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Bamboo dominance reduces tree regeneration in a disturbed tropical forest

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Abstract Human disturbance may change dominance hierarchies of plant communities, and may cause substantial changes in biotic environmental conditions if the new dominant species have properties that differ from the previous dominant species. We examined the effects of bamboos (*Bambusa tulda* and *Cephalostachyum pergracile*) and their litter on the overall woody seedling abundance, species richness and diversity in a mixed deciduous forest in northeastern Thailand. These bamboo species are gaining dominance after human disturbance. Our results show that seedling abundance and species richness were reduced by bamboo canopies. Seedling abundance and species diversity under bamboo canopies were affected by bamboo litter, whereas seedling abundance and species diversity outside bamboo canopies did not respond to the mixed-tree litter manipulation. Removal of bamboo litter increased seedling abundance and species diversity. However, bamboo litter addition did not affect seedling abundance or species diversity compared to either control or litter removal. This may indicate that the effect of natural amount of bamboo litter is as high as for litter addition in preventing seedling establishment by woody species and hence in minimizing resource competition. We conclude that undergrowth bamboos and their litter affect tree seedling regeneration differently from mixed-tree litter, causing changes in plant community composition and species diversity. Increased human disturbance, causing a shift in dominance structure of these forests, may result in a concomitant reduction in their overall woody species abundance, richness and diversity. Thus, management of bamboos by controlling their distribution in areas of high bamboo density can be an important forest restoration method.

Keywords Diversity · Litter · Restoration · Richness · Seedlings

Introduction

Bamboos are perennial grasses (*Poaceae*); widely distributed in tropical, subtropical and temperate forest ecosystems (Söderström and Calderon 1979). In tropical forests, bamboos are naturally occurring structural components, and they often become dominant with human disturbances (Söderström and Calderon 1979; Gardner et al. 2000). The presence of bamboos may significantly impact the establishment of tree species in forests (Marod et al. 1999; Tabarelli and Mantovani 2000; Griscom and Ashton 2003; Guilherme et al. 2004). In relatively undisturbed mixed deciduous forests in Thailand, the abundance of bamboos was earlier controlled by dominant tree species, such as teak (*Tectona grandis*) (Marod et al. 1999; Forest Restoration Research Unit 2006). Increased disturbance in the form of tree cutting and charcoal burning has, however, resulted in a shift in dominance from various tree species to a few bamboo species (Dhillion et al. 2003). Changes in canopy dominants, from trees to bamboos, may changes tree seedling regeneration patterns.

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Bamboos play distinctive roles in the forest ecosystems through their synchronized flowering cycles and subsequent die-off, resulting in substantial changes in the forest dynamics and environment conditions. These flowering and die-off events may occur at intervals of many decades and can lead to changes in the soil nutrient environment, light intensity and the space available for tree seedling regeneration on the forest floor (Taylor and Qin 1992; Marod et al. 1999; Abe et al. 2002; Taylor et al. 2004; Holz and Veblen 2006; Takahashi et al. 2007). Many studies have shown that living bamboos impede tree regeneration through their competitive superiority in terms of the capture of light and other resources (Gratzer et al. 1999; Tabarelli and Mantovani 2000; Abe et al. 2002; Narukawa and Yamamoto 2002; Griscom and Ashton 2003; Guilherme et al. 2004; Taylor et al. 2004, 2006), and a negative relationship between bamboo density and the abundance of tree seedlings has been found (Gratzer et al. 1999; Taylor et al. 2006). Bamboos reduce pioneer species richness by competing for gaps (Tabarelli and Mantovani 2000) and mass loading of bamboos can cause physical damage of tree juveniles (Griscom and Ashton 2006). Although bamboos compete effectively with other tree species, resulting in an increased bamboo dominance, their die-off events may prevent them from taking over and allow other species to coexist (Taylor and Qin 1992; Marod et al. 1999; Abe et al. 2002; Taylor et al. 2004; Holz and Veblen 2006).

