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Dendroecology of *Pinus elliottii* Engelm. reveals waves of invasion in a neotropical savanna

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Abstract Despite advances in understanding the ecology and consequences of pine invasions, information on the patterns of structure, dynamics, and growth needed to manage these invasive populations are still poorly known. Here we used tree ring analysis to elucidate growth dynamics, age distribution and fire effects, by sampling three populations of slash pine invading Cerrado vegetation in southeastern Brazil. We found that the invasion occurred in waves, every 5–7 years. These pulses are likely related to the time needed by founder trees to reach maturity, and to climatic events. We found distinct growth patterns among the three study areas. Individual trees in the open sites, under low competition for light, showed an increasing trend of diameter and of the basal area growth rates with age. In the dense stands, however, the diameter increment rates gradually decreased with age, as the competition for light was intensified, and the basal area growth rate increased at lower rates. Growth rates were markedly reduced after fire, likely due to fire impact on the canopies, reducing photosynthesis. Fire scars in the wood allowed us to confirm that the formation of the tree rings occurs annually. When competition for light intensifies as the canopy of the stand closes, the invasive populations experience reduced individual growth of adult trees and constraints to the recruitment of young individuals. We did not find, however, evidence of self-thinning due to competition that could reduce the population of adult trees, open gaps and allow colonization by shade-tolerant native species. Therefore, a monodominant pine stand—the "pine desert" feature of the invaded sites—tends to be persistent over time.

Keywords Dendrochronology · Diameter increment · Wood production · Growth rings · Fire record · Cerrado

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Introduction

Pinus elliottii Engelm. (slash pine) is a native tree from North America that became one of the most aggressive invaders of savannas and grasslands in the southern hemisphere, after being introduced for timber production (Richardson et al. 1994; Richardson and Higgins 1998; Richardson 2006). Species of the genus *Pinus* L. have significant economic and environmental importance (Nuñez et al. 2017). In Brazil, tax breaks were given to forestry of *Pinus* species after the 1960s, and they became a significant part of forest plantations, reaching 1.8 million hectares in 2008. Today, *Pinus* species are used in several segments of forestry and wood sectors, mainly for pulp, paper, charcoal, panels and lumber production (Vasquez et al. 2007; Sociedade Brasileira de Silvicultura 2008). *P. elliottii* has been reported as invasive in Argentina, Australia (NSW), Brazil, Hawaii, and South Africa (Richardson 2006), promoting structural, floristic and functional changes in plant communities, reducing the biodiversity, changing hydrological regimes, and altering soil nutrients (Vasquez et al. 2007; Simberloff et al. 2009; Abreu and Durigan 2011; Abreu 2013; Fischer et al. 2014). The native range of the species are the floodplains from the Southeast USA, were slash pine experiences a natural fire regime of about 25 fires per century (Carey 1992). The species grows faster in Brazil than in the native habitat, forming invasive stands with twice the density and a litter depth 14 times thicker than in native pine forests of Mississippi (Brewer et al. 2018). *Pinus elliottii* is able to survive light fires due to the thick bark and bark structures that dissipate the heat. Small individuals can die due to fire, but after 10–12 years slash pine trees are high enough to resist to fire that does not crown (Carey 1992). From its introduction to Brazil in the 1940s, *P. elliottii* has become one of the most planted pine species in Brazil, mostly in temperate climates (Kronka et al. 2005; Vasquez et al. 2007).

Slash pine has been recognized in the last two decades as highly invasive in the Brazilian grasslands and savannas of the Cerrado (Zanchetta and Diniz 2006; Vasquez et al. 2007; Abreu and Durigan 2011; Abreu 2013; Bechara et al. 2013). The Brazilian savanna (Cerrado) is a biome which covers around 2 million km^2 and has 12,000 plant species, 4400 of which are endemic (Oliveira-Filho and Ratter 2002), and it has been the region most heavily invaded by *P.*

elliottii (Zanchetta and Diniz 2006; Abreu and Durigan 2011; Abreu 2013). The invasion process in southeastern Brazil is fast; 22 years after the first pine trees arrived at one site, a grassland savanna was converted into a dense *Pinus* forest with 12,455 individuals and 26.44 m^2 of basal area per hectare. The species richness of the understory was reduced from 52 to 16 species, and 90% of native individuals > 50 cm tall was lost, along with the entirety of the herbaceous layer. *Pinus* invasion thus produces profound changes in the vegetation structure, causing significant losses of plant diversity (Abreu and Durigan 2011).

Despite the recent advances in the geography and ecology of pine invasion, aspects such as the structure, dynamics and growth patterns of the invasive populations are still poorly known. Simberloff (2014) argues that the problem of biological invasions could be better addressed by moving from a focus on invasive *species* to addressing invasive *populations*, because reducing the population size of an invader could be a desired goal for invasive species management. The potential for dendrochronology to provide the needed information and to inform management has been demonstrated by several studies in tropical regions, some encompassing *Pinus* species (Biondi 1999; Worbes 1999; Worbes et al. 2003; Couralet et al. 2005; Brienen and Zuidema 2006; Schöngart 2008; Zimmer and Baker 2009; Rozendaal and Zuidema 2011; Locossssseli et al. 2017; Tomazello-Filho et al. 2017; Vlam et al. 2017). *Pinus* species have distinct tree-rings which can be analyzed by dendrochronology. Schulman (1944) developed the first tree-ring chronologies with *Pinus* species in the tropical regions of Mexico. Since then, dendrochronological studies with *Pinus* were developed in many tropical countries, including Honduras, Guatemala, El Salvador, Dominican Republic, Laos, Thailand, Vietnam and Brazil (Johnson 1980; Sarutanon et al. 1995; D'Arrigo et al. 1997; Biondi 2001; Speer et al. 2004; Buckley et al. 2007; Moya and Filho 2009; Zimmer and Baker 2009; Sigal 2011; Zuidema et al. 2011; Venegas-González et al. 2015). These studies provided evidence of annual growth rings and proposed tree-ring chronologies and inferences about growth-climate relationships. Specifically for *P. elliottii*, tree-ring chronologies and dendroclimatological studies were developed in temperate and subtropical climates (Harley et al. 2011). In Brazil, tree-ring analysis in *Pinus* has been used to

provide information about age and to quantify wood growth, including for forestry production and height growth evaluation, pruning and thinning effects, soil nutrition effects and wood density variations (Trovati and Ferraz 1984; Brito et al. 1986; Pereira and Ahrens 2003; Ferreira and Filho 2009; Coelho and Hosokawa 2010; Elesbão and Schneider 2011; Schneider et al. 2013; Ortega Rodriguez et al. 2018). Dendrochronological analyses have also been used to evaluate height growth, to differentiate juvenile and adult wood, to assess thinning effects on wood quality and to explain wood density variations (Palermo et al. 2003, 2013; Pereira and Tomaselli 2004; Schneider et al. 2013). Three studies developed in Brazil so far have used tree-ring analysis to investigate the invasion process and to evaluate the effects on community level of *Pinus* invasion (Abreu and Durigan 2011; Fischer et al. 2014; Tomazello-Filho et al. 2017).

