

WOODY SPECIES REGENERATION AND DIVERSITY IN A SEASONALLY DRY FOREST IN NORTHEASTERN THAILAND

REKRUTTERING OG DIVERSITET HOS TREARTER I EN TØRKEUTSATT SKOG I NØRDØSTRE
THAILAND

PANADDA LARPKERN

NORWEGIAN UNIVERSITY OF LIFE SCIENCES • UNIVERSITETET FOR MILJØ- OG BIOVITENSKAP
DEPARTMENT OF ECOLOGY AND NATURAL RESOURCE MANAGEMENT
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Panadda Larpkern

Dept. of Ecology and Natural resource Management

Norwegian University of Life Sciences

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PhD supervisors:

Professor Stein R. Moe

Department of Ecology and Natural Resource Management
Norwegian University of Life Sciences
P.O. Box 5003
NO-1432 Ås, Norway

Professor Ørjan Totland

Department of Ecology and Natural Resource Management
Norwegian University of Life Sciences
P.O. Box 5003
NO-1432 Ås, Norway

Adjunction committee:

Dr. Graciela M. Rusch

Norwegian Institute for Nature Research
Terrestrisk avd.
NO-7485 Trondheim, Norway

Professor Jens M. Olesen

Department of Biological Sciences
Aarhus University
DK-8000, Denmark

Professor Tron Eid

Department of Ecology and Natural Resource Management
Norwegian University of Life Sciences
P.O. Box 5003
NO-1432 Ås, Norway

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Compilation of papers I-IV

Abstract

Forest communities are complex because many factors are associated with the spatial patterns of woody species. The main objective of this thesis is to provide a better understanding of how woody species composition and diversity, as well as its components, are related and respond to environmental variables within a forest landscape. The environmental variables are both natural environmental factors and human-induced changes to a local environment. To capture a whole forest community assemblage and to understand how woody species respond to the environment through their life span, seedling, sapling and adult stages are thus considered.

The thesis consists of four papers. The studies were conducted in a bamboo-deciduous forest, in northeastern Thailand. Three of the papers are observational studies and one is an experimental study. The first observational study attempts to find the most important determinants of woody species richness and diversity at different life stages. The second study examines if productivity and human disturbance can function as determinants of evenness in the relative abundance of growth stages (seedlings, saplings and adults) of woody species. The third study is concerned with niches of woody species, examining if their niches shift across the life stages. The experimental study was set up to determine effects of bamboos, which have become dominant in the forest, on woody seedlings regeneration.

Overall, the results show that environmental variables rather than human disturbance were important in explaining the variation in woody species richness and diversity (Paper I). Productivity and human disturbance significantly explained the variation in evenness of adults and saplings, respectively, in which evenness decreased with productivity and human disturbance (Paper II). The soil phosphorus content was found to be the most important variable for seedlings as it had a negative relationship to their richness, evenness and diversity (Paper I and II). The sapling stage is the most susceptible to human disturbance which influences sapling richness, evenness and diversity (Paper I and II). Adult richness and diversity can be predicted by forest structure (i.e. number of bamboo clumps and canopy cover) (Paper I). The basal area (i.e. productivity) was the most important determinant for adult evenness (Paper II). When examining the environmental or niche requirements among the growth stages within a species, the nine most abundant species in the forest showed

changes in their niche requirements across the growth stages (Paper III). The results from the experiment clearly showed that bamboos suppress regeneration of woody seedlings through their deep shade and litter on the forest floor. Seedling abundance and species richness were reduced by bamboo canopies, and removal of bamboo litter increased seedling abundance and species diversity (Paper IV).

Although current human activities do not appear to have severe negative effect on community properties, a long term study and experiments are needed to clarify the effects of human disturbance on this forest community. A good management strategy for woody species should consider the situation for each life stage, since the environmental requirements of a species change across the ontogenetic stages. Finally, bamboos should be incorporated in management strategies when the aim is to maintain woody species richness and diversity in these forest ecosystems.

List of papers

This PhD thesis is based on the following papers which are referred to by their roman numerals (I-IV):

- I: The effects of environmental variables and human disturbance on woody species richness and diversity in a bamboo–deciduous forest in northeastern Thailand** (Larpkern, P., Moe, S. R. and Totland, Ø. 2009. Ecological Research 24: 147-156)
- II: Do disturbance and productivity influence evenness of seedling, sapling and adult tree species across a semi-deciduous tropical forest landscape?** (Larpkern, P., Totland, Ø. and Moe, S. R., Oikos, in press) DOI: 10.1111/j.1600-0706.2010.18967.x
- III: Ontogenetic niche shifts within a tropical woody species guild** (Larpkern, P., Totland, Ø. and Moe, S. R., submitted)
- IV: Bamboo dominance reduces tree regeneration in a disturbed tropical forest** (Larpkern, P., Moe, S. R. and Totland Ø. 2011, Oecologia 165: 161-168)

1. Introduction

Community ecologists have attempted to identify potential mechanisms that control plant diversity. Numerous studies have determined important factors that influence the diversity, ranging from environmental conditions such as productivity, edaphic and topographic factors to disturbance regimes such as herbivory and fire as well as human disturbances (e.g. Givnish 1999; Hillebrand 2007; Gardner et al. 2009). Such ecological knowledge is important, not only for the ecologists to get a better understanding of what can determine and control plant community diversity, but also for forest managers to set strategies for forest management and restoration. This is especially important for seasonally dry tropical forests which are among the most threatened tropical ecosystems (Janzen 1988; Sánchez-Azofeifa et al. 2005). The seasonally dry tropical forests cover more than 40% of all forests in tropical and subtropical regions and are subject to human disturbances (Murphy and Lugo 1986; Janzen 1988). Seasonality in these forests is pronounced, with about six months of dry conditions and an annual precipitation between about 400 and 1,700 mm (Gerhardt and Hytteborn 1992). These forests differ from tropical rain forests in structure, diversity, species composition, production and other functional aspects (Murphy and Lugo 1986; Janzen 1988; Gerhardt and Hytteborn 1992). Although, they cover large areas and are unique in their species composition, few studies have been conducted in these forests compared to tropical rain forests or savannas. In particular, studies on regeneration processes of the forests are still needed (Gerhardt 1996; Vieira and Scariot 2006). In order to maintain or manage and restore the seasonally dry forest ecosystems, a predictive understanding of the ecological systems is required.

This thesis attempts to give ecological knowledge, determining important factors that relate to woody species richness, evenness and diversity in the seasonally dry forest in northeastern Thailand. Because forest communities contain trees of different life stages, life stages of woody species, i.e. seedlings, saplings and adults, are thus considered. Recent studies have highlighted on how ontogenetic niche shifts in plants may contribute to plant species coexistence (Eriksson 2002; Barot and Gignoux 2004; Miriti 2006; Quero et al. 2008). The possible niche shifts of woody species across the life stages were examined. Finally, human disturbance may have indirect effects on the forest community by changing species dominance patterns, and may subsequently affect forest regeneration, as shown for bamboos in a case study of this thesis.

1.1 Plant species diversity in relation to forest environmental conditions

Species diversity comprises both species richness; the number of species in a given area, and evenness; the relative contribution of each species to the total number of individuals (Magurran 1988). In forest communities, tree species diversity is fundamental to other forest species, providing resources and habitats. Studies in tropical forests have shown that the number of woody species tends to increase with precipitation, forest stature, soil fertility, rate of canopy turnover and time since catastrophic disturbance, and it decreases with seasonality, latitude, altitude, and diameter at breast height (d.b.h.) (Givnish 1999). Pattern of diversity at one spatial scale can, however, be distinct from patterns at other spatial scales (e.g. from local to regional), and they are controlled by different factors (Whittaker et al 2001). At a local scale, numerous factors such as chemical and physical soil properties, topography, canopy gaps are important drivers of tree diversity and composition in tropical forests (Oliveira-Filho et al. 1998; Miyamoto et al. 2003; Poulsen et al. 2006). Human disturbance variables such as logging, burning and livestock grazing are also found to be important (Silk et al. 2002; Sagar and Singh 2004). In Paper I, we examined woody species richness and diversity at different life stages (seedlings, saplings and adults) in relation to local variability in environmental conditions within a forest landscape of seasonally dry forest in Thailand. The environmental conditions include both natural and human disturbance variables. This was done to get an overview of the forest and uncover associations between local environmental conditions and woody species richness and diversity.

Although the relationships between species richness and diversity, and environmental conditions have attracted considerable interest, species evenness, another key component of diversity has received less attention. Moreover, species richness and evenness in plant communities are not always correlated (Wilsey et al. 2005; Bock et al. 2007). Some studies have pointed out that evenness is more sensitive to changes in human disturbance and productivity than richness because the relative abundance among species changes more rapidly with productivity or disturbance than the actual number of species (Chapin et al. 2000; Chalcraft et al. 2009). Nevertheless, very few studies have examined how productivity may function as a determinant of evenness (Drobner et al. 1998; Laird et al. 2003; Chalcraft et al. 2009). Evenness may decrease with productivity of woody species because highly productive environments tend to have more individuals and a stronger dominance structure (Mulder et al.

2004; Chalcraft et al. 2009). Human disturbances can also affect species evenness by changing the species composition of communities (Hillebrand et al. 2008) because disturbances may differentially affect the density of species. The disturbances may prevent dominant species from gaining high abundance (Kumar and Ram 2005; Sagar and Singh 2006; Reitalu et al. 2009), and therefore they may increase evenness.

In Paper II we examined environmental variables shaping evenness in the relative abundance of life stages (seedlings, saplings and adults) of woody species. We were particularly interested in linking evenness to measures of human disturbance (i.e. number of tree stumps, area covered by charcoal making holes and trail length) and productivity (i.e. total diameter breast high (dbh) and tree volume) (Paper II).

1.2 Plant species coexistence based on the niche concept

The niche concept has long been used to explain species coexistence within communities. It characterizes species requirements for resources and habitat conditions as well as functional roles (Chase and Leibold 2003). According to the “competitive exclusion principle” by Gause (Hardin 1960), two species cannot coexist in the same locality if they have the same niche. In such cases, the best competitor species would eliminate the other species. Therefore, species must have sufficiently different niches to allow coexistence within the same community. The concept of the ecological niche is also used to predict species distributions along environmental gradients.

In plant communities, niche separation (or niche differentiation) seems unlikely to explain plant coexistence because all plants require the same essential resources, such as CO₂, light and various macro- and micronutrients. Moreover, plants occupying the same community are most likely to experience similar environmental conditions. Many mechanisms have been invoked to explain the coexistence of plants in natural communities (Silvertown and Law 1987; Chesson 2000; Barot and Gignoux 2004). However, niche separation, whereby plants use different resources or use different ranges and proportions of resources in space and time, has still been emphasized in explaining plant coexistence (Pacala and Tilman 1994). Recently, Silvertown (2004) stated that niche separation plays a significant

role in explaining plant coexistence. Based on 13 studies, he concluded that niche separation occurred in plants along several axes (Silvertown 2004).

The well known hypothesis of plants having a ‘regeneration niche’ by Grubb (1977) suggests that niche separation takes place at early life stages where different plant species require different conditions for recruitment. This hypothesis is a way to emphasize that the whole plant life, with different stages, must be considered to provide a better understanding of plant coexistence (Barot and Gignoux 2004). Indeed studies have showed that niche requirements of plants can change through the life of individuals, known as ontogenetic niche shifts (Parrish and Bazzaz 1985; Eriksson 2002; Miriti 2006; Quero et al. 2008). Despite this, studies are still few (Eriksson 2002; Silvertown 2004), and they have mostly focused on a few life stages (Quero et al. 2008) commonly only on a few species (e.g. Miriti 2006; Quero et al. 2008). Moreover, few studies attempted to examine the niche shift in woody species (Stohlgren et al. 1998; Quero et al. 2008). This is because such experiments are difficult to conduct in forest ecosystems with long-lived and various tree species.

Therefore in Paper III, ontogenetic niche shifts of 9 abundant woody species in the study area were examined. The abundance of seedlings, saplings and adults along several environmental gradients was measured and used to explore how woody plant species associated with each other during their life span and how abundances at ontogenetic stages related to environmental and human disturbance variables.

1.3 Bamboo dominance reduces tree regeneration: consequences of change in species dominance patterns

General descriptions of species abundance distributions in ecological communities show that species have unequal abundances, with a few dominant species being very common, and many relatively rare (McGill et al. 2007). It has been emphasized that the few common species are important to ecosystems, not only because of their large biomass, but also because many other species may be affected by them, both positively and negatively (Ellison et al. 2005; Gaston and Fuller 2008). Therefore, a shift in the dominance hierarchies of communities may have influence on several other species. Such dominance-shifts may be caused by disturbances, either natural or anthropogenic, that change the relative abundance of

species due to differences in species responses to such disturbances. If the new dominant species have similar properties as the former dominant, communities are likely to be maintained (Symstad et al. 1998; Walker et al. 1999). However, if the new dominant species have contrasting properties compared to the former dominant, large changes in community species composition and diversity and ecosystem function may occur (Ellison et al. 2005; Gaston and Fuller 2008). Indeed, several studies have shown that dominant invasive species with traits that were not present in the community before invasion (e.g. nitrogen fixation, Vitousek and Walker 1989; Hughes and Denslow 2005), may have large effects on other species (Vitousek 1990; D' Antonio 2000).

The increase in bamboo (Box 1) dominance in many tropical and temperate forests may be an example of change in species dominance. Bamboos are important components of many forest types, especially in Asia (Bystrakova et al. 2003; Zhou et al. 2005), and they have been increasing in their cover in disturbed forests (Garner et al 2000; Forest Restoration Research Unit 2006). Disturbances, both natural and anthropogenic, have been related to a shift in bamboo dominance (Söderström and Calderon 1979; Griscom and Ashton 2003). Recently, Franklin et al. (2010) suggested that bamboos may not be facilitated by disturbances, but instead they can persist and be resilient to disturbances like other clonal plants. Although, mechanisms in which bamboos become dominant need to be investigated, the influence of bamboos on tree seedlings has been emphasized (Marod et al. 1999; Tabarelli and Mantovani 2000; Griscom and Ashton 2003; Guilherme et al. 2004). As bamboos become dominant in the intermediate layer of the forests, they may modify micro-environmental conditions through their deep shade and litter. George and Bazzaz (1999) suggested in their work that the understory stratum (i.e. fern) is an important ecological filter in forests through its modification of micro-environmental variables, temperature, soil moisture, and also through its litter distribution.

In Paper IV, the effects of bamboos (*Bambusa tulda* Roxb. and *Cephalostachyum pergracile* Munro.) and their litter on the overall woody seedling abundance, species richness and diversity in the forest were examined. Since bamboos can cast deep shade on the forest floor (Gratzer et al. 1999; Marod et al. 1999; Abe et al. 2002; Narukawa and Yamamoto 2002; Guilherme et al. 2004; Taylor et al. 2004), and have unique leaf shape with low decomposition rates (Tripathi and Singh 1995; Liu et al. 2000), we hypothesized that

bamboos and trees differ in their litter effects on the woody species seedling abundance, and richness and diversity

Box 1. Looking at bamboos



Bamboos are perennial woody grasses in the family Poaceae, sub-family Bambusoideae. They are the fastest growing plants in the world and well known as “pioneer species”. There are approximately 87 genera and about 1,500 species of bamboo worldwide (Zhou et al. 2005). Bamboos are widely distributed in tropical, subtropical and temperate forest ecosystems, especially found in Asia and South America (Söderström and Calderon 1979; Li and Kobayashi 2004; Zhou et al. 2005). Bamboos spread by underground rhizomes, and culms (stalks) arise from the rhizomes to form the aerial parts. The culms sprout branches from nodes, and leaves grow from branches. The flowering habits of bamboo are not well understood. Some bamboos flower annually or within short intervals, while some flower simultaneously after long intervals of several decades (Söderström and Calderon 1979). Rhizomes are an important structure used in bamboo taxonomy. There are two basic types of bamboos, according to the rhizome systems: monopodial (running); and sympodial (clumping) types. Running bamboos produce long fast-spreading rhizomes, which can spread over large areas and become very invasive and competitive in the vegetation. Clumping bamboos produce short-spreading rhizomes and culms close together in a single clump. With the addition of new culms, the clump gets larger each year. This clump can be rather extensive and quite competitive. Tropical bamboos are mostly of the clumping type, while temperate bamboos are the running type (Söderström and Calderon 1979). Bamboos are very important for the culture and economy in Asia and they are used for basic living, including food, household construction, basket making, firewood and furniture. In Thailand, there are 13 genera and 60 species of bamboos recorded (Pattनाविbool 2000). They are found in degraded and open land, and in natural forests throughout the country.

2. Objectives

The main goal of this thesis was to study how woody species composition and diversity as well as its components are related and respond to environmental variables within a tropical seasonally dry forest. The environmental variables are both natural environmental factors and human-made changes to a local environment. This is to get better understanding of the forest community and provide suggestions for management of the forest. I studied these by separating woody species into three life stages, i.e. seedlings, saplings and adults. This approach would give more accurate information of the forest community assembly. The specific objectives, which correspond to the Paper I-IV were:

- 1) To examine the most important determinants of woody species richness and diversity at different life stages.
- 2) To examine if productivity and human disturbance can function as determinants of woody species evenness at different life stages.
- 3) To examine niche requirements of woody species at different life stages and explore niche shifts across the life stages.
- 4) To determine effects of bamboos on woody seedling abundance, species richness and diversity.

3. Study area and methods

3.1 Study area

The study area for all studies, included in this thesis, is located in the Na Haeo Forest Reserve (17° 29'N, 101° 04'E), Loei Province, northeastern Thailand. The area is on a plateau at about 400-600 m elevation. It is characterized by a tropical monsoonal climate with pronounced wet and dry seasons, and high temperatures throughout the year. The seasons comprise rainy

(May-October), a cool-dry (November-February) and a hot-dry season (March-April). The mean annual rainfall is 1551 mm (2001-2005), and during the study year in 2006, the total annual rainfall was 1632 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 a bamboo-deciduous forest (Maxwell 2004) or a mixed deciduous forest (Smitinand 1977; Marod et al. 1999) with some agricultural fields and fallows near the forest edge. The forest generally comprises a mixture of evergreen and deciduous trees and some bamboo species. Although the study area is relatively small it has a high diversity of plant species, and it is representative for much of the remaining forest in the region. Dominating woody species forming the tree-layer are *Cananga latifolia* (Hk. f. & Th.) Fin. & Gagnep., *Lagerstroemia* sp., *Gardenia sootepensis* Hutch. *Spondias laxiflora* (Kurz) Airy Shaw and *Pterocarpus macrocarpus* Kurz. The intermediate layer comprises woody species such as *Quercus kerrii* Craib, *Aporosa octandra* (B.-H. ex D. Don) Vickery var. *octandra*, *Memecylon scutellatum* Naud., *Aporosa octandra* (B.-H. ex D. Don) Vickery var. *yunnanensis* (Pax & K. Hoffm.) Schott and *Harrisonia perforata* (Blanco) Merr. This intermediate layer is dominated by densely distributed clumps of three bamboo species: *Gigantochloa albociliata* (Munro) Kurz, *Bambusa tulda* Roxb. and *Cephalostachyum pergracile* Munro. The upper tree-layer produces a patchy canopy. The intermediate layer of the woody species and bamboos make the canopy more continuous but ample light still penetrates the canopy and reaches the forest floor. The sapling and shrub layer of the forest is from 1-3 m high.

Fires are common and canopy cover is sparse in the dry season since most trees shed their leaves. Ground vegetation is mostly absent during the dry season. In the rainy season, the ground is covered with a diverse grass and herb layer. Seeds of a majority of tree species in the forest mature in the dry season and are dispersed at the beginning of the rainy season when sufficient moisture is available for germination. Although the forest is protected by law, local people use the forest for various purposes, including agricultural expansion, collecting of non-timber forest products, cattle grazing and charcoal making.

3.2 Methods

To obtain data on woody species and environmental conditions in the forest, seven transect lines were randomly positioned in the area in 2006. Along these transects, a total of 50 plots of 20 m × 20 m were placed for sampling and measurements of adults and saplings of woody species. All plots were more than 20 m apart. In 30 of the 50 plots, each plot was divided into four equal squares (10 m x 10 m), and a subplot of 1 m x 1 m was randomly established in each square for sampling and measurements of seedlings. Seedlings were recorded and monitored in the subplots throughout the year. In this thesis, plant height and diameter at breast height (dbh, 1.3 m) were used to define woody species into different growth stages, as follows; adults: ≥ 4.0 cm diameter at breast height, saplings: > 0.5 m height and < 4 cm dbh when their heights were exceeding 1.3 m, seedlings: ≤ 0.5 m height.