Bamboos may produce substantial amounts of leaf litter, depending on their density in the forest stand (Zhou et al. 2005). Bamboo leaves decompose slowly, and contain high lignin:N, lignin:P and N:P ratio (Liu et al. 2000), which can affect litter decomposition (Lisanework and Michelsen 1994; Parsons and Congdon 2008). The linear and flat leaves of bamboo results in a compact litter layer, especially when moist. Consequently, a thick bamboo litter layer usually accumulates on the forest floor. Takahashi et al. (2007) found that the dry mass of bamboo litter was not different between dead (i.e., 1 year after flowering and die-off) and living bamboo, despite the large amount of dead organic materials deposited after bamboo die-off. This was because the decomposition of litter on sites where bamboo had died was faster than on the sites where bamboo was alive, due to the increased soil temperature and moisture. Although bamboo litter is a conspicuous element of many forest ecosystems (Tripathi and Singh 1995; Singh and Singh 1999; Zhou et al. 2005), surprisingly few studies have examined experimentally how bamboo litter affects regeneration of co-occurring species.

Accumulation of plant litter modifies forest floor micro-environmental conditions and can thereby influence seed germination and seedling establishment, and ultimately affect plant community structure (Facelli and Pickett 1991a; Molofsky and Augspurger 1992). In a meta-analysis on effects of litter on four vegetation variables, i.e., seed germination, seedling establishment, species richness and plant biomass, Xiong and Nilsson (1999) found that plant litter generally has negative effect on these variables. It can impede seed germination by preventing shoot emergence or by preventing the downward penetration of radicles into the soil (Molofsky and Augspurger 1992; Green 1999). The decay of litter may modify the chemical environment by releasing both nutrients and phytotoxic substances into the soil (Facelli and Pickett 1991a). Litter can also have indirect effects on environmental conditions. For example, the higher humidity in the litter layer may favor the development of pathogenic fungi, leading to increased seedling mortality (Facelli et al. 1999; García-Guzmán and Benítez-Malvido 2003). Finally, litter accumulation can inhibit seed germination by reducing light availability (Vazquez-Yanes et al. 1990; Facelli and Pickett 1991b). On the other hand, by protecting seeds from seed predators (Cintra 1997), litter may also have positive effects on seedling establishment. Moreover, litter reduces water evaporation, and may thereby enhance germination, especially in relative dry environments (Facelli and Pickett 1991a; Becerra et al. 2004). Thus, litter may have contrasting effects on different species, depending on their environmental conditions for regeneration.

Although the inhibitory effects of bamboos on tree regeneration have been widely studied (Taylor and Qin 1992; Gratzer et al. 1999; Abe et al. 2002; Narukawa and Yamamoto 2002; Taylor et al. 2004, 2006; Holz and Veblen 2006), most of the studies are from temperate or warm temperate forests with *Sasa* and *Bashania* bamboos, which are different from tropical bamboos. Temperate bamboos generally have running rhizomes and spread quickly over wide areas, whereas tropical bamboos have abbreviated rhizomes that form bamboos of the clumping type (Söderström and Calderon 1979). It is probable that the temperate bamboos may affect co-occurring species differently compared to tropical bamboos because both plant characteristics and environmental conditions are different. Furthermore, to our knowledge, no previous bamboo litter manipulation experiment has been conducted to examine the direct effects of bamboo litter on other species, either in tropical or in temperate forests.

In this study, conducted in a mixed deciduous forest in northeastern Thailand, we related the woody seedling abundance, species richness and diversity to differences in canopy types (under bamboo canopy vs under tree canopy). We examined the effects of litter from these contrasting canopy types on the seedling responses by conducting a litter removal/addition experiment within their canopies. We hypothesized that bamboos and trees differ in their effects on the woody species seedling abundance, and richness and diversity. Firstly, because of the deep shade under bamboo canopy (Gratzer et al. 1999; Marod et al. 1999; Abe et al. 2002; Narukawa and Yamamoto 2002; Guilherme et al. 2004; Taylor et al. 2004), we predicted that regeneration of other species will be lower under bamboo compared to under tree canopies. Secondly, we predicted that due to the shape of bamboo leaves, together with the low decomposition rate of its litter (Tripathi and Singh 1995; Liu et al. 2000), the seedling responses to litter manipulation will be more pronounced under bamboo compared to under tree canopies. Since the litter layer can directly inhibit seedling emergence and prevent newly dispersed seeds from reaching the forest floor (Molofsky and Augspurger 1992; Green 1999), our third prediction was that seedling establishment will be positively affected by removal of litter, and that litter addition will negatively affect seedlings under both canopy types.

