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# AGE AND GROWTH RATE OF CONGENERIC TREE SPECIES (*HYMENAEA* SPP. - LEGUMINOSAE) INHABITING DIFFERENT TROPICAL BIOMES

Giuliano M. Locosselli, Stefan Krottenthaler, Philipp Pitsch,
Dieter Anhuf and Gregório Ceccantini

With 7 figures and 2 tables
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**Summary**: Age and radial growth rate are key data on understanding some aspects of tropical forest dynamics and ecology. In species that produce annual tree rings, tree-ring analysis allows the most precise estimate of these two parameters. The present study assessed the age and radial growth rate of three *Hymenaea* species inhabiting four of the six biomes found in Brazil. Out of these four biomes, two harbor the largest rainforests in South America, the Amazon Forest on the west and the Atlantic Forest in the east. The Cerrado biome is an open and seasonally drier vegetation found between them and the Pantanal is a wetland in the west. The *H. courbaril* species inhabits almost the entire Neotropical lowlands while *H. parvifolia* and *H. stigonocarpa* are restricted to the Amazon and Cerrado biomes, respectively. To investigate these species dynamics within different biomes, age and radial growth rate were calculated for 217 trees through tree-ring analyses. The oldest *H. courbaril* and *H. parvifolia* trees were 316 and 371 years old, respectively, while *H. stigonocarpa* trees were considerably younger, up to 144 years old. *Hymenaea courbaril* trees showed the widest variation in average growth rate, from 1.00 to 6.63 mm per year, while the other two species showed a narrower variation from 0.89 to 2.81 mm per year. The studied populations presented distinct trends in the lifetime growth pattern that seems to be related to the biome of provenance. Overall, trees from the Amazon forest showed a trend of increasing growth rate up to about 100 years followed by a decreasing of it, while trees growing in the Pantanal and Atlantic forest showed only decreasing growth rates. In the Cerrado, trees showed a constant pattern of growth rate up to 50 years followed by a clear decline. It is important to highlight that different species of *Hymenaea* showed similar growth trends within the same biome. In larger trees, the average growth rate is lower in the Cerrado, which is characterized by deeper water tables and more dystrophic soils while the growth rates in the Amazon and Atlantic Forests are 60 % and 79 % higher, respectively. This study represents one of the most comprehensive datasets of trees age and growth rate of tropical congeneric species under such large geographical range.

**Zusammenfassung**: Alter und Zuwachsraten von tropischen Bäumen liefern wichtige Daten über das Verständnis verschiedener Aspekte bezüglich der Dynamik und Ökologie von tropischen Wäldern. Bei Baumarten, welche jährliche Zuwachsringe ausbilden, ermöglicht die Jahrringanalyse eine genaue Untersuchung dieser beiden Parameter. Die vorgestellte Studie analysiert Alter und radiale Zuwachsraten von drei *Hymenaea* Arten, in vier der sechs Biome Brasiliens. Von diesen Biomen gehören zwei, der Amazonas Regenwald und der Atlantische Regenwald, zu den größten Regenwäldern Südamerikas. Das Biom Cerrado ist eine offene Savannenlandschaft, welche eine saisonale Trockenzeit aufweist. Bei dem Pantanal handelt es sich um ein Feuchtgebiet. Die Art *H. courbaril* ist in fast allen neotropischen Tiefländern anzutreffen. Die Verbreitungen von *H. parvifolia* und *H. stigonocarpa* ist auf den Amazonas Regenwald bzw. auf den Cerrado beschränkt. Um das Wachstumsverhalten dieser Arten in unterschiedlichen Biomen zu untersuchen, wurden von 217 Bäumen mit Hilfe der Jahrringanalyse das Alter und die radiale Zuwachsrate bestimmt. Die ältesten *H. courbaril* und *H. parvifolia* Bäume wurden 316 bzw. 371 Jahre alt, wohingegen *H. stigonocarpa* mit einem Höchstalter von 144 Jahren deutlich jünger war. Bäume der Art *Hymenaea courbaril* zeigten die größte Schwankung des durchschnittlichen Wachstums, welches sich zwischen 1.00 und 6.63 mm pro Jahr bewegte. Der Schwankungsbereich der andren beiden Arten war mit 0.89 bis 2.81 mm pro Jahr deutlich geringer. Die untersuchten Bestände wiesen unterschiedliche Wachstumsmuster auf, welche an die Bedingungen ihres Herkunftsgebietes gekoppelt zu sein scheinen. Im Allgemeinen zeigten die Bäume im Amazonas Regenwald in den ersten 100 Jahren ein überdurchschnittliches Wachstum, gefolgt von einem abnehmenden Wachstum. Bäume aus dem Atlantischen Regenwald und dem Pantanal wiesen nur abnehmende Wachstumsraten auf. Innerhalb des Cerrados ließ sich in den ersten 50 Jahren ein konstantes Wachstumsverhalten ausmachen, auf welches ein klarer Rückgang folgte. Zu betonen ist, dass unterschiedliche Arten von *Hymenaea* innerhalb des gleichen Bioms ein gleichartiges Wachstumsverhalten an den Tag legten. Im Cerrado, welcher durch nähstoffarme Böden und tiefliegenden Grundwasserspiegel gekennzeichnet ist, war die durchschnittliche Wachstumsrate von großen und alten Bäumen am niedrigsten. Im Amazonas Regenwald und dem Atlantischen Regenwald waren diese Raten von alten Bäumen um 60 % bzw. 79 % über dem Durchschnitt. Diese Studie umfasst einen der größten Datensätze von Alter und Wachstumsraten tropischer artverwandter Bäume über ein großes Untersuchungsgebiet.