Twenty environmental- and human disturbance variables were measured in each plot. Of the 20 variables, 17 variables represented natural environmental conditions, and three variables were related to human disturbance. The environmental variables were characterized as forest structure (i.e. canopy cover, canopy height, number of bamboo clumps and bamboo basal area), edaphic factors (i.e. pH, available phosphorus, available potassium, calcium, magnesium, organic matter, total nitrogen and percent sand), topographic factors (i.e. slope and elevation) and others (i.e. number of termite mounds, termite mound ground surface area and small water ways passing the plots). The human disturbance variables included the number of tree stumps, the length of trails and the area covered by charcoal making holes. The species data and the environmental- and human disturbance variables were used in the Paper I, II and III.

To examine the most important determinants of woody species richness and diversity at different growth stages (Paper I), a stepwise selection method in multiple regression analyses was used. Species diversity was calculated using the Shannon diversity index (H') (Magurran 1998) for each plot and growth stage.

To examine how evenness of growth stages of woody species is related to measures of productivity and aspects of human disturbance (Paper II), the Pielou's species evenness index (Pielou 1975) was calculated for each plot and growth stage. Productivity used in this study was defined in two ways: 1) as a measure of a total dbh (cm) of all trees in each plot, and 2) as

a measure of a total tree volume (m^3) in each plot. Although it can be argued that these two measures represent standing crop and not productivity, other studies have found a relationship between productivity and standing crop (Clark et al 2001). Moreover, total dbh is frequently used as a surrogate measure of tree productivity (Sagar and Singh 2006). It can also be argued that standing crop is a function of previous production associated with our main interest, evenness. Another measure that can be used to represent above ground production is litterfall (Clark et al 2001). We found that litterfall was correlated with total dbh ($r = 0.416$, $p = 0.022$). However, since we only have litterfall data from 30 of the plots we rather used dbh and tree volume since we have data on these variables from 50 plots for adults and saplings. The primary goal of the study was to study the possible effects of productivity and human disturbance on evenness of the three growth stages. However additional information on other environmental variables was included in order to control, in a statistical sense, for their potential influences on evenness. The stepwise multiple regressions were used to determine the relative importance of productivity, human disturbance and environmental variables, in explaining variation in species evenness among the plots.

To examine niche requirements of woody species at different life stages and examine if the niches shift across the growth stages (paper III), nine abundant woody species were selected. The species are *Aporosa octandra* (B.-H. ex D. Don) Vickery var. *octandra* (Euphorbiaceae), *Aporosa octandra* (B.-H. ex D. Don) Vickery var. *yunnanensis* (Pax & K. Hoffm.) Schott (Euphorbiaceae), *Croton roxburghii* N.P. Balakr. (Euphorbiaceae), *Gardenia sootepensis* Hutch. (Burseraceae), *Hydnocarpus* sp. (Flacourtiaceae), *Lagerstroemia* sp. (Lythraceae), *Lithocarpus elegans* (Bl.) Hatus. ex Soep. (Fagaceae), *Memecylon scutellatum* Naud. (Melastomataceae) and *Pterocarpus macrocarpus* Kurz (Fabaceae). Since the study aimed to examine niche shift in a multidimensional niche space, multivariate analyses were performed where each species were examined simultaneously at each growth stage. Canonical correspondence analysis, (CCA) (ter Braak 1986) was used to relate the abundance of species to the environmental and human disturbance variables. By using CCA, the most parsimonious variables explained separation of species at the seedling stage were identified, and then these variables were used to model separation of species at the sapling and adult stages. The process was repeated for the sapling stage too by first identifying the variables that most parsimoniously explaining separation of species at the sapling stage, and applying these variables at the adult stage. The models were finally compared with those that most parsimoniously explained separation of species at the adult

stage. Any change in the identity and magnitude of the variables contributing to separation of the species, and any change in the relative position of species along these variables from the seedling to the sapling and at the adult stage will represent a niche shift from the seedling to the subsequent growth stages.

To determine effects of bamboos on woody seedling abundance, species richness and diversity (Paper IV), an experiment was set up in 20 plots containing bamboo clumps within the forest area. A split-plot experimental design was used with the bamboo/tree canopy as the main plot factor and litter treatments as the sub-plot factor. At each site, three 1 m x 1 m sub-plots, separated by 20 cm, were randomly located under the bamboo canopy. In addition, another three sub-plots were randomly placed under tree canopies, approximately 5-10 m away from each bamboo 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. 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. New recruited seedlings were observed and added to total seedlings throughout the experimental period. Light intensity was measured at each site both under the bamboo canopy and the tree canopy. Repeated measures analysis of variance was used to examine the effects of canopy type (under bamboo canopy vs. under tree canopy) and litter on total seedling abundance, seedling species richness and diversity.

4. Main results and discussions

4.1 Main results

Including all life stages, 136 woody species were found in the study area. A total of 125 species in the adult stage and 111 species in the sapling stage were recorded within the 2 ha total sampling area. Within the 0.012 ha total seedling sampling area, 89 species of seedlings were recorded. Although the forest had been disturbed by local people, it still contained a high number of tree species. Variations in woody species diversity, as well as richness and evenness in the forest were found to be influenced by a number of complex and interacting

variables. Species richness and diversity at each life stage were generally related to different sets of environmental and human disturbance variables (Paper I). The most important variables will be discussed later. When measures of productivity and human disturbance were used to examine species evenness, only evenness at the adult stage was significantly related to productivity (total dbh) (Paper II). In addition, only evenness of saplings was significantly related to human disturbance (area covered by charcoal holes) (paper II). Apart from measures of productivity and human disturbance, other environmental variables also explained the variation in evenness. Human disturbance was not found to have a negative influence on species richness and diversity. However, changes in species dominance, i.e. from trees to bamboos in the forest, as consequence of long term human disturbances, had negative effects on the abundance, richness and diversity of seedlings growing under bamboo canopies (Paper IV). The idea that plants may change environmental requirements from early life stage, i.e. the regeneration niche (Grubb 1977), as individuals develop, is supported by our results. The nine most abundant woody species in the forest generally changed their niche requirements across the life stages (Paper III).

4.2 Life stages of woody species and the important variables that determine their diversity

In general, tree species differ in their morphology and physiology when growing from seedlings to adults (Tuner 2001), and each growth stage may require distinctive environmental conditions and respond differently to human disturbances. For example, seedlings are small in size and hence are more susceptible to small scale variation in environmental conditions, e.g. soil fertility as compared to the later growth stages (Vargas-Rodriguez et al. 2005). This study showed that soil phosphorus was an important determinant for seedling richness and diversity (Paper I) as well as evenness (Paper II). Seedling species richness, evenness and diversity were negatively related to soil phosphorus (Paper I and II). In contrast, other studies have suggested that P could be a limiting resource in tropical dry forest soils and that P addition increased seedling recruitment and survival (Ceccon et al. 2003 and 2004). However, the positive responses of seedlings (i.e. recruitment and survival) to P levels are different among species, in which fast-growing species (early successional species) have a

higher response to P than species from the mature forest (late successional species) (Raaimakers and Lambers 1996; Huante et al. 1995; Ceccon et al. 2003). Studies have shown that species from the mature forests are more common on P deficient soils and have low P dependency (Rincón and Huante 1994; Huante et al. 1995). The negative relationships between species richness, evenness and diversity, and soil P can indicate that P is not a limiting resource for seedlings in this forest. An experiment in a Mexican dry forest showed that addition of P decreased seedling diversity, while it increased the recruitment of only a few species (Ceccon et al. 2004). Moreover, mycorrhizal fungi are known to play important roles in increasing nutrient uptake, improving growth and survival of seedlings in tropical forests where soils are deficient in P (Janos 1980; Burslem et al. 1995). A previous study on mycorrhizal plants in this forest found that woody seedlings were commonly associated with mycorrhizal fungi (Eriksen 2009). This may explain how seedlings can establish well despite low soil available P. Species richness, diversity and evenness of seedlings seemed not to be influenced by human disturbance and productivity as compared to the sapling and adult stages (Paper I and II). This may be because the seedling's growth period is shorter than for saplings and adults, and therefore, seedlings may have lesser exposure and response to disturbances and competition. Seedling establishment largely depends on suitable environmental conditions, i.e. the regeneration niche (Grubb 1977). Also, seedling populations are initially influenced by the availability of seeds (Dalling et al. 2002; Paine and Harms 2009). Although, woody species at the seedling stage in general were not related to human disturbance, some species may largely depend on conditions including human disturbance. For example, the abundance of *Aporosa octandra* var. *octandra* was closely associated with the number of stumps at the seedling stage (Paper III).

Sapling richness and diversity were highest at lower elevation (Paper I). This may be because elevation is related to water availability, and that water availability is higher close to streams at lower elevations. While most seedlings germinate and establish when there is sufficient water during the rainy season, and adults have extensive root systems, rapidly growing saplings have high water requirements and are prone to water deficiency (Kume et al. 2007). Therefore, at lower elevation, higher water availability can support more diverse species of saplings. The sapling stage seemed to be more influenced by human disturbance compared to other life stages. The variations in the sapling species richness and diversity, as well as evenness were partly explained by measures of the human disturbance variables. The results showed that sapling species richness and diversity were positively related to the

number of tree stumps (Paper I). These positive relationships may indicate that there is resource competition between saplings and adult trees. Adult trees can suppress juveniles for resources and/or space, and hence may prevent substantial population densities of saplings to occur. Removing big trees reduces resource competitions for saplings and hence allow more species to occur with higher population densities of saplings. The abundance of some species, *A.octandra* var. *octandra*, *A.octandra* var. *yunnanensis* and *Hydnocarpus* sp., were also closely associated with the number of tree stumps at the sapling stage (Paper III). In addition, evenness of saplings was negatively related to area covered by charcoal making holes (Paper II). Clearing of vegetation to make space for charcoal holes may reduce suppression of saplings from adults, the same case as the disturbance indicated by the number of tree stumps. However, the clearing of vegetation for charcoal holes means more intense disturbance to the area than selective tree cutting. This kind of disturbance might allow only some sapling species to occupy and take advantage of the situation, and consequently become dominant. Rao et al. (1990) and Yadav and Gupta (2006) also found that disturbance decreased evenness of woody species in tropical forests. On the other hands, other studies found human disturbances preventing dominant species from gaining high abundance (i.e. increased evenness) (Kumar and Ram 2005; Sagar and Singh 2006). The difference in direction of the relationship between human disturbance and evenness of trees in this study, compared to others studies may be due to differences in scale and intensity of disturbances. Those studies were conducted in the forests where they have experienced frequent and large-scale disturbances, such as mining, power generation, cattle ranching and tree felling (Kumar and Ram 2005; Sagar and Singh 2006), whereas the human disturbances in our study area are substantially less intense and on a much smaller spatial scale.

We found that productivity (total dbh) explained a significant part of the variation in evenness only at the adult stage where evenness decreased with productivity (Paper II). The negative relationship between productivity (total dbh) and evenness may be due to the interspecific competition in which a high productive environment may facilitate competitively dominant species (Mulder et al. 2004; Chalcraft et al. 2008), and thereby affect evenness in woody communities. For instance, soil nutrient availability at a local scale may cause variation in productivity. Hypotheses have been proposed that competition intensity (for soil nutrients and light) increases with productivity (Grime 1973; Rajaniemi 2002). Fertilizer application increased plant productivity (i.e. plant size) but it may cause a decrease in species diversity through competitive exclusion of weak competitors (Rajaniemi 2002; Rajaniemi et al.

2003). Thus, only a few dominant species are able to capitalize strongly on increased resource availability at the expense of other species, resulting in low evenness. In a meta-analysis, Hillebrand et al. (2007) demonstrated that fertilizer addition reduces both richness and evenness in terrestrial ecosystems. The results in this study showed a similar trend in that higher dbh and higher soil nutrient content were found to decrease the woody species evenness at the adult stage. Our result is in the same line with Vance-Chalcraft et al. (2010), who found a negative above ground biomass - evenness relationship in subtropical forests in Puerto Rico. They suggested that a few species become more dominant at high biomass, rather than the biomass being distributed evenly among all species. Competitions among individuals are probably more intense as plants are developing, due to changes in size and abilities to utilize resources (Callaway and Walker 1997; Li et al. 2008). Our results showed that only sapling and adult evenness were related to measures of human disturbance and productivity, respectively, but such relationships were not found at the seedling stage.

4.2 Bamboo dominance reduces tree regeneration

Adult species richness and diversity were negatively related to the bamboo clumps (Paper I). Bamboos are naturally occurring structural components in the mixed deciduous forest, and the increase in their dominance is often related to human disturbances (Söderström and Calderon 1979; Gardner et al. 2000). The correlations between the number of bamboo clumps and/or bamboo basal area and human disturbance variables (Paper I) did not show this pattern clearly. It might be because bamboos generally have long flowering cycles (Taylor and Qin 1992; Marod et al. 1999; Abe et al. 2002; Taylor et al. 2004; Holz and Veblen 2006; Takahashi et al. 2007), and therefore the processes of replacement after disturbances may also take considerable time.

Because bamboos are dominant at the understory stratum, we hypothesized that they may also have negative effects on young life stages of woody trees, especially seedlings. At the plot scale, seedling species richness and diversity were not found to be related to the density of bamboos (Paper I), while the sapling abundance of four dominant species (*Lithocarpus elegans*, *Memecylon scutellatum*, *Pterocarpus macrocarpus* and *Gardenia sootepensis*) was closely associated with the bamboo density (Paper III). Although bamboos

did not have negative relationship with seedling richness and diversity (Paper I and II), the experiment indicated negative effects of bamboos on seedlings growing under bamboo canopies (Paper IV). Total seedling abundance and species richness were lower under bamboo canopies than under tree canopies. Moreover, seedling abundance and species diversity under bamboo canopies were affected by bamboo litter. Light intensity is significantly lower under bamboo canopies compared to under tree canopies, and may thus cause lower total seedling abundance and species richness under bamboo canopies than under tree canopies. However, light availability generally may not be the most limiting factor for seedlings in seasonally dry tropical forests (Gerhardt 1996; McLaren and McDonald 2003; Vieira and Scariot 2006). The results showed that seedling species richness and diversity were not related to the canopy cover (Paper I). In addition, most of the nine abundant species in the forest were associated with relatively high canopy cover at the seedling and sapling stages (Paper III). These may be due to soil moisture which is related to shade in dry forests (Gerhardt 1996; Vieira & Scariot 2006). Canopy openness could also result in low seedling survival through desiccation in the long dry season (Gerhardt 1996). However, dense shade under bamboo canopies may benefit shade-tolerant species able to germinate and establish. Many studies have also shown that reduced light availability by bamboos is a main factor limiting seedling regeneration in both temperate (Gratzer et al. 1999; Abe et al. 2002; Narukawa and Yamamoto 2002; Taylor et al. 2004) and tropical forest ecosystems (Marod et al. 1999; Guilherme et al. 2004). Our results, therefore, supported these studies in that dense shades of bamboos negatively affect seedling regeneration.

Bamboo litter may be another important factor that can affect the seedling regeneration under bamboo canopies. The results show that total seedling abundance and species diversity under bamboo canopies were affected by bamboo litter, whereas total seedling abundance and species diversity outside bamboo canopies did not respond to the mixed-tree litter manipulation. In addition, removal of bamboo litter increased seedling abundance and species diversity. The different responses of woody seedlings under bamboo and tree canopies can be explained by differences in leaf shape and decomposition rate between bamboo and tree species. Bamboo leaves are linear and flat and accumulate in a compact and thick layer on the forest floor, especially under moist conditions, and hence may intercept seedling emergence and prevent newly dispersed seeds from reaching suitable soil substrate. On the other hand, mixed-tree litter comprise tree leaves of different size, shape and surface structure, forming a looser litter layer, and therefore may be a lesser barrier for

seedlings to emerge or for seeds to reach the soil. Furthermore, bamboo leaves decompose slower 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). Reduced seed dispersal of woody species into the bamboo canopy could also contribute to 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). Further studies need to compare seed dispersal into the bamboo and tree canopies, examine seedling composition under bamboo canopies and investigate which species are able to germinate and establish there as well as looking into how different woody species respond to litter manipulations.

At a patch scale, bamboos negatively affect woody seedling abundance, species richness and diversity through their dense shades and litter (Paper IV). Although, seedling richness and diversity were not found to be related to the density of bamboos at the plot scale, adult species richness and diversity showed negative relationships (Paper I). However, the mechanisms in which bamboos affect adult richness and diversity at the plot scale may be different from those on seedlings at the patch scale. The negative relationships of bamboos on adults may be due to the resource competitions as bamboos can compete effectively for resources by their root systems (Griscom and Ashton 2003). Bamboos may also compete for the space on the forest floor as they can grow and spread faster than trees. Moreover, bamboo branches can also destroy trees growing below their canopies (Griscom and Ashton 2006). Therefore, changes in forest dominance structure, from a high diversity of tree species to a few bamboo species, may result in a concomitant reduction in overall woody species abundance, richness and diversity in these forest ecosystems.

4.4 Ontogenetic niche shift within woody species

We found that the environmental variables that most parsimoniously explained separation of species at the seedling stage (i.e. regeneration niche) differed from the variables that separated species at the sapling and adult stages (Paper III). Rank correlation tests also suggest that species are changing their relative position in environmental niche space from one stage to another. These results confirm ontogenetic niche shifts within the woody species we

examined (Paper III). Changing in the abundance of a plant species along a particular environmental gradient from seedling to adult stages may be caused by numerous processes occurring at earlier stages. At the seedling stage, abundance of seedlings is initially determined by abundant seed sources (reproductive adults), seed dispersal (Haper 1977; Hardesty and Parker 2002; Seidler and Plotkin 2006) and suitable environmental conditions for successful seed germination (regeneration niche). Then, both biotic and abiotic conditions affect growth and survival of seedlings and saplings (Augspurger 1983, 1984; Denslow & Guzman 2000; Nagamatsu et al. 2002), and these processes subsequently affect abundance of new adults recruited to a particular site. These myriads of factors that have different effects on individuals as they develop contribute to the change in relative density of species across life stages and along the environmental gradients.

Elevation was the only variable explaining separation among species at all life stages (Paper III). Most of the species were associated with being located below average elevation, especially at the sapling stage. This was because high elevation areas in the forest are associated with low water availability and areas being more prone to fire during the dry season. For example, *Croton roxburghii* and *Lithocarpus elegans* that were associated with high elevation at the sapling and adult stages, respectively, are reported to occur mainly in fire-prone areas (Gardner et al. 2000).

5. Concluding remarks and management implications

Environmental rather than human disturbance variables were important in explaining the variation in woody species richness and diversity in this forest ecosystem. The current human disturbance regime is not strong enough to impact woody species richness and diversity within the forest. This may be because the use of the forest by local people is limited. Although, human disturbances at the local scale do not necessarily cause direct loss of species richness and diversity in the forest, they may create heterogeneous conditions which influence interactions among plant species, and subsequently change the forest community structure. This study showed that human disturbance may facilitate competitive dominant species, affecting evenness in woody communities. Moreover, human disturbance can also facilitate bamboos, and bamboos can suppress woody seedlings regeneration. Therefore, bamboos

should be incorporated in management strategies when the aim is to maintain woody species richness and diversity in these forest ecosystems. If bamboos cover the forest floor at high densities, it may be necessary to actively control these species for successful tree establishment. A long term study is needed to clarify the effects of human disturbance on the forest community. A longer course of the experiment is also required to monitor if seedlings performance under bamboo canopies changes over long periods.

The woody species requirements to environmental conditions change as individuals develop. These ontogenetic niche shifts may be important in explaining the coexistence of plant species within a community. However, seed arrival may be more important than the niche explaining seedling density and diversity in forest communities (Paine and Harms 2009). Thus, further studies on seed dispersal are needed to clarify whether dispersal assembly or niche assembly play the most important role in generating this community structure. Based on our results, a good management strategy for woody species should consider the situation for each life stage.

6. References

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Paper I

Panadda Larpkern · Stein R. Moe · Ørjan Totland

The effects of environmental variables and human disturbance on woody species richness and diversity in a bamboo–deciduous forest in northeastern Thailand

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Abstract Variations in species richness and diversity at a local scale are affected by a number of complex and interacting variables, including both natural environmental factors and human-made changes to the local environment. Here we identified the most important determinants of woody species richness and diversity at different growth stages (i.e. adult, sapling and seedling) in a bamboo–deciduous forest in northeast Thailand. A total of 20 environmental and human disturbance variables were used to determine the variation in species richness and diversity. In total, we identified 125 adult, 111 sapling (within fifty 20 × 20-m plots) and 89 seedling species (within one hundred and twenty 1 × 1-m subplots). Overall results from stepwise multiple regression analyses showed that environmental variables were by far the most important in explaining the variation in species richness and diversity. Forest structure (i.e. number of bamboo clumps and canopy cover) was important in determining the adult species richness and diversity ($R^2 = 0.48, 0.30$, respectively), while topography (i.e. elevation) and human disturbance (i.e. number of tree stumps) were important in determining the sapling species richness and diversity ($R^2 = 0.55, 0.39$, respectively). Seedling species richness and diversity were negatively related to soil phosphorus. Based on our results, we suggest that the presence of bamboos should be incorporated in management strategies for maintaining woody species richness and diversity in these forest ecosystems. Specifically, if bamboos cover the forest floor at high densities, it may be necessary to actively control these species for successful tree establishment.