Materials and methods

Study area

The study area (17°29′N, 101°04′E) is located in the Na Haeo Forest Reserve, Loei province, Thailand. This area has a tropical monsoonal climate divided into rainy (May–October), cool-dry (November–February) and hot-dry seasons (March–April). The elevation ranges from 400 to 600 m above sea level. The mean annual rainfall is 1,551 mm (2001–2005), and during the study year in 2006, the total annual rainfall was 1,632 mm. The mean monthly temperature was 25°C, with a minimum of 12°C in January and a maximum of 34°C in March. The total study area is approximately 163 ha, comprising 161 ha covered mostly by the mixed deciduous forest, with some agricultural fields and fallows near the forest edge.

The forest comprises a mixture of evergreen and deciduous trees. Canopy cover is spare in the dry season, since most trees drop their leaves. Dominating woody species forming the tree-layer are *Cananga latifolia*, *Lagerstroemia* sp., *Gardenia sootepensis*, *Spondiax laxiflora* and *Pterocarpus macrocarpus*. The upper tree canopy produces a patchy canopy. The intermediate layer of trees make the canopy more continuous but ample light still penetrate the canopy and reach the forest floor. The canopy cover was more than 70% during the rainy season, when measured by a densitometer at 50 sites. The relatively dense canopy cover is largely due to understory trees and bamboos. The intermediate layer is dominated by densely distributed clumps of three bamboo species; *Gigantochloa albociliata, Bambusa tulda* and *Cephalostachyum pergracile*, all characterized as sympodial, or the clump-forming type. Life spans reported for these bamboo species are about 20 years for *C. pergracile,* 30 years for *G. albociliata* and 35–42 years for *B. tulda* (Htun 1998). The sapling and shrub layer of the forest are from 1 to 3 m high. Bamboos are scattered in the forest, but aggregate in some parts of the area with high previous disturbances. Aggregations of bamboos are found where trees were intensively cut for charcoal making, or close to the fringe of the forest. The bamboo basal area covers 198.1 m^2/ha, while the overall basal area of adult trees is 17.1 m^2/ha (Larpkern et al. 2009). Ground vegetation is mostly absent during the dry season. In the rainy season, the ground is covered with a diverse grass and herb layer.

Experimental set-up and sampling

We randomly selected 20 plots containing bamboo clumps within the forest area. The minimum distance between plots was approximately 30 m. Two bamboo species (*B. tulda* and *C. pergracile*) were selected because of their higher abundance compared to *G. albociliata.* Of the 20 plots, 9 had *C. pergracile* and 11 had *B. tulda*. In general, *B. tulda* has a bigger clump size than *C. pergracile*, although clump size depends on the age of bamboos. The bamboo clumps in our study area varied in size between 0.5 and 3 m in diameter.

We used a split-plot experimental design with the bamboo/tree canopy as the main plot factor and litter treatments as the sub-plot factor. At each site, three 1 m × 1 m sub-plots, separated by 20 cm, were randomly located under the bamboo canopy. The sub-plots were placed about 50 cm from bamboo culms, but within the canopy. In addition, we randomly located three sub-plots under tree canopies, approximately 5–10 m away from each bamboo canopy. The sub-plots under tree canopies were randomly placed beneath any tree crown. Shrubs, saplings and herbs occupied transitional zones between the bamboo and tree canopy. The litter treatments: (1) litter removal, (2) litter addition, and (3) control (un-manipulated), were randomly assigned to the sub-plots under bamboo and tree canopies. Because bamboo and most tree species shed their leaves at the same time in the dry season, litter was continuously distributed on the forest floor when the experiment started. A preliminary survey of the litter on the forest floor during the dry season (December 2005) indicated dry litter amount of about 277 g m^{-2} with a litter depth of about 2–4 cm. Under bamboo canopies, bamboo litter comprised at least 90% of the total litter, whereas under tree canopies, bamboo litter comprised less than 10% of the total litter amount. Ground vegetation under bamboo canopy was sparse and dominated by scattered herbs and small seedlings, while a denser cover of herbs, seedlings and saplings dominated the forest floor under tree canopies. Visual estimates of plant cover were typically less than 50% under bamboo canopy and more than 50% under tree canopy for all sub-plots.

At the beginning of the experiment (May 2006), litter was carefully removed by hand from the litter removal sub-plots and this litter was applied to the litter addition sub-plots. Consequently, assuming litter was evenly distributed under canopies, the litter addition plots received about twice as much litter as the corresponding control sub-plots. Leaves falling on top of the litter removal sub-plots were removed and added to the litter addition sub-plots once a week during the experiment.

