A self-perpetuating bamboo disturbance cycle in a neotropical forest

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Abstract: We investigate a hypothesis for explaining maintenance of forest canopy dominance: bamboo (*Guadua weberbaueri* and *Guadua sarcocarpa*) loads and crushes trees, resulting in a self-perpetuating disturbance cycle. Forest inventory data revealed a peculiar pattern of tree form and size class distribution in bamboo-dominated plots within the Tambopata River watershed, Madre de Dios, Peru. Bamboo disproportionately loaded trees 5–29 cm in diameter, and this size class had over seven times more canopy damage than trees in control plots without bamboo. These differences were accompanied by reduced tree basal area and tree density in the 5–29-cm-diameter size class in the presence of bamboo. Elevated tree canopy damage was not apparent for trees ≥ 30 cm dbh, which are beyond the reach of bamboo. Additional evidence for the impact of bamboo was revealed by an experiment using artificial metal trees. Artificial trees in bamboo-dominated forest plots had nine times higher frequency of physical damage and nine times more plant mass loading as compared with control plots. Our results support the hypothesis that bamboo loading causes elevated physical damage to trees and suppresses tree recruitment, particularly for trees 5–29 cm in diameter.

Key Words: clonal growth, community ecology, competition, disturbance, *Guadua*, Peru, succession

INTRODUCTION

In south-western Amazonia, an area of approximately 180 000 km^2 has been classified as bamboo-dominated forest from remote-sensing analysis (Nelson 1994) representing the largest neotropical bamboo-dominated forest formation. The two most common dominant bamboo species in this formation, *Guadua sarcocarpa* Londoño & P.M. Peterson and *Guadua weberbaueri* Pilger (hereafter also referred to as bamboo), are endemic to northern and western Amazonia (Judziewicz *et al.* 1999) and grow to over 20 m in height. Unlike most bamboo species, *G. sarcocarpa* and *G. weberbaueri* depend upon adjacent trees for vertical growth beyond about 10 m in height, employing recurved thorns to climb trees. The widespread occurrence of bamboo dominance on terra firme sites in this region has perplexed scientists because lush tree-dominated forests are usually widespread on such sites in lowland moist tropical eco-regions (Bailey 1989, Judziewicz *et al.* 1999, Whitmore 1998).

Catastrophic disturbance has been proposed as an explanation for bamboo mono-dominance. Balée (1989)

observed that bamboo forests (*Guadua glomerata* Munro) are associated with past horticultural activities by the Ka'apor and Guajajara indigenous groups of eastern Amazonia. Evans & Meggers (1960) reported that Taruma Indians of Guyana planted a stand of bamboo or cane. Balée invokes these observations to support Sombroek's claim that bamboo forests are anthropogenic in the Brazilian Amazon basin (Balée 1989, Sombroek 1966). We have observed that bamboo (*Guadua sarcocarpa* and *Guadua weberbaueri*) invades some modern swidden-fallow sites in south-western Amazonia (Madre de Dios, Peru; Pando, Bolivia; and Acre, Brazil). We suspect, however, that a large proportion of bamboo-dominated forests in south-western Amazonia are not anthropogenic in origin.

Anthropogenic Amazonian *terra preta* soil formations tend to occur at the scale of a few hectares (Whitmore 1998), while these bamboo-dominated forests of south-western Amazonia occur both as patches of a few hectares and at scales of 100 to 10 000 km^2 (Nelson *et al.* 2001). A number of authors, reviewed by Denevan (1996) and Lima *et al.* (2002), report that historically human indigenous settlements in Amazonia were more concentrated in floodplains and adjacent bluffs than in the interior of terra-firme plateaux. In contrast, we have observed that bamboo-dominated forests of

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south-western Amazonia are frequently more widespread on terra-firme plateaux than in the floodplains. At a local scale, we have identified an association between bamboo dominance (*Guadua* spp.) and poorly drained soils with more stressful hydrologic regimes that do not appear preferable for agricultural activities (Griscom 2003). Furthermore, none of the 'mature' bamboo-dominated stands or control stands without bamboo sampled by Griscom (2003) with soil pits (n = 12), soil auger holes (n = 24), and soil cores (n = 300) revealed evidence of *terra preta* anthropogenic soils or other signs of indigenous activity (e.g. pot shards, metates, plough lines, megalithic structures). *Terra preta* soils are characterized by elevated soil carbon and soil fertility, and particularly high phosphorus content in the A horizon (Lima *et al.* 2002). Griscom (2003) found that A-horizon soil in mature terra-firme bamboo-dominated stands, as compared with control stands without bamboo, had significantly lower mean cation exchange capacity (CEC), and no significant difference in per cent carbon or extractable phosphorus. Silman *et al.* (2003) also found no signs of anthropogenic soils associated with bamboo-dominated stands.

Two natural (i.e. non-anthropogenic) causes of bamboo-dominance in forest systems have been discussed in the literature: (1) bamboo exploitation of catastrophic natural disturbances (Choudhury 1986, Henkel 1927, Horn 1989, Keeley & Bond 1999, Platt & Brantley 1997, Rao & Saxena 1995, Stern 1995), and (2) bamboo exploitation of tree-fall gaps, and persistence by suppressing tree recruitment (Gonzàles *et al.* 2002, Griscom & Ashton 2003, Lusk 2001, Nelson *et al.* 2001, Oliveira Filho *et al.* 1994, Tanaka 1988, Taylor & Qin 1988, Veblen 1982, 1989; Veblen *et al.* 1981). Both phenomena may act in concert; if bamboo can persist by inhibiting tree recruitment, then smaller-scale and less-intense disturbance could account for extensive, persistent distribution of bamboo-dominated forests.