Keywords Bamboo–deciduous forest · Human disturbance · Species diversity · Thailand · Woody species

Introduction

A number of complex and interacting variables affect the spatial variation in woody species abundance, richness and diversity. At relatively small spatial scales, environmental variables, such as chemical and physical soil properties (Miyamoto et al. 2003; Eilu et al. 2004; Fu et al. 2004; Poulsen et al. 2006), topography (Oliveira-Filho et al. 1998; Miyamoto et al. 2003; Fu et al. 2004; Cielo-Filho et al. 2007) and canopy gaps (Oliveira-Filho et al. 1998; Svenning 2000), and human disturbance variables, such as logging (Slik et al. 2002; Brown and Gurevitch 2004), burning (Slik et al. 2002; Saha and Howe 2003; Otterstrom et al. 2006) and livestock grazing (McEvoy et al. 2006; Dufour-Dror 2007), are important drivers of community structure. At a larger scale (e.g. landscape), climatic variables (e.g. temperature and precipitation), altitude and soil types are frequently used to explain differences in species diversity and forest types (Archibold 1995; Whitmore 1998).

In seasonally dry tropical forests, water availability is an important factor affecting woody species distribution (Murphy and Lugo 1986) and, therefore, topography (e.g. elevation, slope and aspect) and soil physical properties related to ground moisture are potential controllers of the local species composition (Oliveira-Filho et al. 1998; Cielo-Filho et al. 2007). Tree species richness generally tends to increase with soil fertility (Givnish 1999). Variation in soil and vegetation in the tropical dry forest may occur at a fine scale within kilometers (Rundel and Boonpragob 1995; Oliveira-Filho et al. 1998). However, other factors, such as termite activity, which results in micro-scale improvements of the soil fertility, may contribute to small-scale variations in soil fertility within tropical forest communities (Dangerfield et al.

P. Larpkern (✉) · S. R. Moe · Ø. Totland
Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences,
P.O. Box 5003, 1432 Ås, Norway
E-mail: panadda.larpkern@umb.no
Tel.: +47-64-965399
Fax: +47-64-965801

1998) and to woody species composition (Loveridge and Moe 2004). Canopy openness related to light availability influences seedling establishment in the rain forest, especially pioneer and light-demanding species (Schnitzer and Carson 2001). However, in the tropical dry forest, canopy openness may correspond to water availability with effects on seedling growth and survival during the dry season (Gerhardt 1996).

The seasonally dry tropical forests are generally less complex in terms of vegetation structure than the wet forests and are, therefore, easier to access and utilise for many different purposes (Murphy and Lugo 1986). Intensive and prolonged human disturbances may lead to a decline in species diversity, change in species composition and forest degradation (Murphy and Lugo 1986; Ramirez-Marcial et al. 2001; Sagar et al. 2003; Brown and Gurevitch 2004; Sagar and Singh 2004). However, some studies have shown that tropical forests with an intermediate level of disturbance have the highest diversity (Connell 1978; Sheil 1999; Molino and Sabatier 2001). Thus, within forest management, it is necessary to consider how human activities and natural environmental conditions in concert affect richness and diversity of the forests. If species richness and diversity are maintained despite human utilisation, management strategies may not require the exclusion of human activities.

In Thailand, a bamboo–deciduous forest (henceforth termed bamboo forest) is a form of degraded forest—one previously dominated by teak (*Tectona grandis*) (FORRU 2006)—but which at present comprises a mixture of evergreen and deciduous trees forming the tree-layer and bamboos dominating the intermediate layer. Some researchers (e.g. Smitinand 1977; Marod et al. 1999) refer to this forest type as “a mixed deciduous forest”. Bamboos are pioneer species that dominate disturbed areas (Marod et al. 1999; Gardner et al. 2000), and they are able to effectively compete in forest gaps where they exclude other more light-demanding pioneer species (Tabarelli and Mantovani 2000). The life span of bamboos commonly lasts several decades (Wong 2004), and their simultaneous death after mass flowering may provide a large vacant space for tree regeneration (Marod et al. 1999). The bamboo forest experiences significant human disturbances due to the harvesting of valuable timber species, frequent use of fire, cattle grazing and cultivations (Marod et al. 1999; FORRU 2006). Due to the decline of the forested area in Thailand, there have been many attempts to describe and document Thailand’s vegetation (Maxwell 2004), but few studies have focused on the relative effects of environmental variables and human impacts on woody species richness and diversity. In order to improve management strategies for the bamboo forest, it is necessary to explain the underlying factors that result in spatial variations in woody species richness and diversity.

We report here our investigation of the relative effects of environmental and human disturbance variables on woody species richness and diversity in a bamboo forest

in the Na Haeo Forest Reserve, Thailand. Since trees at different growth stages may respond differently to these explanatory variables, we separated the woody plant into three growth stages according to size classes—i.e. adult, sapling and seedling. Specifically, we asked: (1) which environmental and human disturbance variables are the most important determinants of woody species richness and diversity at each growth stage? (2) how do these variables relate to the species richness and diversity of woody species?

Methods

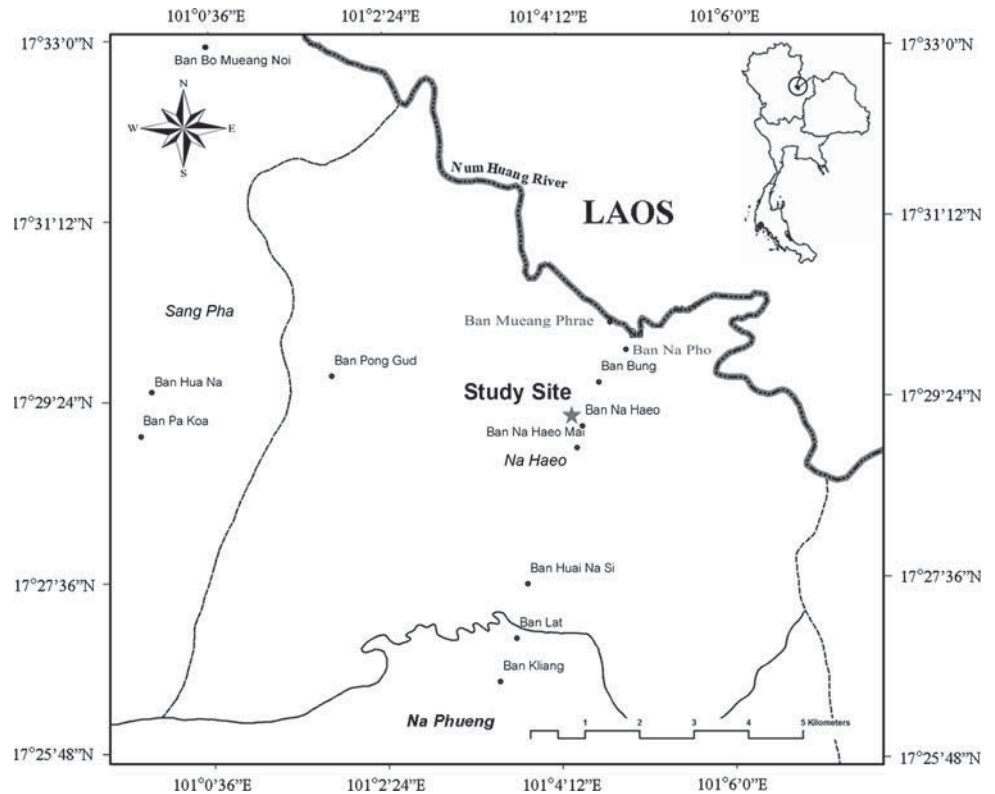
Study area

The study area (17°29'N, 101°04'E) is located in the Na Haeo Forest Reserve, Loei Province, Thailand (Fig. 1). The elevation ranges from 400–600 m a.s.l. The climate is monsoonal and can be divided into a rainy (May–October), a cool-dry (November–February) and a hot-dry season (March–April). The mean annual rainfall is 1551 mm (2001–2005), and during the study year in 2006, the total annual rainfall was 1632 mm. The minimum and maximum temperatures were 5°C in December and 37°C in April, respectively. The study area is typical for remaining fragments of bamboo forest commonly found in northeastern Thailand. The area is approximately 163 ha in total, comprising 161 ha covered mostly by the bamboo forest, with some agricultural fields and fallows near the forest edge. The area also contains small patches of teak trees that were introduced approximately 15 years ago. The forest is locally dominated by species such as *Cananga latifolia*, *Croton roxburghii*, *Gardenia sootepensis*, *Lagerstroemia* sp., *Aporosa octandra* var. *yunnanensis*, *Colona flagrocarpa* and *Pterocarpus macrocarpus*. Most trees shed their leaves in the dry season, and man-made ground fires are common. Although the forest is protected by law, local people have been using the forest for many purposes, including agricultural expansion, non-timber forest product collection, cattle grazing and charcoal making.

Sampling procedures

To quantify woody species richness and diversity in our study system, we constructed seven transect lines from a random chosen point in the area. Fifty plots of 20 × 20 m with at least a 20-m distance between them were established along these transect lines. Within each plot, all adult trees ≥4.0 cm in diameter at breast height (dbh 1.3 m) were counted and identified. The height (using a clinometer) was measured for each individual adult tree. Saplings that were >0.5 m in height and <4 cm dbh when their heights exceeded 1.3 m were counted and identified. The height of each individual

Fig. 1 The study area Na Haeo Forest Reserve, northeastern Thailand



sapling was measured within a 2-week period in June (rainy season), considering the effect of seasonality of rainfall on plant growth. The perimeters of the bamboo clumps were measured in all plots. In 30 of the 50 plots, each plot was divided into four equal squares (10×10 m), and a subplot of 1×1 m was randomly established in each square. Seedlings (≤ 0.5 m height) were recorded and monitored in the subplots throughout the year. Voucher specimens were collected and sent to the Herbarium at Chiang Mai University for species identification and confirmation.

Environmental and human disturbance variables were recorded at each plot (Table 1). Elevation was estimated by a global positioning system (GPS) at the centre of each plot. Slope was measured using an auto level meter, determining the difference in ground level position from the centre of each plot in northern, southern, western and eastern directions. The aspect was determined using a compass. Canopy cover was recorded using a densiometer. The termite mounds within each plot were counted, and the ground surface area of each mound was measured. In our study, the shape of the mound was normally circular; therefore, we used the formula πr^2 to calculate the surface area of the mound. Small waterways passing through the plots during the rainy season were observed (presence or absence). Bamboo clumps within each plot were counted and identified. The bamboo basal area of each clump was estimated using the circular distance around the clump.

Table 1 Dependent variables and environmental and human disturbance explanatory variables used in this study

Dependent variables	Independent variables
Number of woody species at Adult stage ($n = 50$) Sapling stage ($n = 50$) Seedling stage ($n = 30$)	Environmental variables Forest structure Canopy cover (%) Canopy height (m) Number of bamboo clumps Bamboo basal area (m^2)
Shannon diversity index at Adult stage ($n = 50$) Sapling stage ($n = 50$) Seedling stage ($n = 30$)	Edaphic factors pH Available phosphorus (ppm) Available potassium (ppm) Calcium (ppm) Magnesium (ppm) Total nitrogen (%) Organic matter (%) Sand (%)
	Topographic factors Slope ($^\circ$) Elevation (m)
	Others Number of termite mounds Termite mound ground surface area (m^2) Water way passing the plots (presence/absence)
	Human disturbance variables Number of tree stumps Trail length (m) Area covered by charcoal making holes (m^2)

Soil samples were taken in July (in the rainy season) 2006. Twelve soil samples (cores 25 cm long and 2 cm in diameter) were collected in a stratified random manner within each plot. The soil samples in each plot were mixed and kept in a freezer until analysed by the Soil and Water Analysis working group, Agrochemistry Section, Division of Agricultural Research, Ministry of Agriculture, Bangkok. The analyses included soil pH (at a 1:1 soil/water ratio), organic matter (Walkley–Black method), available phosphorus (Bray II), calcium, potassium and magnesium (ammonium acetate 1 N pH 7 extraction), total nitrogen (Kjeldahl method) and percentage of clay, silt, and sand (hydrometer and pipette method).

Any holes from the making of that appeared in any of the plots were counted, and the size (width and length) of each hole was measured. Any walking trails crossing through the plots were observed and the length of the trails in each plot measured. The number of tree stumps within each plot was recorded.

Statistical analyses

The Shannon diversity index (H') was calculated for each plot using the following equation (Magurran 1988):

$$H' = -\sum_{i=1}^S p_i \ln p_i.$$

In the above equation, p_i is the proportional abundance of i th species in the sampling plot, and S equals the total number of species in the sampling plot.

We used a forward stepwise selection method in multiple regression analyses to select the best combination of explanatory variables (Glantz and Slinker 1990) that explained the variation in woody species richness and diversity. The values of alpha to enter and to remove independent variables were both set at 0.15. The analyses were performed using SYSTAT ver. 10 (Systat, Evanston, IL). The details of the variables used in the analyses are shown in Table 1.

Results

Woody species richness and diversity

Within the 2-ha total sampling area we identified 125 species in the adult stage and 111 species in the sapling stage. Within the 0.012-ha total seedling sampling area, we found 89 seedling species. Considering all growth stages, we counted a total of 136 woody species belonging to 44 families. Most species (82) were represented in more than one growth stage, 30 species were found only as adults, 24 species were found only in the sapling stage while no species was represented in the seedling stage only. Family Euphorbiaceae was represented by the highest number of species (15) followed by

Fabaceae and Rubiaceae with 13 and eight recorded species, respectively.

There were 118,000.0 seedlings, 2189.5 saplings and 849.5 adults per hectare, respectively (Table 2). The majority of individuals belonged to a relative small number of species. Many species abundant at the adult stage were also abundant at the sapling and seedling stage (Pearson correlation coefficients 0.70 and 0.59, respectively; $P < 0.001$). *Croton roxburghii* was a distinctive species in the forest due to its high density and frequency at all growth stages (Table 2). The three bamboo species that were present, *Gigantochloa albociliata*, *Bambusa tulda* and *Cephalostachyum pergracile*, dominated the forest (Table 3). These species are characterised as sympodial or clumping-forming type. The basal area of the bamboo basal area was 198.1 m²/ha, while the overall basal area of adult tree species was 17.1 m² ha⁻¹ (Tables 2, 3).

The canopy layer of the forest can be divided into three layers based on the mean height of the major species (Table 2). An upper canopy layer with tree height 10–14 m included tree species such as *Pterocarpus macrocarpus*, *Cananga latifolia*, *Canarium subulatum* and *Castanopsis indica*. A medium layer of height 6–9 m included species such as *Quercus kerrii*, *Aporosa octandra* var. *octandra*, *Memecylon scutellatum*, *Aporosa octandra* var. *yunnanensis* and *Harrisonia perforata*. The medium layer of the forest also included a dense bamboo understory. The sapling layer of the forest covered heights from 1 to 3 m.

Effects of environmental and human disturbance variables

Multiple regression showed that the number of bamboo clumps (negative relationship) and the canopy cover (positive relationship) explained almost 50% of the variation in adult species richness (Table 4). Elevation (negative) and number of tree stumps (positive) were the two most important explanatory variables for sapling species richness, while phosphorus (negative) and canopy height (negative) were the two most important variables explaining the variation in seedling species richness (Table 4). In terms of diversity, the number of bamboo clumps (negative) and canopy cover (positive) were the main explanatory variables for the variation in adults (Table 5). The number of tree stumps (positive) and elevation (negative) were the two most important explanatory variables for sapling diversity, while phosphorus (negative) and elevation (negative) were the two most important explanatory variables of seedling diversity (Table 5).

In general, explanatory variables included in our models after stepwise variable selection explained a large amount of the variation in species richness at all growth stages ($R^2 \geq 0.60$; Table 4). The selected variables also explained a large amount of the variation in the species diversity at the sapling and seedling stage ($R^2 = 0.58$,

Table 2 Density, frequency and basal area of woody species represented in different growth stages (adult, sapling and seedling) in a bamboo–deciduous forest at the Na Haeo Forest Reserve, northeastern Thailand

Species	Density ($n \text{ ha}^{-1}$)			Frequency (%)			Mean height (m) ^a		Basal area ($\text{m}^2 \text{ ha}^{-1}$) ^b
	Seedlings	Saplings	Adults	Seedlings	Saplings	Adults	Saplings	Adults	
<i>Antidesma sootepense</i>	2,000.0	29.0	4.0	20	26	10	2.18	4.50	0.01
<i>Aporosa octandra</i> var. <i>octandra</i>	– ^c	39.5	29.5	–	36	38	1.72	7.70	0.21
<i>Aporosa octandra</i> var. <i>yunnanensis</i>	2,333.3	46.5	31.5	50	58	46	1.77	7.14	0.18
<i>Cananga latifolia</i>	–	12.5	44.5	–	16	78	1.36	13.15	2.10
<i>Canarium subulatum</i>	6,000.0	8.0	16.0	47	6	40	1.75	12.43	0.65
<i>Castanopsis indica</i>	–	29.0	20.5	–	14	12	1.26	12.04	0.42
<i>Colona flagrocarpa</i>	–	24.0	21.5	–	48	50	3.09	11.20	0.20
<i>Cratoxylum cochinchinense</i>	–	44.0	6.5	–	26	18	1.41	11.14	0.11
<i>Cratoxylum formosum</i>	3,250.0	22.5	10.0	53	36	20	1.08	10.84	0.14
<i>Croton roxburghii</i>	12,166.7	568.0	84.5	73	94	78	1.16	10.87	0.46
<i>Dalbergia cana</i> var. <i>cana</i>	–	28.0	19.5	–	40	42	1.77	10.67	0.24
<i>Gardenia sootepensis</i>	1,0250.0	13.5	41.0	67	36	64	2.98	10.09	0.10
<i>Goniothalamus laoticus</i>	–	65.0	14.0	–	50	30	1.68	10.35	0.19
<i>Harrisonia perforata</i>	1,916.7	2.0	8.5	40	8	16	0.79	6.91	0.04
<i>Hydnocarpus</i> sp.	3,916.7	51.5	16.5	37	32	24	0.99	10.69	0.26
<i>Lagerstroemia</i> sp.	2,333.3	178.0	67.0	53	92	12	1.19	11.72	2.04
<i>Lithocarpus elegans</i>	1,416.7	215.0	24.5	30	54	2	1.13	9.93	0.27
<i>Memecylon scutellatum</i>	40,750.0	28.0	54.5	80	36	38	0.98	7.54	0.47
<i>Phoebe lanceolata</i>	–	38.0	–	–	32	–	1.39	–	–
<i>Polyalthia cerasoides</i>	–	65.0	1.5	–	62	4	1.73	5.50	0.002
<i>Pterocarpus macrocarpus</i>	2,833.3	26.5	18.0	50	52	46	1.15	14.08	0.74
<i>Pterospermum semisagittatum</i>	1,916.7	180.0	5.5	27	58	12	0.97	10.60	0.10
<i>Quercus kerrii</i>	–	55.0	31.5	–	30	30	1.02	8.48	0.41
<i>Suregada multiflorum</i>	2,000.0	26.0	7.0	13	36	24	1.15	11.46	0.15
<i>Terminalia triptera</i>	4,166.7	95.0	11.5	43	60	32	1.24	11.20	0.18
Other species	20,749.9	300.0	179.0	–	–	–	–	–	7.38
Total	118,000.00	2,189.5	849.5	–	–	–	–	–	17.06

The species shown are based on a combination of the 15 most abundant species at each growth stage

^aThe heights were measured only for sapling and adult stages

^bThe basal areas were measured only for adult stage

^cSpecies did not occur

Table 3 Density, frequency and basal area of bamboo species represented in a bamboo–deciduous forest at the Na Haeo Forest Reserve, northeastern Thailand

Species	Density (no. of clumps ha^{-1})	Frequency (%)	Basal area ($\text{m}^2 \text{ ha}^{-1}$)
<i>Bambusa tulda</i>	4.5	8	13.50
<i>Cephalostachyum pergracile</i>	174.5	70	122.70
<i>Gigantochloa albociliata</i>	67.5	70	61.90
Total	246.5	–	198.10

0.69, respectively) but only moderately at the adult stage ($R^2 = 0.40$) (Table 5). In general, more variables were included in the models explaining the variation in species richness than in those explaining diversity. For adults and saplings, the variables explaining the variation in species diversity also explained the variation in species richness, except for pH, which only contributed to the variation in species diversity of saplings. Seedling richness and diversity were explained by different variables, with the exception of phosphorus, which significantly explained the variation in both species richness and diversity.

The independent variables in our study generally showed low intercorrelation (Table 6). For all final models, all tolerance values were greater than 0.46, indicating that the assumption of low collinearity among predictor variables was not seriously violated in our analyses (Tables 4, 5).