As in other grassy ecosystems, natural and anthropogenic fires are common in the Cerrado (Klink and Machado 2005; Miranda et al. 2009), including in areas invaded by *P. elliottii*. Fire is an essential factor for maintaining natural communities in the Cerrado (Miranda et al. 2009) and has been used in experiments to manage invasive species (Abreu 2013). Fire events can be recorded by fire scars marked in the wood and dated by the tree ring analysis (Brandes et al. 2018), and the formation of fire scars has been verified in *Pinus* species (Speer et al. 2004; Harley et al. 2011). Fire-scar dating of *P. elliottii* could provide information about fire events and the effects of fire on the structure of the invasive populations.

In this study, we used tree ring analysis to elucidate growth dynamics, wood production, and age distribution in three populations of slash pine invading Cerrado vegetation in southeastern Brazil. Among the questions we address are: (1) Can the fire scars demonstrate the annual nature of the growth rings? (2) Does the pine population age structure and growth dynamics differ among open and closed invaded habitats? We searched for distinct patterns in population structure and growth dynamics depending on the type of habitat invaded, namely open grasslands and riparian forests.

Materials and methods

Study areas

The study was carried out in two reserves located in São Paulo state, Southeast Brazil, within the Cerrado biome: Itirapina Ecological Station (IEcS) and Santa Barbara Ecological Station (SBEcS) (Fig. 1). Both reserves protect typical savanna vegetation (cerrado sensu lato), ranging from grasslands (campo cerrado, campo sujo, campo limpo) to woodlands (cerradão). The climate is classified as Cwa following Köppen's system (humid subtropical with dry winter and hot summer). Biological invasion is amongst the major challenges for management and conservation of the reserves. *Pinus* species planted for forestry purposes in the 1960s in the vicinity promote constant propagule pressure over the Cerrado remnants, with large areas already invaded (Silva et al. 2006; Melo and Durigan 2009; Miashike 2015).

The IEcS (22°11′S–22°15′S, 47°51′W–48°00′W—Fig. 1) covers 2300 ha, with altitude ranging from 710 to 830 m a.s.l. (Silva et al. 2006). Mean annual temperature is 21.9 °C, the hottest months were January (24.9 °C) and February (24.8 °C), and the coldest months were June (17.8 °C) and July (17.9 °C). The average annual precipitation is 1459 mm, with means ranging from 1128 mm (77%) in the rainy season (Oct–Mar) and 331 mm (23%) in the dry season (Apr–Sep). The monthly average precipitation in the driest months is 24 mm in July and 42 mm in August (Silva et al. 2006). At Itirapina we sampled two distinct sites with invaded patches of similar size, around 0.03 ha. Area 1 (or IEcS1) (22°11′52.15″S, 47°53′19.94″W) was in a grassland savanna recently invaded, in well drained soils despite being close to a water dam. Pine trees were at low density, with sunlight able to penetrate the canopies and reach the ground. Area 2 (or IEcS2) (22°14′42.24″S, 47°51′28.15″W) was in the riparian zone of a stream, likely invaded for longer than Area 1. Previous vegetation was a low-biomass riparian forest, characterized by a shaded environment with high competition for light in the understory, with no sunlight reaching the ground. Temporal series of climate data for these areas (1 and 2) were available from São Carlos meteorological station, placed 25 km far from the study sites (INMET 2018). In Areas 1 and
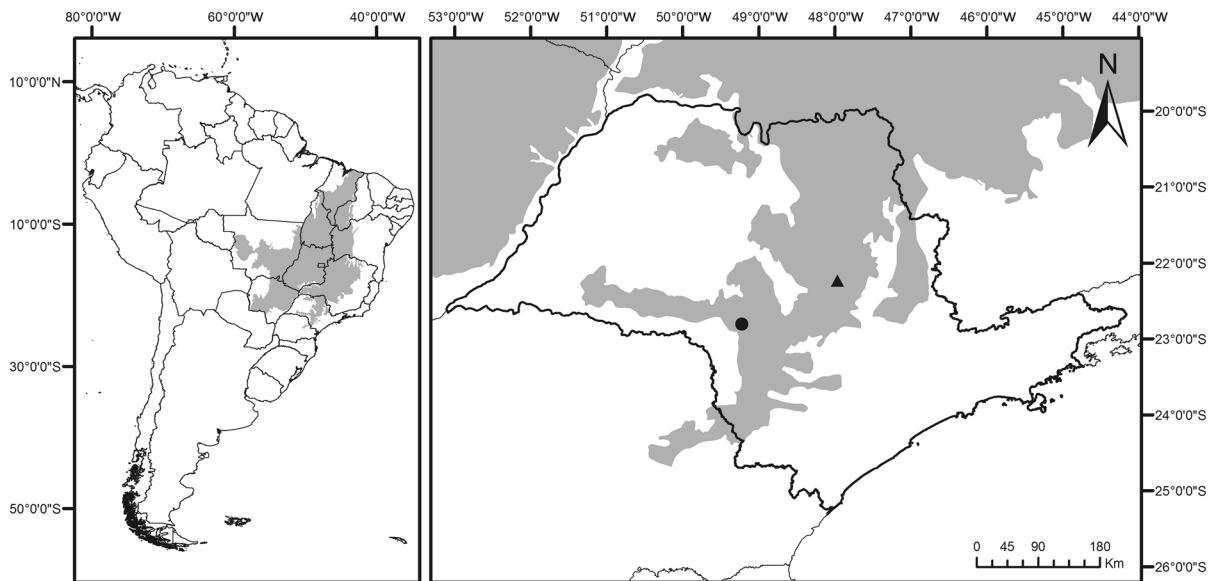
Fig. 1 Map of South America and detail of São Paulo State, Brazil. Gray = Cerrado biome; circle = Santa Barbara Ecological Station (SBEcS—Area 3); triangle = Itirapina Ecological Station (IEcS—Areas 1 and 2)

2 all individuals of *P. elliottii* within the invaded patches were sampled.

The third study site (Area 3) was located at SBEcS, a reserve covering 2715 ha (22°46′33″S–22°50′33″S, 49°10′27″W–49°15′36″W, Fig. 1). Monthly temperature ranges from 16 to 24 °C and annual precipitation from 1100 to 1300 mm. The grassland physiognomies (campo cerrado and campo sujo), where trees are scarce, occupy 225 ha. Of these grasslands, approximately 136 ha were lost due to a massive *Pinus* invasion, especially in the riparian zones (Melo and Durigan 2009). Area 3 (22°47′7.92″S and 49°14′44.21″W) corresponded to a large invaded site composed by 5 blocks (with 10 plots of 10 m × 10 m each) covering around 0.5 ha where the effects of slash pine invasion were assessed in 2010 (Abreu 2013). At this site, we sampled all pine individuals within the plots. In 2011, a wildfire reached the established sample units, and 2 years later we collected the basal cross-sections of all surviving individuals of *P. elliottii* within the 50 plots. Despite observing many dead saplings in the understory or burned after the wildfire in 2011, we must highlight that we did not observe dead adult trees standing in any of the study sites. A time series of meteorological data for Area 3 was obtained from a meteorological station in Avaré, 45 km from the sample area (INMET 2018).