Nelson (1994) hypothesized that bamboo-dominance in south-western Amazonia may be attributable to a natural form of catastrophic disturbance: large-scale fire events associated with rare El Niño droughts. Bamboo-dominated forests of south-western Amazonia occur, however, in a moist tropical climatic regime with no observed cases of large-scale catastrophic natural fire we are aware of. Nelson *et al.* (2001) have since conjectured that bamboo-dominance may not depend upon such catastrophic disturbance, but may be attributed to bamboo competitive mechanisms resulting in suppression of tree recruitment.

Judziewicz *et al.* (1999), Nelson *et al.* (2001), Griscom & Ashton (2003) and Silman *et al.* (2003) have observed that trees tend to be physically damaged in bamboo-dominated forests of south-western Amazonia, and that physical loading by bamboo may contribute to the cause. Griscom & Ashton (2003) recorded higher mortality of tree saplings in stands dominated by bamboo (*Guadua weberbaueri* and *Guadua sarcocarpa*) suggesting suppressed tree recruitment in bamboo-dominated stands despite higher understorey light levels. Griscom (2003) and Silman *et al.* (2003) also reported physical damage and reduced basal area in larger tree size classes in the presence of high densities of bamboo, and hypothesize that bamboo interference of tree performance due to mass loading may extend over a substantial range of tree size classes.

In this paper, we present new descriptive and experimental data from the study sites described in Griscom & Ashton (2003) and Griscom (2003) to investigate the following concept and hypotheses:

Concept: bamboo physically damages tree canopies by loading them with high densities of large, water-filled bamboo (*Guadua weberbaueri* and *Guadua sarcocarpa*) equipped with recurved thorns functioning as grappling hooks. This phenomenon results in a self-perpetuating bamboo disturbance cycle.

Hypothesis 1: physical damage to trees is higher in bamboo-dominated stands due to loading by bamboo.

Hypothesis 2: bamboo-induced physical damage to trees results in reduced tree density and recruitment.

This study addresses hypothesis 1 with both (1) descriptive data on tree physical damage, tree form, and bamboo loading, for trees of all size classes above 1 m in height, and (2) experimental data on physical damage to artificial trees placed in stands with and without bamboo. Our descriptive and experimental results also inform hypothesis 2.

SITE DESCRIPTION

Two study sites were selected within terra firme tropical moist Amazonian forests of the Tambopata watershed, south-eastern Peru. The bamboo-dominated forests of these sites represent disjunct patches (with distinct geology and soils) to the south of the centre of distribution of this forest type as described by Nelson (1994). Based on a visual analysis of Landsat imagery (from 1980, 1991, 1996 and 2000) and aerial photography (from 1964), as well as informal interviews of local informants, we found no evidence of natural or anthropogenic catastrophic disturbance of the terra-firme forest canopy at our plot locations for the past 40 y. We use the term 'catastrophic disturbance' in reference to a disturbance strong enough to fell the majority of tree basal area over an area substantially larger than that associated with single or multiple tree-fall gaps.

The two study sites will be referred to as 'Bahuaja' (accessed through Bahuaja Lodge camp site) and 'TRC' (accessed through the Tambopata Research Center). The Bahuaja study site is located along the lower section of

the Tambopata River, just above the confluence with La Torre River, 30 km upriver (SSW, towards the Andes) from the city of Puerto Maldonado, Peru. TRC study site is located closer to the foothills of the Andes in the upper reaches of the Tambopata River, 75 km upriver from the city of Puerto Maldonado and 45 km upriver from Bahuaja site. While we do not know the age of bamboo rhizome systems at each site, bamboo culms at both sites had achieved full size, based on our observations of the two bamboo species in the region. We witnessed a gregarious monocarpic mortality event at our TRC study site during 2002, demonstrating that the TRC bamboo population was mature when we collected our data (1999–2001). The soils at each of the two study sites have been classified as either deep, well-drained Ultisols (Ortic Acrisol) or poorly drained Inceptisols (Dystric Gleysol) (ONERN 1972). Bahuaja receives approximately 2000 mm y^{-1} rainfall increasing heading upriver towards the Andes, due to an orographic effect, reaching approximately 3500 mm y^{-1} at TRC site (as interpolated from Johnson 1976). The dry season extends approximately April through September as defined by monthly rainfall *c.* $\leq$ 200 mm for TRC and *c.* $\leq$ 100 mm for Bahuaja.

While average monthly wind velocity is consistently low, at $\sim$ 7–9 km h^{-1} (Johnson 1976), higher velocity wind events causing tree damage have been reported (Forsyth & Miyata 1984, Foster & Terborgh 1998, Ortiz 2002). The only form of natural catastrophic disturbance reported (to our knowledge) for terra firme lowland rain forests of south-eastern Peru are convective downbursts, which can cause flattening of forests over many hectares (Garstang *et al.* 1998). This disturbance phenomenon is reported to be concentrated, however, in predominantly tree-dominated forests from Venezuela in the north to Acre and Rondonia in the south (Garstang *et al.* 1998, Nelson *et al.* 1994).