Discussion

Overall effects of environmental and human disturbance variables

Environmental variables were by far more important than human disturbance variables in explaining the variation in species richness and diversity. The only significant human disturbance variable in our models was the number of tree stumps, which was the most important variable explaining the diversity of saplings ($R^2 = 0.26$) and the second most important variable in explaining the variation in sapling species richness ($R^2 = 0.13$). Both sapling species richness and diversity were positively related to the number of tree stumps. Human abrasion (trail length) and man-made fires (the presence of charcoal making holes) did not relate to the

Table 4 Stepwise multiple regression analyses on species richness as a function of 20 independent variables (see Table 1)

Variable	ΔR^2	Coefficient	Standard error	Standard coefficient	Tolerance	t	P (two-tailed)
Number of adult species, $n = 50$ (multiple $R^2 = 0.74$, $F = 11.32$, $P < 0.001$)							
Constant		1.251	10.298	0.000	–	0.121	0.904
Number of bamboo clumps	0.280	–0.324	0.084	–0.456	0.465	–3.836	<0.001
Canopy cover (%)	0.478	0.273	0.086	0.298	0.743	3.170	0.003
Bamboo basal area (m ²)	0.549	–0.454	0.110	–0.451	0.546	–4.115	<0.001
Small water way (present/absence)	0.596	4.743	1.369	0.335	0.702	3.465	0.001
Canopy height (m)	0.649	–0.856	0.320	–0.244	0.792	–2.676	0.011
Phosphorus (ppm)	0.674	–0.782	0.485	–0.158	0.681	–1.612	0.115
Termite mound ground surface area (m ²)	0.691	0.093	0.044	0.204	0.718	2.127	0.040
Nitrogen (%)	0.708	94.102	40.016	0.245	0.606	2.352	0.024
Trail length (m)	0.726	0.074	0.040	0.176	0.727	1.847	0.072
Potassium (ppm)	0.744	–0.034	0.021	–0.172	0.592	–1.632	0.111
Number of sapling species, $n = 50$ (multiple $R^2 = 0.76$, $F = 18.90$, $P < 0.001$)							
Constant		93.509	22.114	0.000	–	4.229	<0.001
Elevation (m)	0.427	–0.192	0.036	–0.465	0.767	–5.379	<0.001
Number of tree stumps	0.553	0.430	0.144	0.257	0.772	2.982	0.005
Calcium (ppm)	0.612	0.015	0.007	0.199	0.618	2.069	0.045
Potassium (ppm)	0.666	–0.081	0.023	–0.303	0.794	–3.564	0.001
Number of bamboo clumps	0.697	–0.200	0.084	–0.208	0.758	–2.390	0.021
Canopy cover (%)	0.727	0.305	0.104	0.246	0.806	2.920	0.006
Magnesium (ppm)	0.759	0.048	0.020	0.238	0.559	2.350	0.024
Number of seedling species, $n = 30$ (multiple $R^2 = 0.60$, $F = 5.74$, $P = 0.001$)							
Constant		3.437	21.100	0.000	–	0.163	0.872
Phosphorus (ppm)	0.179	–0.090	0.023	–0.687	0.573	–3.944	0.001
Canopy height (m)	0.309	–1.291	0.435	–0.411	0.907	–2.969	0.007
Potassium (ppm)	0.416	–0.090	0.023	–0.687	0.573	–3.944	0.001
Small water way (present/absence)	0.466	3.398	1.582	0.352	0.650	2.149	0.042
Number of termite mounds	0.552	1.097	0.427	0.421	0.648	2.567	0.017
pH	0.600	6.667	4.008	0.249	0.780	1.663	0.110

Forward selection of variables was used with the following criteria: $\alpha = 0.15$ to enter and 0.15 to remove

Table 5 Stepwise multiple regression analyses on the Shannon diversity index (H') as a function of 20 independent variables (see Table 1)

Variable	ΔR^2	Coefficient	Standard error	Standard coefficient	Tolerance	t	P (2 Tail)
H' of adult species, $n = 50$ (multiple $R^2 = 0.40$, $F = 7.35$, $P < 0.001$)							
Constant		0.913	0.666	0.000	–	1.369	0.178
Number of bamboo clumps	0.156	–0.016	0.007	–0.348	0.588	–2.302	0.026
Canopy cover (%)	0.304	0.022	0.007	0.377	0.961	3.190	0.003
Bamboo basal area (m ²)	0.359	–0.019	0.009	–0.296	0.686	–2.116	0.040
Phosphorus (ppm)	0.395	–0.069	0.042	–0.221	0.744	–1.646	0.107
H' of sapling species, $n = 50$ (multiple $R^2 = 0.58$, $F = 12.23$, $P < 0.001$)							
Constant		0.644	2.530	0.000	–	0.255	0.800
Number of tree stumps	0.260	0.030	0.013	0.258	0.798	2.362	0.023
Elevation (m)	0.387	–0.011	0.003	–0.380	0.835	–3.560	0.001
Canopy cover (%)	0.476	0.028	0.009	0.332	0.852	3.145	0.003
pH	0.541	0.763	0.360	0.225	0.840	2.118	0.040
Magnesium (ppm)	0.581	0.003	0.001	0.219	0.844	2.065	0.045
H' of seedling species, $n = 30$ (multiple $R^2 = 0.69$, $F = 18.96$, $P < 0.001$)							
Constant		6.268	2.193	0.000	–	2.858	0.008
Phosphorus (ppm)	0.417	–0.245	0.038	–0.733	0.939	–6.466	<0.001
Elevation (m)	0.628	–0.014	0.003	–0.530	0.898	–4.570	<0.001
pH	0.686	0.754	0.342	0.251	0.930	2.203	0.037

Forward selection of variables was used with the following criteria: $\alpha = 0.15$ to enter and 0.15 to remove

species richness or the diversity in this area. Our findings that human disturbance variables had no—or relatively minor—impact (except on sapling species richness and diversity) and that a combination of the environmental variables explained a very large amount of the variation for all growth stages suggests that environmental conditions, rather than human impact, are the main drivers

of community species richness and diversity in the bamboo forests. It should be noted that human activities within the forest may be partly incorporated in some of the environmental variables (e.g. canopy cover). However, based on the relatively low correlations (Table 6) between human disturbance and environmental variables (the largest was 0.44, between trail length and the

Table 6 Pearson correlation coefficients between independent variables

	Canopy cover	Canopy height	Bamboo clumps	Bamboo basal area	pH	Phosphorus	Potassium	Calcium	Magnesium	Total nitrogen
Environmental variables										
Canopy cover	-0.276									
Canopy height	0.024	0.237								
Bamboo clumps	0.104	0.131	0.551							
Bamboo basal area	0.164	-0.182	-0.265	-0.042						
pH	-0.163	-0.203	-0.480	-0.322	-0.114					
Phosphorus	0.154	0.013	0.078	0.228	0.161	-0.035				
Potassium	-0.035	-0.217	-0.125	0.085	0.602	-0.144	0.356			
Calcium	-0.284	0.002	-0.110	-0.022	0.178	-0.035	0.292	0.564		
Magnesium	-0.044	0.035	0.184	0.215	0.048	-0.032	0.536	0.560	0.360	0.999
Total nitrogen	-0.041	0.040	0.191	0.224	0.042	-0.038	0.539	0.555	0.357	-0.428
Organic matter	-0.232	-0.078	-0.109	-0.081	-0.003	0.298	-0.551	-0.178	-0.120	0.999
Sand	0.148	0.101	0.274	0.283	0.045	-0.393	0.270	0.242	0.462	0.246
Slope	-0.209	0.406	0.329	0.237	-0.057	-0.228	0.103	0.011	0.191	0.245
Elevation	-0.136	0.120	0.324	0.303	-0.127	-0.199	0.285	0.081	-0.139	0.412
Number of termite mounds	-0.043	0.149	0.296	0.444	-0.047	-0.263	-0.043	-0.017	-0.018	-0.079
Termite mound ground surface area	0.375	0.000	-0.058	0.092	0.272	-0.190	0.262	0.141	0.150	-0.089
Water way										
Human disturbance variables										
Number of tree stumps	0.137	-0.277	-0.401	-0.369	0.316	0.070	-0.033	0.014	0.044	-0.336
Trail length	0.109	-0.110	0.441	0.264	-0.333	-0.157	0.078	-0.192	-0.156	0.045
Charcoal making holes (area)	-0.332	-0.074	-0.136	0.094	0.024	0.072	-0.305	0.041	-0.076	-0.069
	Organic matter	Sand	Slope	Elevation	Number of termite mounds	Termite mound ground surface area	Water way	Number of tree stumps	Trail length	Charcoal making holes (area)
Environmental variables										
Canopy cover										
Canopy height										
Bamboo clumps										
Bamboo basal area										
pH										
Phosphorus										
Potassium										
Calcium										
Magnesium										
Total nitrogen										
Organic matter										
Sand	-0.432									
Slope	0.243	-0.306								
Elevation	0.254	-0.062	0.054							
Number of termite mounds	0.418	-0.336	0.021	0.231						
Termite mound ground surface area	-0.066	0.039	0.074	-0.040	0.336	-0.057				
Water way	-0.090	-0.242	0.304	-0.089	-0.164					
Human disturbance variables										
Number of tree stumps	-0.340	-0.126	0.010	-0.330	-0.219	-0.248	0.240			
Trail length	0.045	0.001	0.313	-0.278	0.089	0.038	-0.079	-0.106		
Charcoal making holes (area)	-0.074	0.226	-0.126	0.115	-0.029	0.008	-0.137	-0.190	-0.101	

Statistical significant correlations ($P < 0.05$) are indicated with bold numbers

number of bamboo clumps), it would appear that such indirect human influences may be of relatively low importance in our system. Nevertheless, we admit that long-term experiments would be required to truly decouple the effects of “environmental” and “human” influences on richness and diversity on this forest ecosystem.

Effects of environmental and human disturbance variables on different growth stages

Species richness and diversity at each growth stage were related to different environmental and human disturbance variables, indicating that each growth stage has distinctive environmental requirements and responds differently to human disturbances. Forest structure (i.e. the number of bamboo clumps and canopy cover) was important in determining adult species richness and diversity, while topographic factors (i.e. elevation) and human disturbance (i.e. number of tree stumps) were important in determining sapling species richness and diversity. Phosphorus was the most important variable in explaining the seedling species richness and diversity, supporting Vargas-Rodriguez et al. (2005) who found that edaphic factors appear to be more important at the early stage of tree development than at later life stages. Because of their small size, seedlings are more susceptible to small-scale variation in environmental conditions, such as soil fertility compared to variables like forest structure, topography and human disturbance. The strong negative impact of phosphorus on seedling richness and diversity may be due to a low number of nutrient-demanding species having a competitive advantage at high levels of available phosphorus. An experiment in a Mexican dry forest showed that the addition of phosphorus decreased seedling diversity while it increased the recruitment of only a few species (Ceccon et al. 2004).

Sapling richness and diversity were highest at the lower elevation. While seedlings establish during the wetter parts of the year and adults have extensive root systems, rapidly growing saplings have high water requirements and are prone to water deficiency (Kume et al. 2007). Water availability is higher close to streams at lower elevations. Furthermore, higher elevations are more prone to fire during the dry season. The number of tree stumps had a positive effect on sapling species richness and diversity. This may indicate that there is resource competition between saplings and adult trees (Goldberg 1990).

The variables assessed in this study explained a large proportion of the variation in species richness of all growth stages, but they had less explanatory power on the variation in diversity (except for the seedling stage). Mechanisms controlling species diversity are typically more complex than those controlling richness (Ozinga et al. 2005; Wilsey and Stirling 2007). The Shannon index of diversity accounts for both evenness and species

richness (Magurran 1988), but these two components can be influenced by different processes, with richness being more influenced by seed dispersal and evenness more by species interactions, such as competition (Ma 2005; Wilsey and Stirling 2007).

Effect of bamboos

Some of the tree species that are the main components of a typical naturally occurring bamboo forest, such as *Xylia xylocapa* var. *kerrii*, *Afzelia xylocarpa* and *Chukrasia tabularis* (FORRU 2006), did not occur in our study area. These species are valuable timber species and, as is frequently the case for teak, they may have become locally extinct through excessive harvesting. This forest has been through a period of secondary growth, and less valuable tree species, such as *Cananga latifolia*, *Croton roxburghii* and *Memecylon scutellatum*, have partly replaced the former vegetation. However, other valuable timber species, such as *Lagerstroemia* sp. and *Pterocarpus macrocarpus*, still exist in high abundance in this forest.

Although the bamboo species occurring in our study area are the non-invasive clump-forming types (Wong 2004), their long life spans and their large clumps at high densities make the continuous recruitment and development of seedlings difficult (Marod et al. 1999). We found that adult species richness and diversity and sapling species richness were negatively related to the number of bamboo clumps. However, bamboo density was not related to the richness and diversity of seedlings. Many studies have revealed that a bamboo understory impedes seedling establishment, mainly due to reduced light intensity (e.g. Taylor et al. 2004, 2006). Unlike tropical rain forests, light limitation or gap dynamics may not be important for seedling regeneration in tropical dry forests (Gerhardt and Hytteborn 1992; Mooney et al. 1995; Gerhardt 1996). In seasonally dry forests, light is commonly of less importance due to the lower stature and vertical structural simplicity of the forests and to seasonal deciduousness causing spatial and temporal variability in the availability of light (Murphy and Lugo 1986). Therefore, seedling establishment and the survival of the seasonally dry forest may not be impeded by low light intensity under bamboo canopies. However, at a small scale, bamboo canopies may affect seedling establishments more than at a plot scale.

Conclusions

Based on the findings of our investigation, we conclude that environmental variables, rather than human disturbances, are the main drivers of spatial variation in woody species richness and diversity of the Na Haeo forest Reserve. Current human activities do not appear to have severe negative effect on community

properties. We suggest that the presence of bamboos should be incorporated in management strategies for maintaining tree richness and diversity in the bamboo-deciduous tropical forest ecosystem. Specifically, if bamboos cover the forest floor at high densities, it may be necessary to actively control these species for successful tree establishment. Cutting back the shoots may be an effective approach for controlling the clumping bamboos. However, it is important to account for the fact that bamboos are natural elements in—and characteristic of—this forest type and that they represent an important ecosystem service by supplying food, housing, tools and handicrafts for local people. Therefore, any forest management programme should not completely eliminate the bamboo species.

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Paper II



Do disturbance and productivity influence evenness of seedling, sapling and adult tree species across a semi-deciduous tropical forest landscape?

Panadda Larpkern, Ørjan Totland and Stein R. Moe

P. Larpkern (panadda.larpkern@umb.no), Ø. Totland and S. R. Moe, Dept of Ecology and Natural Resource Management, The Norwegian Univ. of Life Sciences, PO Box 5003, NO–1432 Ås, Norway.

Disturbance and productivity may influence and alter community structure by affecting the partitioning of resources among species. Here, we examined how evenness in the relative abundance of growth stages (seedlings, saplings and adults) of woody species is related to measures of productivity (i.e. total diameter breast high (dbh) and tree volume) and aspects of human disturbance (i.e. number of tree stumps, area covered by charcoal making holes and trail length) in a bamboo-deciduous forest, northeastern of Thailand. Our results using stepwise multiple regressions showed that productivity (total dbh) explained a significant part of the variation in evenness only at the adult stage where evenness decreased with productivity. We found a decreased evenness of saplings with the area covered by charcoal making holes. Evenness of seedlings was not related to productivity or human disturbance variables and other environmental variables contribute more to explain the variation in evenness at this stage. Evenness was correlated consistently between the growth stages but the strength of relationships diminishes across the stages. Our results suggest that high productivity and human disturbance may facilitate competitive dominant species, affecting evenness in woody communities.

The understanding of how productivity is related to species diversity has long been of great interest to ecologists (Tilman 1996, Hector et al. 1999, Tilman et al. 2001, Chalcraft et al. 2009). Often species richness has been used as a surrogate of species diversity. However, species diversity comprises both species richness; the number of species in given area, and evenness; the relative contribution of each species to the total number of individuals (Magurran 1988). Species richness and evenness in plant communities are not always correlated (Wilsey et al. 2005, Bock et al. 2007), and may be influenced by different processes; with richness mainly controlled by migration (the available species pool), and evenness mainly by local biotic interactions (competition or facilitation) (Stirling and Wilsey 2001, Wilsey and Stirling 2007). Thus, it appears that evenness, at least in plants, represent a unique property of diversity. Moreover, explaining plant diversity of communities using the number of species may overlook the quantitative structure of communities, such as the relative abundance of rare and dominant species and their roles in the communities.

Recently, many studies have addressed how plant species evenness is an important community property that influences productivity (Wilsey and Porvin 2000, Polley et al. 2003, Mulder et al. 2004, Wilsey and Polley 2004, Mwangi et al. 2007, Hillebrand et al. 2008). On the other hand, very few studies have examined how productivity may function as a determinant of evenness (Drobner et al. 1998, Laird et al.

2003, Chalcraft et al. 2009). In this study we therefore focus on how landscape-scale spatial variation in productivity and disturbance may explain variation in evenness within natural plant communities. According to McGill et al. (2007), little is known about how evenness, presented by species abundance distributions (SADs), is affected by productivity. Based on large scale observations in natural communities, Whittaker (1960, 1975), Hubbell (1979), Hurlbert (2004) and McGill et al. (2007) concluded that productivity most likely positively influences species evenness, without proposing any mechanism behind such pattern. In addition Sagar and Singh (2006), using tree basal area as a surrogate of biomass and productivity, found that evenness was positively related with productivity in dry tropical forest in India. On the other hand, Vance-Chalcraft et al. (2010) found that evenness in general was negatively related to above ground biomass in a subtropical forest of Puerto Rico. We propose that productivity could also negatively influence species evenness at a local scale. Unproductive environments can only support small population densities of species. Hence, interspecific competition is expected to be low, resulting in a more even distribution of species compared with intense competitive situations, where a few highly competitive species often gain strong dominance (Drobner et al. 1998, Rajaniemi 2002, Rajaniemi et al. 2003, Mulder et al. 2004, Hillebrand et al. 2007, Chalcraft et al. 2009). Thus, as an indirect effect of high productivity, competitively dominant

species may suppress the population densities of other species, resulting in decreased evenness. Highly competitive environments, with high productivity are also hypothesized to generate skewed (i.e. uneven) distributions of individual plant sizes (Obeid et al 1967).

In addition to productivity, human disturbances can also affect species evenness by changing the species composition of communities (Hillebrand et al. 2008) because disturbances may differentially affect the density of species. Such changes may influence interactions among species at the same trophic level (Ellison et al. 2005), which may cascade into effects on their relative abundance, and thus evenness (Hillebrand et al. 2007, 2008). Evenness may increase following disturbances, due to a reduction in population density of competitively strong species (i.e. potentially dominant species) which are sensitive to disturbances (Kumar and Ram 2005, Sagar and Singh 2006, Sahu et al. 2008, Reitalu et al. 2009). However, if the potentially dominant species are not affected by disturbances, the disturbances will likely decrease evenness because competitive weak species may be reduced in abundance (Yadav and Gupta 2006). It is conceivable that evenness is more sensitive to changes in productivity and disturbance than richness because the relative abundance among species likely changes more rapidly with productivity or disturbance than the actual number of species (Chapin et al. 2000, Chalcraft et al. 2009). Therefore, understanding how productivity and disturbance may influence evenness is important because they can influence and alter community structure before any species are lost, by affecting the partitioning of resources among species.

In this study we examine how evenness of growth stages (seedlings, saplings and adults) of tropical tree species is related to measures of productivity and aspects of human disturbance. To our knowledge, this is the first study that examines such relationships in concert. We predict that: 1) evenness decreases with productivity for all growth stages because highly productive environments tend to have more individuals and a stronger dominance structure (Mulder et al. 2004, Chalcraft et al. 2008), and that; 2) this relationship is strongest for adults, because they exert stronger competitive effects on each other compared with seedlings and saplings (Callaway and Walker 1997, Li et al. 2008), and because the community of adult individuals have been exposed longer to the dominance hierarchy of the community than seedlings and saplings (Collins and Carson 2004). Because disturbance may prevent dominant species from gaining high abundance (Kumar and Ram 2005, Sagar and Singh 2006, Reitalu et al. 2009), we predict that; 3) human disturbances increase evenness of all growth stages. Finally, we predict that; 4) evenness is not correlated consistently between the growth stages, because of an increased intensity of competition from seedlings to adults (Callaway and Walker 1997, Li et al. 2008, Paine et al. 2008).

Methods

Study area

The study was conducted in the Na Haeo Forest Reserve, Loei Province, northeastern Thailand, 17°29'N, 101°04'E.