**Keywords**: Tree rings, dendrochronology, tree ecology, Pantanal, Amazon, Mata Atlântica, Cerrado, Latin American-locust, Brazilian copal

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## 1 Introduction

The tropical zone comprises a variety of terrestrial environments covering about 10% of the globe's land surface (Lewis 2006). The highest diversity of trees is found within this area, where more than 53,000 tree species (Slik et al. 2015) suffered different histories of distribution expansion and contraction through time (Ledru et al. 2002; Lomolino et al. 2010). Their current distribution is the result of long histories in which some retained their distribution within a singular biome, while others were able to colonize adjacent biomes or cross unfavorable ones and established in farther biomes. Some species even remained in these unfavorable biomes being subject or not to speciation, for example by vicariance (Donoghue and Edwards 2014). By definition, a biome is categorized by its vegetation composition and history together with climate characteristics (Woodward et al 2004), and therefore, tropical tree species inhabiting different biomes are living under different biotic and abiotic conditions, which impose distinct growth strategies.

Despite the presence of single species and/or genus covering large geographical areas, large-scale comparative dendroecological research has only been applied to few species so far. (but see Therrel et al. 2007). For all species owning visually distinct and annually formed tree rings, both age and growth rate can be easily assessed by identifying and measuring the width of tree rings (Schweingruber 1989). These are key parameters required to understand some aspects of tropical forest dynamics and ecology (Dünisch et al. 2003). Despite the relevant results obtained by such studies, they are relatively few in number especially considering the diversity of tree species in the tropics. Clearly, there is a strong potential to apply tree-ring analysis to study growth strategies within species or genera that present a wide distribution range and fulfil the basic needs for dendroecological studies.

For instance, the genus *Hymenaea* belongs to the Leguminosae family, which is one of the most abundant families in the tropics (Gentry 1988). In the Neotropics, some of these species are widely distributed and are present in most lowland biomes. The species *H. courbaril* is found in distinct biomes from Brazil to Mexico, while other species like *H. stigonocarpa* and *H. parvifolia* are restricted to the Cerrado and Amazon Forest biomes respectively (Lee and Langenheim 1975). In Brazil, these *Hymenaea* species are found in the Amazon biome in the northwest, in the Atlantic Forest in the East, as well as in the two contiguous drier biomes in between: the Cerrado and Caatinga. Actually, these last two biomes form a vast area of seasonal vegetation crossed by riparian forests that connect the floras of the Amazon and Atlantic Forests, the two largest rainforests in South America (Prado and Gibbs 1993; Oliveira-Filho and Ratter 1995). Actually, some elements of these two floras crossed this large drier area through riparian forests. Meanwhile, some *H courbaril* populations remained in the Cerrado biome together with *H. stigonocarpa* populations, but inhabiting different environments (Ramos et al. 2009).

The present study aimed to perform a comprehensive tree-ring analysis of three *Hymenaea* species over a large geographical area covering the two largest rainforests in South America and the seasonally dry vegetation in between. Based on age and radial growth rates, and considering the variability in growth conditions in which *Hymenaea* species occur in Brazil, we assessed: 1) whether different species would present different maximum ages and growth rates; 2) if growth rates and ages of trees differed among distinct populations and biomes; 3) the differences in ontogenetic trends in growth among populations from different biomes and among distinct species inhabiting the same biome; and 4) whether growth rates in each biome differed within similar ontogenetic classes.

## 2 Material and Methods

### 2.1 Species and Sampling Sites

A total of 217 trees were sampled in ten sites across Brazil comprising twelve populations of three *Hymenaea* species (Fig. 1 and Tab. 1). Out of these populations, nine are *Hymenaea courbaril* L., two are *Hymenaea stigonocarpa* Mart ex. Hayne and one is *Hymenaea parvifolia* Huber. Sampling took place in four of the six biomes found in Brazil: Amazon, Cerrado (the Brazilian Savanna), Atlantic Forest (Mata-Atlântica) and Pantanal (wetlands). Three populations were sampled in the non-flooded areas of the Amazon biome in the northern region of Brazil, including one population of *H. parvifolia* and two populations of *H. courbaril.* We also sampled one population of *H. courbaril* in the Pantanal biome in the west central part of the country, along with a population of *H. stigonocarpa* found in permanent drylands within the Pantanal/Cerrado transition. Another population of *H. courbaril* was sampled in the dry forest on karst in central Brazil, and four