METHODS

Forest inventory

Twelve inventory plots were established between June 1999 and August 2001, six at TRC site and six at Bahuaja site. Plots were distributed in pairs, each plot of a pair separated by a minimum of 30 m and located on either side of the boundary between a bamboo-dominated forest stand and a forest stand without bamboo (Figure 1). Plots were located in pairs so as to both minimize and facilitate measurement of factors influencing plant growth aside from the presence or absence of bamboo (e.g. topography, drainage, disturbance history and availability of plant propagules). Paired plot sets were located a minimum of 0.5 km from other paired plot sets.

Potential locations of paired plots were limited for logistical reasons to the terra-firme forests within 3 km of each base camp at Bahuaja and TRC sites. A 1996 Landsat TM image was used to randomly select potential paired plot locations perpendicular to the transition zone between bamboo-dominated forest stands and forest stands without bamboo. In order to ensure sufficient contrast between bamboo-dominated and bamboo-free stands, we defined bamboo-dominated stands a priori as having ten or more bamboo culms per 100 m^2, and bamboo-free (control) stands as having zero canopy-occupying bamboo culms. Potential paired plot locations were visited in the field using a GPS device and accepted if stands met the above criterion for bamboo density. Thus, we avoided cases of low densities of bamboo stems within a forest matrix.

Plot locations were composed of three different plot sizes for measurement of different components of the plant community (Figure 1). A linear series of five 10 ×
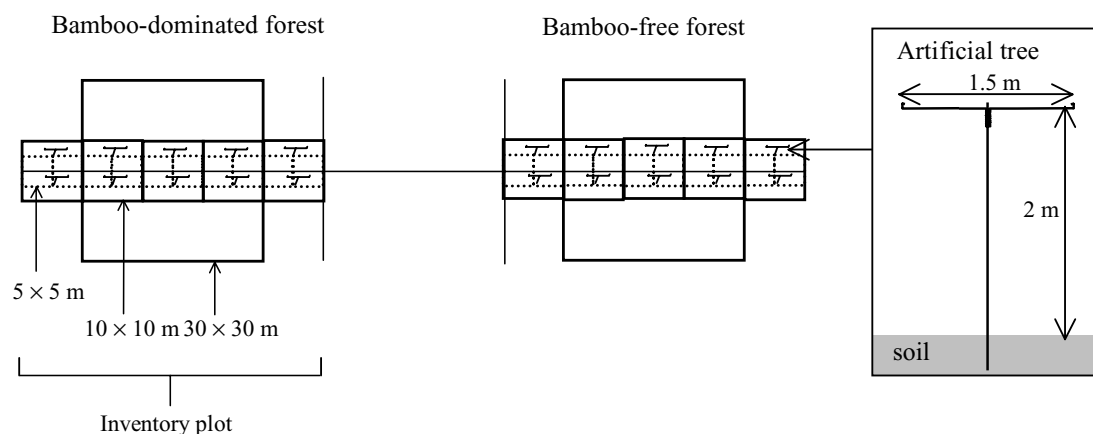

Figure 1. Inventory plots were located in pairs centred on a transect line crossing between the two forest types. Three different inventory plot dimensions were used for sampling different plant categories: 5 × 5-m plots for sapling and understorey plants, 10 × 10-m plots for bamboo, and 30 × 30-m plots for trees. Within Bahuaja site plots, four sets of artificial trees were placed at 10-m intervals.

10-m plots was established for measurement of bamboo culms. Within each 10×10-m plot, all mature bamboo culms (those with ramified branches and leaves) were measured for diameter at breast height (dbh). Bamboo culms were defined as individuals at 10 cm above the ground. In August of 1999, numbered aluminium tags were attached to all mature bamboo culms in the five 10×10-m plots of one randomly selected Bahuaja inventory location (total of 96 mature culms) and one randomly selected TRC inventory location (72 mature culms). Tagged bamboo culms were re-censused in August 2000 for calculations of per cent annual mortality of bamboo culms.

Within each 10×10-m plots at all inventory locations, two 5×5-m nested plots were established for collection of data on all 'large saplings' (trees 1–4.9 cm dbh) and 'small saplings' (trees > 1 m height and ≤ 1 cm dbh). All saplings were measured for dbh with a tape measure, and for height with a telescoping height pole. Some of the data on saplings presented here are re-census data from stems reported in Griscom & Ashton (2003). Liana stems > 2 cm dbh were also tallied in 5×5-m nested plots of four of the paired plot locations.

One set of paired plots at TRC site contained four 10×10-m plots each, thus eight nested plots each (two 10×10-m plots were discarded retroactively due to human trail-clearing disturbance). Thus, the total number of mature-forest 10×10-m plots was 58 (116 nested plots), evenly distributed between the two forest types (with and without bamboo).

For measurements on trees ≥5 cm dbh (referred to hereafter as 'trees'), twelve 30×30-m plots were established centred on each series of 10×10-m plots (Figure 1). All trees were measured for dbh. Height measurements were taken with a clinometer on all trees within bamboo-dominated plots, and on a randomly selected 1/3 subset of trees in bamboo-free plots (to balance for at least three-fold higher tree density in bamboo-free plots).

Data on trees and saplings with canopy damage and bamboo loading were collected within inventory locations at Bahuaja site plots. Within the 10×10-m plots at each of the three Bahuaja inventory sites, all stems were tallied for presence of 'severe canopy damage'. All stems with visual evidence of more than 2/3 of their primary branch basal area recently broken off were classified as having 'severe canopy damage'. Recently broken branch stumps were defined as those without shed bark or signs of cambium callus growth around the branch stump base. Stems loaded with one or more bamboo culms were tallied.