The area is on a plateau at about 400–600 m elevation. It is characterized by a tropical monsoonal climate with pronounced wet and dry seasons, and high temperatures throughout the year. The seasons are divided into a rainy (May–October), a cool–dry (November–February) and a hot–dry season (March–April). The mean annual rainfall is 1 551 mm (2001–2005), and during the study year in 2006, the total annual rainfall was 1632 mm. The mean monthly minimum and maximum temperature ranges were 12–24°C and 28–34°C, respectively.

The study area (163 ha) consists mostly of bamboo–deciduous forest or mixed deciduous forest. Although the study area is relatively small it has a high diversity of plant species, and it is representative for much of the remaining forest in the region. The bamboo forest comprises a mixture of evergreen and deciduous trees. The dominant tree species are *Cananga latifolia*, *Lagerstroemia* sp., *Gardenia sootepensis*, *Spondiix laxiflora* and *Pterocarpus macrocarpus*. An upper tree canopy (ca 10–14 m high) is dominated by *Pterocarpus macrocarpus*, *Cananga latifolia*, *Canarium subulatum* and *Castanopsis indica*. A medium tree canopy (ca 6–9 m high) includes *Quercus kerrii*, *Aporosa octandra* var. *octandra*, *Memecylon scutellatum*, *Aporosa octandra* var. *yunnanensis* and *Harrisonia perforate*. The three bamboo species; *Gigantochloa albociliata*, *Bambusa tulda* and *Cephalostachyum pergracile* are common in the understorey. Fires are common and canopy cover is sparse in the dry season since most trees shed their leaves. Agricultural expansion, non-timber forest product collection, cattle grazing and charcoal making are the main human-disturbance factors in the area.

Sampling procedures

We randomly positioned seven transect lines in the area in 2006. Along these transects we placed a total of 50 plots of 20 × 20 m for measurements of density of adults and saplings of woody species. All plots were more than 20 m apart. We divided each plot into four squares of 10 × 10 m, and randomly positioned a 1 × 1 m subplot within each square for measurements of seedling densities. We counted adults and saplings within the whole 20 × 20 m square in each of the 50 plots, whereas seedlings were counted within the four 1 × 1 m subplots, and only in 30 of the 20 × 20 m plots.

We separated individuals of the woody species into adults, saplings and seedlings by using plant height and diameter at breast height (dbh; at 1.3 m stem height); adults (dbh ≥ 4cm), saplings (height > 0.5 m and dbh < 4 cm when their height were exceeding 1.3 m) and seedlings (height ≤ 0.5 m). Voucher specimens were collected and sent to the herbarium at Chiang Mai University for species identification and confirmation.

To estimate productivity we measured dbh with diameter tape and height with a clinometer for all adult trees. We quantified productivity in two ways: 1) as a measure of a total dbh (cm) of all trees in each plot and 2) as a measure of a total tree volume (m³). Although it can be argued that these two measures represent standing crop and not productivity, other studies have found a relationship between productivity and standing crop (Clark et al. 2001) and total dbh is frequently used as a surrogate measure of tree productivity (Sagar and Singh 2006). It can also be argued that

standing crop is a function of previous production associated with our main interest, evenness. Another measure that can be used to represent above ground production is litterfall (Clark et al. 2001). We found that litterfall was correlated with total dbh (Pearson correlation coefficient: $r = 0.416$, $p = 0.022$). However, since we only have litterfall data from 30 of the plots we rather used dbh and tree volume since we have data on these variables from 50 plots for adults and saplings. The tree volume includes both the dbh and height, and is calculated for each tree as $\pi/4 d^2 \times ht$ where $d =$ dbh (m) and $ht =$ height (m), and then summarize the tree volume of all trees over each plot. Since these two estimates of productivity were not highly correlated in our study (Pearson correlation coefficient: $r = 0.4$), we decided to use both the total dbh and total tree volume as productivity variables in our analyses. We measured three variables to represent the local-scale human disturbance intensity, i. e. number of tree stumps, the area covered by charcoal making holes, and trail length. Within each 20×20 m plot: 1) the tree stumps were counted, 2) the size (width and length) of any charcoal making holes was measured and then summarized as area covered (m^2), and 3) the length (m) of any walking trails crossing through the plots was measured.

Because of the longevity of trees, an experimental approach (where we manipulated productivity and disturbance) was not practically possible in our study. However, although our primary goal was to study the possible effects of productivity and human disturbance on evenness of the three growth stages, we included additional information on several abiotic (e.g. edaphic and topographic factors) and biotic (e.g. bamboo and termite mound density) variables in order to control, in a statistical sense, for their potential influences on evenness. This was also based on other studies suggesting that the strengths of relationships between above ground biomass and multiple measures of biodiversity (including evenness) are often quite weak, and may be reduced by other local environmental factors, such as soil fertility, topography and elevation (Chalcraft et al. 2009, Vance-Chalcraft et al. 2010). Methods of measurement of these variables in this study are described fully in Larpkern et al. (2009).

Data analyses

We calculated the Pielou's species evenness index for each plot by dividing the Shannon diversity index (H') by \ln (species richness) (H_{max}') (Pielou 1975). Initially, we calculated "odds measure of evenness" since it has been suggested as more appropriate measure of evenness (Kvålseth 1991). The two measures evenness were, however, highly correlated ($r = 0.9$) and we therefore used Pielou's species evenness because it is the most commonly applied evenness in many studies.

We used stepwise multiple regressions, with forward selection of variables, to determine the relative importance of productivity, human disturbance and environmental variables, in explaining variation in species evenness among our plots. The criteria to enter and to remove variables from the models was set to $\alpha = 0.15$. Initial analyses included the categorical variable transect, but this variable did not contribute significantly ($p > 0.05$ in all cases) to explain variation in evenness in any of the growth stages. Therefore, we removed transect from further analyses. Before the analyses,

we checked the predictor variables for intercorrelations, and generally they showed low intercorrelations, only rarely $r > 0.5$ (Larpkern et al. 2009). However, we removed soil organic matter content and calcium from the analyses, due to high correlations ($r > 0.6$) with other variables. The tree volume, number of tree stumps and number of bamboo clumps were log-transformed to improve normality. According to Murtaugh (2009) the variable-selection methods can provide useful predictive models when many explanatory variables are used. Moreover, Murtaugh (2009) suggested that there is little difference in predictive ability among the methods of variable selection.

The Pearson's correlation coefficient was used to examine the correlation of evenness between growth stages, and correlation between evenness and richness and diversity at each growth stage. All statistical analyses were done with SYSTAT 10 (SPSS 2000).

Results

All stepwise multiple regression models significantly explained variations in species evenness at all growth stages (Table 1). Evenness of saplings was negatively related to productivity (tree volume, Table 1, Fig. 1a), but not statistically significant (Table 1). Evenness of adults was significantly negatively related to the total dbh (Table 1, Fig. 1b). Evenness of saplings was significantly negatively related to disturbance (area covered by charcoal making holes) (Table 1, Fig. 2a). The number of tree stumps, another disturbance variable also partly explained variation in evenness at the sapling stage (Table 1, Fig. 2b), but it was not statistically significant (Table 1). Evenness of seedlings and adults were not related to any human disturbance variables (Table 1). Evenness of seedlings was negatively related to phosphorus and elevation, while evenness of saplings was positively related to pH, elevation and slope, and negatively related to magnesium (Table 1). Evenness of adults was negatively related to percentage of sand in soil (Table 1). Tolerance values of the predictor variables in all final models were high (Table 1), indicating that there was low multicollinearity in our analyses.

Evenness at the seedling and sapling stages (Pearson correlation coefficient; $n = 30$, $r = 0.43$, $p = 0.02$), and at the sapling and adult stages ($n = 50$, $r = 0.32$, $p = 0.02$), were positively correlated, whereas the correlation of evenness between seedling and adult stages was not significant ($n = 30$, $r = 0.32$, $p = 0.08$). There was no significant correlation between evenness and species richness for any growth stage (seedlings: $n = 30$, $r = -0.004$, $p = 0.99$; saplings: $n = 50$, $r = -0.14$, $p = 0.32$; adults: $n = 50$, $r = 0.001$, $p = 0.99$). On the other hand, correlations between evenness and diversity were significantly positive for all growth stages (seedlings: $n = 30$, $r = 0.70$, $p < 0.0001$; saplings: $n = 50$, $r = 0.30$, $p = 0.03$; adults: $n = 50$, $r = 0.38$, $p = 0.007$).

Discussion

Our study shows that evenness of woody species is related to productivity and human disturbance, at least for one of the three growth stages we measured. The relationship between

Table 1. Stepwise multiple regression¹ on the relationship between species evenness at seedling, sapling and adult growth stages (response) and productivity, human disturbance and environmental variables (predictor)² in the semi deciduous forest in northeast Thailand.

Effect	ΔR^2	Coefficient	SE	Std Coef	Tolerance	t	P(2 Tail)
Seedlings (n = 30, R ² = 0.41, p = 0.001)							
Constant		2.756	0.706			3.905	0.001
P (ppm)	0.28	-0.048	0.018	-0.446	0.712	-2.701	<0.0001
Elevation (m)	0.41	-0.003	0.001	-0.363	0.905	-2.481	0.019
Saplings (n = 50, R ² = 0.51, p < 0.0001)							
Constant		-1.702	0.577			-2.948	0.005
Tree volume (m ³)	0.14	-0.098	0.061	-0.201	0.756	-1.614	0.114
pH	0.24	0.231	0.081	0.326	0.889	2.842	0.007
Elevation (m)	0.32	0.002	0.001	0.406	0.905	3.572	0.001
Charcoal making holes (m ²)	0.38	-0.009	0.004	-0.240	0.927	-2.140	0.038
Number of tree stumps	0.43	0.113	0.058	0.228	0.871	1.970	0.055
Mg (ppm)	0.46	-0.001	0.000	-0.347	0.627	-2.539	0.015
Slope (°)	0.51	0.006	0.003	0.292	0.611	2.109	0.041
Adults (n = 50, R ² = 0.28, p = 0.002)							
Constant		1.438	0.175			8.205	<0.0001
Total dbh (cm)	0.16	-0.000	0.000	-0.394	0.999	-3.146	0.003
Sand (%)	0.22	-0.006	0.002	-0.399	0.696	-2.660	0.011
K (ppm)	0.28	-0.001	0.000	-0.298	0.696	-1.986	0.053

¹models are based on a forward selection of variables, alpha to enter and remove = 0.15

²the predictors in the analyses are productivity (total dbh and tree volume), human disturbance (area covered by charcoal making holes, number of tree stumps and trail length), and environmental variables (number of bamboo clumps, bamboo basal area, number of termite mounds, termite mound ground surface area, canopy cover, slope, elevation, pH, available phosphorus, potassium, magnesium, total nitrogen and sand)

productivity and evenness did not occur at the seedling stage, and although it was included in the final model for sapling it was not significant. It appears that other variables contribute more to explain the variation in evenness at these stages (Table 1). However, productivity, in term of total dbh, explained a significant part of the variation in evenness at the adult stage (Table 1). Thus, our first prediction is not fully supported since evenness significantly decreased with productivity only for adults. Our second prediction is, however, supported in that evenness of adults was more strongly related to productivity than the other two stages. A negative relationship between evenness and productivity has been reported in herbaceous wetland vegetation (Weiher and Keddy 1999), across different vegetation types in a temperate oceanic area (Drobner et al. 1998), in a glass house experimental study with serpentine plants (Chiarucci et al. 2004) and also in a subtropical forest (Vance-Chalcraft et al. 2010). At local scale, soil nutrient availability may cause variation in productivity that consequently influences species evenness. For instance, an experimental study in an old field, Michigan, USA has shown that fertilizer application generally increases plant productivity (i.e. plant size) but reduces diversity (Rajaniemi 2002). Grime (1973) and Rajaniemi (2002) hypothesized that competition (for soil nutrients and light) intensity increases with productivity. In a meta-analysis, Hillebrand et al. (2007) demonstrated that fertilizer addition reduces both richness and evenness in terrestrial ecosystems. Fertilization may cause a decrease in species richness through competitive exclusion of weak competitors (Rajaniemi 2002, Rajaniemi et al. 2003, Hillebrand et al. 2007). Thus, only a few dominant species are able to capitalize strongly on increased resource availability at expense of other species, resulting in low evenness. Low nutrient availability, on the other hand, limits productivity and may keep population density of strong

competitors at low levels (Drobner et al. 1998, Chalcraft et al. 2009). Our results show that higher dbh and higher soil nutrient content decrease woody species evenness at the adult stage (Table 1). Soil nutrients, such as phosphorus, magnesium and potassium, were also negatively related to evenness of seedlings, saplings and adults, respectively (Table 1). Variation in productivity may also depend on the extent by which specific species can use the available resources efficiently, and subsequently gain dominance. Vance-Chalcraft et al. (2010), who found a negative above ground biomass- evenness relationship in subtropical forests in Puerto Rico, suggested that a few species become more dominant at high biomass, rather than the biomass being distributed evenly among all species. In contrast, Sagar and Singh (2006) found a positive relationship between the total tree basal area and evenness in disturbed dry forests of India. They argued that such positive relationship might be because recurring disturbances do not allow concentration of biomass or stems in only a few strong competitors (Sagar and Singh 2006).

We only found a decreased evenness of saplings with higher human disturbance, represented by the area covered by charcoal making holes (Table 1). Our initial prediction was that human disturbances should prevent dominant species from gaining high abundance (i.e. increased evenness) (Kumar and Ram 2005, Sagar and Singh 2006, Reitalu et al. 2009). This prediction was based on studies of human disturbances in relation to evenness of tree species only at the adult stage. However, saplings, rather than adults sensitively responded to the disturbance in our study. The difference in direction of the relationship between human disturbance and evenness of trees in this study, compared to others studies may be due to differences in scale and intensity of disturbances. For example, Kumar and Ram (2005) and Sagar and Singh (2006) found

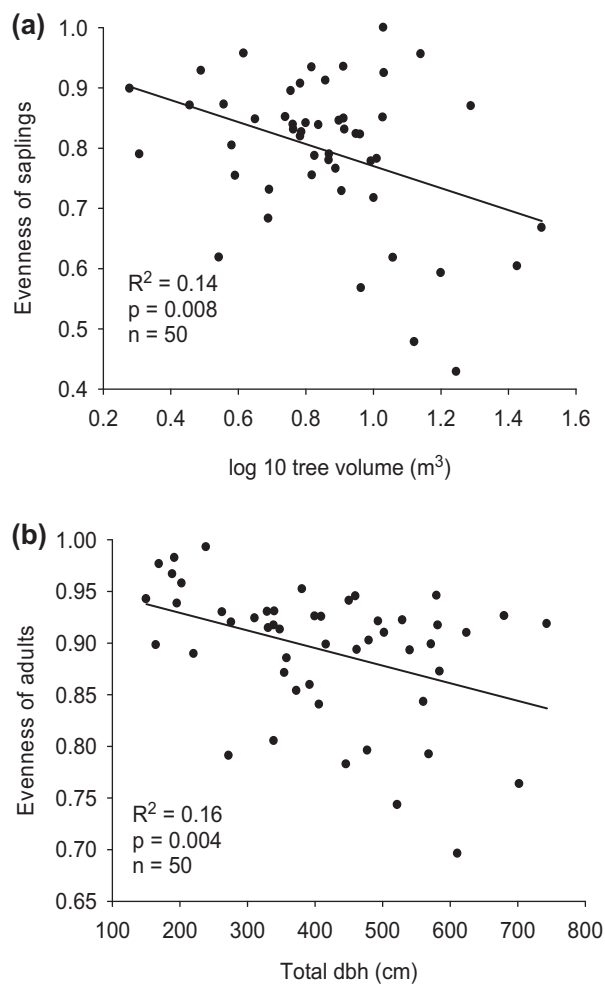


Figure 1. Relationships between measures of productivity and evenness of tree species at a) sapling and b) adult growth stages, in a semi deciduous forest in Thailand. Tree volume and total dbh of tree were measured from a 20 × 20 m plot. The coefficient of determination (R^2), probability value (p), from a simple linear regression, and number of observations (n) are shown.

human disturbances decreased the dominant of single species in highly disturbed tropical forests, where the forests have experienced frequent and large-scale disturbances, such as mining, power generation, cattle ranching and tree felling. In contrast, the human disturbances in our study area are substantially less intense and on a much smaller spatial scale than in these other studies. Adult trees can suppress juveniles for resources and/or space, and hence may not allow substantial population densities of saplings to occur. The clearing of vegetation to make space for charcoal holes may reduce suppression of saplings from adults and might allow some sapling species to take advantage and consequently become dominant. Rao et al. (1990) and Yadav and Gupta (2006) found that disturbance decreased evenness of woody species.

Evenness of trees did not appear to relate consistently to productivity or human disturbance at any growth stage (Table 1), and appear to be more strongly related to abiotic environmental variables such as phosphorus and elevation at the seedling stage. This may be because seedling establishment largely depends on suitable environmental conditions,

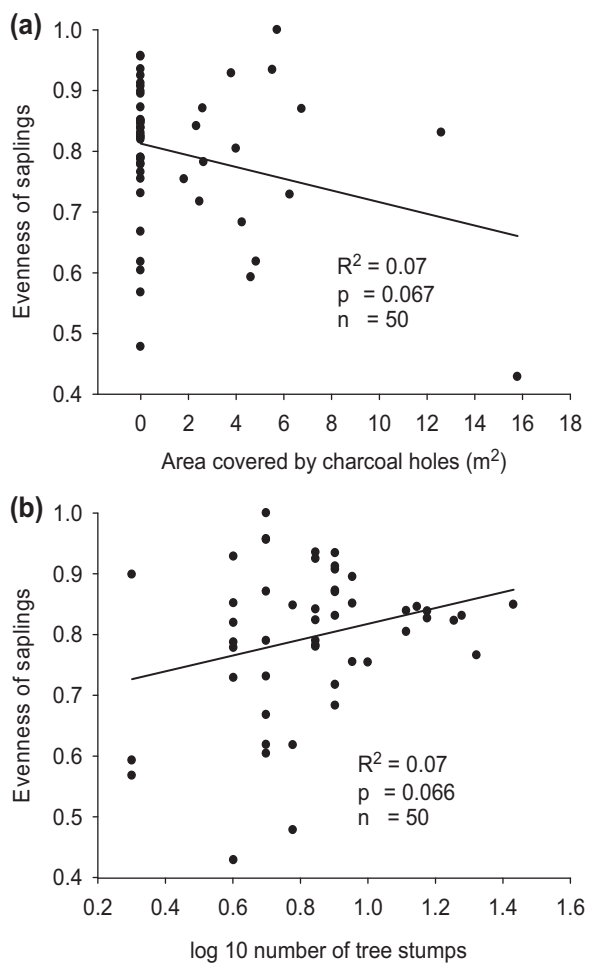


Figure 2. Relationships between measures of human disturbance: a) area covered by charcoal holes and b) number of tree stumps and evenness of tree species at the sapling stage, in a semi deciduous forest in Thailand. Area covered by charcoal holes and number of tree stumps were measured from a 20 × 20 m plot. The coefficient of determination (R^2), probability value (p), from a simple linear regression, and number of observations (n) are shown.

i.e. the regeneration niche (Grubb 1977). Seedling populations are also initially influenced by the availability of seeds (Dalling et al. 2002, Paine and Harms 2009). Previous studies have found that resource competitions between seedlings do not seem to be important for seedling performance and survival (Paine et al. 2008, Svenning et al. 2008). In addition, the exposure to both the biotic and abiotic environment has been shorter for seedlings than for saplings and adults, so competition and disturbances may have less influence on evenness of seedlings. At later growth stages, competitions among individuals are probably more intense due to changes in size and abilities to utilize resources (Callaway and Walker 1997, Li et al. 2008), and therefore saplings and adults are likely more strongly influenced by productivity and disturbance than seedlings.

We predicted that evenness would not be correlated among growth stages. However, evenness was correlated between seedlings and saplings and between saplings and adults, but not between seedlings and adults. This suggests that species abundance distribution did not change across all the growth

stages. However, the strength of relationships diminishes across the stages, ($r = 0.43$ and $r = 0.32$, between seedlings and saplings, and between saplings and adults, respectively). This may be explained by the differences in growth period that is shorter from seedlings to saplings than from saplings to adults so that the abundance distribution pattern of seedlings more closely resembles saplings than adults.

To our knowledge, this is the first study examining the relationships between productivity, human disturbance and evenness across growth stages. Overall, our results indicate that high productivity and human disturbance cause low evenness. However, this effect did not occur across all growth stages. We suggest that interspecific competition may be an underlying process affecting evenness in plant communities. High productivity and disturbance may facilitate competitive dominant species, affecting evenness in woody communities, and that competition intensity increases across plant development.

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Paper III

Ontogenetic niche shifts within a tropical woody species guild

Panadda Larpkern^{*}, Ørjan Totland and Stein R. Moe

Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway

^{*}Corresponding author. E-mail: panadda.larpkern@umb.no

Summary

1. As plants develop from seedlings, saplings to adult stages, their niche requirements may change. Although ontogenetic changes may have fundamental effects on how plants respond to environmental conditions and on intra- and interspecific relationships, studies of ontogenetic shifts have mainly been focusing on animals.