Our experiment was started in May, the beginning of rainy season, since this is an important time for seedlings to germinate and establish. Most tree seeds in the forest ripen and disperse during the (hot) dry season (March–April), and germinate during the rainy season (May–October). Woody seedlings (≤50 cm height) in each sub-plot were counted at the beginning of the experiment in May 2006 and repeatedly counted every month until December 2006. However, it was difficult to determine if seedlings came from roots or stem sprouts at the beginning of the experiment. New recruited seedlings were observed and added to total seedlings throughout the experimental period. All seedlings in the sub-plots were identified to species. The Shannon diversity index (Magurran 1988) was calculated for seedling diversity in each sub-plot. Light intensity (lux) under the bamboo canopy and the tree canopy was measured weekly at each site with a light meter (Digicon, LX-50) at mid-day. We measured the light by holding the light meter sensor (4.5 cm in diameter) above the sub-plots under both canopies. Our experiment was conducted mainly during the rainy season, accordingly there was no difference between evergreen and deciduous trees in term of foliage cover. Rain prevented us from measuring light intensity in some few weeks during the experimental period.

Data analysis

Repeated measures analysis of variance was used to examine if canopy type (under bamboo canopy vs under tree canopy) affected total seedling abundance, seedling species richness, diversity and average seedling abundance per species. We used only the seedling data from the control sub-plots in this analysis because we wanted to exclude the litter effects (addition/removal) on seedlings. The control sub-plots therefore represent natural conditions both under bamboo and tree canopy. Canopy type (fixed factor) and plot (random factor, $n = 20$) were the between-subject factors, and month (May–December) was the within-subject repeated measures factor (random).

We used repeated measures analysis of covariance to examine the effects of the litter removal/addition treatment on seedling responses. Litter treatment (fixed factor) and plot (random, $n = 20$) were the between-subject factors, and month (June–December) was the within-subject factor. We used the data from the beginning of the experiment (May) as a co-variable in each analysis in order to account for differences in response variables (i.e., total seedling abundance, seedling species richness, diversity and average seedling abundance per species) before the experiment started. We conducted separate analyses on the data from bamboo canopies and tree canopies, because our litter manipulation essentially represented different experiments since different types and amounts of litter was removed/added inside and outside bamboo canopies. Initial analysis, using the two bamboo species instead of plot as the between-subject factor, showed that bamboo species did not contribute to differences in total seedling abundance ($P = 0.34$), seedling species richness ($P = 0.53$), diversity ($P = 0.46$), and average seedling abundance per species ($P = 0.30$). In addition, there were no significant interactions between the bamboo species and month or the bamboo species and litter treatment. We therefore did not use bamboo species as a factor in our analyses. Accordingly, plot was used as the between-subject factor.

Since assumptions of sphericity were violated in all cases (Mauchly's sphericity test, $P < 0.0001$), we corrected the degrees of freedom with Greenhouse-Geisser adjustments, as implemented in SPSS. Data on total seedling abundance and average seedling abundance per species were log-transformed prior to analysis to normalize the data. The analyses were performed with SPSS version 15.0 for Windows (SPSS 2006), using the general linear model procedure. Type III sum of squares was used which is the default in SPSS.

Results

Effects of bamboo canopy versus tree canopy on seedlings

Total seedling abundance (mean ± SE) was higher under tree canopy (12.96 ± 2.50 seedlings m^{-2}), than under bamboo canopy (5.88 ± 2.50 seedlings m^{-2}) ($F_{1,19} = 6.19$, $P = 0.02$; full ANOVA is shown in the Electronic supplementary material, ESM, Table S1; Fig. 1a). Total seedling abundance changed over time ($P = 0.03$), in a similar way in both canopy types (no month by canopy interaction: $P = 0.10$) (Fig. 1a). Seedling species richness was also higher in the plots under the tree canopy (3.91 ± 0.42 species m^{-2}) than the plots under the bamboo canopy (2.32 ± 0.42 species m^{-2}) ($F_{1,19} = 7.13$, $P = 0.02$; ESM Table S1; Fig. 1b). There was no difference in seedling species diversity ($F_{1,19} = 4.03$, $P = 0.06$; ESM Table S1) and average seedling abundance per species ($F_{1,19} = 2.07$, $P = 0.17$; ESM Table S1) between the canopy types. However, a significant month by canopy interaction on seedling diversity