Botanical specimens of fertile bamboo were collected in August–September 2001 and 2002. Herbarium specimens were analysed at The New York Botanical Garden (NYBG).

Artificial tree experiment

Sixty-four artificial metal trees were located in the forest understorey of four paired plots at Bahuaja Site, including the three paired plots used for other measurements, and one additional paired plot.

Within each of the eight plot locations (four of each forest type), eight artificial trees were located in pairs of two (see Figure 1 for layout design). Artificial trees were placed in October 2001. Artificial stem and branch tips were re-measured for height in October 2002, and any loading plant material was noted.

The main 'stem' of each tree was a 230-cm-long straight piece of 6-mm-diameter industrial steel rod. Branches were constructed from a piece of 3-mm-diameter industrial steel wire 170 cm in length. The wire was bent into a hook at each end, and bent into a 'U' in the centre for attaching to the main stem. This branch element was attached to the main stem rod with 2-mm-diameter industrial wire at a point 5 cm below the tip of the stem rod. Branch ends were bent vertically 5 cm in height, with the tip doubled over to simulate branch nodes. The main stem rod was placed 30 cm into the ground. Thus, the artificial trees were 150 cm wide and 200 cm in height after planting (Figure 1).

Data analysis

Mean values per plot (n = 6) were used as replicates for purposes of statistical analysis for tree stem density, basal area and height. For each of these tree metrics, the mean of six bamboo-dominated plot values were compared with bamboo-free plot values for each tree size class. Data from the two sites (TRC and Bahuaja) were pooled for each forest type after finding no significant difference between sites for each variable. The non-parametric Wilcoxon rank-sum test was used to compare differences between mean plot values.

Percentage of trees and saplings with canopy damage, and percentage of trees with bamboo loading (only collected at Bahuaja site) were calculated by size class. Statistical significance of difference between mean values was tested with one-way ANOVA, using arcsine-transformed (square root of arcsine) data. In the case of canopy damage data, tests were done comparing bamboo-dominated vs. bamboo-free plot values within each tree size class. In the case of bamboo-loading data, we tested for differences between size classes in bamboo-dominated plots using the Tukey extension for pairwise comparisons.

Per cent height loss of artificial trees (branch and main stem tips) over 1 y was calculated for each forest type as grand mean values of tree pair means. Artificial tree pairs were considered the experimental unit (n = 16, four pairs within each of four plots). The proportion of artificial trees

in two damage classes was also calculated: (1) 'damaged': trees with 25% height loss or more for one or more branch or stem tip, and (2) 'severe damage': trees with 50% height loss or more for one or more branch or stem tip. Plots were the experimental unit ($n = 4$). Due to substantial numbers of artificial tree pairs with zero height loss in bamboo-free plots, the data (both per cent height loss and damage class proportion) could not be transformed to a normal distribution, thus differences between bamboo-dominated vs. bamboo-free plots were tested with the non-parametric Wilcoxon rank sum test.

RESULTS

Tree size class distribution

In 30×30-m plots, both mean basal area and mean stem density of trees ≥ 10 cm dbh were 87% lower in bamboo-dominated forest plots as compared with adjacent bamboo-free plots (Table 1). The proportional difference between bamboo-dominated and bamboo-free values for both tree basal area and stem density was greater in the 10–29-cm-dbh size class than in larger and smaller size classes (5–9, 30–49) (Figure 2a, b). Tree basal area peaked in a lower size class in bamboo-free plots (10–29 cm) than in bamboo-dominated plots (30–49 cm) (Figure 2a).

Lianas ≥ 2 cm dbh occurred at a seven-fold higher mean density in the bamboo-free plots sampled than in the bamboo-dominated plots sampled (Table 1), reflecting an approximately similar liana density per tree stem for the two forest types.

Bamboo diameter, density, basal area and mortality

Guadua weberbaueri was characterized by lower mean stem diameter (4.2 cm dbh) and higher mean stem density (3860 stems ha^{-1}), and lower mean basal area (5.4 m^2 ha^{-1}) as compared with *Guadua sarcocarpa* (6.7 cm dbh, 2375 stems ha^{-1}, 8.3 m^2 ha^{-1}), although only diameter and density means were significantly different (Table 2). On average, 47.7% of the *Guadua* culms (both species) tallied in 1999 had died 1 y later. Mortality was approximately balanced by recruitment: the number of new culms in 2000 was 44.4% of the number tallied in 1999

Table 1. Grand mean ± standard error of plot means of basal area and stem density for all trees ≥ 10 cm dbh and lianas > 2 cm dbh are presented, comparing bamboo-free plots (B−) with bamboo-dominated plots (B+). Non-parametric Wilcoxon rank sum test was used.

	B−	B+	P
Tree basal area (m^2 ha^{-1})	37.9 ± 9.9	4.8 ± 0.5	0.012
Tree density (stems ha^{-1})	616 ± 101	83.3 ± 56.7	0.008
Liana density (stems ha^{-1})	283 ± 83.9	41.7 ± 31.9	0.028

(Table 2). Mortality of *G. weberbaueri* culms was 34.4%, and recruitment of culms 41.6%. Mortality of *G. sarcocarpa* culms was 61.1%, and recruitment of culms 47.2%. Elevated culm mortality of *G. sarcocarpa* as compared with *G. weberbaueri* may have been influenced by a synchronized monocarpic mortality event of *G. sarcocarpa* that began between 2001 and 2002 at TRC site, but did not occur at Bahuaja site for *G. weberbaueri*.