2. We studied ontogenetic niche shifts of 9 abundant woody species across seedling, sapling and adult life stages in a seasonally dry bamboo-deciduous forest in northeastern Thailand. Using 20 environmental- and human disturbance variables to characterize the species niche for each ontogenetic stage, we claim that any change in the identity and strength of the variables contributing to separate the species, and any change in the relative position of species along these variables from the seedling to the sapling and at the adult stage will represent a niche shift from the seedling to the subsequent life stages.

3. The environmental variables that explained separation of species at the seedling stage differed from the variables that explained separation of species at the sapling and adult stages. The species also changed their relative position in environmental niche space between seedling and adult stages and between the sapling and the adult stages, indicating ontogenetic niche shifts. Elevation was the only variables explaining separation among species at all life stages.

4. *Synthesis and applications.* Our results suggests that the requirements (or responses) to environmental conditions changes as individuals develop. Such ontogenetic niche shifts may be important in explaining the coexistence of plant species within a community. We propose that such differences in niche requirements among life stages should be taken into consideration when management strategies, particularly forest restoration, of tree species are developed.

Key-Words: Abundance, environmental gradients, human disturbance, life stages, regeneration, restoration, Thailand

Introduction

Plants vary far more morphologically and physiologically when passing through life stages from seeds to adults, than between individuals of the same age group and even between species belonging to the same guild (Donovan & Ehleringer 1991; Thomas & Ickes 1995; Cavender-Bares & Bazzaz 2000; Turner 2001). These ontogenetic changes may have fundamental effects on how plants respond to environmental conditions and on intra- and interspecific relationships.

Because all plants require the same essential resources, such as CO₂, light and various macro- and micronutrients, one could believe that niche differentiation is less possible in plants compared to animals. Indeed in his Unified Neutral Theory, Hubbell (2001) postulated that niche differences in plants are irrelevant in explaining plant species coexistence. However, other studies have emphasized the huge alpha diversity found in many plant communities and the shortcomings of our current understanding of plant coexistence (Silvertown 2004). When reviewing 13 studies, Silvertown (2004) concluded that niche differentiation occurred in plants along several axes. One particularly important factor, which can contribute to the explanation of plant species coexistence, is the regeneration niche (Grubb 1977). The supply of seeds and their access to suitable germination sites are thought to be the main processes determining recruitment in plant populations (Eriksson & Ehren 1992; Schupp 1995; Norden 2007; Duncan *et al.* 2009). After seed dispersal, many biotic and abiotic microsite factors influence the seed germination success, and the seedling establishment and growth (Augsburger 1983, 1984; Denslow & Guzman 2000; Nagamatsu *et al.* 2002). However, niche requirements of plants can change through the life of individuals, known as ontogenetic niche shifts (Parrish & Bazzaz 1985; Eriksson 2002; Miriti 2006; Quero *et al.* 2008). Schupp (1995) proposed that a microhabitat which is optimal for seed germination may be detrimental for seedling survivorship. Such ontogenetic changes in habitat requirement can also occur between the juvenile and adult stages (Webb & Peart 2000; Comita *et al.* 2007). These differences in niche requirements between life stages of individuals may facilitate species coexistence (Parrish & Bazzaz 1985; Miriti 2006). Understanding the combined effect of the adult abundance and environmental conditions on the abundance of earlier growth stages (i.e. seedlings and saplings) is important for the understanding of factors determining natural regeneration processes. Since plants, unlike most animals, are sessile ontogenetic niche shifts are either caused by changes in environmental conditions during the life span of individuals or by interspecific interactions affecting

survival. Thus, to improve our understanding of the dynamics and composition of plant communities, and subsequently the management of plant communities, we need to understand the magnitude of ontogenetic niche shifts in plant species assemblages.

Although most studies on ontogenetic shifts have been on animals (e.g. Olson 1996; Claessen & Dieckmann 2002; Persson & Brönmark 2002), it is recognized that ontogenetic niche shifts are also important in plants (Parrish & Bazzaz 1985; Silvertown 2004). Despite this, studies are few (Eriksson 2002; Silvertown 2004), have mostly focused on few life stages (Quero *et al.* 2008), and commonly only on a few species (e.g. Miriti 2006; Quero *et al.* 2008). When studying ontogenetic shifts in old-field annuals, Parrish & Bazzaz (1985) found that plant response to moisture and nutrient levels was more similar to other species of similar age than to the same species at a different age. Studies on *Vaccinium oxycoccos* (Eriksson 2002) and on *Acer opalus* ssp. *granatense* (Quero *et al.* 2008) found a niche contraction towards the adult stage. This may suggest an increased interspecific competition resulting in niche contractions (Alley 1982).

Assessing the environmental conditions affecting the abundance of individual growth stage is not only theoretically interesting, but also important for management, because restoration efforts should include a focus on the growth stages that is most limiting for the population survival and growth (Lieberman 1996; Collin & Carson 2004; Quero *et al.* 2008).

We studied ontogenetic niche shifts of 9 abundant woody species in a seasonally dry bamboo-deciduous forest in northeastern Thailand. By measuring the abundance of seedlings, saplings and adults along several environmental gradients we explored how woody plant species associated with each other during their life span and how abundances at ontogenetic stages relate to environmental and human disturbance variables.

We specifically asked (i) can adult species assemblages be predicted with the same environmental variables as for younger life stages (e.g. seedlings and saplings)? (ii) which environmental variables are the most important determinants of the species assemblages at each ontogenetic stage? and (iii) do species change their relative positions along environmental gradients across ontogenetic stages? Thus, any change in the identity and strength of the variables contributing to separate the species, and any change in the relative position of species along these variables from the seedling to the sapling and at the adult stage will represent a niche shift from the seedling to the subsequent life stages.

Materials and methods

STUDY SITE

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 a rainy (May-October), a cool-dry (November-February) and a hot-dry season (March-April). The elevation ranges from 400-600 m above sea level. The mean annual rainfall is 1551 mm (2001-2005), and during the study year in 2006, the total annual rainfall was 1632 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 bamboo-deciduous forest, with some agricultural fields and fallows near the forest edge. The bamboo forest comprises a mixture of evergreen and deciduous trees forming the tree-layer and bamboos dominating the intermediate layer. Dominating woody species are *Cananga latifolia* (Hk. f. & Th.) Fin. & Gagnep., *Lagerstroemia* sp., *Gardenia sootepensis* Hutch. *Spondias laxiflora* (Kurz) Airy Shaw and *Pterocarpus macrocarpus* Kurz. Bamboo species occurring in these forests are *Gigantochloa albociliata* (Munro) Kurz, *Bambusa tulda* Roxb. and *Cephalostachyum pergracile* Munro. In the dry season, most trees shed their leaves, and man-made ground fires are common. Although the forest is protected by law, local people use the forest for various purposes, including agricultural expansion, non-timber forest product collection, cattle grazing and charcoal making.

SAMPLING PROCEDURES

We separated individuals of the woody species into adults, saplings and seedlings by using plant height and diameter at breast height (dbh; 1.3 m); adults (dbh \geq 4cm), saplings (height $>$ 0.5 m and dbh $<$ 4 cm when their height were exceeding 1.3 m) and seedlings (height \leq 0.5 m). Sapling and adult abundance of each selected species were measured by counting each individual of each species within 30 plots of 20 m \times 20 m. The plots were set up along two transect lines (separated by approximately 260 m) placed east-west from a random chosen point in the forest area. Twelve plots were set up in one transect line and 18 plots were set up in the other. The plots along a transect line were at least 20 m apart. We counted and measured saplings during two weeks in June 2006 (rainy season) because they may grow

rapidly during seasonality of rainfall. Voucher specimens were collected and sent to the Herbarium at Chiang Mai University for species identification and confirmation.

Each of the 30 plots was divided into four equal squares (10 m × 10 m), and a subplot of 1 m × 1 m was randomly located in each square for sampling and measurements of seedlings. We monitored seedling abundance in the subplots throughout the year. At the initial census (January 2006), we identified and tagged all individual tree seedlings in the subplots, and mapped the position of each tree seedling. New recruited seedlings were observed throughout the year.

ENVIRONMENTAL- AND HUMAN DISTURBANCE VARIABLE MEASUREMENTS

We used 20 environmental- and human disturbance variables to characterize the species niche for each ontogenetic stage. Of the 20 variables, 17 variables represented natural environmental conditions, and three variables were related to human disturbance. We characterized the environmental variables according to forest structure (i.e. canopy cover, canopy height, number of bamboo clumps and bamboo basal area), edaphic factors (i.e. pH, available phosphorus, available potassium, calcium, magnesium, organic matter, total nitrogen and percent sand), topographic factors (i.e. slope and elevation) and others (i.e. number of termite mounds, termite mound ground surface area and small water way passing the plots). The human disturbance variables included the number of tree stumps, the length of trails and the area covered by charcoal making holes.

We measured canopy cover (%) with a densitometer and the height of all adult trees in each plot with a clinometer. Canopy height was an average of all adult tree heights in each plot. Moreover, we counted bamboo clumps within each plot, and estimated the bamboo basal area of each clump using the circular distance around all the stems in the clump.

We collected soil samples in July (in the rainy season). Twelve soil samples (cores 25 cm deep and 2 cm in diameter) were collected in a stratified random manner within each plot. The soil samples were mixed and placed in a freezer the same day as they were collected and stored there until analyzed by the Soil and Water Analysis working group, Agrochemistry Section, Division of Agricultural Research, Ministry of Agriculture, Bangkok. The analyses included soil pH (at a 1:1 soil/water ratio), organic matter (Walkley-Black method), available phosphorus (Bray II), calcium, potassium and magnesium (ammonium acetate 1 N pH 7 extraction), total nitrogen (Kjeldahl method) and percentage of sand (Hydrometer and Pipette method).

We estimated elevation by GPS at the center of each plot and slope with an auto level meter. Termite mounds within each plot were counted and their surface area measured. In our study, the shape of the mound was normally circular, and we therefore used the formula πr^2 to calculate the surface area of the mound. Small waterways passing through the plots, during the rainy season, were observed as present or absent. We measured the size (width \times length) of charcoal making holes. Finally, we measured the length of any walking trails crossing through the plots, and counted the tree stumps within each plot.

DATA ANALYSIS

Of the 136 identified woody species, we examined for the presence of ontogenetic niche shift in 9 species: *Aporosa octandra* (B.-H.ex D.Don) Vickery var. *octandra* (Euphorbiaceae), *Aporosa octandra* (B.-H. ex D.Don) Vickery var. *yunnanensis* (Pax & K.Hoffm.) Schott (Euphorbiaceae), *Croton roxburghii* N.P.Balakr. (Euphorbiaceae), *Gardenia sootepensis* Hutch. (Burseraceae), *Hydnocarpus* sp. (Flacourtiaceae), *Lagerstroemia* sp. (Lythraceae), *Lithocarpus elegans* (Bl.) Hatus. ex Soep. (Fagaceae), *Memecylon scutellatum* Naud. (Melastomataceae), *Pterocarpus macrocarpus* Kurz (Fabaceae). We chose these species because they had a relatively high abundance, representing 66%, 56% and 48% of the total seedling, sapling and adult abundance, respectively and all of these species had > 15 individuals in each ontogenetic stage. Although data are available for the whole woody assemblage, we only included the nine selected species in the analysis, in order to avoid the other species to influence the results on ontogenetic niche shift in the selected species.

Since we aimed at examining niche shift in a multidimensional niche space, we used multivariate analyses where each species were examined simultaneously at each ontogenetic stage. Preliminary detrended correspondence analysis (DCA; Hill & Gauch 1980) showed that change in species composition, as measured by the gradient length in standard deviation (SD) units, were 2.78 (seedlings), 2.23 (saplings), and 3.2 (adults). Ter Braak & Prentice (1988) suggested that if the gradient length is short (< 1.5 SD), redundancy analysis (RDA) is appropriate for linear responses, whereas canonical correspondence analysis (CCA) is most appropriate for unimodal responses if the gradient is long (> 3 SD), while both RDA and CCA can be used if the length of the gradient lies between 1.5 and 3 SD. We used CCA (ter Braak 1986), as implemented in CANOCO version 4.5 (ter Braak & Smilauer 2002) because of the need to use the same analysis on all stages, and because comparisons of model output suggested that CCA better explained separation among species than RDA. It is also suggested

that species data with many zeroes, as is the case with our data, are often best analyzed with a unimodal method (ter Braak & Smilauer 2002). The default settings of CANOCO v. 4.5 were applied both in DCA (detrending by segments) and CCA (scaling with focus on species distances and biplot scaling) (ter Braak & Smilauer 2002). All environmental and human disturbance variables were collected from the plots located along two different transects. Therefore, we used transects as a covariable (coded 0 and 1 as a dummy variable). The analyses were done separately for the three life stages.

Our analysis of niche shift was conducted over several steps. First, we identified the variables that most parsimoniously explained separation of species at the seedling stage, and then used these variables to model separation of species at the sapling and adult stages. These models were then compared with the models that contained the variables that most parsimoniously explained separation of species at the sapling and adult stages. Second, we repeated this process for the sapling stage, by first identifying the variables that most parsimoniously explained separation of species at the sapling stage, and applying these variables at the adult stage and finally comparing this model with the model containing the variables that most parsimoniously explained separation of species at the adult stage. We took this approach to model niche shift under the assumption that plants have little ability of choosing their habitat (both at small and large spatial scale). Thus, the variables identified as important at the seedling stage conform to the regeneration niche (Grubb 1977). Any change in the identity of variables that contribute significantly to separate the species, and any change in the relative position of species along these variables at the sapling and at the adult stage represent, in our approach, a niche shift from the seedling to the subsequent life stages.

Identification of the most parsimonious model was done by first examining the explanatory power and significance of each variable separately with CCA, using 999 Monte Carlo permutations. Variables with a P-value > 0.10 was excluded for further analyses. We used a P = 0.10 as a cutting point (instead of the conventional P = 0.05) in order to avoid excluding variables whose contribution to the separation of species could be influenced by other variables in the model. The variables with a P-value ≤ 0.10 were then included as predictor variable in a second CCA, and their significance assessed with 999 permutations. We then repeated the process of excluding variables with P > 0.10 , and ran a final CCA model. In the final model, we considered the variables with a P ≤ 0.05 as statistical significance.

From these final models, we used CanoDraw to produce CCA biplots with species and environmental variables. Preliminary CCAs showed high collinearity, as indicated by variance inflation factors larger than 20, between some of the variables. We therefore removed organic

matter and calcium from the analyses because they correlated with total nitrogen and magnesium.

We used Spearman rank correlation (r_s), based on the species scores along the first and second DCA axis from three DCAs conducted separately for each of the three stages. We used the species scores from DCA, rather than from the CCAs because different variables were used to constrain the axes in the CCAs. These rank correlations test if species changes their relative position along niche dimensions from one stage to another. A non-significant r_s suggest that species are changing their relative position in environmental niche space from one stage to another.

Results

Canopy cover, elevation, number of stumps, number of bamboo clumps and area covered by charcoal holes contributed significantly to separate species at the seedling stage (Table 1, Fig 1 a). When these variables were used to separate species at the sapling stage, only four of them (canopy cover, elevation, number of stumps and number of bamboo clumps) were significant, and area covered by charcoal holes lost its explanatory power (Table 1, Fig 2 a). At the adult stage only two of the variables from the seedling model (canopy cover and elevation) contributed to separate species, whereas the other variables lost their ability in explaining separation among species (Table 1, Fig 2 b).

Canopy cover, elevation, number of stumps, number of bamboo clumps and number of termite mounds best explained separation among species at the sapling stage (Table 1, Fig 1 b). Of these, only canopy cover and elevation contributed significantly in explaining separation of species at the adult stage (Table 1, Fig 2 c). Only two variables (elevation and small water ways) were identified as contributing significantly to separate species at the adult stage (Table 1, Fig 1 c). Thus, elevation was the only variable that explained separation among species at all three stages. The significance of the first canonical axis and of the overall model (all axes) was affected by which variable was included in the models (Table 1). The “best models” of all stages were significant both for the first and for all axes. The model on saplings with the best variables from seedlings was also significant, whereas the model on adult with seedling variables was not significant for the first axis. Moreover, the model on adults with sapling variables was not significant for the first axis (Table 1).

The best CCA models for the seedling, sapling and adult stages show that species are changing their relative position along environmental gradients (Fig. 1 a-c). The first two axes

of the best models explained 36 %, 37%, and 22% of the variance in species data at seedling, sapling and adult stage, respectively (Table 2). These axes explained a fairly high amount of the species-environmental relation and explained more than a half of the variation that could be attributed to the variables in the models. Along the canopy cover gradient, almost all of the species had their niche optimum at above-average canopy cover at the seedling and sapling stages (Fig 1a and b). Only *M. scutellatum* and *C. roxburghii* were clearly associated with below-average canopy cover at the seedling and sapling stage, respectively (Fig 1a and b). At the adult stage, however, three species, *M. scutellatum*, *Lagerstroemia* sp. and *G. sootepensis* were associated with below-average canopy (Fig 1c). Among all species, *L. elegans* had the high score along the canopy cover gradient at all life stages.

Species also shifted their position from one stage to another along the elevation gradient; an environmental proxy that does not change in time. At the adult stage, *L. elegans*, *G. sootepensis*, *M. scutellatum* and *Lagerstroemia* sp. had the highest scores along the elevation gradient, and all of these were associated with above-average elevations (Fig 1 c). However, only *M. scutellatum* and *C. roxburghii* had a clear distribution towards high-elevations at the seedling and sapling stage, respectively (Fig 1a and b). Species also changed relative position to each other in the multi-dimensional niche space. For example *L. elegans* and *A. octandra* var. *yunnanensis* had similar niche requirements (are positioned close together) at the seedling stage (Fig 1a) but were widely separated (indicative of different niche requirements) at the sapling and adult stages (Fig 1b and c). *P. macrocarpus* and *M. scutellatum* were closely associated at the sapling stage (Fig 1 b) but were widely separated from each other at the seedling and adult stages (Fig 1a and c). *P. macrocarpus* and *C. roxburghii* were closely associated at the seedling stage (Fig 1 a), separated from each other at the sapling stage, and then closely associated again at the adult stage (Fig 1b and c). In general, it does not appear that any species pairs remain closely associated across all the life stages.

The shifts in relative positions of species in niche space across their life stages are also shown in the Spearman rank correlation analyses (Table 3). Along the first canonical axis the species scores at the seedling and sapling stages is significantly related, whereas there is no significant relationship between species scores at the seedling and adult stages or between the sapling and the adult stages. Along the second canonical axis the species scores at the seedling and adult stages is significantly related, whereas there is no significant relationship between species scores at the seedling and sapling stages or between the sapling and the adult

stages. A non-significant r_s suggest that species are changing their relative position in environmental niche space from one stage to another.

Discussion

We know of no other studies that have attempted to examine niche shifts across life stages of several species simultaneously along several niche gradients (but see Stohlgren *et al.* 1998). Our results suggests that the requirements (or responses) to environmental conditions changes as individuals develop. We found that the environmental variables that most parsimoniously explained separation of species at the seedling stage (i.e. regeneration niche) differed from the variables that separated species at the sapling and adult stages. When the most parsimonious seedling and sapling models were applied at the adult stage, many of the variables lost their ability to explain niche separation. Therefore, adult species assemblages could not be predicted with the same environmental variables as for younger life stages (seedlings and saplings). Species were also changing their relative position in environmental niche space between seedling and adult stages and between the sapling and the adult stages, indicating ontogenetic niche shifts. In plants, the abundance of a species along a particular environmental gradient (niche dimension) at the adult stage is affected by numerous processes occurring at earlier stages. First, the number of seeds produced by the adults determines the potential for acquiring a certain population density under a given set of environmental conditions that affect the adults (Haper 1977). Second, seed dispersal and location of seeds, which the adults in general have little control over, determine the abundance of seed across the landscape (Hardesty & Parker 2002; Seidler & Plotkin 2006). Third, both the biotic and environmental conditions where seeds are deposited (the regeneration niche) affect the germination success of seeds. Fourth, the survival of seedling and growth of saplings, affected by both biotic (predators, herbivores, competitors, facilitators) and abiotic (nutrient, water and light availability) conditions, affect the number of new adults recruited to a particular site (Augspurger 1983, 1984; Denslow & Guzman 2000; Nagamatsu *et al.* 2002). Clearly, these myriads of factors that have different effects on individuals as they develop contribute to the change in relative density of species across life stages along environmental gradient, as suggested by our results.

Parrish & Bazzaz (1985) found that six old-field annual plants had narrow responses to temperature and moisture gradients but broad responses to nutrient gradients at the germination and seedling stages, and these responses were changed at more mature stages.

