Biological Conservation 147 (2012) 32–39

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Bamboo overabundance alters forest structure and dynamics in the Atlantic Forest hotspot

Renato A.F. Lima [a,*], Débora C. Rother [b], Ana E. Muler [c], Igo F. Lepsch [d], Ricardo R. Rodrigues [c]

[a] Programa de pós-graduação em Ecologia, Instituto de Biociências – Universidade de São Paulo (USP), Rua do Matão, travessa 14, 321, CEP 05508-090 São Paulo, Brazil
[b] Programa de pós-graduação em Biologia Vegetal, Campus Rio Claro – Universidade Estadual Paulista (UNESP), Av. 24A, 1515, Caixa Postal 199, CEP 13506-900 Rio Claro, SP, Brazil
[c] Departamento de Ciências Biológicas, ESALQ – Universidade de São Paulo (USP), Av. Pádua Dias, 11, Caixa Postal 9, Piracicaba, CEP 13418-900 São Paulo, Brazil
[d] Departamento de Ciência do Solo, ESALQ – Universidade de São Paulo (USP), Av. Pádua Dias, 11, Caixa Postal 9, Piracicaba, CEP 13418-900 São Paulo, Brazil

A R T I C L E I N F O

Article history:
Received 18 May 2011
Received in revised form 3 January 2012
Accepted 10 January 2012
Available online 9 February 2012

Keywords:
Brazil
Forest conservation
Guadua
Physical damage
Soil
Tree regeneration

A B S T R A C T

With fast growth rates and clonal reproduction, bamboos can rapidly invade forest areas, drastically changing their original structure. In the Brazilian Atlantic Forest, where recent mapping efforts have shown that woody bamboos dominate large areas, the present study assessed the differences in soil and vegetation between plots dominated (>90% of bamboo coverage) and not dominated (<10% of coverage) by the native *Guadua tagoara*. Surface soil was physically and chemically analyzed, and trees at three size classes (seedling, sapling, and adult) were counted, identified and measured. New inventories were conducted to assess recruitment, mortality, and damage rates. Bamboo plots had more fertile soils (higher bases saturation and lower potential acidity) due to the preferential occurrence of *G. tagoara* on more clayey soils. Bamboo-dominated plots had lower density of adult trees (diameter >5 cm) and lower species density. In addition, overall tree diameter distribution was very different between environments, with bamboo plots having greater concentration of small-sized trees. Such differences are probably related to the general tendency of higher mortality, recruitment, and damage rates in bamboo plots. Greater physical (wind and bamboo-induced damages) and physiological stress (heat and light) in bamboo plots are probable causes of bamboo-dominated plots being more dynamic. Finally, we discuss the differences between Atlantic and Amazonian *Guadua*-dominated forests, causes, and possible consequences of bamboo overabundance to the Atlantic Forest conservation.

1. Introduction

Records of biological invasions are widespread in the ecological literature. Classic examples come from alien species that are introduced by man into a new environment (e.g. Vitousek et al., 1987) where they become dominant for different reasons (e.g. lack of predators or competitors). The consequences vary from the addition of new species to drastic disruptions on the community structure (Simberloff and von Holle, 1999; Mack et al., 2000). Nevertheless, there are records of native species becoming increasingly dominant in its original range, a phenomenon known as overabundance (Garrot et al., 1993). Generally, overabundant species are opportunists that respond positively to changes in the original community, a common feature of human-modified landscapes. Traditionally seen as a phenomenon that needs control, biological invasions by exotic species are one of the most conspicuous impacts in natural ecosystems, and its study has provided some important ecological and evolutionary insights (Rejmánek, 1996; Sax et al., 2007). Although regarded as a phenomenon with similar impacts (Garrot et al., 1993), the effects of overabundant native species are less known.