Growth dynamics, age structure, and fire record

In December 2009, 169 trees were felled in Area 1, and 192 in Area 2. In September 2013, 168 trees were felled in Area 3. In each area, all *P. elliottii* trees with a basal diameter ≥ 1.0 cm were collected. The total of sampled trees was 529. The samples (wood discs) were obtained with a chainsaw operating close to the tree base (∼ 10 cm above ground). The wood discs were polished using an orbital sander. Four radii were delineated, then tree rings were cross-dated within trees to detect wedging and false rings. Cross-dating between trees was not performed because of complacent and short tree-ring width series. Leica® Stereomicroscope was used for tree ring observations. The tree rings dates followed Schulman's (1956) convention for tree ring studies in the South Hemisphere, where growth ring formation starts in the spring (September–December) and the rings are labeled with the year that they started to develop. We scanned each disc with an HP 2400 scanner and measured ring width with Image Pro Plus software, version 3.0 for Windows (Media Cybernetics Inc). Each individual establishment year was inferred by the year of the first ring, and the tree ages were inferred from the total number of annual rings. Some trees may be older than the age estimated because we did not sample in the exact root-stem boundary. The age structures of the

three populations were analyzed by age classes with 2 years range.

For each tree, we calculated the annual diameter increment as the average of the four measured ring widths, multiplied by two. We calculated the cumulative diameter increment by summing the annual diameter increment as the age of the tree increased. For the cumulative basal area increment we used the squared radius (sum of the ring widths per tree) multiplied by π. The annual basal area increment was calculated subtracting the previous year cumulative basal area from the subsequent year. For each site, we calculated the mean annual diameter and the basal area growth rate, the standard deviation, the standard error, and the maximum and minimum values. When comparing growth rates among the study areas, we analyzed the mean annual diameter and basal area increments at different age and size classes to avoid ontogenetic bias. The analysis was performed in ranges of 5 years, from 1 to 20 years (1–5, 6–10, 11–15, 16–20) and six diameter classes (every 10 cm). The non-parametric Kruskal–Wallis test was used in the comparison and the results presented in boxplots. The analyses were performed using the software Statistica 6.0 (StatSoft Inc). To evaluate the range of growth rates in each population, we plotted individual cumulative growth curves by study site. An average cumulative curve was built for each population using the mean annual diameter and the basal area increment values (Stahle et al. 1999; Worbes et al. 2003; Brienen and Zuidema 2006; Schöngart 2008). To evaluate the lifetime growth trends of the trees in each site, we plotted the annual diameter and the basal area increment by the age of the trees.

The fire record was evaluated by the presence of fire scars in the samples collected at Area 3, where a wildfire occurred in the winter of 2011 (17th July). By matching fire scars with the year of the growth rings, we evaluated growth ring periodicity formation (Worbes 1995; Harley et al. 2011). We calculated the mean diameter and the basal area increments in 2009, 2010, 2011 and 2012 to evaluate growth before and after the fire event. To eliminate the influence of size and/or age we standardized the data dividing the annual increment by the mean growth (Speer 2010) from 2009 to 2012. A paired *t* test with standardized data was performed to evaluate differences in diameter and basal area growth from 2 years before

(2009–2010) and 2 two years after (2011–2012) the wildfire event.

The sample processing was done in Wood Anatomy and Dendrochronology Laboratory (LAMAD—Laboratório de Anatomia da Madeira e Dendrocronologia) in Fluminense Federal University (Universidade Federal Fluminense). Samples were deposited in the Rio de Janeiro Botanical Garden Wood Collection (RBw—Xiloteca do Instituto de Pesquisas Jardim Botânico do Rio de Janeiro) and Niterói Herbarium Wood Collection (NITw—Xiloteca do Herbário de Niterói).

Results

Fire records

In Area 3, 48 trees showed fire scars before the formation of early wood of the year 2011 (Fig. 2). The wildfire event that reached the sample site happened in 17th July 2011, before the early wood formation. The fire scars allow us to confirm the annual nature of the growth ring formation due to the matches between the date of the wildfire and the growth ring date. Tree growth was faster in the 2 years before fire than in the 2 years after fire either for diameter increment ($t = -11.252$, $df = 335$, $P < 0.0001$) or for basal area increment ($t = -6.0853$, $df = 335$, $P < 0.0001$). Before fire, the average diameter increment was 45–60% and the basal area increment was 22–48% higher than after fire. Diameter increment before fire was 14.7 mm/year (± 0.6 SE) in 2009 and 13.2 mm/year (± 0.7 SE) in 2010. After fire, diameter increment was 8.8 mm/year (± 0.6 SE) in 2011 and
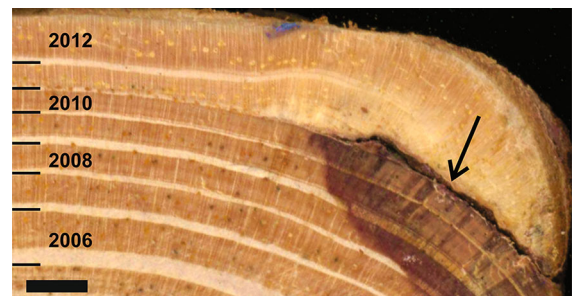
Fig. 2 Transverse stereomicroscope section of *P. elliottii*. The black arrow highlights a fire scar in the year of 2011. Scale bar = 1 cm

9.1 mm/year ($\pm$ 0.5 SE) in 2012. The average basal
area increment before fire was 3572.1 mm^2/year
($\pm$ 280.0 SE) in 2009 and 3390.7 mm^2/year
($\pm$ 299.4 SE) in 2010. After fire, basal area increased
2409.0 mm^2/year ($\pm$ 207.3 SE) in 2011 and
2780.9 mm^2/year ($\pm$ 255.0 SE) in 2012.

Age structures

Area 1

Tree ages ranged from 2 to 19 years. The greatest
number of individuals was in the class of 4–5 years
with 84 trees, followed by 6–7 years with 53 trees.
Trees were absent in two classes 12–13 years and
16–17 years. Young trees were found at low fre-
quency (2–3 years). One founder arrived in the year
1990, and 5 years later (1995) two other founders.
After another 5 years (year 2000) the colonization of
pine trees started to accelerate. An invasion pulse
happened between 2002 and 2005, with the establish-
ment of 137 trees, 7 years after the establishment of
the first founders, in 1995 (Fig. 3).

Area 2

Tree ages ranged from 4 to 20 years. The greatest
number of individuals was in the class of 18–19 years
with 40 trees, followed by 8–9 years with 30 trees. The
class with the lowest density was the 20-year class,
with seven trees. Young trees were in low abundance
(4–7 years). In this area, a continuous colonization
started with the arrival of founders in 1989 and with
the establishment of 40 trees between 1990 and 1991.
Seven years later, an invasion wave occurred between
1998 and 2001, with the establishment of 59 trees
(Fig. 3).