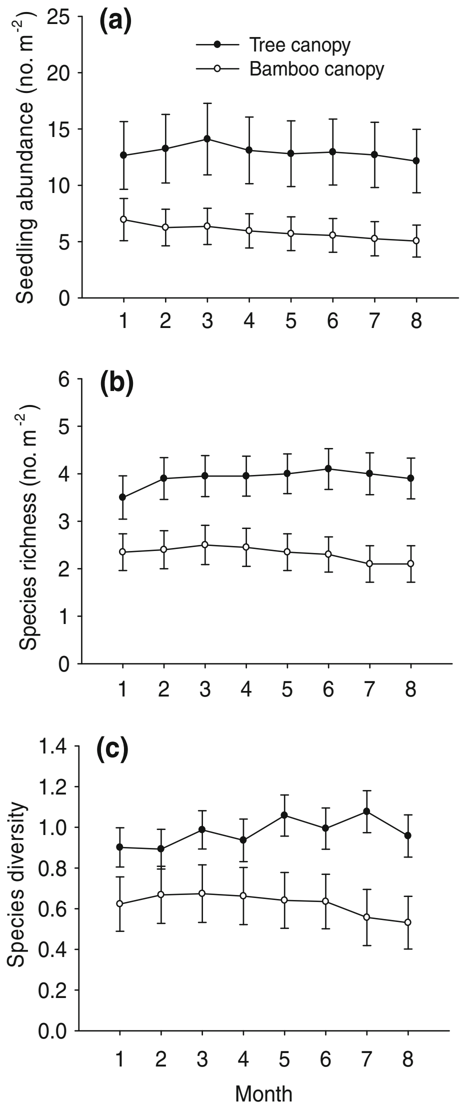

Fig. 1 The effects of canopy type on woody seedling **a** abundance, **b** species richness, and **c** species diversity. The canopy types are under bamboo canopy (*open circles*) and under tree canopy (*filled circles*). Months (1–8) are May–December. Values are means ± SE ($n = 20$)

($P = 0.04$) suggests that seedling diversity differed between bamboo and tree canopies at some time during the monitoring. The difference in species diversity between bamboo and tree canopies is highest during November (Fig. 1c).

None of the seedling responses differed among the plots (ESM Table S1). When the plot factor was omitted from the analysis, thus increasing error degree of freedom, seedling diversity differed significantly between canopy types, and was higher under tree canopy (0.98 ± 0.11) than under bamboo canopy (0.62 ± 0.11) ($F_{1,38} = 4.04$, $P = 0.036$).

Light intensity under the tree canopies was substantially higher (14,940 ± 1,557 lux) than under bamboo canopies (4,379 ± 604 lux) (one-way ANOVA, $P < 0.0001$; ESM Fig. S2).

Effects of bamboo and tree litter on seedlings

There was a significant difference in total seedling abundance among the litter treatments under bamboo canopies ($F_{2,37} = 4.30$, $P = 0.02$; full ANOVA in ESM Table S3; Fig. 2). Total seedling abundance was significantly higher ($P = 0.02$, Bonferroni pairwise comparisons) in the removal treatment (6.36 ± 0.53 seedlings m^{-2}) than in the control (4.79 ± 0.53 seedlings m^{-2}) whereas total seedling abundance in the litter addition treatment was not significantly different from the removal treatment ($P = 0.34$) or the control ($P = 0.60$). The total seedling abundance in May (covariate) was positively related to the total seedling abundance in later months ($P < 0.0001$). Under tree canopies, total seedling abundance was not affected by any litter treatment ($F_{2,37} = 0.73$, $P = 0.49$; ESM Table S3). The total seedling abundance in May (covariate) was positively related to the total seedling abundance in later months ($P < 0.0001$).

There was also a significant difference in seedling species diversity among the litter treatments under bamboo canopies ($F_{2,37} = 3.82$, $P = 0.03$; full ANOVA in ESM Table S4; Fig. 3). Seedling diversity was higher ($P = 0.03$, Bonferroni pairwise comparisons) in the removal treatment (0.80 ± 0.04) than in the control (0.64 ± 0.04), whereas seedling species diversity in the litter addition was not significantly different from the removal treatment ($P = 0.87$) or the control ($P = 0.32$). The seedling diversity in May (covariate) was positively related to the seedling diversity in later months ($P < 0.0001$). Under tree canopies, seedling diversity was not affected by any litter treatment ($F_{2,37} = 1.11$, $P = 0.34$; ESM Table S4). The seedling diversity