Many woody bamboos (Poaceae: Bambuseae) are typical examples of invasive plants, having many attributes of successful invaders. The production of large amounts of small seeds and small periods of dormancy promote efficient colonization of new sites (Rejmánek and Richardson, 1996; Williamson and Fitter, 1996; Veldman and Putz, 2011), especially disturbed ones (Burman and Filgueiras, 1993). Once established, fast growth and clonal reproduction (sometimes including reiterative growth) increase bamboos' ability to compete for space, and to form dense stands (Silveira, 2005). Its reproduction and growth strategies work together to sustain the occupancy for long periods of time (Young, 1991; Griscom and Ashton, 2006). Since woody bamboos are essentially forest species (Clark, 1997; Judziewicz et al., 1999), bamboo-dominated areas usually play an important part on the structure and dynamics of forest ecosystems (Veblen, 1982;

* Corresponding author. Tel.: +55 11 50522171.
E-mail addresses: raflima@usp.br (R.A.F. Lima), dcrother@rc.unesp.br (D.C. Rother), ana.muler@usp.br (A.E. Muler), igo_lepsch@yahoo.com.br (I.F. Lepsch), rrr@esalq.usp.br (R.R. Rodrigues).

0006-3207/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2012.01.015

Okutomi et al., 1996). In this sense, there is a general agreement that bamboos compete with other species, reducing woody species density and diversity (Taylor and Zisheng, 1988; Silveira, 2005) and sometimes bringing forest succession to a standstill (Griscom and Ashton, 2006). Bamboos also affect seed dispersal patterns, influencing forest regeneration on its early stages (Rother et al., 2009). Forest soils and nutrient cycling are also affected by high bamboo dominance that may have soils and litter poorer in some nutrients (Veblen, 1982; Tripathi et al., 2006).

Unconstrained bamboo expansion can lead to the formation of the so-called bamboo forests, well-known in Eastern Asia (Taylor and Zisheng, 1988; Okutomi et al., 1996). In South America, there are vast areas in southwestern Amazon dominated by native *Guadua* species (>160,000 km^2), where density varies from 1.900 to 3.800 culms ha^{-1} (Griscom and Ashton, 2006; Nelson et al., 2006). More recently, attention was directed to southeastern Brazil where mapping efforts revealed that considerable parts of the remaining Atlantic Forest are dominated by woody bamboos. In southern São Paulo State, for instance, there is evidence that one third of the forest remnants may be dominated by woody bamboos, mainly *Guadua tagoara* (Fantini and Guries, 2007; Araujo, 2008). Other important remnants in Rio de Janeiro state (i.e. Itatiaia, Bocaina, and Serra dos Orgãos National Parks) also present areas dominated by this species (R.A.F. Lima, pers. observation). Although *G. tagoara* is native, the situation is somewhat alarming since there is evidence of bamboo expansion (Alves, 2007). After analyzing aerial photographs between 1962 and 2000 in a 40,000-ha protected area, Araujo (2008) reported an increase of ca. 2000 ha in the forest class enclosing bamboo-dominated forests. Thus, in the highly threatened Atlantic Forest (Ribeiro et al., 2009), conservationists currently see the overabundance of *G. tagoara* and other woody bamboos as major threats (Araujo, 2008).

However, the origin of *G. tagoara* overabundance is still unclear. Some have argued that it is induced by human activities, such as crops, timber, and/or palm-heart extraction (Fantini and Guries, 2007; Araujo, 2008). But natural disturbances or specific types of soil may also create suitable environments to bamboo colonization (Griscom and Ashton, 2006; Nelson et al., 2006). Independently of their origin, the overabundance of bamboos in the Atlantic Forest is an issue that deserves close attention. Obviously, any intervention should be preceded by the understanding of the expansion processes and consequences. Similarly to southwestern Amazon (Nelson et al., 2006; Griscom and Ashton, 2003), forests dominated by *G. tagoara* have lower densities of adult trees (Fantini and Guries, 2007). Despite of the effects of *G. tagoara* on forest structure, studies on the underlying processes that generate such differences are largely missing. In addition, we still do not know what the influences of *G. tagoara* overabundance are on species density and soil nutrient availability.