Area 3

Tree ages ranged from 4 to 19 years. The highest
abundance was found in the class of 12–13 years with
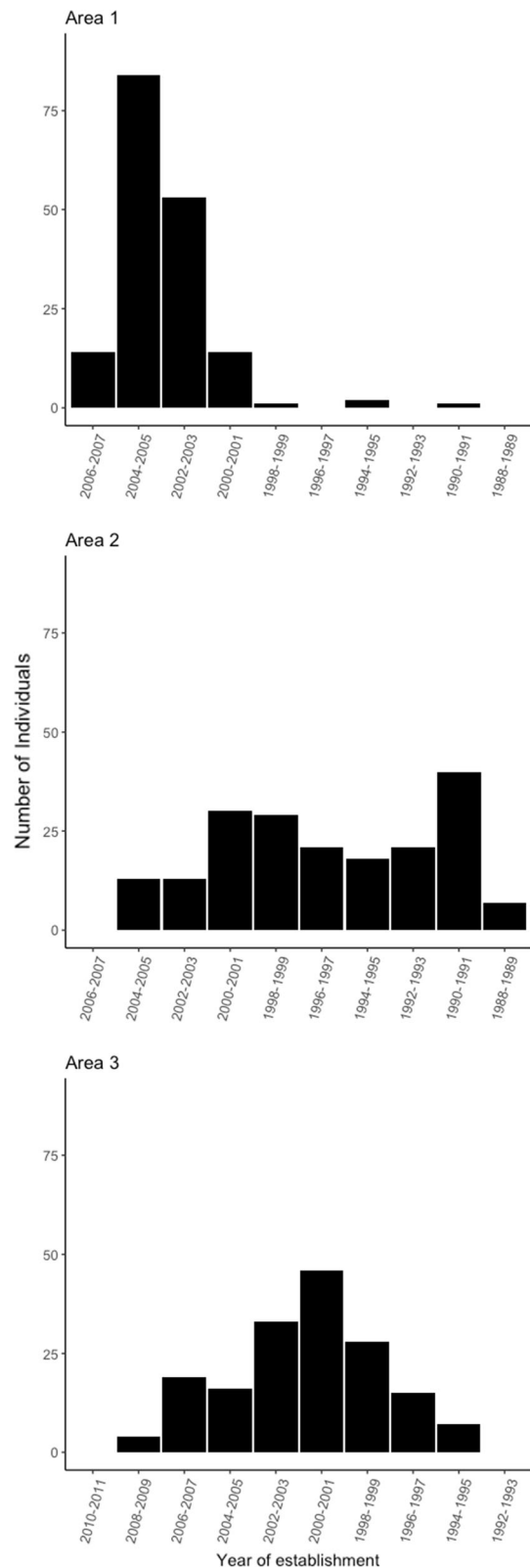
46 trees, followed by 10–11 years with 33 trees. The class with the lowest density was 4–5 years. The founders arrived in the year of 1994 and the first invasion wave happened between 1998 and 2003, 7 years after the first founders, with the establishment of 107 trees (Fig. 3).

Growth dynamics

Area 1

In this area, 3714 annual rings were measured in 169 trees. The analysis period ranged from the year 1990 to the year 2008, covering a 19-year timespan. The mean annual diameter increment was 10.5 mm/year ($\pm$ 0.3 SE) and basal area increment was 1101.0 mm^2/year ($\pm$ 100.1 SE) (Table 1). Despite the wide range of the annual increments for diameter (from 0.7 to 57.2 mm/year) and for basal area (from 0.7 to 29,359.1 mm^2/year), the individual cumulative diameters and basal area curves had similar shapes (Fig. 4).

We observed a pattern of constant increase in diameter growth rate until the tree reaches the age of 10 years (Fig. 4). After this age, we observed an oscillation on the growth rate, but only a few individuals reached more than 10 years of age in this area. During the first 5 years, the diameter growth rate was higher than that observed in Area 2 and lower than that observed in Area 3 (Fig. 5). Considering trees from 6 to 10 years old, the growth rate was higher than observed in Area 2 and similar to that observed in Area 3. We could not analyze the last age classes (the youngest) due to the small number of individuals. Considering the diameter size class 1–10 cm, diameter growth rate in Area 1 was higher than observed in Area 2 and lower than observed in Area 3 (Fig. 6). For all other size classes (11–20, 21–30, 31–40, 41–50 cm), diameter growth rate was higher in Area 1 than observed in Areas 2 and 3.

Basal Area growth rate exponentially increased until trees reached the age of 10 years (Fig. 4). After this age, an oscillation on basal area increment was detected, but few individuals compound this data. Considering 1–5 years and 6–10 years age classes, basal area increment rate in Area 1 was higher than observed in Area 2 and lower than observed in Area 3 (Fig. 7). In the diameter size class 1–10 cm, basal area growth rate in Area 1 was higher than observed in Area 2 and lower than observed in Area 3 (Fig. 8). For all

Table 1 Number of trees (sample size), total number of tree rings measured, annual diameter increment, annual basal area increment, standard deviation (SD), standard error (SE), maximum (max) and minimum (min), timespan of the chronology, number of years

Local	Sample size	Total measurements	Diameter growth (mm/year)	SD	SE	Max	Min	BAI (mm^2/year)	SD	SE	Max	Min	Time span	Number of years
IEcS1	169	3714	10.5	8.6	0.28	57.2	0.7	1101.0	3055.7	100.1	29,359.1	0.7	1990–2008	19
IEcS2	192	9570	4.5	3.7	0.08	24.3	0.3	336.5	474.1	9.6	3166.5	0.3	1989–2008	20
SBEcS	168	7726	15.1	9.2	0.20	58.2	0.1	2683.4	3132.5	70.6	32,596.0	0.0	1994–2012	19
Total	529	21,010												

Itirapina Ecological Station—Areas 1 (IEcS1) and 2 (IEcS2), and Santa Barbara Ecological Station—Area 3 (SBEcS)
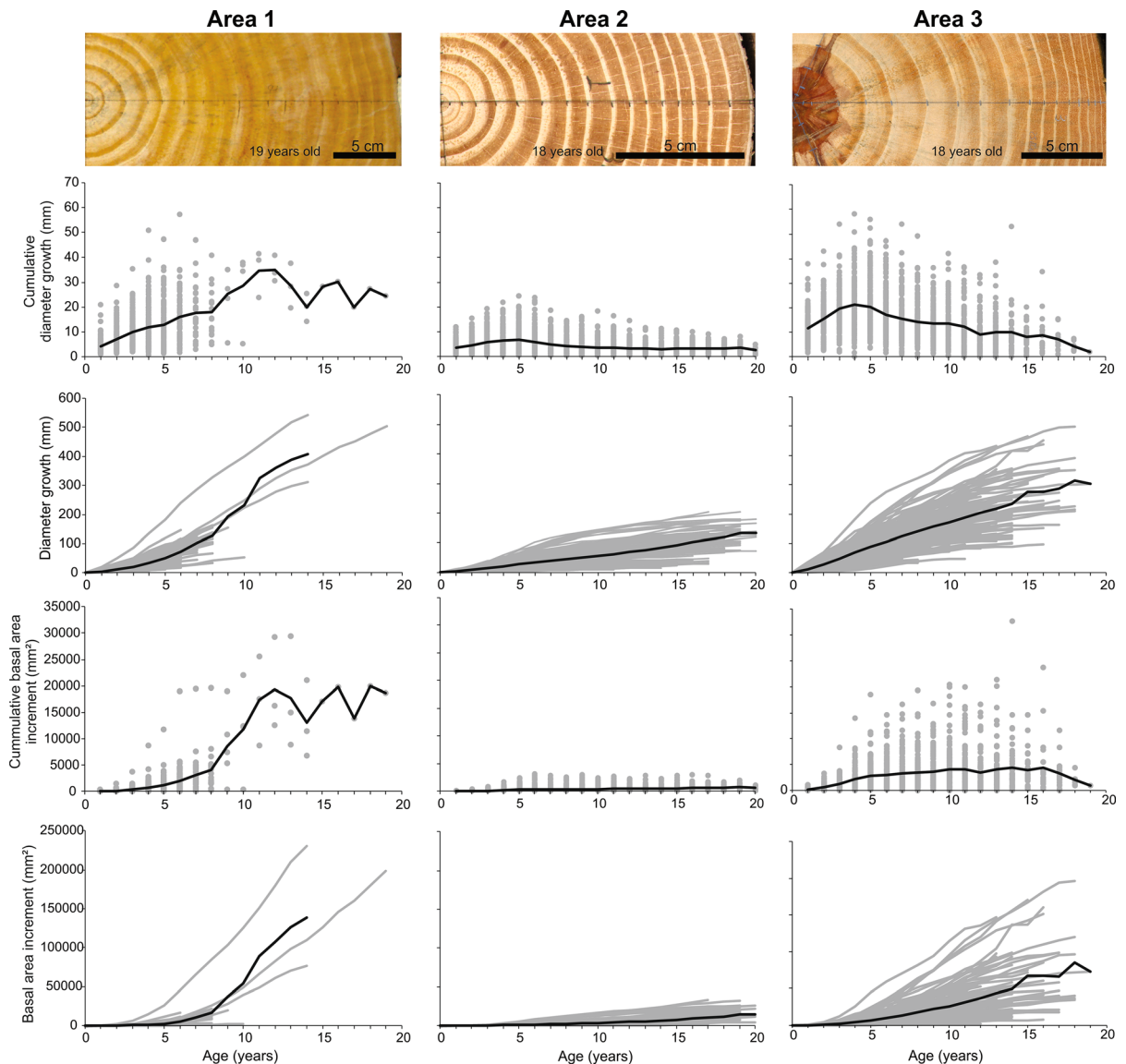
Fig. 4 From the top to the bottom—samples of the growth rings in each study site. Cumulative diameter growth curves of invasive trees of *P. elliottii*. Diameter growth trends, cumulative basal area growth, basal area growth trends. Gray lines = individual cumulative curves; black line = average curve; gray dots = individual annual increment. Area 1 (IEcS1) and Area 2 (IEcS2) from Itirapina Ecological Station; Area 3 (SBEcS) from Santa Barbara Ecological Station

