare large tree within its boundary (Chave et al., 2003), a Kolmogorov–Smirnov test for normality indicated that our data for AGB were normally distributed among the 16 sites we inventoried (Zar, 1998).

We carried out a power analysis of our above-ground biomass data, which was the largest source of variation in our C stock estimates. This was accomplished using the model of Krebs (1999): $n = (s/x)^2 (t_\alpha^2 / r^2) \times 100^2$, where n is the number of sites needed for a certain level of precision, t_α the Student t -value for $n - 1$ degrees of freedom for the $1 - \alpha$ level of confidence, s the standard deviation of the variable, and r is the desired relative error.

Species composition was contrasted among land-use types using a Jaccard similarity index. The Jaccard similarity index uses species presence/absence data for two sample sets (in this case land-use types) and is calculated as $J = M / (M + N)$, where M is the number of species that occur in both land-use types and N is the number of species that occur in only one of the two land-use types.

Pearson correlation analyses were used to explore relationships between morphospecies richness, above-ground biomass and soil C stocks both among and within land-use types. Unidentified individuals in our plots posed a problem to species richness calculations, and we therefore estimated the number of morphospecies per site by taking the average of the “maximum” number of morphospecies (in which we assume that all unidentified individuals are different morphospecies) and the “minimum” number of morphospecies (in which we assume that all unidentified tree, palm, or liana individuals in a plot belong to the same species). On average, in all land-use types, less than 2% of individuals ≥ 10 cm DBH in a plot were unidentified; and in only 3 of the 96 sample plots were more than 6% of individuals unidentified.

We repeated these analyses within each land-use type replacing morphospecies richness with two indices of diversity: the Shannon–Wiener index ($H' = -\sum_{i=1}^s p_i \ln p_i$) and Simpson’s index of diversity ($D = 1 / \sum_{i=1}^s p_i \ln p_i$) where s is the total number of species and p is the relative abundance of species i . In contrast to direct measures of species richness, these indices take into account the relative abundances of species (Legendre and Legendre, 1998). One site with outlying soil C values in the 0–10 cm layer was removed from the correlation analysis as it alone was responsible for a negative trend among soil C and Simpson’s diversity index in agroforest sites. Once removed, the trend disappeared ($r = 0.02$; $p = 0.942$; Table 3).

In order to examine the contribution of individual species to C storage across sites, we calculated the average contribution of

Table 3
Results of correlation analyses between tree-species diversity, above-ground biomass (AGB), and soil organic carbon at two depths (0–10 cm and 30–40 cm). Three indices of diversity were used: species richness, Shannon–Weaver H' , and Simpson’s D . For each relationship, the R -squared and p -value are given (p -value is in parentheses)

	Above-ground biomass			Soil organic carbon (0–10 cm depth)			Soil organic carbon (30–40 cm depth)		
	Forest	Agroforest	Pasture	Forest	Agroforest	Pasture	Forest	Agroforest	Pasture
Richness	0.17 (0.526)	0.31 (0.237)	0.68 (0.046)	0.41 (0.116)	0.03 (0.600)	0.04 (0.600)	0.23 (0.116)	0.14 (0.046)	0.06 (0.877)
Shannon–Wiener H'	0.23 (0.400)	0.01 (0.961)	0.62 (0.074)	0.09 (0.723)	0.03 (0.902)	0.09 (0.820)	0.03 (0.723)	0.19 (0.074)	0.08 (0.844)
Simpson’s D	0.28 (0.301)	0.02 (0.940)	0.48 (0.189)	0.24 (0.376)	0.02 (0.942)	0.10 (0.621)	0.13 (0.798)	0.29 (0.275)	0.19 (0.621)

each species to C storage per hectare across sites in forests and agroforests. We did not perform this analysis for pastures because of the small number of individuals and species in pasture sites. For the species storing approximately 85% of C in the two land-use types (the ‘major contributors’), we then calculated the average number of individuals per species per hectare by averaging across sites. Next, we calculated the average biomass of one individual of each of the ‘major contributor’ species, and compared this to the global average, which we base on all individuals ≥ 10 cm DBH measured in that land-use type. Finally, because we were also interested in how the use of the ‘major contributor’ species by community members could be important to the management of a project in this landscape, we assigned a ‘dominant use’ to each species based on the number of times a use was recorded for that species during the carbon inventory.

Regression analysis was used to examine the relationship of tree AGB in forest sites to the distance of the site from the village, and logistic regression was used to relate the history of timber harvesting of different sites (yes/no) to distance of the site from the village. In all cases an alpha of 0.05 was used.

3. Results

3.1. Carbon stocks

When all above-ground components were considered together, AGB increased from pasture to agroforest to intact forest ($F = 340$; $p < 0.0001$; Table 2). Trees ≥ 10 cm DBH accounted for over 90% of above-ground carbon stocks in forest and agroforest and over 50% in pastures (Fig. 1). Separating trees, including palms, into size-class bins reveals that the relatively low C stock of pastures is a result of the near absence of stems ≥ 10 cm DBH in pasture sites, whereas the difference

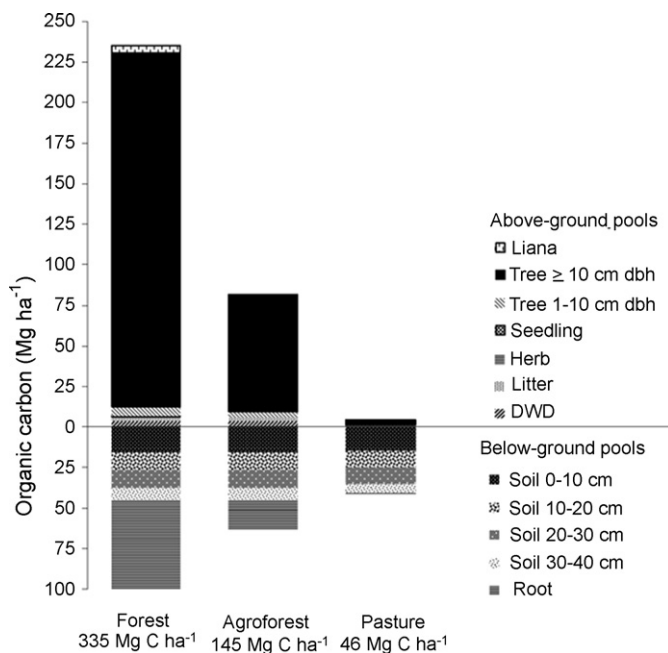


Fig. 1. Total carbon pools of forests, agroforests and pastures.

between agroforests and forests is explained by the near absence of stems ≥ 50 cm DBH in agroforests (Fig. 2). While 54% of forest biomass is stored in trees 10–89.9 cm DBH, 46% of forest biomass is stored in trees 90–176 cm DBH (Fig. 2).