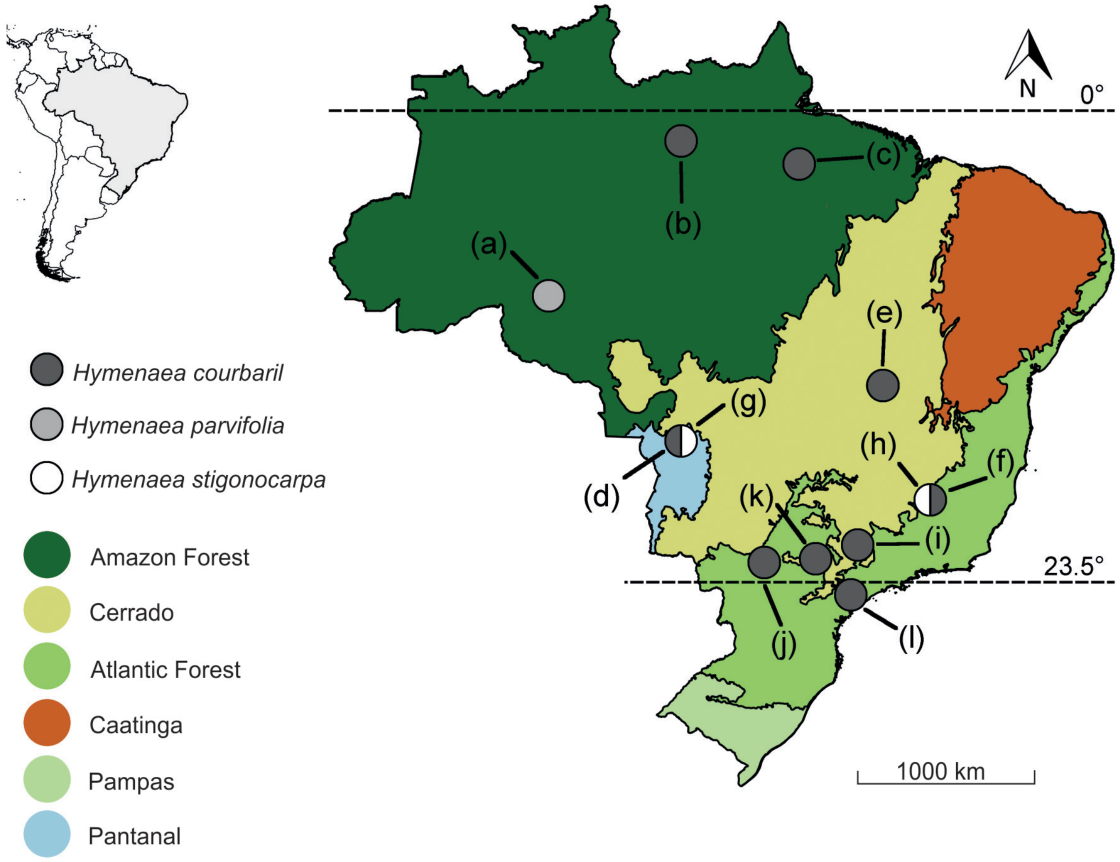

**Fig. 1: Location of the 12 populations of *Hymenaea* spp. sampled in Brazil. Colors on the Brazilian map indicate biome distribution.**

populations of that species were also sampled in the Atlantic Forest in Southeastern Brazil. In addition, a *H. stigonocarpa* population was sampled in a transition zone between the Atlantic Forest and Cerrado in Southeastern Brazil.

We used stem discs and cores for the present study. Stem discs were only obtained from legal logging companies in the northern region of Brazil and in Minas Gerais State (Matozinhos), while cores were collected in all other sites where we sampled from one to four cores per tree. Since these tree species are characterized by high wood density, 15 mm-wide cores were obtained using a special increment borer coupled with a motor drill (Krottenthaler et al. 2015). After sampling, injuries were treated with a solution of copper sulfate and calcium oxide and closed with a natural cork. The diameter at breast height (DBH) was recorded for each tree in the field. It is important to note that these species rarely form buttresses; therefore, sampling height was restricted to a range between 0.5 to 1.5 meters above ground.

During field work, we sampled a wide variety of stem sizes from small to large trees to better characterize each studied population. However, trees sampled in the northern part of Brazil were restricted by the minimum logging diameter of 50 cm (according to Federal regulation - CONAMA 2009). After field work, all samples were left to dry for weeks to months, depending on their type and size.

## 2.2 Sample preparation and measurements

After drying the samples, their transversal surfaces were carefully polished using sandpaper with different grits from roughest (50) to finest (2000). The finest grits were used with water to produce a fine surface that was subsequently cleaned with high-pressure water to clear the vessel lumen. *Hymenaea* species have tree rings delimited by the presence of marginal parenchyma (Fig. 2). Tree rings were identified and marked in 494 radii using a stereomicroscope, and tree-ring width was

**Tab. 1: Sampling sites characteristics, including biome and vegetation type, species, number of samples (n), maximum age (MA, years), average growth rate (AGR, mm/year), latitude and longitude of provenance and altitude (alt, meters a.s.l.). All lettered populations correspond to the letters in Fig. 1.**

| Site | Biome | Vegetation type | Species | n | MA | AGR | Lat | Long | Alt |
|---|---|---|---|---|---|---|---|---|---|
| (a) | Amazon Forest | Non-flooded forest | *H. parvifolia* | 19 | 371 | 1.7 | 9°13‘S | 62°57‘W | 120 |
| (b) | Amazon Forest | Non-flooded forest | *H. courbaril* | 21 | 288 | 1.86 | 1°37‘S | 56°02‘W | 70 |
| (c) | Amazon Forest | Non-flooded forest | *H. courbaril* | 20 | 316 | 1.93 | 2°40‘S | 56°30‘W | 50 |
| (d) | Pantanal | Riparian forest | *H. courbaril* | 21 | 179 | 1.91 | 16°30‘S | 56°24‘W | 125 |
| (e) | Cerrado | Dry forest on karst | *H. courbaril* | 19 | 184 | 1.71 | 13°44‘S | 46°21‘W | 650 |
| (f) | Atlantic Forest | Semi-deciduous forest | *H. courbaril* | 10 | 119 | 3.06 | 19°27‘S | 43°57‘W | 650 |
| (g) | Cerrado | Murundu fields | *H. stigonocarpa* | 35 | 135 | 1.58 | 16°30‘S | 56°24‘W | 125 |
| (h) | Cerrado | Cerrado stricto sensu | *H. stigonocarpa* | 10 | 144 | 1.89 | 19°28‘S | 43°57‘W | 650 |
| (i) | Atlantic Forest | Semi-deciduous forest | *H. courbaril* | 12 | 306 | 2.88 | 21°42‘S | 47°35‘W | 600 |
| (j) | Atlantic Forest | Semi-deciduous forest | *H. courbaril* | 21 | 188 | 2.61 | 22°33‘S | 52°14‘W | 400 |
| (k) | Atlantic Forest | Semi-deciduous forest | *H. courbaril* | 20 | 287 | 1.43 | 22°24‘S | 49°4‘W | 550 |
| (l) | Atlantic Forest | Ombrophilous forest | *H. courbaril* | 9 | 273 | 1.41 | 24°12‘S | 47°55‘W | 150 |

measured using the Lintab 6 system (Rinntech-Germany). Whenever possible, false rings and missing rings were checked using visual crossdating among all radii of each tree to ensure better age and growth rate estimation. The tree-ring series of the population growing in a transition zone in Southeastern Brazil and in the dry forest in central Brazil have been dated before (for further details, please refer to Locosselli et al. 2013 and 2016b, respectively)

However, we missed the inner rings in some sampled trees because they were hollowed or because we failed to hit the pith. To address this problem, we used a modified methodology proposed by Hietz (2011). First, we scanned all samples (EPSON V300) at 2400 dpi resolution. Then, we drew lines parallel to the wood rays and estimated the pith position at their intersection using the GIMP software (version 2.8.10), followed by measurement of the missing distance to the pith using ImageJ (Schneider et al.