other size classes (11–20, 21–30, 31–40, 41–50 cm), basal area growth rate was higher in Area 1 than observed in Areas 2 and 3.

Area 2

We measured 9570 tree-rings in 192 trees. The analysis period ranged from the year 1989 to the year 2008, covering 20 years of growth. Annual diameter and basal area increments were 4.5 mm/year (± 0.1 SE) and 336.5 mm²/year (± 9.6 SE), respectively (Table 1). Annual diameter increment ranged from 0.3 to 24.3 mm/year and basal area increment ranged from 0.3 to 3166.5 mm²/year. Both cumulative curves—diameter and basal area—had similar shapes (Fig. 4).

We observed a growth pattern with variations and slow growth rate during all the lifetime of the trees

Fig. 5 Boxplots of the average diameter growth rate of trees growing in the study sites by different age classes. Itirapina Ecological Station—Area 1 (IEcS1) and Area 2 (IEcS2); and Santa Barbara Ecological Station—Area 3 (SBEcS). Different letters means difference by Kruskal–Wallis test
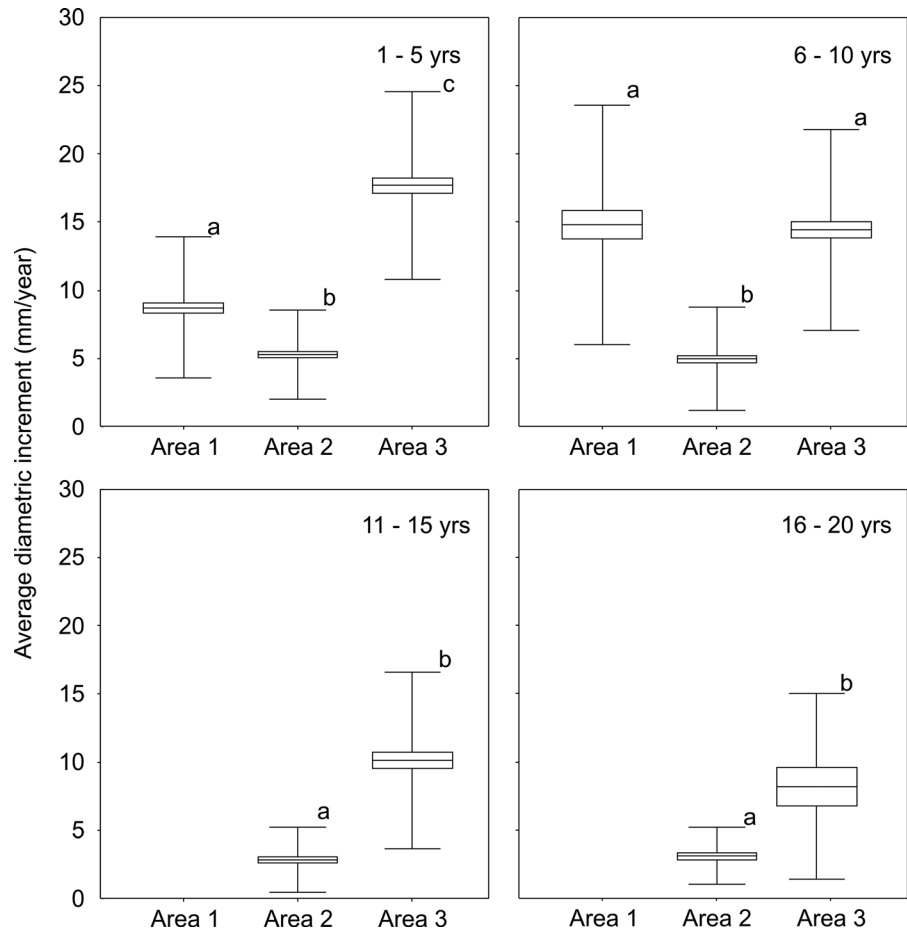

(Fig. 4). Diameter and basal area growth rates showed increase in the first 5 years. After this age, diameter growth rate decreased and basal area growth rate had a small increase. Compared to the other sites, the diameter and the basal area growth rates were the lowest in Area 2 for all age and size classes (Figs. 5, 6, 7, 8).

Area 3

We measured 7726 tree-rings in 168 trees with the analysis period ranging from 1994 to 2012 (covering 19 years). The mean annual diameter and the basal area increments were 15.1 mm/year (± 0.2 SE) and 2683.4 mm²/year (± 70.6 SE), respectively (Table 1). This area had the greatest variation in annual diameter increment (from 0.0 to 58.2 mm/year) and basal area increment (from 0.0 to 32,596.0 mm²/year). The individual cumulative diameter and basal area curves had similar shapes (Fig. 4).

We observed a pattern of increasing growth rate in the first 5 years, followed by a constant decrease in the diameter growth rate and a small increase in the basal area growth rate as the trees got older (Fig. 4). During the first 5 years, the diameter growth rate was higher than observed in the other sites (Fig. 5). When observing trees from 6 to 10 years old, the growth rate was similar to the observed in Area 1 and higher than the observed in Area 2. In the classes of 11–15 and 16–20 years, the growth rate was still higher than that observed in Area 2, but there was a noticeable reduction in the growth rate in the 16–20 years age-class. Considering the size classes, diameter growth rate was higher in Area 3 than observed in the other sites in the size class 1–10 cm (Fig. 6). In the other size classes, basal area growth rate in Area 3 was higher than the observed in Area 2 and lowest than the observed in Area 1.