A post hoc sample size analysis showed that the precision of our AGB estimates for forests could be improved to $\pm 10\%$ of the mean with 95% confidence with 91 sites. The actual precision of our AGB estimates for forests was $\pm 24.9\%$ of the mean with 95% confidence.

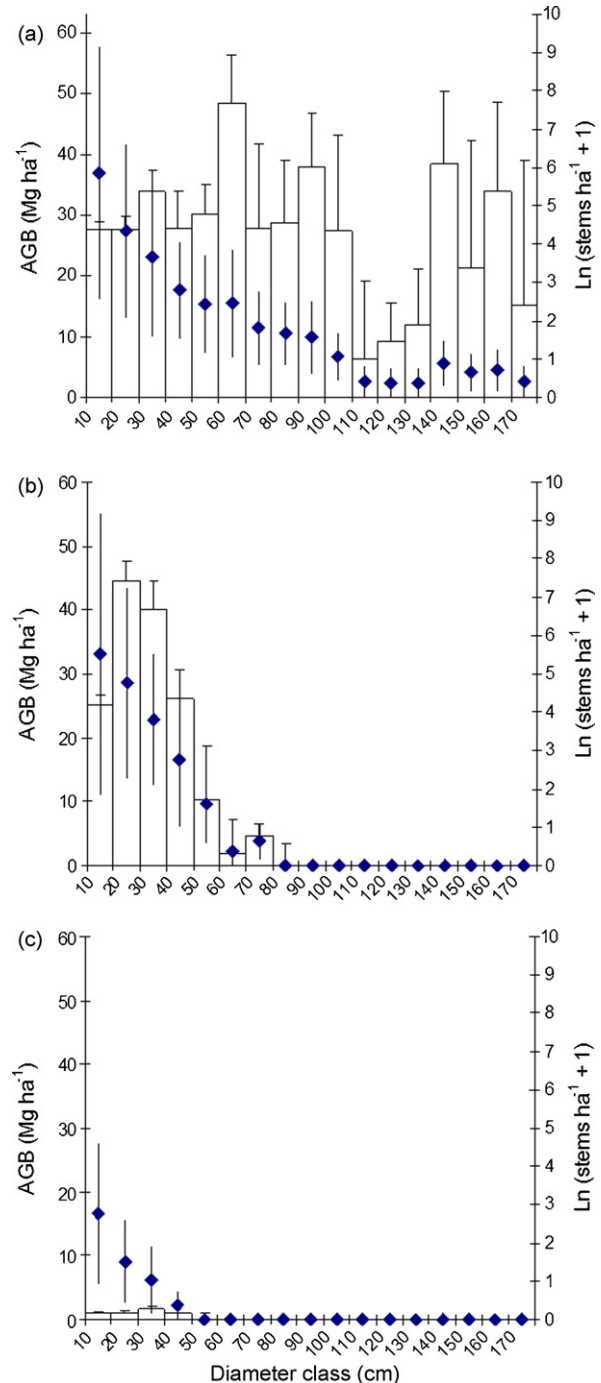


Fig. 2. Distribution of biomass and stem numbers among 10 cm diameter classes in (a) forests, (b) agroforests, and (c) pastures.

Soil organic carbon (SOC) did not differ significantly among land-use types (0–10 cm depth: $F = 0.15$, $p = 0.8621$; 30–40 cm depth: $F = 2.32$, $p = 0.1095$; Table 2). Of the quantified C-stocks in pastures, 89.6% were in soils (Fig. 1). In forests and agroforests this figure was much lower at 13.4% and 31.1%, respectively. Soils were variable both among plots at a single site and among sites within a land-use type. For example, the average coefficient of variation for %C in the 0–10 cm layer of two plots at a single site was 32% in forests, 21% in agroforests, and 22% in pastures. The coefficient of variation for %C in the 0–10 cm layer for all sites within a land-use type was 25% in forests, 46% in agroforests, and 40% in pastures.

Local taxonomic knowledge of the team members allowed us to identify 96% of the 2468 trees, palms and lianas ≥ 5 cm DBH that we inventoried. These names corresponded to 129 morphospecies, 87 of which were linked to a scientific species, and 11 to a genus. Over all plots, 98 morphospecies were identified in forests, 61 in agroforests, and 19 in pastures. Of the 61 morphospecies encountered in agroforests, 29 (48%) were not encountered in forest plots, and 8 of the 29 (13%) were not native to the Neotropics. In pastures, 7 of the 19 morphospecies (37%) were not encountered in forests, and 1 of the 7 (5%) was exotic.¹ Jaccard similarity indices between the three land-use types were: forest–agroforest: 0.252; forest–pasture: 0.114; agroforest–pasture: 0.194. The number of morphospecies per sampling site (1414 m²), ranged from 25 morphospecies per forest site, to 13 per agroforest site, to 1 per pasture site. When data on C stocks and morphospecies richness from sites in all land-use types were pooled, there was positive relationship between above-ground C stocks and morphospecies richness ($r^2 = 0.59$; $p < 0.001$).

Total AGB and AGB of trees (including palms and lianas) ≥ 10 cm DBH were uncorrelated to species richness in forest or agroforest plots (Table 3). In pasture, AGB of trees was positively correlated to richness ($r = 0.68$, $p = 0.046$), reflecting the small number of species in pastures and the quick increase in biomass as another species (and individual) is added. There was no correlation between species richness and soil C in any of the land-use types (Table 3). We observed the same results when we replaced species richness with either the Shannon–Weaver or Simpson diversity index (Table 3).

3.2. Species' relative contribution to C storage

The role of large trees in determining forest C stocks is well illustrated in Fig. 2. However, further analysis indicates that while all morphospecies encountered are represented by individuals 10–89.9 cm DBH, only 12 morphospecies are represented by individuals ≥ 90 cm; these 12 species thus contribute almost half of the biomass per hectare. To further explore the evenness of species' contributions, we calculated the average contribution of each species to C stocks per hectare. Average contributions were highly skewed in forests, with the first-ranked species, espave (*Anacardium excelsum*), having the

same average contribution as the 70 lowest ranked species together (approximately 16% of total C stocks per hectare; Fig. 3a). This is particularly notable given that only 1% of the 1106 individuals ≥ 10 cm DBH that we inventoried in forests were espave trees, while 63% were trees of the 70 lowest ranked species (Fig. 3c).