The shifts in responses to the gradients were more pronounced in some species than others. In contrast, Eriksson (2002) studied ontogenetic niche shifts in three clonal species and found that niche shift did not occur from seed to seedling stages and that the recruitment was seed limited, rather than constrained by environmental conditions. However, niche shift occurred from the juvenile to adult stage Eriksson (2002). A niche contraction towards the adult stage was also found by Quero *et al.* (2008) in an endangered Mediterranean tree species. Undoubtedly, detailed experimental studies that manipulate seed availability under contrasting biotic and abiotic environmental conditions, and that monitor development of individual plants and population densities over time, would be required to reveal how the plants change in their environmental requirements across ontogenetic stages. However, in our study system, with long lived trees and many tree species, such experiments would be difficult to conduct.

Elevation was the only variable that explained separation among species at all life stages. Although short elevation gradients within a landscape are not a typical variable explaining species composition in tropical areas (Miyamoto *et al.* 2003; Vargas-Rodriguez *et al.* 2005), we found that elevation explained niche separation among species at all life stages, and most of the species were associated with below average elevation, especially at the sapling stage. Because the elevation range is narrow in our study system (from 498 m to 567 m), we do not believe this is a temperature effect, but rather caused by other factors that are associated with elevation (Miyamoto *et al.* 2003; Eilu *et al.* 2004; Vargas-Rodriguez *et al.* 2005). High elevation areas in the forest have a low water availability and are more prone to fire during the dry season. Species like, *C. roxburghii* and *L. elegans* that were associated with high elevation at the sapling and adult stages, respectively, are reported to occur mainly in fire-prone areas (Gardner *et al.* 2000). Canopy cover was significantly explained species separation at the seedling and sapling stages and close to significant at the adult stage. In closed canopy forests, light is generally the most limiting factor for establishment, survival and growth of juvenile trees (Withmore 1996; Poorter & Arets 2003). However, light may not be the most limiting factor for seedlings in seasonally dry tropical forests where seasonal variability of moisture is more critical for seed germination and seedling survival (Gerhardt 1996; McLaren & McDonald 2003; Vieira & Scariot 2006). Shade, which in general is related to soil moisture, provided optimum conditions for seedling survival during the dry period in tropical seasonal dry forests (Gerhardt 1996; Vieira & Scariot 2006). Gerhardt (1996) concluded that competition for moisture and possibly nutrients has significant effects on seedling performance in seasonally dry forests. Most of the species in our study were

associated with relatively high canopy cover at the seedling and sapling stages, and species were changing their relative position along the canopy gradient at the later stage. However, *M. scutellatum*, a small evergreen tree growing to approximately 10 m, evidently required open canopy area at both seedling and adult stages. This species is common in dry and open area (Gardner *et al.* 2000). *L. elegans* is a shade-tolerant and small to medium-sized evergreen tree species growing to 15-20 m (FORRU 2006). Their distribution was associated with low light conditions in the forest at all growth stages. Previous studies have shown that tall species commonly go through a comparatively large switch from low light conditions at the seedling stage to high light exposure at the adult stage (Rijkers *et al.* 2000). For example, *Lagerstroemia* sp., a large deciduous upper canopy tree growing above 30 m, preferred low light conditions under canopy at the seedling stage but preferred high light conditions at below-average canopy cover at the sapling and adult stages. *P. macrocarpus*, a large deciduous upper canopy tree above 20 m, was associated with above-average canopy cover at the seedling and sapling stages but at the adult stage it was associated with an average canopy cover. The life stages differed in relative abundance across the elevation and canopy cover gradients for all species. Apart from elevation and canopy cover, different variables explained niche separation for each of the life stages. Although, many studies have shown that bamboos may negatively influence the establishment of tree species (Marod *et al.* 1999; Tabarelli & Mantovani 2000; Griscom & Ashton 2003; Guilherme *et al.* 2004) we found that four species, *L. elegans*, *M. scutellatum*, *P. macrocarpus* and *G. sootepensis* at the sapling stage were closely associated with high density of bamboos.

Our results have implications for managements of plant populations since they suggest that environmental requirements change across ontogenetic stages. Thus, the most optimal management strategy in term of actively changing environmental conditions may vary among life stages. Accordingly, to optimize management, detailed knowledge of how different life stages respond to environmental conditions is needed. For example, our results suggest that the three species; *Lagerstroemia* sp., *M. scutellatum* and *G. sootepensis* were associated with below-average canopy cover at the adult stage, whereas only *M. scutellatum* is associated with such canopy conditions at the seedling stage. Thus, management of canopy cover could be a feasible strategy to maintain a species like *M. scutellatum* in the landscape, whereas the success of canopy cover management would be dependent on the relative contribution of e.g. seedling and adult survival for the population persistence in *Lagerstroemia* sp. and *G. sootepensis*. Human disturbance variables, i. e. the number of tree stumps and the area covered by charcoal holes, do not appear to separate the species examined here, although *A.*

octandra var. *octandra* was closely associated with the number of stumps at the seedling and sapling stages. It is possible that the use of the forest by local people is so limited, perhaps because it is protected by law, that the current human disturbance regime is not strong enough to impact the distribution and abundance of species within the forest. However, it is important to keep in mind that human disturbances may eventually have negative effects on community properties, particularly as it increases in intensity. Overall, we suggest that there are differences in niche requirements between life stages of individuals. These differences may be important in explaining the coexistence of plant species. Assessing the environmental conditions affecting the abundance of individual growth stage can therefore provide an approach to efficient forest management. We propose that such differences in niche requirements among life stages should be taken into consideration when management strategies of tree species are developed.

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Table 1. P-values of variables identified as most parsimonious and CCA model summary.

	Seedlings (Best model)	Saplings (Best model)	Saplings (Seedling model)	Adults (Best model)	Adults (Seedling model)	Adults (Sapling model)
Canopy cover	0.002	0.006	0.006	0.079	0.031	0.031
Elevation	0.001	0.054	0.040	0.005	0.005	0.005
Number of stumps	0.001	0.012	0.012		0.415	0.278
Number of bamboos	0.010	0.048	0.048		0.290	0.681
Slope	0.073		0.286		0.170	
K	0.065		0.316		0.101	
Area covered by charcoal making holes	0.049		0.236		0.157	
Number of termite mounds		0.049				0.731
Small waterways				0.013		
CCA model summary: F-						
ratio (P-value) of						
1 st canonical axis	6.26 (0.001)	7.69 (0.011)	7.42 (0.001)	3.75 (0.048)	4.26 (0.151)	3.23 (0.179)
All axes	3.53 (0.001)	3.85 (0.001)	2.88 (0.001)	2.92 (0.002)	1.97 (0.014)	1.72 (0.026)

Table 2. Cumulative % variation explained of species data by all 4 axes, eigenvalues and species-environment relations in all 6 models.

	Axis 1	Axis 2	Axis 3	Axis 4
<u>Seedlings (Best model)</u>				
Eigenvalues	0.304	0.175	0.124	0.070
Cum. % var. species data	23.0	36.2	45.6	50.8
Cum. % var. spec. environm. relations	42.5	67.0	84.2	94.0
<u>Saplings (Best model)</u>				
Eigenvalues	0.309	0.152	0.072	0.019
Cum. % var. species data	25.1	37.3	43.2	44.7
Cum. % var. spec. environm. relations	55.0	81.9	94.8	98.1
<u>Saplings (Seedling model)</u>				
Eigenvalues	0.322	0.143	0.071	0.042
Cum. % var. species data	26.1	37.7	43.5	46.9
Cum. % var. spec. environm. relations	53.4	77.1	88.9	95.8
<u>Adults (Best model)</u>				
Eigenvalues	0.270	0.176	0.090	0.590
Cum. % var. species data	13.1	21.6	25.9	54.5
Cum. % var. spec. environm. relations	50.3	83.2	100.0	0.0
<u>Adults (Seedling model)</u>				
Eigenvalues	0.349	0.249	0.092	0.088
Cum. % var. species data	16.9	28.9	33.3	37.6
Cum. % var. spec. environm. relations	42.5	72.9	84.1	94.8
<u>Adults (Sapling model)</u>				
Eigenvalues	0.254	0.230	0.039	0.024
Cum. % var. species data	12.3	23.4	25.3	26.5
Cum. % var. spec. environm. relations	45.3	86.2	93.1	97.4

Table 3. Spearman correlation coefficient (r_s) between the species scores along the first (upper panel) and second (lower panel) DCA axis of seedling, sapling, and adult stages. Critical value for $P \leq 0.05 = 0.683$ with $N = 9$, indicating by *.

	Seedling	Sapling
<u>The first DCA axis</u>		
Sapling	0.69*	
Adult	0.38	0.34
<u>The second DCA axis</u>		
Sapling	0.42	
Adult	0.73*	0.07

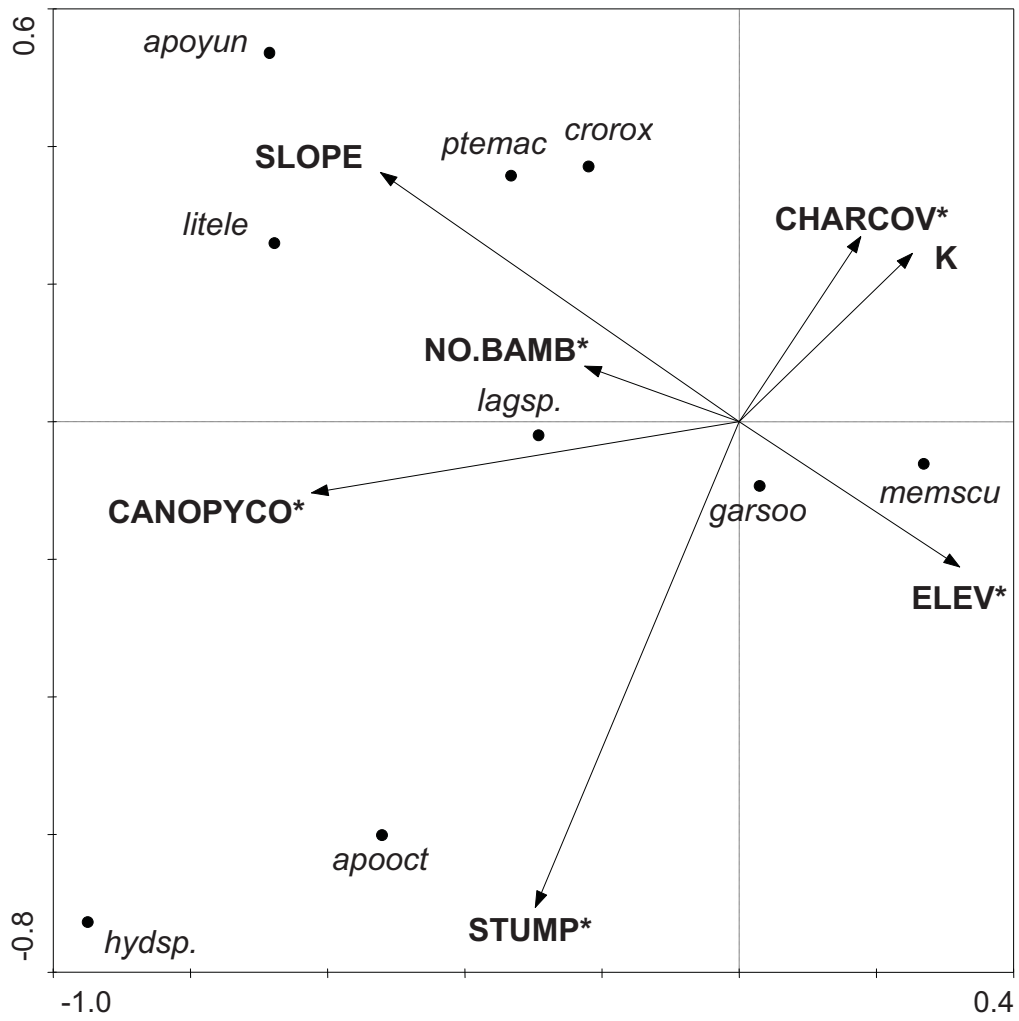
Figure captions

Figure 1. CCA ordination diagrams of the 9 most abundant woody species and environmental variables that most parsimoniously explained separation of species (best model) at: a) seedling, b) sapling and c) adult stages. Abbreviations of species' names are (*Aporosa octandra* var. *octandra* (apooct), *Aporosa octandra* var. *yunnanensis* (apoyun), *Croton roxburghii* (crorox), *Gardenia sootepensis* (garsoo), *Hydnocarpus* sp. (hydsp.), *Lagerstroemia* sp. (lagsp.), *Lithocarpus elegans* (litele), *Memecylon scutellatum* (memscu), *Pterocarpus macrocarpus* (ptemac). Abbreviations of environmental variables are area covered by charcoal holes (CHARCOV), Canopy cover (CANOPYCO), Elevation (ELEV), Number of bamboos (NO.BAMB), Number of stumps (STUMP), Number of termite mounds (NO.TERM), Potassium (K), Slope (SLOPE) and Small waterways passing through the plots (WATERWAY). * indicates a significant variable ($P \leq 0.05$). F and P values of the models: see Table 1.

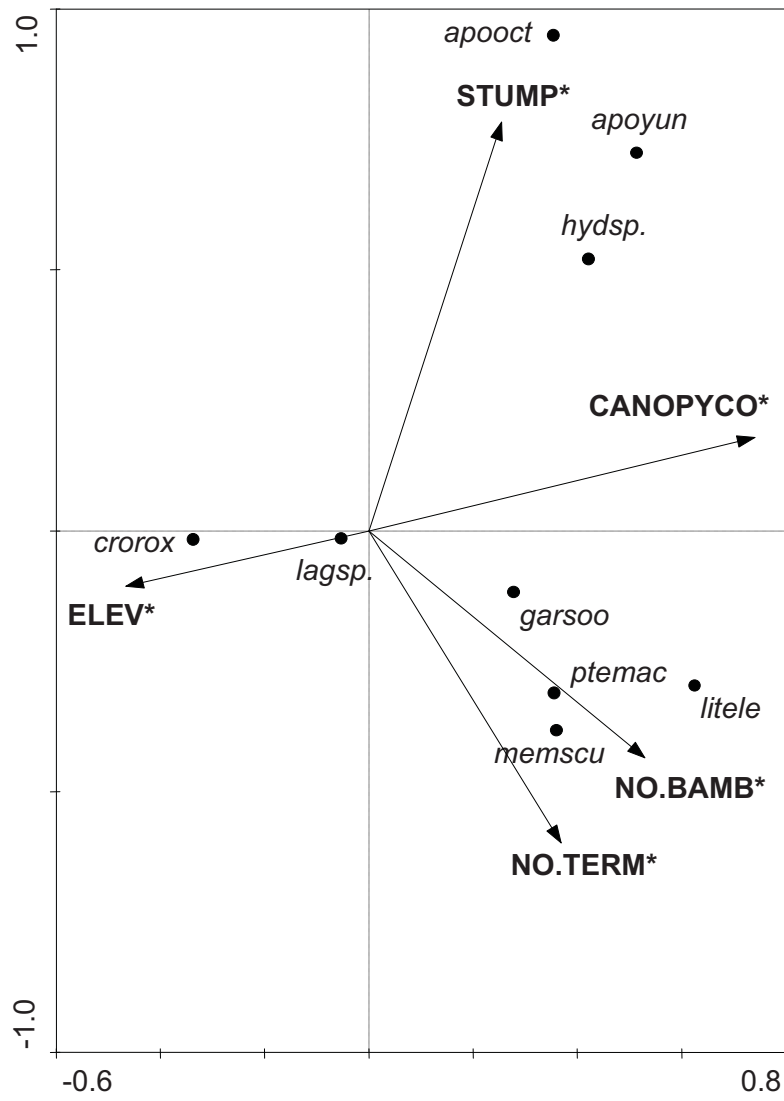
Figure 2. CCA ordination diagrams when use: a) saplings modeled with the best seedling model, b) adult modeled with the best seedling model and c) adult modeled with the best sapling model. The abbreviation of species' name and environmental variables see: Fig 1. * indicates a significant variable ($P < 0.05$). See Table 1 for F and P values.

Figure 1.

a) Seedling stage



b) Sapling stage



c) Adult stage

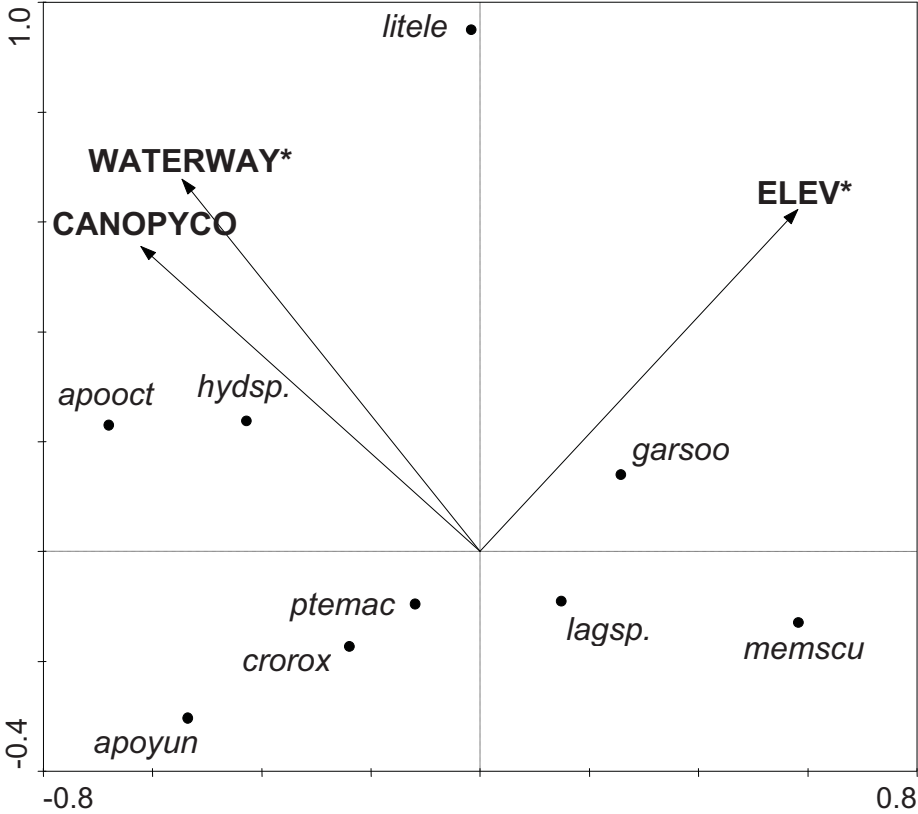
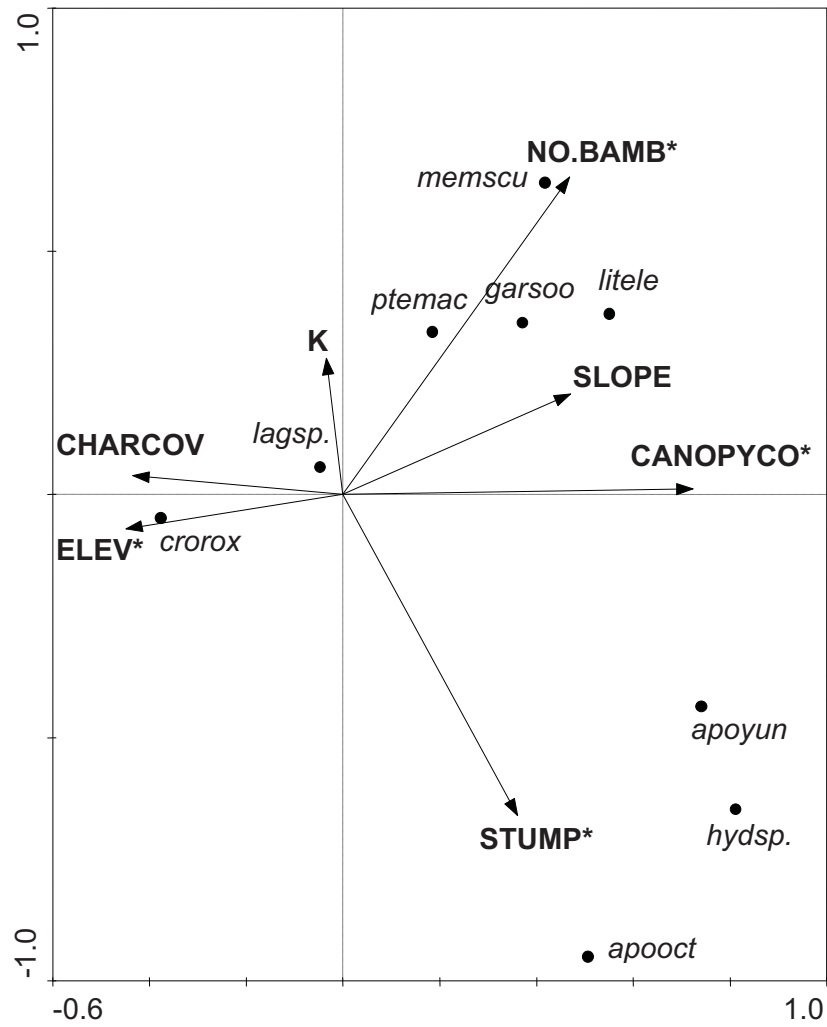
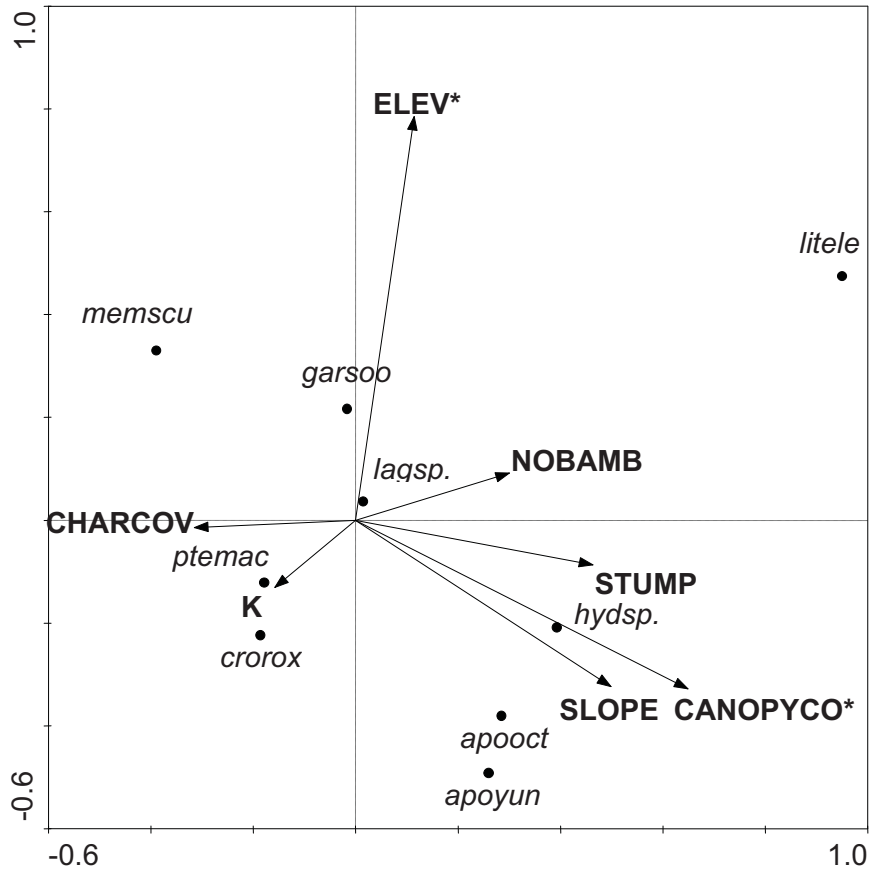


Figure 2.