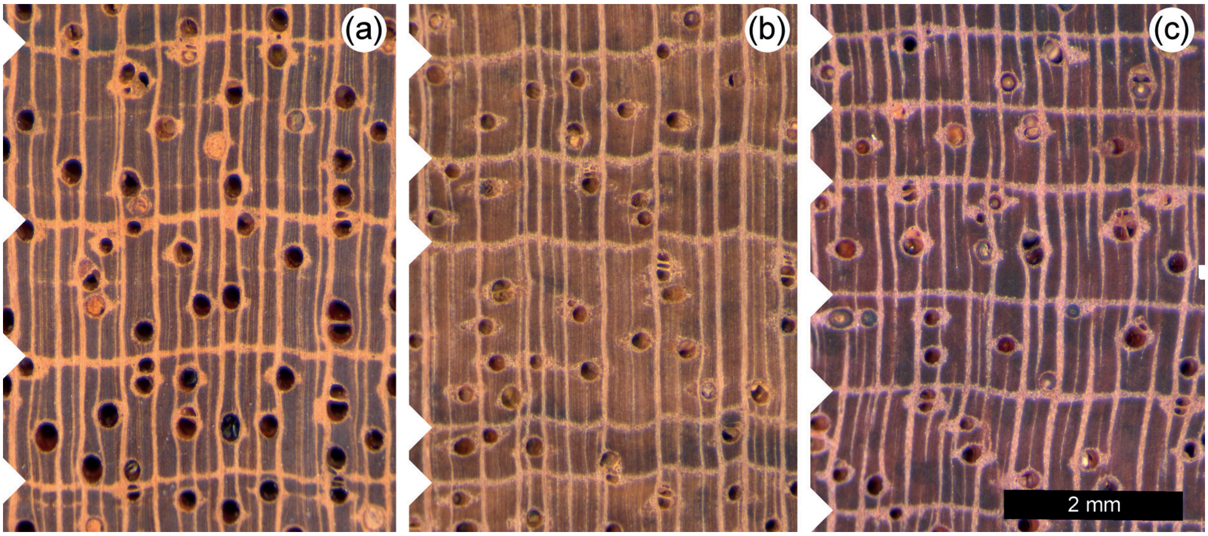

**Fig. 2: Examples of tree rings of a) *Hymenaea courbaril*, b) *H. parvifolia*, and c) *H. stigonocarpa*. All three species possess tree rings (white arrows) delimited by marginal parenchyma.**

2012). When we failed to use this method as a consequence of a slightly higher distance between the inner part of the sample and the pith, we estimated this distance by using the measured diameter at breast height obtained in the field. To accomplish this, we calculated the pith position, considering it central. By using the average width of the innermost ten tree rings, we were able to calculate the number of missing rings and better estimate the age of each tree.

### 2.3 Data analysis

We characterized both age and growth rate distribution of each species using histograms. We calculated mean, standard deviation, maximum and minimum values of age and growth rate for each species.

To assess the differences in the age and growth rate of the studied populations, we built cumulative diameter growth plots for each population. To do this, we built a mean growth curve for each tree, which was calculated as the average tree-ring width among different radii of each tree multiplied by two. The cumulative growth is the sum of the current diameter growth and all previous tree ring widths. In the present work, we added simulated growth curves with constant radial growth rate (0.5, 1, 2, 3, 4 and 5 mm per year) to these plots in order to facilitate interpretation and comparison of growth curves. In addition, the average cumulative diameter growth per site was calculated in order to compare differences in growth among sites. We also evaluated the lifetime growth pattern of each species in all studied biomes. For this purpose, we plotted the radial growth rate by the cambial age of each *Hymenaea* tree in the four biomes. We also plotted the smoothed average radial growth of each species found within these biomes using a locally weighted scatterplot smoothing (LOESS).

Finally, we compared the growth rate of *Hymenaea*'s trees inhabiting each biome. In order to avoid ontogenetic bias, we compared the growth rate at different size classes as suggested by Peters et al. (2015). The growth rate was compared in 10 cm incremtent diameter classes, from 10 to 80 cm, with a minimum of 10 trees per biome. The non-parametric Kruskal-Wallis analysis and the Dunn's test were used in comparison of three or more biomes, and the Wilcoxon test was used for the comparison between two biomes. All results are presented in Boxplots. All analyzes were performed using R. The Dunn's test was performed using the 'dunn.test' package (Dinno 2014).

## 3 Results

Age distribution shows that both *Hymenaea courbaril* and *H. parvifolia* trees can reach an age of 300 years and more (Fig. 3, Tab. 2). More precisely, the maximum estimated tree ages were 316 and 371 for *H. courbaril* and *H. parvifolia*, respectively. On the other hand, individuals of *H. stigonocarpa* were considerably younger with a maximum age of 144 years (Fig. 3, Tab. 2). This last species also presented the lowest average value of age, 71 years, while *H. courbaril* and *H. stigonocarpa* showed considerable higher average values of age, 154 and 215 years respectively. Concerning growth rate, the studied species showed similar average growth rates (Tab. 2 and Fig. 3). Nonetheless, the distribution of the growth rate of these species are different. While *H. courbaril* showed a higher frequency of slow growing and a few fast growing trees (Fig. 3), which is reflected by the higher standard deviation values of growth rate (Tab. 2), the other two species showed a narrower range of growth rates and, therefore, lower standard deviation values (Fig. 3 and Tab. 2). None of these trees grew as fast as the fastest growing trees of *H. courbaril*.