Basal area growth rate in Area 3 was higher than observed in the other sites for all age classes, and in the
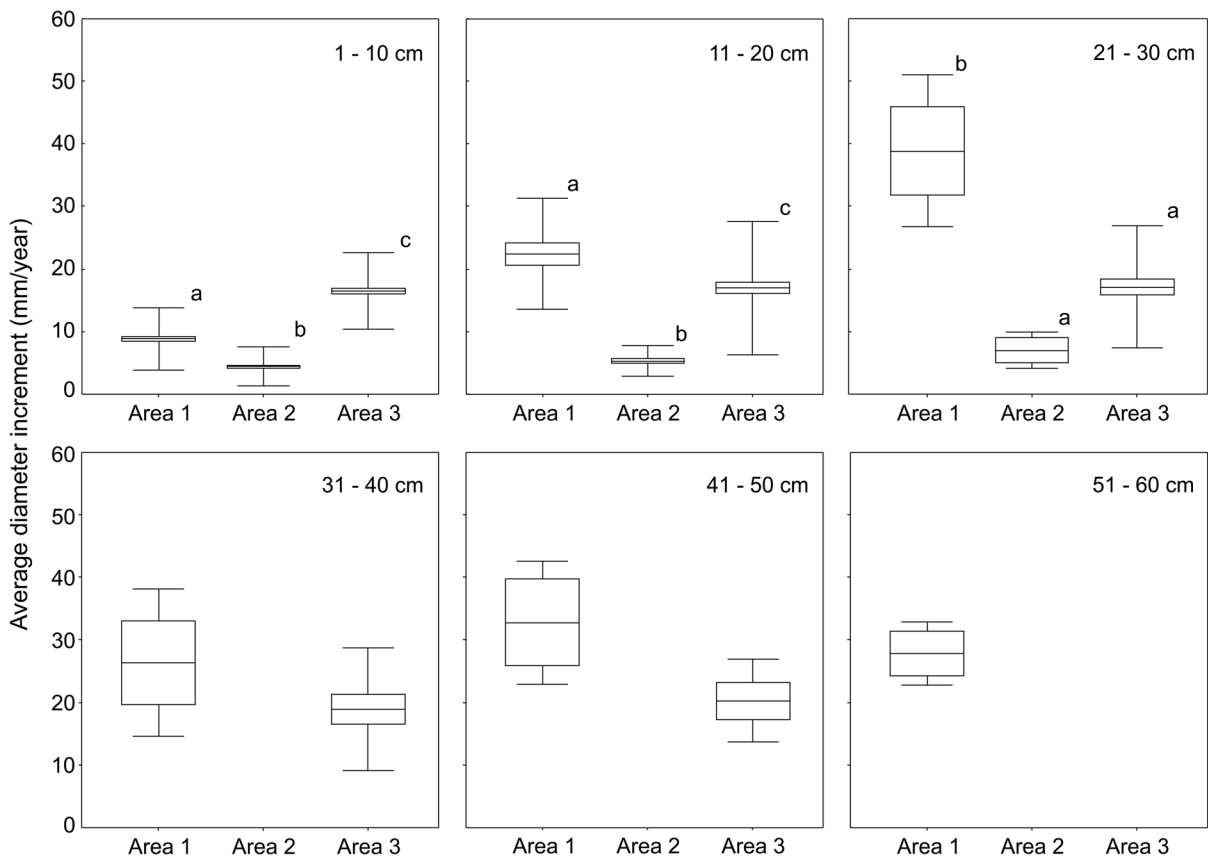
Fig. 6 Boxplots of the average diameter growth rates of trees by different size classes. Itirapina Ecological Station—Area 1 (IEcS1) and Area 2 (IEcS2); and Santa Barbara Ecological Station—Area 3 (SBEcS). Different letters means difference by Kruskal–Wallis test

first size class (1–10 cm; Figs. 7, 8). However, it was lower than Area 1 and higher than Area 2 in the other size classes.

Discussion

Fire record and effect

We detected a reduction in the increment for both diameter and basal area after the wildfire in most trees, even in trees without fire scars. Diameter and basal area increments after fire (2011 and 2012) were lower than increments recorded before fire (2009 and 2010). In Brazil, many studies demonstrating the presence of annual growth rings in *Pinus* species, including *P. elliottii*, were developed in plantations of known age (Trovati and Ferraz 1984; Brito et al. 1986; Palermo et al. 2003, 2013; Pereira and Ahrens 2003; Pereira and Tomaselli 2004; Ferreira and Filho 2009; Coelho

and Hosokawa 2010; Elesbão and Schneider 2011; Schneider et al. 2013). However, in the Brazilian savanna, the periodicity of growth rings formation for *P. elliottii* has not been tested yet.

Fire scars have previously been used to indicate the annual tree-ring formation in *P. elliottii* in Florida savannas (Harley et al. 2011). We used fire scars in this study to demonstrate that rings formation of *P. elliottii* was also annual in the invaded Cerrado sites. The wildfire that burned into Area 3 in 2011 was recorded in the wood of 48 *P. elliottii* trees by fire scars. The fire scars were detected before the early wood of the year 2011. This is expected because the fire occurred in 17th July, in the middle of the winter, historically the coldest and driest month of the year in that region (Melo and Durigan 2009).

It is expected that the *Pinus* trees present a reduction in growth in the years of fire occurrence (Seifert et al. 2017). During the period after fire, we observed that most adult pine trees were not killed by