Loading and physical damage to trees

Mean per cent of trees loaded by one or more bamboo culms in the three Bahuaja plots was not significantly different between 5–9 cm and 10–29 cm dbh size classes (56% and 66% respectively), but both were significantly different from the > 30 cm dbh size class (ANOVA with Tukey extension for pairwise comparison on arcsine-transformed data). For all tree size classes less than 30 cm dbh except small saplings, the per cent of stems 'severely damaged' was over four times higher in bamboo-dominated than in bamboo-free plots ($P < 0.05$). No severe canopy damage was recorded in either plot type among trees ≥ 30 cm dbh. In bamboo-dominated plots, the peak percentage of stems with severe canopy damage occurred in the 5–9 cm dbh size class (69% severe damage), followed by 10–29 cm dbh (35% severe damage) (Figure 2d).

Mean stem height was significantly lower in bamboo-dominated plots vs. bamboo-free plots for tree dbh size classes 1–4, 5–9 and 10–29 cm. Mean height was not significantly different for small saplings, and trees ≥ 30 cm dbh. The largest difference between bamboo-dominated and bamboo-free plot mean stem height was for trees 10–29 cm dbh. In this size class, bamboo-dominated plot trees were on average half the height (53%) of bamboo-free plot trees ($P < 0.01$) (Figure 2c).

Artificial tree experiment

Damage to artificial trees 1 y after being placed in the forest understorey was both more common and more severe in bamboo-dominated plots. Mean per cent height loss of artificial tree main stem tips was over an order of magnitude higher in bamboo-dominated plots than in bamboo-free plots (Table 3, $P < 0.01$). Mean per cent height loss of branch tips was over five times higher in bamboo-dominated plots ($P < 0.01$). Over seven times more trees were classified as 'damaged' (0.25 height loss or more) in bamboo-dominated plots ($P < 0.05$). No trees in bamboo-free plots had 'severe damage' (0.5 height loss or more), while 19% of trees in bamboo-dominated plots had 'severe damage' ($P < 0.10$). In bamboo-free plots, 9.4% of artificial trees were bearing the load of
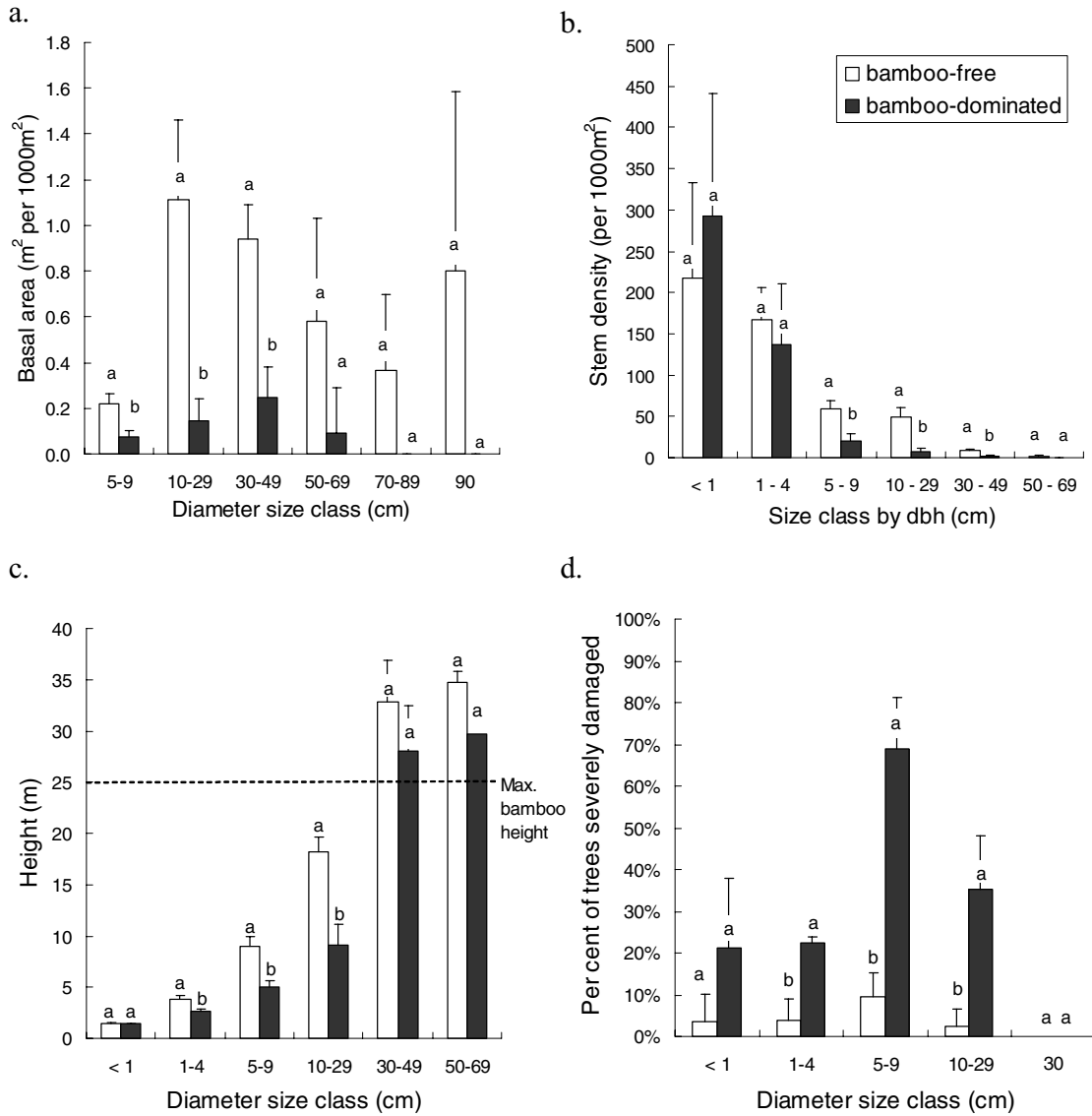
Figure 2. Measurements of tree stand structure in forest stands with and without bamboo-dominance. Basal area (a), density (b), mean height (c) and canopy damage by tree size class (d), are shown. Trees were classified as having 'severe canopy damage' if 2/3 or more of primary branch basal area was recently broken off. Trees of size class '<1 cm' include all trees less than 1 cm dbh that are 1 m in height or more. Bars indicate standard deviation from the mean of plot values. For a–c, Wilcoxon rank sum method was used to test for significant differences between bamboo-dominated vs. bamboo-free plots (n = 6) within each size class. For d (n = 3), one-way ANOVA was performed on arcsine-transformed data. Letters quantitatively indicate significant differences within each size class (a > b at P ≤ 0.05).