Average contributions of agroforest species were also skewed, though species' average contributions were more in line with their relative abundances (Fig. 3a and b). For example, mango (*Mangifera indica*) was the top-ranked species across our sites in terms of C storage (29.2% of C stocks per ha) but was also very common and represented 20.7% of all individuals inventoried.

3.3. Land management and use of tree species

The interviews revealed that less than half of the forest owners had ever harvested trees from their landholdings. Among those who had harvested trees, the average time since last harvest was 7.9 years, with three forest owners having harvested in the last 2 years, and three not having harvested for 10 or more years. Those who were currently harvesting timber indicated they could sell sawn planks for about US\$ 0.25/board foot, earning upwards of US\$ 600 per tree. In contrast, forest owners who had harvested trees more than 10 years ago reported receiving an average of US\$ 15 to US\$ 20 per tree. We found that forest owners were more likely to have harvested timber from their landholding if it was closer to the village ($p = 0.04$); however, we found no effect of reported selective logging or of distance of sample plot to village on AGB or tree-species richness.

The average age of agroforests was 23.2 years, with the majority having been established shortly after the owner's arrival in the community. Ninety-three percent of agroforest owners reported using a machete to thin the understorey of their agroforest. Owners also reported adding trees to their agroforests through time such that agroforests contain trees of a range of ages. Indeed, there was only a weak trend of increasing AGB of trees ≥ 10 cm DBH in with agroforest age ($r^2 = 0.46$; $p = 0.09$). All owners reported consuming at least part of their agroforest harvest in their home, and 53% indicated that they sold some of the produce from their agroforests.

The average age of pastures was 12.5 years. Pasture owners indicated that their pastures were an important source of income; at the time of the study, 33% of pasture owners were renting their pasture to cattle farmers from outside the community and another 20% owned cattle that were currently grazing in their pasture.

In addition to examining the relative contributions of forest and agroforest species to C storage, we also explored the uses of these species by local inhabitants. Fig. 3 displays the uses of the top-ranked contributors to C storage in forests and agroforests. In total, 11 of the 21 “major contributor” species (52%) were destructively harvested for timber or construction and an additional 7 of the 21 (33%) were firewood species. We were particularly interested in “preferred timber species,” as we felt these species might be at highest risk of being destructively

¹ We assume all unidentified individuals are native species.

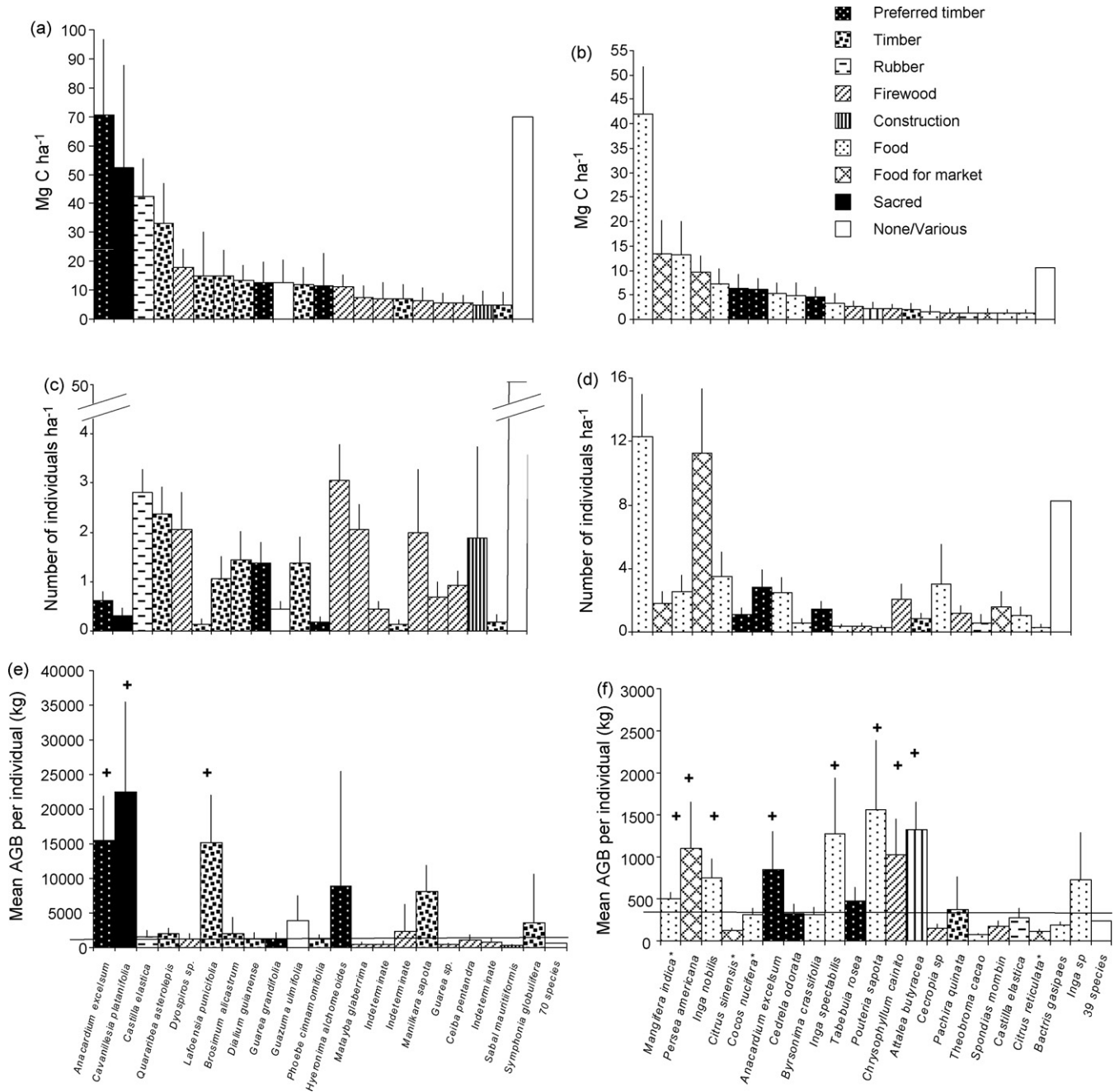


Fig. 3. Top panels (a) and (b) show average contribution of species (trees, palms and lianas ≥ 10 cm DBH) to carbon stocks per hectare across forest and agroforest sites (\pm I.S.E.). Only contributions from the 21 top-ranked species are shown in each land-use type; contributions from remaining species are grouped in the right-most bar on each graph. Middle panels (c) and (d) show the average number of individuals per hectare of each of the 21 species in each land-use type, again averaged across sites (\pm I.S.E.). The bottom panels (e) and (f) show the average biomass per individual of each of the 21 species in each land-use type, with 95% confidence intervals. The horizontal line in these two figures shows the average biomass of individuals from all species in that land-use type. A ‘+’ above a bar indicates that, for that species, the average biomass per individual differs significantly from the average biomass of individuals of all species in that land-use type. Finally, the dominant use for each species is indicated by the fill pattern, and species exotic to the Neotropics are indicated by a ‘*’.