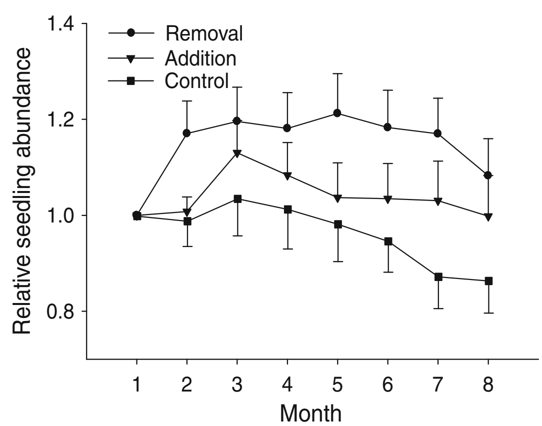

Fig. 2 Mean relative woody seedling abundance ($n = 20$) under the bamboo canopies after litter removal (*filled circles*), litter addition (*filled triangles*) and control (*filled squares*). *Vertical bars* are 1SE. Months (1–8) are May–December. The number of seedlings in May was used as a reference and the relative seedling abundance was, therefore, calculated by dividing the number of seedlings in the later months by the initial number of seedlings

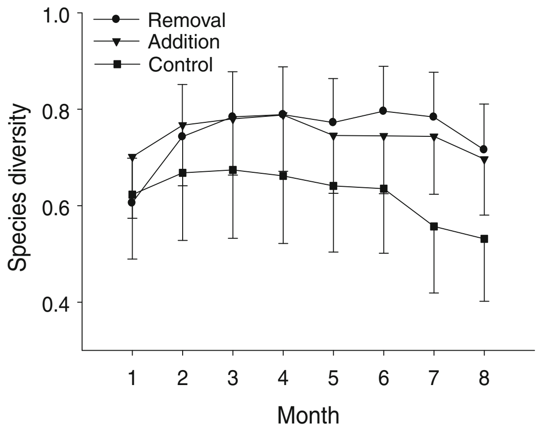

Fig. 3 Mean woody seedling species diversity ($n = 20$) under the bamboo canopies after litter removal (*filled circles*), litter addition (*filled triangles*) and control (*filled squares*). Months (1–8) are May–December. *Vertical bars* are 1SE

in May (covariate) was positively related to the seedling diversity in later months ($P < 0.0001$). Seedling diversity changed over time ($P = 0.03$), in a similar way in all litter treatments (no month by litter treatment interaction: $P = 0.58$).

Both total seedling abundance ($F_{19,37} = 2.48$, $P = 0.009$) and seedling species diversity ($F_{19,37} = 3.21$, $P = 0.001$) under bamboo canopies differed significantly among plots (ESM Tables S3 and S4). Seedling species richness and average seedling abundance per species were not significantly affected by the litter manipulation ($P > 0.05$), under any canopy type (ESM Tables S5 and S6).

Discussion

Our main hypothesis that bamboos are different from trees in affecting woody seedling abundance, and species richness and diversity, was supported**.** The results show that seedling abundance and species richness are reduced by bamboo canopies. Light intensity was significantly lower under bamboo canopies compared to adjacent forest areas, suggesting that light may be one of the limiting factors for seedling regeneration under bamboos in these forest ecosystems, thus supporting our first prediction. Reduced light availability by bamboos is one of the main factors that limit seedling regeneration in many temperate tree species (Gratzer et al. 1999; Abe et al. 2002; Narukawa and Yamamoto 2002; Taylor et al. 2004). Other studies in tropical forests have also suggested that shade from bamboo inhibits woody species regeneration (Marod et al. 1999; Guilherme et al. 2004). The woody species found under bamboo canopies may be shade-tolerant and thus able to germinate and establish under the dense shade of bamboos. Further, Griscom and Ashton (2003) proposed that root competition and the mechanical crushing by bamboo, rather than light competition, explain the arrested forest succession.