Table 2. *Guadua weberbaueri* inventory data was collected at Bahuaja site and *Guadua sarcocarpa* data was collected at TRC site. Grand mean values for diameter, density and basal area ± SE are reported. Differences between diameter and density grand means for each site (Bahuaja vs. TRC) were tested with Welch's modified two-sample t-test (n = 3). Mortality and recruitment data were collected from one plot at each site (thus no statistical analyses), and were calculated as the number of culms recruited or dead in 2000 as a proportion of all live culms in 1999.

	Bahuaja Site (*G. weberbaueri*)	TRC Site (*G. sarcocarpa*)	P	Mean of both
Mean stem diameter (cm)	4.2 ± 0.4	6.7 ± 0.1	0.01	5.4 ± 1.4
Mean stem density (stems ha^{-1})	3860 ± 265	2375 ± 618	0.03	3117 ± 918
Mean basal area (m^2 ha^{-1})	5.4 ± 1.1	8.3 ± 2.2	>0.10	6.9 ± 2.2
Per cent annual culm mortality	34.4	61.1	–	47.7
Per cent annual culm recruitment	41.6	47.2	–	44.4

Table 3. Mean per cent height loss of main stem tips and branch tips of artificial tree pairs ± standard error are presented for bamboo-free plots (B−) and bamboo-dominated plots (B+). Wilcoxon rank-sum method was used to test for significant difference between plot type mean values (n = 16). Also presented are mean per cent of trees 'damaged' (≥25% height loss) and 'severely damaged' (≥50% height loss), and mean proportion of trees mass-loaded with plant matter. Wilcoxon rank-sum method was used to test for significant differences between plot types (n = 4 plots, 8 trees per plot).

	B−	B+	P
Per cent height loss – main stem	0.2 ± 0.6	7.6 ± 14.9	0.008
Per cent height loss – branches	2.9 ± 3.0	19.8 ± 16.0	0.000
Per cent of trees 'damaged'	6.3 ± 7.2	56.3 ± 7.2	0.027
Per cent of trees 'severely damaged'	0.0 ± 0.0	18.8 ± 16.1	0.069
Per cent of trees mass loaded	9.4 ± 12.0	84.4 ± 12.0	0.028

plant matter after 1 y. In all cases the loading plant matter was fallen tree wood. In bamboo-dominated plots, 84.4% of artificial trees were bearing the load of plant matter. Almost all load-bearing artificial trees (81%) were loaded with live or dead *Guadua* stems, and 6% were also loaded with wood from dead fallen trees (Table 3).

DISCUSSION

Based on our results, bamboo loading of trees is the best explanation for elevated tree physical damage in bamboo-dominated plots. Bamboo loading also offers an explanation for the bottleneck in tree recruitment after the sapling size classes (trees > 4 cm dbh). Tree size classes most loaded by bamboo (5–29 cm dbh) had the greatest evidence of physical damage, both in terms of visual evidence of crown damage, and reduced tree height compared with bamboo-free plots. Artificial trees in bamboo-dominated plots experienced nearly an order of magnitude more loading (due to bamboo) and physical damage than in bamboo-free plots.

While the tree size class analogous in height to the artificial trees (large saplings) also had greater physical damage in bamboo-dominated plots, the most pronounced evidence of physical damage to trees, bamboo loading of trees, and a bottleneck in tree recruitment was for the intermediate tree size classes: 5–29 cm dbh. These patterns suggest that the crushing force of bamboo loading reaches a peak for the intermediate tree size classes, at levels high enough to suppress tree recruitment. We will discuss the lines of evidence that support this conclusion as well as various alternative explanations for our results.

Different tree species may grow to different heights for a given diameter class, and may have different susceptibility to crown or stem damage (Oliver & Larson 1996). Thus, it might be hypothesized that the differences in tree size class distribution and tree form between bamboo-dominated and bamboo-free plots are due to floristic differences between the two forest types. However, a floristics-based hypothesis is not consistent with results from our plots reported by Griscom (2003): the same patterns of size class distribution and tree form reported here (Figure 2) was also found when results were calculated for only tree species shared in both bamboo-dominated and bamboo-free plots.