These differences in the range of growth rates are also found at the population level. For instance, populations of *H. courbaril* from the eastern Amazon and from the Atlantic Forest in southeastern Brazil (Fig. 4 b and h, respectively) have a range of radial growth rate from 1 mm to almost 5 mm per year. On the other hand, populations from the same species have a more limited growth rate range from slightly less than 1 mm to 2 mm, similar to those populations found in the Atlantic Forest of southeastern Brazil (Fig. 4 k and l, respectively). Other populations comprise trees with even higher growth rates, 5 mm or more, in the Atlantic Forest biome (Fig. 4 f and j, respectively). The growth rates of the other two species seem to be more limited, ranging from slightly less than 1 mm to more than 2 mm for *H. parvifolia* and from 1 to 2 mm per year for *H. stigonocarpa*. The cumulative growth rate of the populations from the Amazon, Cerrado and Pantanal biomes seems to be more similar than the growth rate of the Atlantic Forest populations (Fig. 5). These last populations can be divided in two groups, one with fast growing trees (Fig. 5 "i", "j" and "f") and another one with slow growing trees (Fig. 5 "l" and "k").

The growth rate of the studied populations is considerably different among ontogenetic periods in each biome. Overall, the sampled trees showed

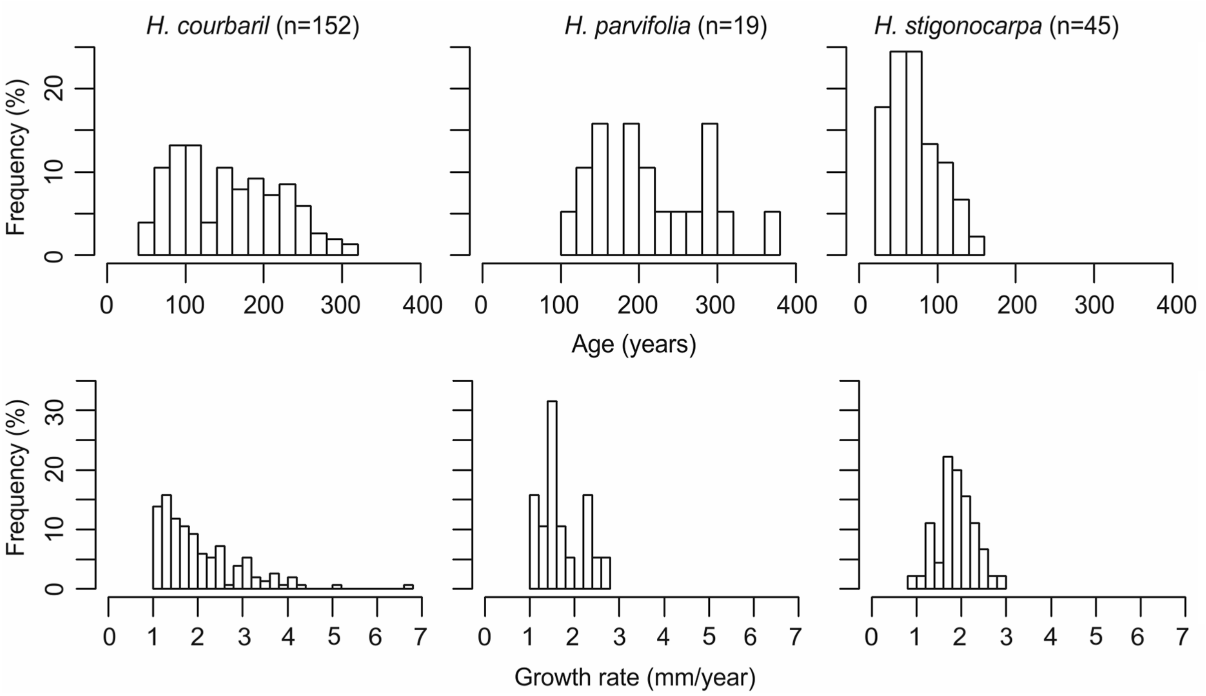

**Fig. 3: Histograms of age and growth rate distributions of *H. courbaril*, *H. parvifolia* and *H. stigonocarpa* specimens, including all studied populations. Total sample size is given for each species.**

different growth trajectories throughout their lives in the different biomes. In the Amazon Forest, tree growth rate increases up to an age of 100 years, and decreases afterwards (Fig. 6a). Trees sampled in the Atlantic Forest usually have a high growth rate at the beginning of their lives, which tends to decreases steadily (Fig. 6b). In the Pantanal biome, the sampled trees grow fast at the beginning of their lives, but then this growth gradually decreases up to 100 years old (Fig. 6c). Finally, trees from the Cerrado have a relatively fast growth rate up to 50 years, which decreases afterwards (Fig. 6d). It is interesting to note that these patterns are shared by the different *Hymenaea* species inhabiting the same biome. For instance, *H. courbaril* and *H. parvifolia* share the same lifetime growth pattern in the Amazon biome and *H. courbaril* and *H. stigonocarpa* share the same lifetime growth pattern in the Cerrado biome.

Due to the presence of the aforementioned ontogenetic trends, the growth rates among biomes were tested in different diameter classes (Fig. 7). Overall, the growth rates of small trees, up to 10 cm of diameter, are higher in the Cerrado and the

**Tab. 2: Descriptive statistics of age and radial growth rate of *Hymenaea* species and biomes of provenance, including mean, standard deviation (STD), maximum (Max) and minimum (Min) values**

| | Age (years) | | | | Growth rate (mm/year) | | | |
|---|---|---|---|---|---|---|---|---|
| **Species** | **Mean** | **STD** | **Max** | **Min** | **Mean** | **STD** | **Max** | **Min** |
| **H. *courbaril*** | 154.43 | 66.76 | 316 | 40 | 2.04 | 0.91 | 6.63 | 1.00 |
| **H. *parvifolia*** | 215.84 | 71.74 | 371 | 119 | 1.70 | 0.48 | 2.06 | 1.12 |
| **H. *stigonocarpa*** | 71.09 | 30.86 | 144 | 26 | 1.89 | 0.41 | 2.81 | 0.89 |
| **Amazon Forest** | 203.20 | 56.44 | 371 | 92 | 1.83 | 0.69 | 4.38 | 1.01 |
| **Atlantic Forest** | 157.42 | 68.27 | 305 | 50 | 2.24 | 1.06 | 6.63 | 1.00 |
| **Cerrado** | 83.70 | 38.35 | 195 | 26 | 1.85 | 0.49 | 3.08 | 0.89 |
| **Pantanal** | 90.80 | 30.38 | 157 | 40 | 1.91 | 0.72 | 3.80 | 1.13 |