Fig. 7 Boxplots of the average basal area growth rates of trees by different age classes. Itirapina Ecological Station—Area 1 (IEcS1) and Area 2 (IEcS2); and Santa Barbara Ecological Station—Area 3 (SBEcS). Different letters means difference by Kruskal–Wallis test
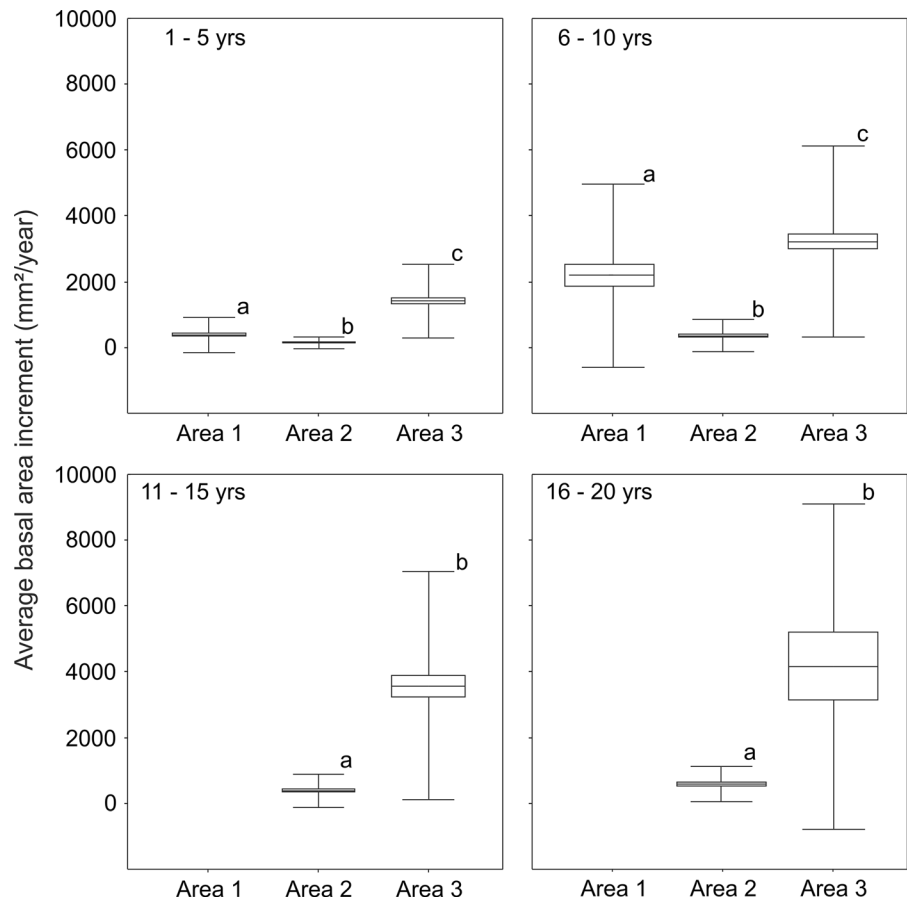
fire, but had their canopies severely reduced by fire, reducing their photosynthetic activity and growth rates. A similar phenomenon has been observed for native trees in Australian savannas (Murphy et al. 2010). The absence of fire scars in some trees can be explained by the intensity of fire that reached each individual, by the fire type (surface fire, crown fire or ground fire), and by other environmental conditions (Taylor and Skinner 2003; Speer 2010; Brandes et al. 2018) whereby the fire was not able to damage the vascular cambium and produce a fire scar, but still affected the cambial activity, reducing wood production.

Age structure and invasion

Some species of pine are aggressive invaders in the Southern Hemisphere, allowing their inclusion in the category of "transformers" (Simberloff and Rejmánek 2011), due to the radical changes they cause to the native vegetation. Their invasion potential is associated with species attributes like small seed mass, which facilitates wind dispersal, the short juvenile phase allowing them to quickly reach reproductive size (e.g. in less than 10 years), and high seed production (Richardson and Rejmánek 2004). They can change the structure of the native vegetation, promote losses of plant diversity (Zanchetta and Diniz 2006; Abreu and Durigan 2011), and rapidly convert grasslands and savannas into pine forests (Langdon et al. 2010). In the three study areas we verified that the invasion pulses occurred every 5–7 years after the establishment of the first invaders (hereafter founders). This same pattern was found in a previous study that used time-series of aerial photographs and satellite images for historical evaluation (Abreu and Durigan 2011). The invasion of grasslands in pulses was also noticed for other *Pinus* species in the Chilean Patagonia (Langdon et al. 2010). Those pulses, also called waves of invasion, could be related to climatic
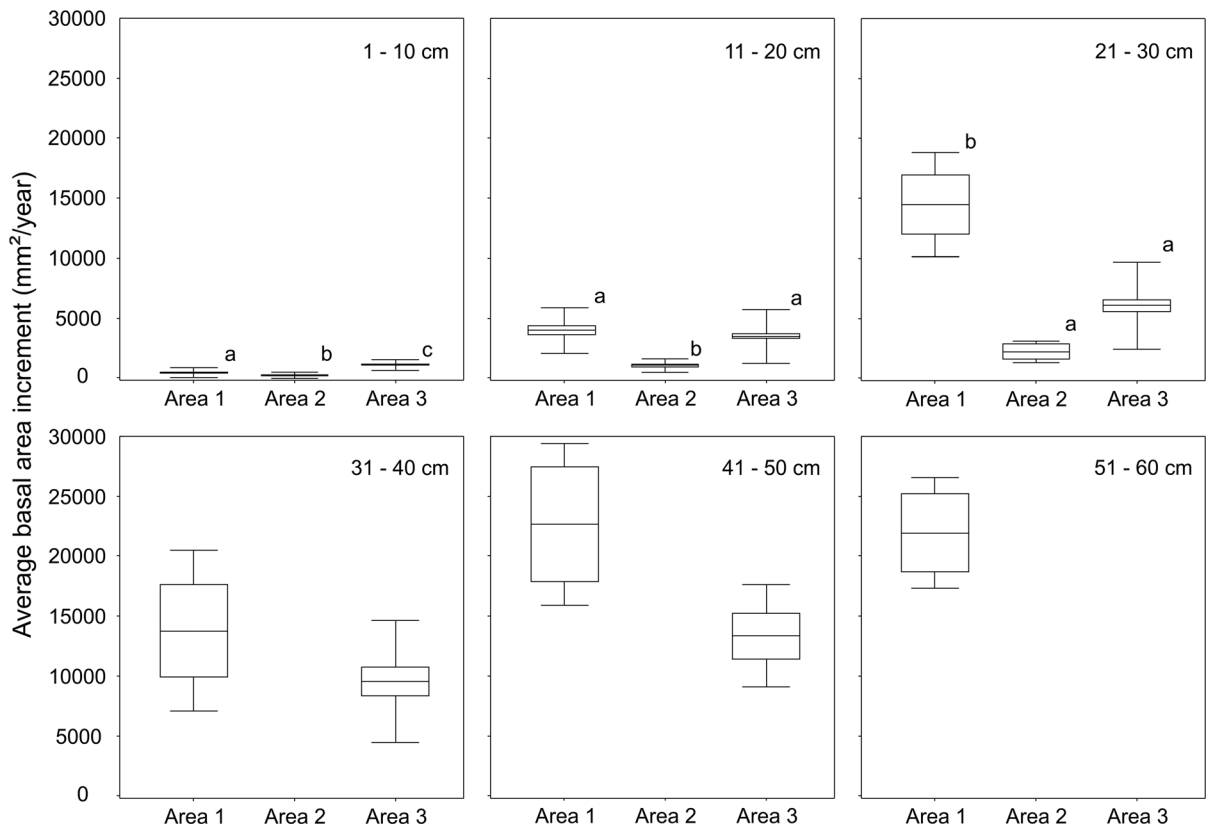
Fig. 8 Boxplots of the average basal area growth rate of trees by different size classes. Itirapina Ecological Station—Area 1 (IEcS1) and Area 2 (IEcS2); and Santa Barbara Ecological Station—Area 3 (SBEcS). Different letters means statistical difference by Kruskal–Wallis test

conditions like temperature and precipitation, or to founder populations reaching mature size and increasing propagule pressure (Abreu and Durigan 2011; Bourscheid and Reis 2011; Diez et al. 2012; Bechara et al. 2013).