harvested in the future. Forest owners reported having sold wood from six species: espave, zapatero (*Heyeronia alchorneoides*), cedro macho (*Guarea grandifolia*), cedro amargo (*Cedrela odorata*), quira (*Platymiscium pinnatum*), and roble (*Tabebuia rosea*). In addition to espave, which was the first ranked species in terms of average C storage per hectare in forests, zapatero and cedro macho were also among the top-

ranked C-storing forest species (Fig. 3a). Together these three species represented only 3.2% of individuals in our inventory but stored an average of 21.6% of the C in the forest sites.

In agroforests, three of the ‘preferred timber’ species (*A. excelsum*, *C. odorata*, and *T. rosea*) and two other timber species, cedro espino (*Pachira quinata*) and teak (*Tectona grandis*), which were never encountered in forest plots, were

being grown for future harvest (Fig. 3b). Interestingly, espave was again a ‘disproportionate contributor’ to C storage, with significantly higher-than-average per capita biomass. Although we focus on preferred timber species here as we feel the economic value of these species makes them particularly vulnerable to logging, demand for tree species used in construction and for firewood would also be expected to increase with population growth in the TC.

We were also interested in the contributions to C storage of agroforest species from which agroforest owners reported harvesting some fruit for resale, as these might represent species with multiple livelihood benefits if used in reforestation projects for C storage. Avocado (*Persea americana*), orange (*Citrus sinensis*) and mandarin (*Citrus reticulata*) were all top-ranked C-storers from which fruits were sold on local markets; these species stored an average of 16.9% of the C stored per ha in agroforests and represented 24.5% of agroforest individuals (Fig. 3d–f).

4. Discussion

4.1. C storage and biodiversity

Experimental studies looking at diversity–function relationships have only recently been initiated in forest ecosystems and have yet to produce results (Scherer-Lorenzen et al., 2005; Vilà et al., 2005). In the meantime, analyses of forest inventory data have produced conflicting support for diversity–function relationships in forests, showing either a positive relationship between diversity and productivity (Caspersen and Pacala, 2001), no relationship (Enquist and Niklas, 2001), or a positive or negative relationship depending on the identity of the dominant species in a mixed-species stand (Frivold and Frank, 2002).

While the majority of such observational studies have focused on relationships between tree-species diversity and productivity (growth), our analyses explore relationships between diversity and biomass storage. Understanding these relationships will be particularly important in attempts to maintain the C stocks of forests over the long term. We hypothesized that the same mechanisms that have been proposed for increased growth in more diverse stands (i.e., more complete use of resources; disproportionate contributions by functionally important species) could also lead to greater storage of biomass in forest stands over the long-term.

We were unable to find any evidence for a relationship between tree-species diversity and above-ground carbon stocks at our sites, and therefore no support for a niche-complementarity hypothesis (Table 3). However, our work underlined the disproportionate contribution of a small number of species to stand-level carbon stocks. Although differences in the functional traits of tree species (such as average DBH, wood density, and life span) are a well-known principle of community ecology (e.g., Körner, 2005), the magnitude of the effect of such differences on stand-level carbon storage is rarely emphasized in the context of C-sink initiatives (but see Balvanera et al., 2005; Bunker et al., 2005).

We also did not find evidence for a relationship between tree-species diversity and the percent carbon content of either the 0–10 cm or 30–40 cm layer of the soil (Table 3). A number of mechanisms have been proposed by which tree-species diversity could influence the storage of C in soils. These include effects of tree-species on water availability, litter quantity and quality, the amount and composition of root exudates, and the distribution of C in the soil profile (Grayston et al., 1997; Rothe and Binkley, 2001; Gleixner et al., 2005; Hättenschwiler, 2005). The absence of a relationship between diversity and SOC within land-use types may reflect the high variability of soils in this landscape; we observed significant variability among soil samples from a single site, suggesting that future attempts to link tree-species diversity to soil C in this landscape should sample soils more intensively.

4.2. The potential for forest conservation-based C-sink activities

In Ipetí-Emberá, protecting forests from further clearing (“avoided deforestation” as it is referred to in international policy debates; UNFCCC, 2005) would have the largest impact on landscape-level C stocks: forests store 57% more C per hectare than agroforests and 86% more than pastures. This is particularly interesting given that the forests we surveyed would be considered “non-intact” *sensu* Achard et al. (2005) as they are actively managed by community members for timber and non-timber forest products. Although selective logging removes only a limited number of desirable trees from a forest leaving an intact, but ‘thinned’, forest canopy, previous studies have shown that this practice can have a large negative impact on forest C stocks (Putz and Pinard, 1993; Pinard and Cropper, 2000; Asner et al., 2005). For example, Putz and Pinard (1993) estimated that conventional selective logging in Sabah, Malaysia, reduced the C stocks of unlogged forests by one-third. Similarly, Asner et al. (2005) showed that estimates of anthropogenic emissions of C from the Brazilian Amazon increased by 25% when selective harvesting was included in the estimate.

Our estimates of the C stocks of the forests of Ipetí-Emberá, where selective logging by community members takes place at low intensities, are comparable with those for protected forests in the floristically similar Panama Canal Watershed (PCW) (Heckadon-Moreno et al., 1999; Gonzalez, 2000 in Dale et al., 2003; Chave et al., 2004). For example, Chave et al. (2004) estimated that late-secondary and primary forests in the PCW store 251.7 Mg C ha⁻¹ above ground in trees ≥1 cm DBH. Using the same model as Chave et al. (2004; Appendix A), the forests of the TC store 343.3 Mg C ha⁻¹ above ground in trees ≥1 cm DBH. Our higher estimate, which is within one standard deviation of that of Chave et al. (2004), seems to be explained by the higher density of large trees in our study area. This in turn may reflect the land-use histories of the two areas: Ipetí-Emberá was settled relatively recently in the 20th century, while the PCW was managed for agriculture until 1914, when land use was restricted and forests were left to regrow for the protection of the canal (McKay, 1984; Condit et al., 2001).