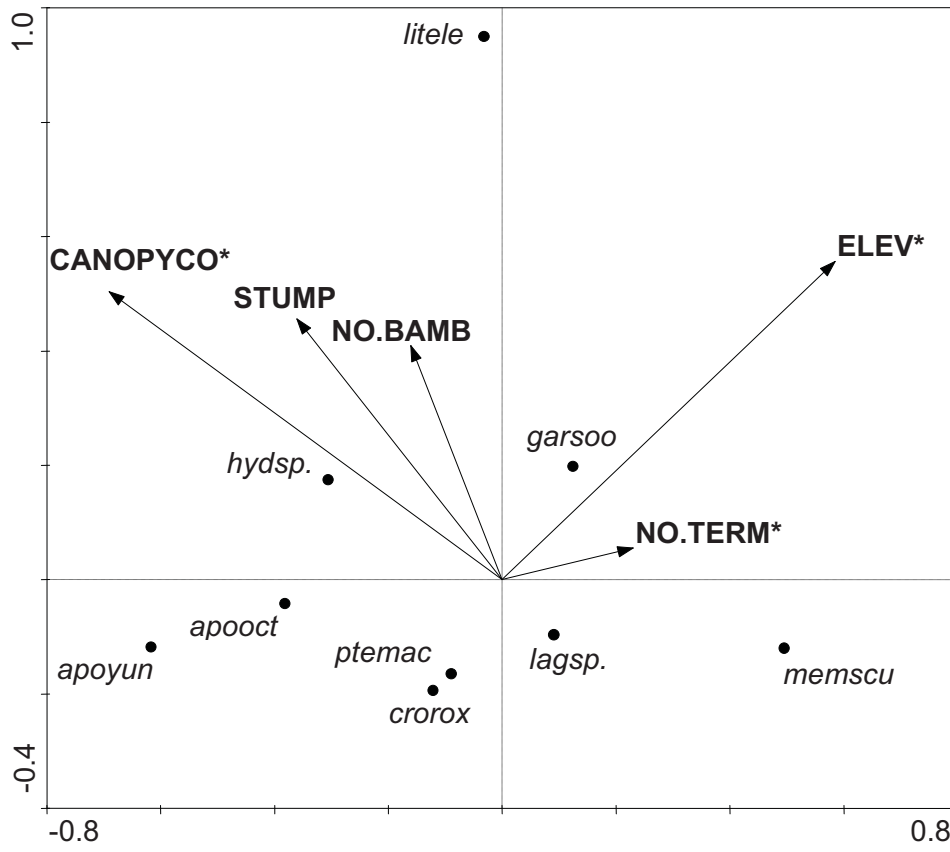
a) Saplings modeled with the best seedling model



b) Adults modeled with the best seedling model



c) Adult modeled with the best sapling model



Paper IV

Bamboo dominance reduces tree regeneration in a disturbed tropical forest

Panadda Larpkern · Stein R. Moe · Ørjan Totland

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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 (Dhillon et al. 2003). Changes in canopy dominants, from trees to bamboos, may change tree seedling regeneration patterns.

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P. Larpkern (✉) · S. R. Moe · Ø. Totland
Department of Ecology and Natural Resource Management,
The Norwegian University of Life Sciences,
P.O. Box 5003, 1432 Ås, Norway
e-mail: panadda.larpkern@umb.no;
larpkern.panadda@gmail.com

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 (Lisanewok 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 sparse in the dry season, since most trees drop their leaves. Dominating woody species forming the tree-layer are *Cananga latifolia*, *Lagerstroemia* sp., *Gardenia sootepensis*, *Spondias 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 m²/ha, while the overall basal area of adult trees is 17.1 m²/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 \pm 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

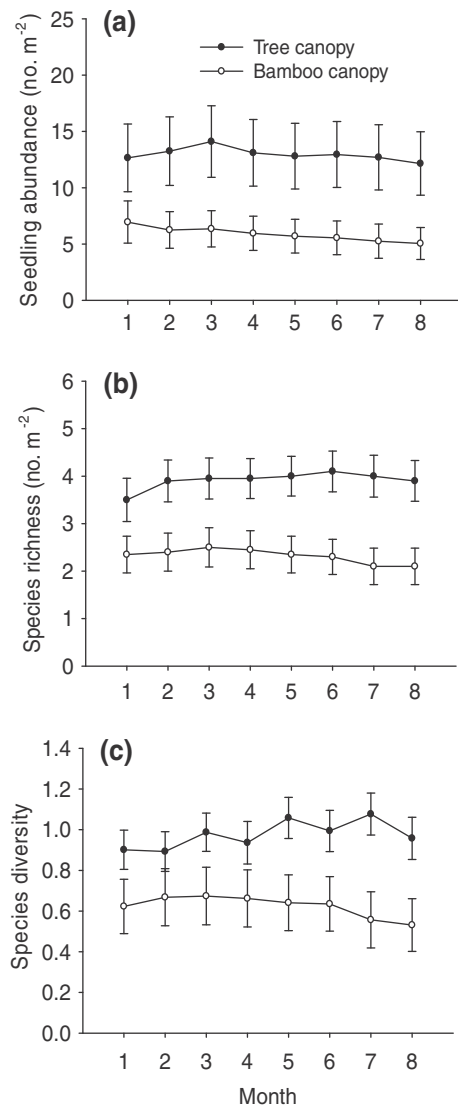


Fig. 1 The effects of canopy type on woody seedling **a** abundance, **b** species richness, and **c** species diversity. The canopy types are under bamboo canopy (*open circles*) and under tree canopy (*filled circles*). Months (1–8) are May–December. Values are means \pm SE ($n = 20$)

($P = 0.04$) 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 ($14,940 \pm 1,557$ lux) than under bamboo canopies ($4,379 \pm 604$ 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

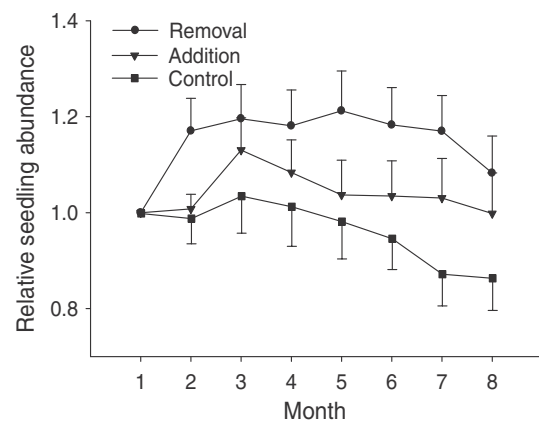


Fig. 2 Mean relative woody seedling abundance ($n = 20$) under the bamboo canopies after litter removal (*filled circles*), litter addition (*filled triangles*) and control (*filled squares*). Vertical bars are 1SE. Months (1–8) are May–December. The number of seedlings in May was used as a reference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

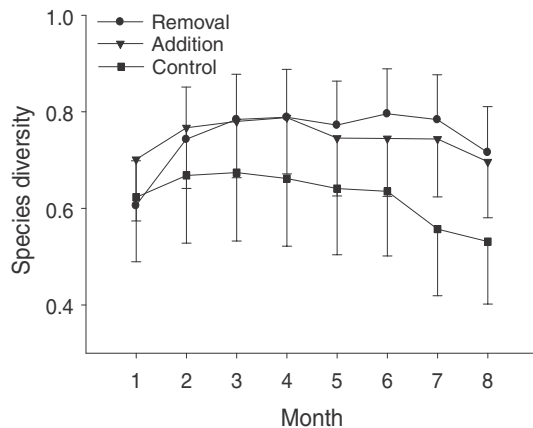


Fig. 3 Mean woody seedling species diversity ($n = 20$) under the bamboo canopies after litter removal (filled circles), litter addition (filled triangles) and control (filled squares). Months (1–8) are May–December. Vertical bars are 1SE

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 (Larppern 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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Electronic Supplementary Material for:

Bamboo dominance reduces tree regeneration in a disturbed tropical forest by Panadda Larpkern, Stein R. Moe, Ørjan Totland

Table S1. The effects of canopy type (below bamboo canopy vs. below tree canopy), plot and month on woody seedlings monitored from May to December 2006 in a mixed deciduous forest, Thailand. Repeated-measures ANOVA on log-transformed seedling abundance and average seedling abundance per species data. Analyses used Type III SS. The fractional degrees of freedom are derived from the Greenhouse-Geisser correction for the within-subjects factors.

Parameters	Abundance			Species richness			Species diversity			Average seedling abundance per species						
	df	MS	F	P	df	MS	F	P	df	MS	F	P				
Between-subjects																
Canopy type (C)	1	8.30	6.19	0.022	1	203.20	7.13	0.015	1	9.88	4.03	0.059	1	1.16	2.07	0.167
Plot (P)	19	1.14	0.851	0.635	19	22.89	0.80	0.681	19	1.73	0.70	0.775	19	0.41	0.73	0.747
Error	19	1.34			19	28.50			19	2.45			19	0.56		
Within-subjects																
Month (M)	2.68	0.05	3.64	0.030	2.39	1.42	2.25	0.108	3.27	0.11	1.87	0.139	2.83	0.024	4.37	0.009
M x C	2.68	0.03	2.23	0.103	2.39	1.75	2.77	0.064	3.27	0.18	2.87	0.039	2.83	0.003	0.54	0.644
M x P	50.82	0.01	0.84	0.727	45.42	0.64	1.01	0.487	62.21	0.07	1.14	0.310	53.70	0.006	1.11	0.355
Error (M)	50.82	0.01			45.42	0.63			62.21	0.06			53.70	0.005		

Figure S2. Light intensity (mean \pm SE, n = 20) measured for 21 weeks under the tree (filled circles) and the bamboo (open circles) canopy during last week of May to December.

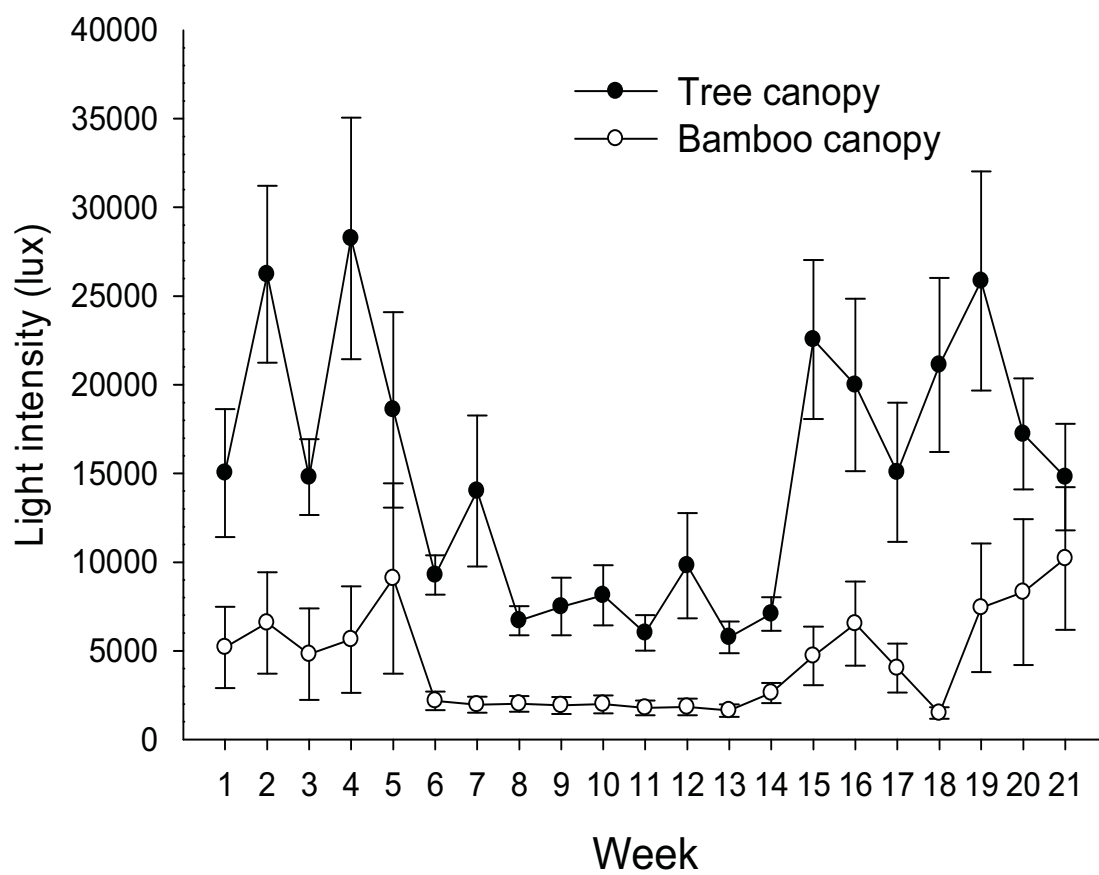


Table S3. The effects of litter, plot and month on total woody seedling abundance monitored from May to December 2006 in a mixed deciduous forest, Thailand. Repeated-measures ANCOVA on log-transformed total seedling abundance data. The seedling abundance in May was used as a covariate. Analysis used Type III SS. The fractional degrees of freedom are derived from the Greenhouse-Geisser correction for the within-subjects factors.

Parameters	Total seedling abundance							
	Bamboo canopy				Tree canopy			
	df	MS	<i>F</i>	<i>P</i>	df	MS	<i>F</i>	<i>P</i>
Between-subjects								
Litter (L)	2	0.30	4.30	0.021	2	0.03	0.73	0.488
Plot (P)	19	0.18	2.48	0.009	19	0.10	3.04	0.002
Covariate (C)	1	13.94	197.70	<0.0001	1	6.25	186.15	<0.0001
Error	37	0.07			37	0.03		
Within-subjects								
Month (M)	2.44	0.01	1.15	0.244	2.54	0.003	0.53	0.634
M x L	4.87	0.01	0.85	0.609	5.08	0.003	0.68	0.642
M x P	46.28	0.01	1.02	0.050	48.21	0.007	1.40	0.083
M x C	2.44	0.01	0.44	0.665	2.54	0.006	1.21	0.310
Error (M)	90.12	0.01			93.88	0.005		

Table S4. The effects of litter, plot and month on total woody seedling species diversity monitored from May to December 2006 in a mixed deciduous forest, Thailand. Repeated-measures ANCOVA with seedling species diversity in May as a covariate. Analysis used Type III SS. The fractional degrees of freedom are derived from the Greenhouse-Geisser correction for the within-subjects factors.

Parameters	Seedling species diversity							
	Bamboo canopy				Tree canopy			
	df	MS	<i>F</i>	<i>P</i>	df	MS	<i>F</i>	<i>P</i>
Between-subjects								
Litter (L)	2	0.90	3.82	0.031	2	0.39	1.11	0.342
Plot (P)	19	0.76	3.21	0.001	19	0.69	1.98	0.037
Covariate (C)	1	39.91	169.43	<0.0001	1	17.22	49.27	<0.0001
Error	37	0.24			37	0.35		
Within-subjects								
Month (M)	3.01	0.03	0.79	0.501	2.70	0.13	3.29	0.028
M x L	6.02	0.03	0.72	0.638	5.40	0.03	0.77	0.584
M x P	57.21	0.04	1.00	0.486	51.33	0.05	1.32	0.116
M x C	3.01	0.01	0.25	0.863	2.70	0.09	2.41	0.077
Error (M)	111.41	0.04			99.95	0.04		

Table S5. The effects of litter, plot and month on total woody seedling species richness monitored from May to December 2006 in a mixed deciduous forest, Thailand. Repeated-measures ANCOVA with seedling species richness in May as a covariate. Analysis used Type III SS. The fractional degrees of freedom are derived from the Greenhouse-Geisser correction for the within-subjects factors

Parameters	Seedling species richness							
	Bamboo canopy				Tree canopy			
	df	MS	<i>F</i>	<i>P</i>	df	MS	<i>F</i>	<i>P</i>
Between-subjects								
Litter (L)	2	6.37	3.20	0.052	2	8.76	2.58	0.089
Plot (P)	19	6.40	3.22	0.001	19	7.34	2.16	0.022
Covariate (C)	1	288.77	76.12	<0.0001	1	258.37	76.12	<0.0001
Error	37	1.99			37	3.39		
Within-subjects								
M	2.91	0.33	1.110	0.347	3.39	0.47	2.77	0.038
M x L	5.823	0.19	0.63	0.702	6.77	0.28	1.68	0.123
M x P	55.35	0.29	0.98	0.530	64.34	0.28	1.63	0.010
M x C	2.91	0.11	0.37	0.770	3.37	0.60	3.56	0.013
Error (M)	107.79	0.30			125.29	0.17		

Table S6. The effects of litter, plot and month on average woody seedling abundance per species monitored from May to December 2006 in a mixed deciduous forest, Thailand.

Repeated-measures ANCOVA on log– transformed seedling abundance per species data. The seedling abundance in May was used as a covariate. Analysis used Type III SS. The fractional degrees of freedom are derived from the Greenhouse-Geisser correction for the within-subjects factors.

Parameters	Average seedling abundance per species							
	Bamboo canopy				Tree canopy			
	df	MS	<i>F</i>	<i>P</i>	df	MS	<i>F</i>	<i>P</i>
Between-subjects								
Litter (L)	2	0.03	0.81	0.454	2	0.02	0.58	0.566
Plot (P)	19	0.04	0.99	0.488	19	0.05	1.58	0.116
Covariate (C)	1	7.49	188.78	<0.0001	1	4.58	138.09	<0.0001
Error	37	0.04			37	0.03		
Within-subjects								
M	3.26	0.003	0.90	0.450	3.04	0.003	0.94	0.425
M x L	6.52	0.002	0.51	0.816	6.089	0.003	0.73	0.579
M x P	61.95	0.008	2.05	<0.0001	57.85	0.004	1.20	0.209
M x C	3.26	0.005	1.154	0.293	3.04	0.006	1.85	0.141
Error (M)	120.63	0.004			112.65	0.003		

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NORWEGIAN UNIVERSITY OF LIFE SCIENCES
NO-1432 Ås, NORWAY
PHONE +47 64 96 50 00
www.umb.no, e-mail: postmottak@umb.no