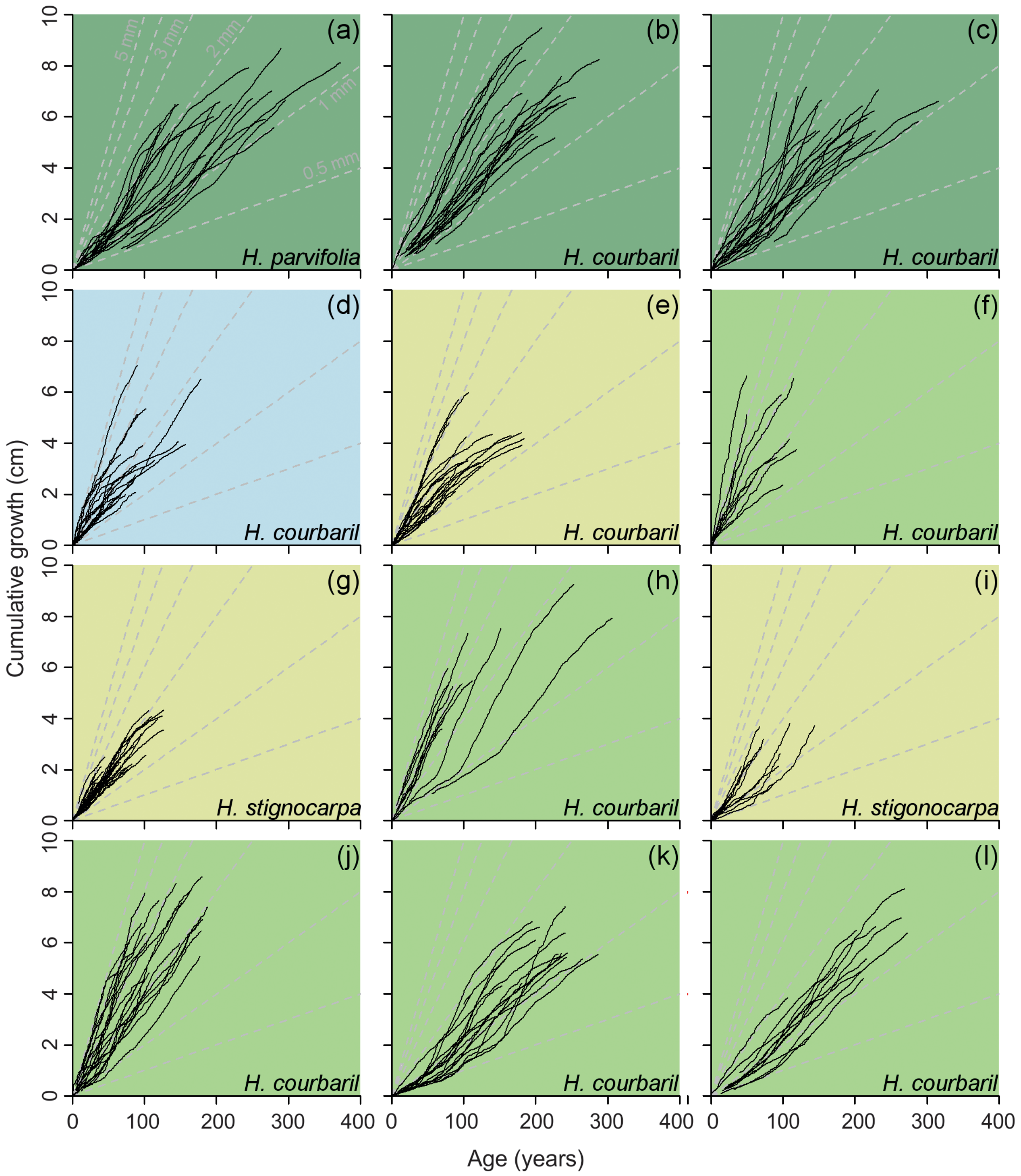

**Fig. 4: Cumulative diameter growth of twelve populations of three congeneric species: *Hymenaea courbaril, H. parvifolia* and *H. stigonocarpa*. Populations "a", "b" and "c" were sampled in the Amazon Forest, population "d" was sampled in the Pantanal (wetlands), and populations "f", "h", "j", "k" and "l" were sampled in the Atlantic Rain Forest. Populations "g", "e" and "i" were sampled in the Cerrado (Brazilian savanna). All lettered populations correspond to the letters in Fig. 1. Dashed grey lines are simulated cumulative diameter growths with constant radial growth of 0.5, 1, 2, 3, 4, and 5 mm per year.**