We did not detect an effect of selective logging on forest C stocks in Ipetí-Emberá at present: sites closer to the village, which were more likely to be selectively logged, did not have lower tree AGB than did sites farther from the village. However, two lines of evidence suggest that the intensity of selective logging may increase in the future. First, in a participatory exercise that was carried out at the same time as our study, community members predicted that without a carbon project or other external source of financing participation in logging would rise from the current level of 40% of households to 100% of households by 2020 (Potvin et al., 2006). Second, our analyses indicate that forest owners were more likely to have harvested timber from their landholding if the landholding was closer to the village. As of 2003, the construction of a road that would cut through the TC to provide communities beyond it with access to the Pan-American Highway was planned. This road would make forest landholdings that are currently a 2 h walk from the village much more accessible.

Our findings also suggest that a scenario of increased selective logging could lead to C-impooverished forests because of preferences for timber species that are disproportionately important C-storers. The impact on C-stocks of biased selective logging has recently been explored by two simulation studies (Balvanera et al., 2005; Bunker et al., 2005). The findings of both studies emphasize that the key to accurately predicting the impact of selective logging on C storage lies in the highly unequal contribution of species to C storage.

The type of analysis that we report here could allow managers to prioritize species for management using (1) species' overall contribution to C storage in the landscape; (2) their relative abundance; and (3) their per capita contribution to C storage (Fig. 3a–f). For example, in forests, espave, cuipo and amarillo pepita (*Lafoensia punicifolia*) store significantly more C per individual than other top-ranked contributors (Fig. 3e). Removing or conserving these individuals in the landscape will therefore have important effects on overall C stocks. A future extension of our work will be to incorporate species-specific lifespans and growth rates into estimates of the contributions of individual species to long-term C storage, allowing sustainable harvesting levels to be determined directly. Unfortunately, such data are unavailable for many tropical tree species. Information on the longevity of wood products would also allow for a more complete analysis of the effects of harvesting on atmospheric C concentrations.

A novel finding of our study surrounds the potential for species-specific cultural taboos to have a large impact on the C stocks of a landscape. *Cavanillesia platanifolia*, or cuipo, was the second most important species in terms of its contributions to C stocks per hectare in this landscape (Fig. 3a). In Ipetí-Emberá, cuipo is considered to be a sacred species and is not harvested for wood nor is it felled when forest is being cleared for agriculture (C. Potvin, unpublished data). The conservation literature has paid attention to the role of taboo and sacred sites in protecting biological diversity (e.g., Ramakrishnan, 1996; Colding and Folke, 2001; Potvin et al., 2002; Xu et al., 2005). In this case, a species-specific taboo might be instrumental in helping to maintain C stocks in the landscape.

4.3. Reforestation for long-term C storage

In contrast to “avoided deforestation,” reforestation is already approved as an eligible Land use, Land-use Change, Forestry and Agriculture (LUCF) activity under the CDM (UNFCCC, 1997). We estimated that the agroforests of Ipetí-Emberá, which could be eligible as a reforestation activity under the CDM if they were established on pastures or other previously cleared areas, store an average of 145 Mg C ha⁻¹ (Table 2). This is higher than the median estimate of 95 Mg C ha⁻¹ for agroforestry systems worldwide (including any agricultural land-use system in which trees are deliberately retained or where trees are introduced with agricultural crops, pastures, or livestock) and well above the range of 39–102 Mg C ha⁻¹ for agroforestry systems in tropical America (Albrecht and Kandji, 2003). When we recalculate tree AGB using the allometric model of Brown (1997) and considering SOC to only 30 cm depth, the values for Ipetí are very similar to those of Roshetko et al. (2002) for homegardens of small-scale farmers in Indonesia that were comprised of a similarly diverse mix of fruit and timber tree species (116.5 Mg C ha⁻¹ (ours) versus 107 Mg C ha⁻¹ (theirs); see Appendix A and Table 2 for calculation).

Although we do not have information on species growth rates and therefore cannot recommend species for reforestation based on the rate at which they would be expected to sequester carbon, our data do allow us to identify tree species that store a disproportionate amount of carbon in agroforests approximately 23 years after establishment. Until species-specific growth rates are available, managers might decide to use this information to select species for long-term reforestation projects. Four examples of such species, each of which also provides livelihood benefits in the form of fruit for home consumption or for resale, are mango, avocado, guaba (*Inga spectabilis*) and mamey (*Pouteria sapota*) (Fig. 3f).

We also compared the C storage potential of agroforests with that of plantations of teak, which is the most common form of reforestation in Panama (Kraenzel et al., 2003). The C stocks of harvest-age (20-year old) teak plantations are 120.2 Mg C ha⁻¹ (including trees ≥10 cm DBH and their roots; Kraenzel et al., 2003). This is comparable to the 89.2 Mg C ha⁻¹ stored in trees ≥10 cm DBH (including roots) in the agroforests we inventoried which were 23 years of age, on average (see Appendix A and Table 2 for calculation). A key difference between the agroforests we surveyed and the harvest-age teak plantations is that 89.1% of the agroforest individuals (representing 85.9% of C stored per hectare) were non-timber species and therefore would be expected to continue storing C until they senesce. Our interviews confirmed that landowners add trees to agroforests through time. As a result, C that is lost from senescing trees should be offset by C sequestered by individuals that are planted in anticipation of the older trees' senescence. This active management should thus allow mature agroforests to maintain their C stocks through time. In contrast, teak plantations are completely cleared when they are harvested and the mean carbon storage of teak plantations over multiple rotations is therefore substantially lower than the C stored in a

harvest-age teak stand (72 Mg C ha^{-1} compared to $120.2 \text{ Mg C ha}^{-1}$; Kraenzel et al., 2003). This average will be slightly higher if the final wood products are long-lived.

Therefore, aroforests would seem to provide an attractive alternative to teak plantations: they sequester a comparable amount of C and provide advantages from a biodiversity conservation perspective. A further benefit of agroforestry-based reforestation is that it represents a traditional Emberá land use (Covich and Nickerson, 1966; De Arauz, 1970) and could therefore be developed and implemented using local expertise (De Jong et al., 1995).