Our study clearly shows that bamboo litter has an effect on woody seedling diversity and abundance. While the litter manipulation affected seedling regeneration under the bamboo canopy, no such effect occurred outside bamboo canopies, supporting our second prediction that effects of litter manipulation will be stronger under bamboo canopies. The different response under bamboo and tree canopies can be explained by differences in leaf shape and decomposition rate between bamboo and woody species. While bamboo leaves are linear and flat and accumulate in a compact and thick layer on the forest floor, especially under moist conditions, mixed-tree litter comprise tree leaves of different size, shape and surface structure, and they therefore form a more open litter layer. Furthermore, bamboo leaves decompose more slowly than tree leaves, and normally contain lower nutrient concentrations compared to litter of other species growing in the same forest (Toky and Ramakrishnan 1983; Tripathi and Singh 1995; Liu et al. 2000).

Accumulation of bamboo litter may influence seedling recruitment by intercepting seedling emergence and prevent newly dispersed seeds from reaching suitable soil substrate. Chou and Yang (1982) suggested that bamboos interfere with the regeneration of herb species in Taiwan through production of allelopathic substances from their leaves. It is possible that this may also have reduced tree seed germination and seedling establishment in our study area.

Interestingly, while removal of bamboo litter increased the total seedling abundance and diversity compared with the control plots, litter addition did not have an opposite effect in control plots. Thus, our third prediction was only partly supported. Actually, addition of bamboo litter had a positive, although not statistically significant, effect on total seedling abundance and species diversity. This may indicate that the effect of natural amount of bamboo litter is as high as for litter addition in preventing seedling establishment by woody species and hence in minimizing resource competition. We do not have any specific explanations to why total seedling abundance and species diversity did not decrease when bamboo litter was added. One possible explanation could be that, despite different litter types, the addition of litter reduces the intensity of competition from herbs and consequently improves the growth and establishment of the woody seedlings (Facelli and Pickett 1991c). Also, litter addition may reduce water evaporation during dry periods (Facelli and Pickett 1991a; Becerra et al. 2004), and protect seeds from seed predators (Cintra 1997), thereby increasing seed germination and seedling and survival. However, bamboo litter addition may gradually affect seedlings negatively over a longer time periods since bamboo leaves decompose slowly.

We found spatial differences in the effects of litter on the total seedling abundance and diversity. These results suggest that the effect of bamboo litter on seedlings may be altered by habitat differences or by complex interactions with other environmental factors, such as moisture, soil nutrient availability and light conditions. For example, experimental studies have shown that litter in some cases positively affects seedling germination and emergence, but only under low water availability or when fungicides are added (Facelli et al. 1999; Becerra et al. 2004). Molofsky and Augspurger (1992) showed that litter improved seedling emergence of *Gustavia superba*, a shade-tolerant species, under open conditions, but not under shade.

A previous study in the same area found that woody seedling species richness and diversity were not related to the basal area of bamboos and the number of bamboo clumps, and that soil phosphorus content was the most important variable for the seedling species richness and diversity (Larpkern et al. 2009). However, the present study suggests that both bamboo canopies and bamboo litter significantly affect woody seedling abundance, species richness and diversity. These seemingly contradictory results may be explained by differences in the spatial scale of measurements. Probably, bamboos have a very local effect on seedlings that do not reach far outside their canopies. At a larger scale, seedlings are influenced by a number of additional environmental variables.

Reduced seed dispersal of woody species into the bamboo canopy could also contribute to the low seedling abundance and species richness under bamboo canopies (Abe et al. 2002; Holz and Veblen 2006). Furthermore, litter may have contrasting effects on different woody species (Molofsky and Augspurger 1992). The effects of litter on the total seedling abundance, species richness and diversity may therefore be partly influenced by the spatial distribution of seeds of woody species.

We conclude that bamboos and trees differed in their effects on the total seedling abundance, species richness and diversity in these forest ecosystems through the environmental conditions (especially light) created under the canopies, and through litter effects. At a patch scale, bamboos negatively affect woody seedling abundance, species richness and diversity. Thus, the presence of undergrowth bamboos creates heterogeneous woody seedling regeneration patterns. A mixed forest of deciduous and some evergreen tree species with small proportions of bamboos is, undergoing change where tree species abundance has declined and bamboo species abundance has increased. Because the natural distribution of bamboos is considerably altered by human intervention (Söderström and Calderon 1979; Gardner et al. 2000), increased disturbance may facilitate bamboo expansion. Since bamboos are an effective dominant competitor in these forests, they will aggravate negative effects of human disturbance in further reducing overall woody species abundance, richness and diversity. This phenomenon may drive changes in the future forest composition into bamboo-dominated forests. Thus, management of bamboos by controlling their distribution in high density areas can be an important forest restoration method.

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