Different soil characteristics are a common explanation for differences between stands in tree height-diameter ratio (Oliver & Larson 1996). Soil differences would not, however, explain why average tree height was significantly different for intermediate tree size classes but not significantly different for trees ≥ 30 cm dbh, particularly when comparing tree species occurring in both plot types (Griscom 2003). Also, Griscom (2003) found that soils of bamboo-dominated stands of our study area supported high rates of tree growth: a number of tree stems reached over 15 cm in dbh after 3 y of growth from seed in three artificial gaps created in bamboo-dominated stands (bamboo was experimentally excluded from regenerating stands).

Wind is the only documented form of natural disturbance that causes stand-scale tree damage in terra-firme forests of our study area. Wind damage does not, however, account for the consistent and peculiar pattern of damage to trees in our plots: high levels of physical damage to intermediate tree size classes, yet low levels of physical damage to large tree size classes (> 30 cm dbh). Potential wind disturbances reported for the region tend to either selectively damage larger trees in the case of rare storms (Foster & Terborgh 1998), or knock down virtually all trees over many hectares, in the case of convective downbursts (Garstang *et al.* 1998). Furthermore, elevated levels of physical damage to artificial trees in all bamboo-dominated plots demonstrated that trees are subjected to chronic physical damage that is remarkably consistent across the landscape, unlike the acute and spatially heterogeneous disturbances associated with severe storms or downbursts. Our results do not preclude the prior occurrence of wind disturbance in stands currently dominated by bamboo, but they do suggest that wind disturbance alone does not explain the current pattern of tree form and size class distribution.

It is conceivable that the pattern of tree density in our plots could have an anthropogenic explanation if intermediate size trees were selectively cut from stands; however, the stand structure we recorded is not consistent with the forms of anthropogenic disturbance we have observed in the region. Furthermore, as discussed in the introduction, we encountered no evidence in our study plots of either prehistoric anthropogenic impacts (e.g. *terra preta*, pot shards) or modern human impacts (e.g. skidding roads, A-horizon charcoal). While we may never know if prehistoric impacts occurred at our sites, we

conclude that anthropogenic impacts do not account for the current anomalous pattern of stand structure in our bamboo-dominated plots.

Physical damage to trees has been recorded from a biotic source other than humans: lianas (Putz 1980, 1984, 1991; Putz & Brokaw 1989). However, liana loading also does not explain our results: we recorded similar densities of lianas per tree stem in the two forest types (Table 1).

The dominant bamboo species of our study sites (*G. sarcocarpa* and *G. weberbaueri*), like lianas, are structural parasites. Unlike lianas in the studies reported above (Putz 1980, 1984, 1991; Putz & Brokaw 1989), *G. sarcocarpa* and/or *G. weberbaueri* are the dominant canopy species over large areas and occur at stem densities approximately an order of magnitude higher than commonly reported for lianas (mean of 3120 bamboo stems ha^{-1} recorded here vs. approximately 100–500 liana stems ha^{-1} reported by Putz (1984) and Putz & Chai (1987)).

The branches of *G. sarcocarpa* and *G. weberbaueri* are equipped with re-curved barbs that function as grappling hooks for loading trees. Bamboo culms (of *G. sarcocarpa* and *G. weberbaueri*) have poor structural properties, and are unable to support their own weight beyond about 10 m in height, at which point they bend or buckle without external structural support. However, we have observed that buckled culms maintain vigorous crowns. Bamboo loading of tree canopies is renewed each growing season, due to the high turnover of bamboo culms (approximately 50% each year, Table 2). The hollow internodes of bamboo culms fill with water, adding substantially to their mass. Bamboo (*G. weberbaueri* and *G. sarcocarpa*) thus presents a growth form that generates substantial mass loading on adjacent trees. Unlike lianas, bamboo does not tend to intertwine multiple canopy trees, but loads a single canopy tree adjacent to the culm base.

The maximum height we have recorded for *Guadua weberbaueri* and *Guadua sarcocarpa* is approximately 25 m. This maximum bamboo height threshold corresponds with both (1) a tree height threshold beyond which bamboo rarely reaches and loads trees and (2) the height threshold beyond which trees did not have elevated levels of physical damage or reduced mean height/diameter ratio (Figure 2c, d). In contrast, trees growing in the midst of the bamboo canopy (5–29 cm dbh) experienced high probabilities of bamboo loading, and had the highest levels of physical damage to canopies (Figure 2d). The artificial tree experiment provided the most direct evidence that bamboo is crushing trees.

We frequently observed a distinctive 'zig-zag' tree trunk form in bamboo-dominated stands across all tree size classes, particularly those within the bamboo canopy. This trunk form suggests repeated trunk breakage and/or leaning events, followed by re-sprouting of a stem leader. Typical stand structures in bamboo-dominated and bamboo-free study plots, representing patterns discussed above, are presented schematically in Figure 3.