5. Conclusions

As in many agricultural frontiers, measures will have to be taken if forest-based C stocks are to be maintained in the landscape of the *tierra colectiva* of Ipetí-Emberá. Our study suggests that protecting forests from conversion to pasture would have the greatest impact on landscape-level C stocks, even though the forests are managed by community members for timber and non-timber forest products. There is a positive correlation between biodiversity and C storage across land use types in Ipetí-Emberá, emphasizing the potential for a single project to optimize both C storage and biodiversity conservation. We found no evidence for a positive relationship between tree-species diversity and above-ground biomass or soil carbon in either forests or agroforests. However, our results highlight the disproportionate contribution of a small number of species to stand-level carbon stocks. In turn, this finding suggests that the future intensification of selective logging that is biased towards tree species with high C-storage potential could lead to C impoverishment of these forests. To counter this, we propose species-based management of timber extraction activities.

In terms of reforestation, our data indicate that the agroforestry systems of Ipetí-Emberá could rival monoculture teak plantations in terms of long-term C storage while providing biodiversity benefits that the teak plantations do not. Additional information on species-specific growth rates and life spans, which are currently unavailable for many tropical tree species, would allow species-level management in both forest conservation and reforestation projects to be optimized. In the meantime, managers of C-sink projects will have to adopt an adaptive management approach, combining inventory data with information on species-specific uses and harvest levels to maintain or maximize C in managed systems over the long-term.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2007.03.072.

References

- Achard, F., Belward, A.S., Eva, H.D., Federucu, S., Mollicone, D., Raes, F., 2005. Accounting for avoided deforestation of intact and non-intact forests. Technical options and a proposal for a policy tool. European Commission, Joint Research Center. UNFCCC COP 11, side event.
- Albrecht, A., Kandji, S.T., 2003. Carbon sequestration in tropical agroforestry systems. *Agric. Ecosyst. Environ.* 99, 15–27.
- Asner, G.P., Knapp, D.E., Broadbent, E.N., Oliveira, P.J.C., Keller, M., Silva, J.N., 2005. Selective logging in the Brazilian Amazon. *Science* 310, 480–482.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patino, S., Pitman, N.C.A., Silva, J.N.M., Vasquez Martinez, R., 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biol.* 10, 1–18.
- Ball, D.F., 1964. Loss-on-ignition as an estimate of organic matter and organic carbon in non-calcareous soils. *J. Soil Sci.* 15, 84–92.
- Balvanera, P., Kremen, C., Martinez-Ramos, M., 2005. Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. *Ecol. Appl.* 15 (1), 360–375.
- Bloomfield, J., Pearson, H., 2000. Land use, land-use change, forestry and agricultural activities in the clean development mechanism: estimates of greenhouse gas offset potential. *Mitig. Adapt. Strat. Global Change* 5, 9–24.
- Brown, S., 1997. Estimating Biomass and Biomass Change of Tropical Forests, vol. 134. Forest Resources Assessment Publication, Forestry Papers, FAO Rome, 55 pp.
- Brown, S., 2002. Measuring, monitoring, and verification of carbon benefits for forest-based projects. *Phil. Trans. Roy. Soc. Lond. A* 360, 1669–1683.
- Brown, J.K., Roussopoulos, P.J., 1974. Eliminating biases in the planar intersect method for estimating volumes of small fuels. *Forest Sci.* 20, 350–356.
- Brown, S., Schroeder, P., Birdsey, R., 1997. Above-ground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. *Forest Ecol. Manage.* 96, 37–47.
- Bunker, D.E., DeClerk, F., Bradford, J.C., Colwell, R.K., Perfecto, Y., Phillips, O.L., Sankaran, M., Naeem, S., 2005. Species loss and above-ground carbon storage in a tropical forest. *Science* 310, 1029–1031.
- Cairns, M.A., Brown, S., Helmer, E.H., Baumgardner, G.A., 1997. Root biomass allocation in the world's upland forests. *Oecologia* 111, 1–11.
- Caspersen, J.P., Pacala, S.W., 2001. Successional diversity and forest ecosystem function. *Ecol. Res.* 16, 895–903.
- CBD (Convention on Biological Diversity), 2006. Global Biodiversity Outlook 2. Available at: www.biodiv.org/GBO2.
- Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B., Hubbell, S.P., 2003. Spatial and temporal variation of biomass. *J. Ecol.* 91, 240–252.

- Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S., Perez, R., 2004. Error propagation and scaling for tropical forest biomass estimates. *Phil. Trans. Roy. Soc. Lond. B* 359, 409–420.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145, 87–99.
- Clark, D.B., Clark, D.A., Brown, S., Oberbauer, S.F., Veldkamp, E., 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. *Forest Ecol. Manage.* 164, 237–248.
- Colding, J., Folke, C., 2001. Social taboos: “invisible” systems of local resource management and biological conservation. *Ecol. Appl.* 11, 584–600.
- Condit, R., 1998. *Tropical Forest Census Plots*. Springer-Verlag, Berlin.
- Condit, R., Robinson, W.D., Ibáñez, R., Aguilar, S., Sanjurjo, A., Martínez, R., Stallard, R.F., García, T., Angehr, G.R., Petit, L., Wright, S.J., Robinson, T.R., Heckadon, S., 2001. The status of the Panama Canal Watershed and its biodiversity at the beginning of the 21st century. *Bioscience* 51, 389–398.
- Covich, A.P., Nickerson, N.H., 1966. Studies of cultivated plants in Choco dwelling clearings, Darien, Panama. *Econ. Bot.* 20, 285–301.
- CTFS (Center for Tropical Forest Science), 2004. *Tree Atlas of the Panama Canal Watershed*. Available at: <http://ctfs.si.edu/webatlas/maintreeatlas.html>. Accessed August 2003–August 2004.
- Dale, V.H., Brown, S., Calderon, M.O., Montoya, A., Martinez, R.E., 2003. Estimating baseline carbon emissions for the eastern Panama Canal watershed. *Mitig. Adapt. Strat. Global Change* 8, 248–323.
- Dalle, S.P., Potvin, C., 2004. Conservation of useful plants: an evaluation of local priorities from two indigenous communities in eastern Panama. *Econ. Bot.* 58, 38–57.
- Dames and Moore, 2001. *Programa de Desarrollo Sostenible de Darién: Estrategia de Ordenamiento Territorial y Protección de la Calidad Ambiental, Volumen 2*. Dames and Moore Group Company, Panama City, Panama, 200+.
- De Arauz, R.T., 1970. Human ecology of Route 17 (Sasarti-Morti) Region, Darien, Panama. 172 pp.
- De Jong, B., Montoya-Gomez, G., Nelson, K., Soto-Pinto, L., Taylor, J., Tipper, R., 1995. Community forest management and carbon sequestration: a feasibility study from Chiapas, Mexico. *Interciencia* 20, 409–416.
- Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A., Quintero, N.B., 1998. The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. *Biotropica* 30, 2–11.
- Duke, J.A., Porter, D.M., 1970. *Darien Phytosociological Dictionary*. Bioenvironmental and Radiological-safety Feasibility Studies of the Atlantic-Pacific Interoceanic Canal. Battelle Memorial Institute, Columbus, 70 pp.
- Elias, M., Potvin, C., 2003. Assessing inter- and intra-specific variation in trunk carbon concentration for 32 neotropical tree species. *Can. J. Forest Res.* 33, 1039–1045.
- Enquist, B.J., Niklas, K.J., 2001. Invariant scaling relations across tree-dominated communities. *Nature* 410, 655–660.
- Fearnside, P.M., 1997. Wood density for estimating forest biomass in Brazilian Amazonia. *Forest Ecol. Manage.* 90, 59–87.
- Frivold, L.H., Frank, J., 2002. Growth of mixed birch-coniferous stands in relation to pure coniferous stands at similar sites in south-eastern Norway. *Scand. J. Forest Res.* 17, 139–149.
- Fujisaka, S., Castilla, C., Escobar, G., Rodrigues, V., Veneklaas, E.J., Thomas, R., Fisher, M., 1998. The effects of forest conversion on annual crops and pastures: estimates of carbon emissions and plant species loss in a Brazilian Amazon colony. *Agric. Ecosyst. Environ.* 69, 17–26.
- Gleixner, G., Kramer, C., Hahn, V., Sachse, D., 2005. The effect of biodiversity on carbon storage in soils. In: Scherer-Lorenzen, M., Körner, Ch., Schulze, E.-D. (Eds.), *Forest Diversity and Function*. Temperate and Boreal Systems. Ecological Studies, vol. 176. Springer, Berlin, Heidelberg, New York, pp. 347–376.
- Gonzalez, F.M., 2000. Comparación de la Capacidad de Fijación de Dióxido de Carbono en los Bosques de los Parques Soberanía, Chagras y Camino de Cruces. Tesis de Maestro en Ciencias Ambientales, Programa de Maestría en Ciencias Ambientales Opción: Gestión Ambiental, Universidad de Panamá, Republica de Panamá.
- Graça, P.M.L.A., Fearnside, P.M., Cerri, C.C., 1999. Burning of Amazonian forest in Ariquemes, Rondônia, Brazil: biomass, charcoal formation and burning efficiency. *Forest Ecol. Manage.* 120, 179–191.
- Grayston, S.J., Vaughan, D., Jones, D., 1997. Rhizosphere carbon flow in trees, in comparison with annual plants—the importance of root exudation and its impact on microbial activity and nutrient availability. *Appl. Soil Ecol.* 5, 29–56.
- Hardner, J.J., Frumhoff, P.C., Goetze, D.C., 2000. Prospects for mitigating carbon, conserving biodiversity, and promoting socioeconomic development objectives through the clean development mechanism. *Mitig. Adapt. Strat. Global Change* 5, 61–80.
- Hättenschwiler, S., 2005. Effects of tree species diversity on litter quality and decomposition. In: Scherer-Lorenzen, M., Körner, Ch., Schulze, E.-D. (Eds.), *Forest Diversity and Function*. Temperate and Boreal Systems. Ecological Studies, vol. 176. Springer, Berlin, Heidelberg, New York, pp. 347–376.
- Heckadon-Moreno, R., Ibanez, D., Condit, R., 1999. La cuenca del Canal: Deforestacion, urbanizacion y contaminacion. USAID, Smithsonian, ANAM.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123–1127.
- Hooper, D.U., Vitousek, P.M., 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277, 1302–1305.
- Houghton, R.A., 2005. Aboveground forest biomass and the global carbon balance. *Global Change Biol.* 11, 945–958.
- Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* 80, 1892–1907.
- Instituto Geográfico Nacional, 1988. *Atlas Nacional de la Republica de Panamá*. Instituto Geográfico Nacional Tommy Guardia, Panama.
- IPCC (Intergovernmental Panel on Climate Change), 2001. *Climate Change 2001: The Scientific Basis*. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.
- Jobbagy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.* 10, 423–436.
- Körner, Ch., 2005. An introduction to the functional diversity of temperate forest trees. In: Scherer-Lorenzen, M., Körner, Ch., Schulze, E.-D. (Eds.), *Forest Diversity and Function*. Temperate and Boreal Systems. Ecological Studies, vol. 176. Springer, Berlin, Heidelberg, New York, pp. 347–376.
- Kotto-Same, J., Wooster, P.L., Appolinaire, M., Zapfack, L., 1997. Carbon dynamics in slash-and-burn agriculture and land use alternatives of the humid forest zone in Cameroon. *Agric. Ecosyst. Environ.* 65, 245–256.
- Koziell, I., Swingland, I.R., 2002. Collateral biodiversity benefits associated with ‘free-market’ approaches to sustainable land use and forestry activities. In: Swingland, I.R. (Ed.), *Capturing Carbon and Conserving Biodiversity: The Market Approach*. Earthscan, London, 368 pp.
- Kraenzel, M.B., Moore, T., Castillo, A., Potvin, C., 2003. Carbon storage of harvest-age teak (*Tectona grandis*) plantations, Panama. *Forest Ecol. Manage.* 173, 213–225.
- Krebs, C., 1999. *Ecological Methodology*, 2nd ed. Benjamin Cummings for Addison Wesley Longman Inc., Menlo Park, CA, 620 pp.
- Leader-Williams, N., 2002. Animal conservation, carbon and sustainability. In: Swingland, I.R. (Ed.), *Capturing Carbon and Conserving Biodiversity: The Market Approach*. Earthscan, London, 368 pp.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*, 2nd English ed., Developments in Environmental Modelling, vol. 20. Elsevier Science, Amsterdam, Netherlands.
- Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72–76.

- Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Di Fiore, A., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Nunez, V., Patiño, P., Pitman, S., Quesada, N.C.A., Silva, C.A., Lezama, J.N.M., Vasques Martinez, A.T., Terborgh, R., Vinceti, J., Lloyd, B.J., 2004. The above-ground coarse wood productivity of 104 neotropical forest plots. *Global Change Biol.* 10, 563–591.
- McKay, A., 1984. Colonización de tierras nuevas en Panamá (1975). In: Heckadon-Moreno, S., McKay, A. (Eds.), *Colonización y destrucción de bosques en Panamá*. Asociación Panameña de Antropología, pp. 45–62.
- MEA (Millennium Ecosystem Assessment), 2005. www.millenniumassessment.org.
- Muller-Landau, H.C., 2004. Interspecific and inter-site variation in wood-specific gravity of tropical trees. *Biotropica* 36, 20–32.
- Nascimento, H.E.M., Laurance, W.F., 2002. Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. *Forest Ecol. Manage.* 68, 311–321.
- Nelson, D.W., Sommers, L.E., 1982. Total carbon, organic carbon and organic matter. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties*. ASA Monograph Number 9, pp. 539–579.
- Pinard, M.A., Cropper, W.P., 2000. Simulated effects of logging on carbon storage in dipterocarp forest. *J. Appl. Ecol.* 37, 267–283.
- Potvin, C., Patenaude, G., O'Badaki, K., Hutton, J., Revérét, J.-P., 2002. Implementation of article 8j of the convention of biological diversity: cultural differences, and conservation priorities. In: Le Prestre, P. (Ed.), *Governing Global Biodiversity: The Evolution and Implementation of the CBD*. Ashgate Pub., UK, pp. 159–176.
- Potvin, C., Tschakert, P., Lebel, F., Kirby, K., Barrios, H., Bocariza, J., Caisamo, J., Caisama, L., Cansari, C., Casamá, J., Casamá, N., Chamorra, L., Dumasa, N., Goldenberg, S., Guainora, V., Hayes, P., Moore, T., Ruíz, J., 2006. A participatory approach to the establishment of a baseline scenario for a reforestation CDM project. *Mitig. Adapt. Strat. Global Change*. doi:10.1007/s11027-006-9056-3.
- Putz, F.E., 1983. Liana biomass and leaf area of a “tierra firme” forest in Rio Negro Basin, Venezuela. *Biotropica* 15, 185–189.
- Putz, F.E., Pinard, M., 1993. Reduced impact logging as a carbon offset method. *Conserv. Biol.* 7, 755–757.
- Ramakrishnan, P.S., 1996. Conserving the sacred: from species to landscapes. *Nat. Resour.* 32, 11–19.
- Roshetko, J.M., Delaney, M., Hairiah, K., Purnomosidhi, P., 2002. Carbon stocks in Indonesian homestead systems: can smallholder systems be targeted for increased carbon storage? *Am. J. Altern. Agric.* 7, 1–11.
- Rothe, A., Binkley, D., 2001. Nutritional interactions in mixed species forests: a synthesis. *Can. J. Forest Res.* 31, 1855–1870.
- Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Scherer-Lorenzen, M., Potvin, C., Koricheva, J., Schmid, B., Hector, A., Bornik, Z., Reynolds, G., Schulze, E.D., 2005. The design of experimental tree plantations for functional 834 biodiversity research. In: Scherer-Lorenzen, M., Körner, Ch., Schulze, E.-D. (Eds.), *Forest Diversity and Function. Temperate and Boreal Systems*. Ecological Studies, vol. 176. Springer, Berlin, Heidelberg, New York, pp. 347–376.
- Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., van Mantgem, P.J., 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* 122, 297–305.
- Smith, J., Scherr, S.J., 2003. Capturing the value of forest carbon for local livelihoods. *World Dev.* 31, 2143–2160.
- Spehn, E.M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E., Beirkuhnlein, C., Caldeira, M.C., Diemers, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Jumpponen, A., Koricheva, J., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Palmberg, C., Pereira, J.S., Pfisterer, A.B., Prinz, A., Read, D.J., Schulze, E.-D., Siamantziouras, A.-S.D., Terry, A.C., Troumbis, A.Y., Woodward, E.I., Yachi, S.Y., Lawton, J.H., 2005. Ecosystem effects of biodiversity manipulations in European grasslands. *Ecol. Monogr.* 75, 37–63.
- Srivastava, D., Vellend, M., 2005. Biodiversity-ecosystem function research: is it relevant to conservation? *Annu. Rev. Ecol. Evol. Syst.* 36, 267–294.
- Stewart, R., 1966. *The Rio Bayano Basin: A Geological Report*. Panama Canal Company, Canal Zone, 16 pp.
- Swingland, I.R. (Ed.), 2002. *Capturing Carbon and Conserving Biodiversity: The Market Approach*. Earthscan, London, 368 pp.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Barend, F., Erasmus, N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379, 718–720.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in the long-term grassland experiment. *Science* 294, 843–845.
- Tschakert, P., Coomes, O., Potvin, C., 2007. Indigenous livelihoods, slash-and-burn agriculture and carbon stocks in Eastern Panama. *Ecol. Econ.* 60, 807–820.
- UNEP (United Nations Environment Programme), 1992. *Convention on Biological Diversity*. United Nations Environment Programme, Nairobi, Kenya Available at <http://www.biodiv.org/convention/default.shtml>.
- UNFCCC (United Nations Framework Convention on Climate Change), 1992. *United Nations Framework Convention on Climate Change*, Geneva, UNEP/WMO. Available at <http://www.unfccc.int/>.
- UNFCCC (United Nations Framework Convention on Climate Change), Conference of the Parties, Third Session, 1997. *Kyoto Protocol to the United Nations Framework Convention on Climate Change*. FCCC/CP/1997/7/Add.1. Available at: <http://www.unfccc.int/>.
- UNFCCC (United Nations Framework Convention on Climate Change). Conference of the Parties, Eleventh Session, 2005. *FCCC/CP/2005/L.2* Available at: <http://cdm.unfccc.int/>.
- Van Wagner, C.E., 1968. The line-intersect method in forest fuel sampling. *Forest Sci.* 14, 20–26.
- Vilà, M., Inchausti, P., Vayreda, J., Barrantes, O., Gracia, C., Ibáñez, J.J., Mata, T., 2005. Confounding factors in the observed productivity-diversity relationship in forests. In: Scherer-Lorenzen, M., Körner, Ch., Schulze, E.-D. (Eds.), *Forest Diversity and Function. Temperate and Boreal Systems*. Ecological Studies, vol. 176. Springer, Berlin, Heidelberg, New York, pp. 347–376.
- Wali, A., 1993. The transformation of a frontier: state and regional relationships in Panama 1972–1990. *Hum. Organ.* 52, 109–123.
- World Bank, 2002. *Biocarbon Fund*. Home page. www.biocarbonfund.org. Accessed January 2006.
- Xu, J., Ma, E.T., Tashi, D., Fu, Y., Lu, Z., Melick, D., 2005. Integrating sacred knowledge for conservation: cultures and landscapes in southwest China. *Ecol. Soc.* 10 7. [online] URL: <http://www.ecologyandsociety.org/vol10/iss2/art7/>
- Zar, J.H., 1998. *Biostatistical Analysis*, 4th ed. Prentice Hall, 929 pp.