This study was conducted in São Paulo state, where woody bamboos have become a real issue for biodiversity conservation. The aim was to understand the effects of *G. tagoara* overabundance on different environmental features. More specifically, we assessed how *G. tagoara* affects soil physical–chemical properties, forest structure and tree species diversity by comparing bamboo-free and bamboo-dominated areas within a 10.24-ha plot. We evaluated if differences on forest structure between environments were accompanied by different dynamics, in terms of recruitment and mortality. In addition, we assessed Griscom and Ashton's (2006) hypothesis that bamboo-induced damages are the main causes of the self-perpetuating cycle in *Guadua*-dominated forests. Finally, we discuss the origin of bamboo overabundance, and its influence in the Atlantic Forest conservation.

2. Material and methods

2.1. Study site

The study site is the Carlos Botelho State Park (PECB) which covers 37 644 ha of the Atlantic Forest of southern São Paulo State, Brazil, one of the largest and well-conserved Atlantic Forest continuums. Data collection was carried out in 10.24-ha (320 × 320 m) permanent plot established in 2002 in the Sete Barras county (plot coordinates: 24°10′S and 47°56′W) subdivided into 20 × 20-m subplots. Local climate is classified as humid subtropical with no dry season (Cfa) with mean annual temperature and precipitation of 22 °C and 1584 mm, respectively. Although there is no dry season, rainfall gets below 50 mm from April through September, especially during El-Niño years. The plot was placed at steep slopes with altitudes varying from 350 to 450 m a.s.l. Plot soils developed over granites and colluvionar deposits, and were classified as Haplic Cambisols (Inceptisols) and Fluvisols/Leptosols (Fluvents/Udorthents; Rodrigues, 2005). Plot vegetation is an old-growth Lower Montane Rain Forest, with an average canopy height of 20 m. Palms and tree ferns are abundant, while Marantaceae and Araceae are common in the herb stratum. Families rich in tree species inside the plot are Myrtaceae, Fabaceae, Rubiaceae, Lauraceae, and Sapotaceae. Although there is no recent record of large human impacts, disturbances related to the illegal extraction of palm-heart (*Euterpe edulis*) are common.

2.2. Bamboo species

Almost one third of the 10.24-ha plot is covered by large areas (mainly >1000 m^2) with great dominance of woody bamboos, regionally known as *taquaral* (see online Supplementary material), where the great density of culms makes it hard to walk through. The canopy is markedly lower and discontinuous, enhancing light entrance (Lima and Gandolfi, 2009). In the studied plot, the *taquarais* are formed solely by *G. tagoara* (Nees) Kunth, a large-sized, semi-scandent woody bamboo. Culms are green, hollow (often filled with water), and scandent towards the top, with heights and girths of 8–15(−20) m and 5–10 cm, respectively (Londoño, 2001). They grow fast upwards (up to 20 cm day^{-1} – Alves, 2007) and then bend over the surrounding vegetation, aided by their sharp recurved thorns. Description of *G. tagoara* showed that the species has long-necked, pachymorph rhizomes that allow combined running and clumping growth strategies (Alves, 2007). The species is monocarpic (lifespan is probably 10–25 yr) with locally synchronized, mast-flowering spread over three or more years (Alves, 2007). The massive amounts of seeds promptly form dense seedling banks below and around senescent clumps (around 300 seedlings m^{-2}). *G. tagoara* is endemic to the Atlantic Lower Montane and Montane Rain Forests of Brazil, ranging from Bahia to Santa Catarina States (Londoño and Clark, 2002). Morphology and growth strategies are similar to the Amazonian *Guadua weberbaueri* and *Guadua sarcocarpa* (Silveira, 2005; Griscom and Ashton, 2006).

2.3. Study design

The 10.24-ha plot was completely surveyed in January 2006 and all areas dominated by *G. tagoara* were delimited. The resulting map was used to classify the 20 × 20-m plots into two groups: bamboo plots, i.e., plots containing ⩾90% of its area covered by *G. tagoara*-dominated stands; and non-bamboo plots, i.e., plots containing <10% of bamboo-dominated stands. This last group includes the other types of canopy conditions of the plot, namely