In the year of 1994, the study sites experienced a severe winter including several rare frost episodes (Brando and Durigan 2004; INMET 2018), at the same time that the first founders were established in Area 1 and Area 3. Another severe winter with frost episodes happened in the year 2000 (Brando and Durigan 2004; INMET 2018) and it coincided with a wave of seedling establishment in Areas 2 and 3, as well as an increase in colonization in Area 1. These particularly cold winters were also wetter than average (INMET 2018). Severe winters with frosts and above-average precipitation can play an important role in the pine invasion process, perhaps by lessening the potential for native species to act as a biotic filter (Colautti and MacIsaac 2004). Most Cerrado species are not frost resistant

(Brando and Durigan 2004; Hoffmann et al. 2019), and frost may temporarily reduce the ground cover by vegetation and open gaps of bare soil, potentially facilitating the invasion by providing germination microsites (Richardson et al. 1994; Diez et al. 2012). Frost, combined with rainy winters, can promote ideal conditions for pine seed germination as *P. elliottii* invades preferably places with high water availability (Zanchetta and Diniz 2006; Melo and Durigan 2009; Almeida et al. 2010; Abreu 2013). Pine seed dispersal occurs mostly in autumn and winter (Bechara et al. 2013), resulting in large amounts of viable propagules when frosts occur. Frost and high rainfall, together, could enhance colonization by the pine invaders.

Another important factor related to the invasiveness of the pine trees is the distance from the seed sources (Zenni and Simberloff 2013; Miashike 2015; Pauchard et al. 2016). Both reserves have *Pinus* plantations in the surrounding areas that act as propagule sources (Zanchetta and Diniz 2006; Melo and Durigan 2009),

but despite these nearby propagule sources, we suggest that dispersal limitation restrains population growth rates until the maturation of founder individuals. *P. elliottii* needs 5–7 years to reach maturity (Zanchetta and Diniz 2006; Zanchetta and Pinheiro 2007). In all study sites, dendrochronology showed that invasion waves happened every 5–7 years after the arrival of the founders. Thus, the founders are likely responsible for the rapid population growth. After they reach maturity, these founders become a new dispersal source in the area (Langdon et al. 2010; Abreu and Durigan 2011), increasing the propagule pressure at the site (Richardson et al. 1994). This period of 7 years since the arrival of the founders and the invasion wave, as the invasion pulse in Area 3 in the year 2000, was also noticed in a previous study at the same reserve of Area 3 (Abreu and Durigan 2011). Based on these findings, the suppression of founders before they reach maturity could hinder the *Pinus* invasion waves.

The low density of young trees in the sample area indicates low recruitment in the population and limitations for establishment of seedlings in the understory of the pine stands (Abreu and Durigan 2011; Bechara et al. 2013). In the SBEcS, another explanation for this age structure could be related to the wildfire event occurred in 2011 that caused the death of small trees. The absence of young trees after fires reinforces that management using prescribed fire can easily prevent the onset of intense colonization (Pyke et al. 2010; Abreu 2013). In fire-prone savanna ecosystems, where the native plant species are resistant to fire (Lawes et al. 2011), prescribed burning can be a management option. However, as our results showed and as demonstrated by Sah et al. (2010), old *P. elliottii* trees can survive fire, so other techniques to eradicate them are necessary to limit seed dispersal and reduce new recruitment of the invaders (Abreu 2013).

Growth dynamics

We found different patterns of individual growth among the study areas. At Area 1, the trees showed an increasing trend in diameter and basal area growth rate as they got older, while at Area 2, the trees showed narrow variation in growth among years. The diameter growth rate decreased over the lifetime of trees and the basal area increment rate had a small increase. The highest values of growth rates were recorded in Area 3 for all age classes, and the trees presented a unimodal pattern of growth rates, with diameter growth rates increasing at young ages and declining later, and basal area growth rate increasing at lower rates after 5 years old. This last pattern is also found in pine plantations, where even-aged stands grow quickly until the onset of canopy closure (Worbes 1999). Variation in growth rates was also described for *P. montana* populations where trees with the highest early growth continually decreased the growth rates as the age increased (Bigler 2016), a pattern similar to that observed in Area 3. Trees with the lowest early growth had slow growth with little variation until they reach the age of 50–150 years, when they experienced abrupt growth releases (Bigler 2016). We found this trend in Area 2, except the growth release, likely because the trees did not reach that age. In Area 1, trees were too young to have the long-term trend assessed. The diameter growth rates found for *P. elliottii* invaders in our study were similar to the values reported for cultivated *P. caribaea* in Venezuela (8.5 mm/year) (Worbes 1999), *P. taeda* (11.3 and 26.8 mm/year) (Inoue et al. 2011) and *P. elliottii* (10.8 mm/year) (Figueiredo Filho et al. 1994) in Paraná state, Brazil.

Several environmental factors can modulate the radial growth of the invasive *P. elliottii* trees in the Cerrado. In the native habitat, the southeast USA, the wood production and growth dynamics of *P. elliottii* are influenced by the water availability (Harley et al. 2011). However, another important factor regulating growth is the light environment and the age of the tree. Reduction in growth rates over time, known as "age trend", may happen due to physiological and/or environmental conditions (Fritts 1976; Cook 1985; Weiner and Thomas 2001; Coelho and Hosokawa 2010). The age trend was detected in the individuals of Area 3, and also described in an invasive population of *P. taeda* in southern Brazil (Tomazello-Filho et al. 2017). This growing pattern was also found in the Cerrado native species *Hymenaea courbaril* L. and *H. stignocarpa* Hayne (Locossselli et al. 2017) where the trees presented a fast growth in the first 50 years of life followed by a substantial reduction in the growth rate after that period.

Changes in light availability can influence growth rates. A high light incidence can increase growth rates, while a low light incidence, such as under closed canopy conditions, can reduce growth rates (Worbes

1999). In our findings, the reduction of growth rates was remarkable in the invaded area with the densest population, where the trees experienced fierce competition for light (Area 2). For that reason, despite competition for light not killing the adult pines, we can assume that light availability is an important limiting factor in the growth of invasive pines in the Neotropical Savanna. Moreover, experiments with *P. elliottii* and *P. taeda* demonstrated that tree-ring width and diameter growth increased with increased light availability (Pereira and Tomaselli 2004; Coelho and Hosokawa 2010; Inoue et al. 2011). Although we did not evaluate the relationship between light intensity and tree growth in this study, we found a high average growth for most age and size classes in the area at the earliest stage of invasion (Area 1), where the canopy was not fully closed, large trees were less frequent, and sunlight was able to reach some portions of the ground.

Conclusions

The dendroecology of the invasive populations of *Pinus elliottii* in the Cerrado revealed that, as the trees aged, diameter growth decreased and basal area continued to increase, at lower rates. Fire scars confirmed that the tree rings were formed annually in invasive populations of *P. elliottii* in the Cerrado. The fire-scar analysis indicated that this species can potentially be used to reconstruct the fire record in invaded areas in the tropics. We also found that the invasion occurred in pulses (waves of invasion), with an intense establishment of individuals every 5–7 years, likely related to periods of seed production and dispersal. The low frequency of young trees indicated limitations to the establishment of seedlings and a reduction of recruitment in the understory. When competition for light intensifies as the canopy closes, the response of the invasive populations is indicated by lower individual diameter growth of adult trees, lower increase in basal area, and reduced recruitment of young individuals. We did not find, however, evidence of self-thinning due to competition that could reduce the population of adult trees, open gaps and allow colonization by shade-tolerant native species. Therefore, the pine monodominance feature of the invaded sites tends to be persistent over time. Further studies to investigate climate-growth relationships are

suggested, as well as experimentation to disentangle the factors triggering the invasion waves.

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