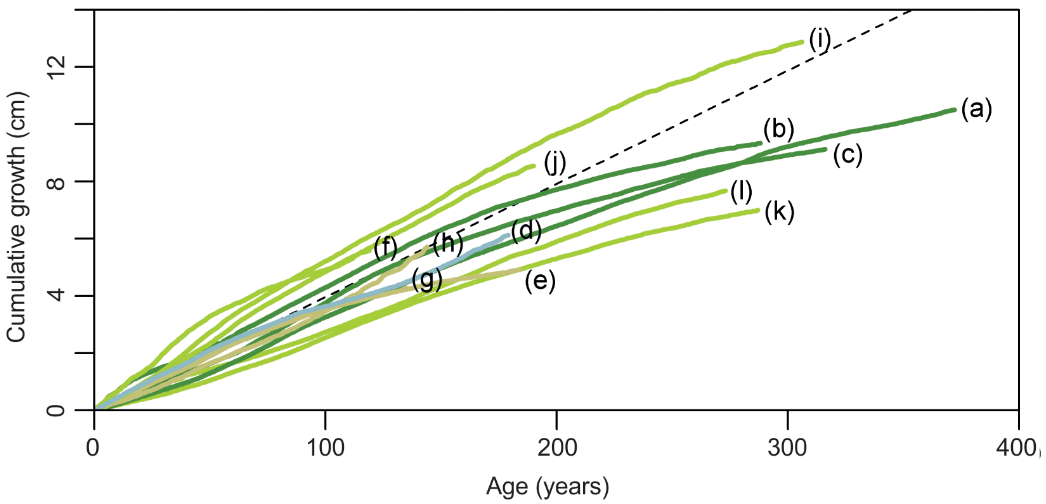

**Fig. 5: Average cumulative diameter growth of twelve populations of *Hymenaea* species. Lines colors indicate the biome of each population. Lines in dark green, light green, light brown and blue represent populations from the Amazon, Atlantic Forest, Cerrado and Pantanal biomes. All lettered populations correspond to the letters in Figures 1 and 2. The dashed line represents the overall average of these populations growth rate.**

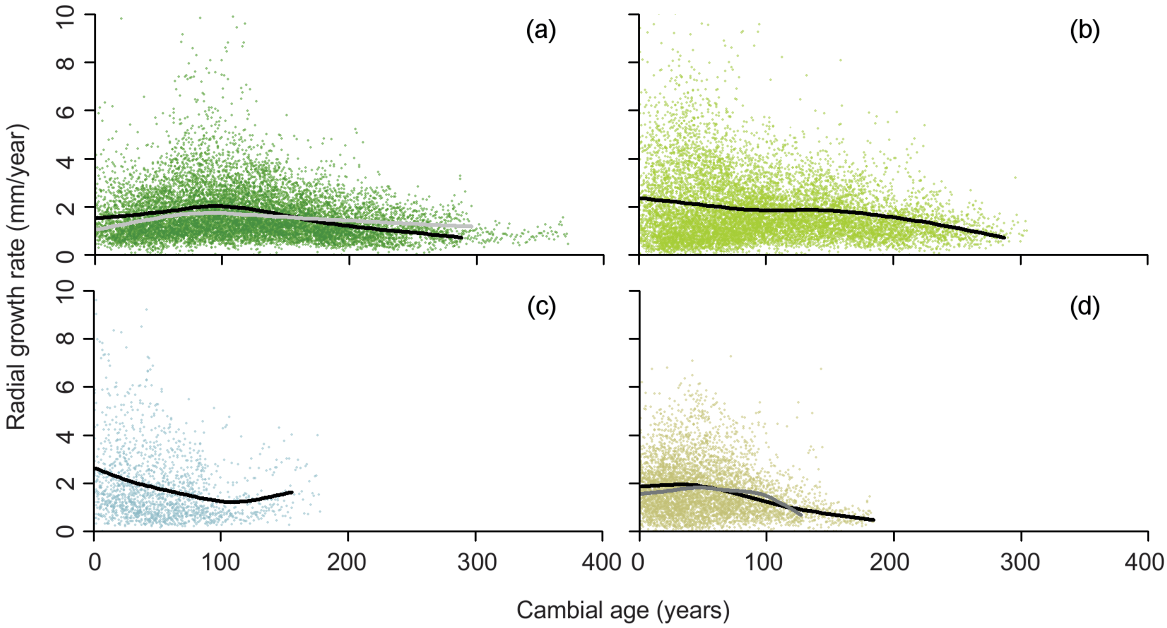

**Fig. 6: Lifetime growth patterns of the studies *Hymenaea* species in the following biomes: a) Amazon biome b) Atlantic Forest biome, c) Pantanal biome and d) Cerrado biome. The smoothed averages lines are presented by species: *H. courbaril* in black, *H. parvifolia* in light grey and *H. stigonocarpa* in dark grey.**

Pantanal biomes and smaller in the Amazon biome. Growth rate of larger trees becomes relatively higher in the Amazon and Atlantic Forest biomes. In the 40–50 cm diameter class, the growth rate of these two biomes is higher than in the Cerrado. In even larger diameter classes, the growth rate at the Atlantic Forest is statistically higher than in the Amazon biome.

## 4 Discussion

Our results show that both *Hymenea courbaril* and *H. parvifolia* trees are able to grow older than 300 years, which can be considered relatively old for tropical standards (Brienen et al. 2016). It is on a par with other tropical species like *Afzelia africana* (349 years), *Cedrela odorata* (308 years), *Daniellia oliveri* (368 years) (Dünisch et al. 2003; Brienen and Zuidema 2006; Schöngart et al. 2006). Only few species like *Hymenolobium mesoamericanum, Dipteryx panamensis, Fokienia hodginsii, Minquartia guianensis* can be considered exceptions because these trees can live beyond 600 years (Fichtler and Clark 2003; Sano et al. 2009). *Tectona grandis* is another long-lived species that can reach more than 500 years (Borgaonkar et al. 2010) These findings agree with Worbes and Junk (1999), who suggested that trees in the tropics are generally not much older than 400 to 600 years, with small probability for a few exceptions. Older trees would require extremely low growth rates and larger diameters, characteristics which are rare in the tropics.

For Cerrado species, *H. stigonocarpa* individuals are considerably younger, with a maximum age of 144 years, which is comparable to species like *Celtis adolfi-friederici* and *Podocarpus lambertii* (Worbes et al. 2003, Locosselli et al. 2016a). It is interesting that trees from forest biomes like the Amazon and Atlantic Forests can be older than trees from the Cerrado. This last biome is usually characterized by the presence of deeper water tables and dystrophic soils as well as the strong influence of fire (Coutinho 1990). In fact, fire is regarded as a key regulator of floristic and physiognomic equilibrium of this biome (Coutinho 1990) that could also limit the maximum age of trees found there.