We did not find any significant differences in physical structure of trees (canopy damage or height-diameter ratios) as a function of site and bamboo species present (*G. sarcocarpa* vs. *G. weberbaueri*). We suspect that further sampling might uncover differences; however, the two species appear to have a parallel physical impact on tree
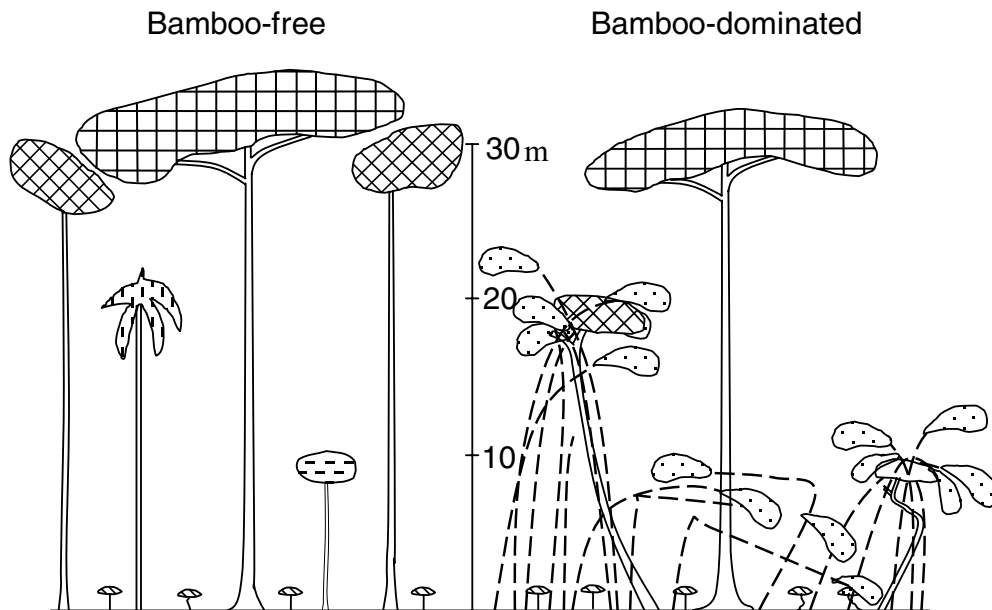

Figure 3. Schematic canopy stratification profiles are presented for hypothetical stands of the two forest types investigated. Bamboo culms are represented by dashed lines and stippled canopies in the right-hand diagram. Dominant, co-dominant, upper mid-canopy, lower mid-canopy and understorey strata (tree saplings only) are represented. 'Zig-zag' trunk formation is depicted in the far-right tree.

structure. We suspect that the higher mean diameter and lower mean density of *G. sarcocarpa* culms (at TRC) as compared with *G. weberbaueri* culms (at Bahuaja) is primarily due to genetic differences between species, but this may also result from soil differences, higher rainfall at TRC site and/or older bamboo cohorts at TRC site.

Bamboo forest dynamics and distribution

Physical damage to juvenile trees due to litterfall has been identified as an important cause of seedling mortality in neotropical forests (Clark & Clark 1989, 1991; Uhl 1982). However, to our knowledge, bamboo forests of south-western Amazonia are the first system in which enough evidence has surfaced to implicate physical damage from mass loading as causing suppressed tree recruitment, severe damage to a large range of tree size classes, and associated changes in forest structure at landscape scales.

Based on the results and observations from this study and others (Griscom & Ashton 2003, Nelson *et al.* 2001; Silman *et al.* 2003), we propose the following 'bamboo crushing hypothesis': bamboo imposes a self-perpetuating disturbance cycle in which physical damage to trees induced by bamboo loading is a principal cause of suppressed tree recruitment, reduced tree density, and reduced tree basal area for trees 5–29 cm dbh in bamboo-dominated stands.

If bamboo can impose a self-perpetuating disturbance cycle by loading trees as evidenced from the data presented here, and if bamboo can invade partially open tree canopies as it appears well adapted to do, then catastrophic disturbance is not necessary for the establishment or persistence of bamboo-dominated forests. We suspect that the distribution of bamboo-dominated patches is determined by a complex interaction of factors that may tip the balance between competitive dominance by trees vs. bamboo including: (1) the distribution and frequency of disturbances causing partial or complete destruction of the forest canopy, (2) the vulnerability of common tree species at a given site to bamboo invasion (e.g. growth rate, capacity to regenerate after physical damage, wood strength properties), (3) gregarious monocarpy of bamboo which invokes pulsed spatial distributions from one decade to the next, (4) the dynamics of understorey plants such as *Olyra latifolia* that may proliferate after *Guadua* monocarpic events and inhibit tree recruitment and (5) soil properties that provide a competitive advantage to trees vs. bamboo.

Studies have reported dominance by *G. sarcocarpa* and *G. weberbaueri* on very different soil types including very well-drained sandy soils (Silman *et al.* 2003) and loams with perched water tables (Griscom 2003). This range suggests that these two species are soil generalists, and are more competitive with trees on more stressful

soil types (associated with either too much or too little water). We suspect that these generalized soil associations drive the distribution of bamboo at the largest regional scales (within the context of climatic distribution limits), while gregarious bamboo monocarpy influences bamboo distribution at intermediate scales ($>1 \text{ km}^2$), and largely stochastic variables (disturbance, floristic patterns of plant recruitment) drive bamboo distribution at local (i.e. stand-level) scales. These multi-scale interactions can account for the difficulty in explaining the occurrence of bamboo-dominated patches when viewed at any one spatial scale.

Aside from the phenomenon of physical damage to trees, other aspects of *Guadua weberbaueri* and *Guadua sarcocarpa* ecology remain poorly understood and are critical to understanding the dynamic distribution of bamboo-dominated forests, such as: (1) details of seed dispersal and dormancy (or lack thereof), (2) successional patterns following stand initiation in the presence of bamboo rhizomes vs. seeds, (3) bamboo growth rate in response to different light and soil conditions and (4) response of bamboo distribution to changes in climate and natural disturbance regimes.

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