An important finding of the present study involves the presence of strong growth variability in some of the sampled populations. For instance, some populations of *H. courbaril* showed strong heterogeneity in tree growth with fast- and slow-growing trees inhabiting the same site. Actually, this species showed the highest growth variability among the sampled *Hymenaea* species. Similar wide growth variability was reported by Brienen and Zuidema (2006) for a population of *Cedrela odorata* from the Bolivian Amazon and *Pterocarpus angolensis* in southern Africa (Therrel et al. 2007). These differences in growth rate could be explained by either exogenous or endogenous factors. For example, different environmental conditions may result in distinct growth rates within a population. Schöngart et al. (2015) reported significant differences between trees growing under different light conditions in the Amazon Forest. It is also possible that some individuals are simply able to grow faster than other trees based on genetic variability (Schweingruber 1996). Moreover, both endogenous and exogenous factors may act together. However, any firm conclusions on this matter can only be reached as a result of further studies, and also is outside the scope of the present paper.

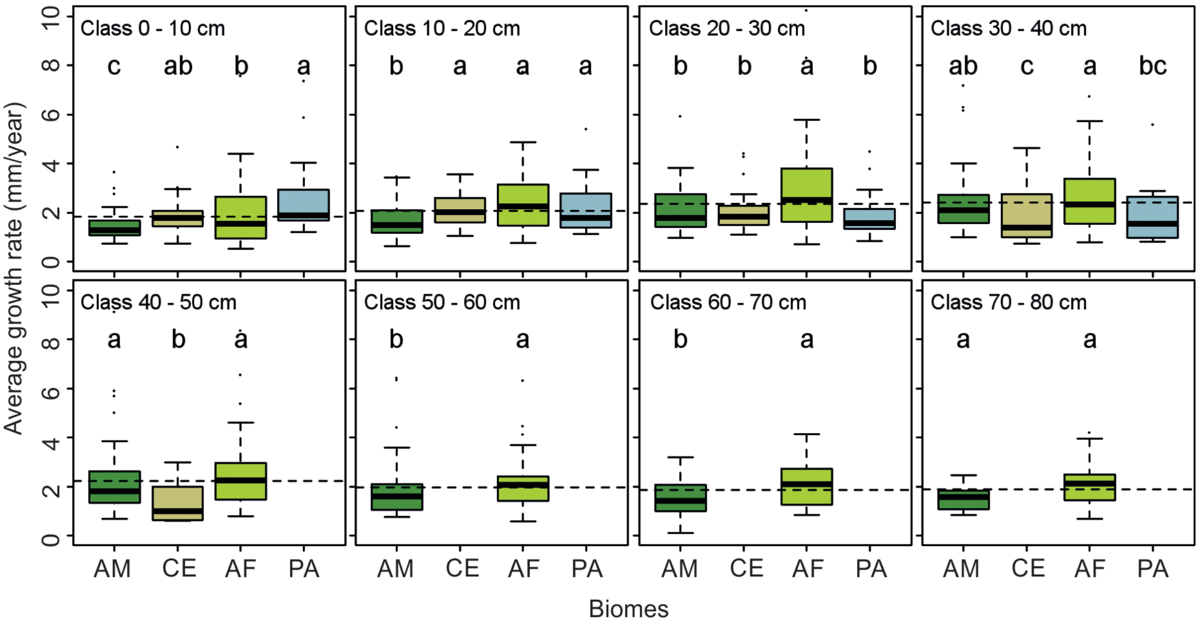

**Fig. 7: Boxplots of the average radial growth rate of trees inhabiting four Brazilian biomes in different diameter classes. Colors and abbreviations indicate the biomes of provenance: Amazon Forest (AM, dark green), Cerrado (CE light brown), Atlantic Forest (AF light green) and Pantanal (PA light blue). The dashed line indicates the overall average growth rate for each diameter class. Letters show the results for the Kruskal-Wallis test and the Dunn's test, or the results of the Wilcoxon's test. Different letter refer to statistically different growth rates.**

At the biome level, the studied species showed distinct trends in the lifetime growth pattern that seems to be related to the biome of provenance. It is important to highlight that different species of *Hymenaea* showed similar growth trends within the same biome, which could be an evidence that they share similar growth strategies according to the environmental demands. This is not always the case, since different species may show completely different growth patterns within the same environment (Groenendijk et al. 2014). Overall, trees growing in the two largest rainforest in South America showed distinct growth patterns throughout their lives. For instance, trees from the Amazon forest showed a trend of increasing growth rate from the beginning of their lives up to about 100 years followed by a decreasing growth rate, while trees growing in the Pantanal and Atlantic forest showed only decreasing growth rates.

In the Cerrado, an open and seasonally drier environment (Prado and Gibbs 1993), trees showed a consistent fast growth rate up to about 50 years followed by a strong decrease of it. A different trend was reported for *H. courbaril* inhabiting the Cerrado in Bolivia (López et al. 2012). In this site, *H. courbaril* trees showed a rather constant growth rate along their lives, which is different from the common pattern described for both *H. courbaril* and *H. stigonocarpa* in the Brazilian Cerrado biome. Even though the *H. courbaril* trees did not actually inhabit the Cerrado vegetation, but rather a dry forest, they showed similar growth pattern to *H. stigonocarpa* a typical Cerrado species. Probably, these differences between the populations from Bolivia and Brazil could be related to distinct vegetation structures. Even the average growth rate of *H. courbaril* inhabiting the Bolivian Cerrado is about 67% higher than the same species inhabiting the dry forest within the Cerrado biome in Brazil.

Differences among biomes are also evident when the growth rates are compared in each diameter class. For smaller trees, the low light stress found in the understory of the taller Amazon forest seems to limit the growth of *Hymenaea* trees. For medium sized trees, the growth rate is higher in the Amazon and Atlantic Forest biomes, and it is about 22% slower in the Cerrado. A lower growth rate could be expected in the Cerrado since it has deeper water tables and more dystrophic soils (Coutinho 1990), as aforementioned. In addition, the higher investment of assimilates to produce thicker barks for fire protection in savannas (Dantas and Pausas 2013) could also constrain trees growth rate there. For even larger trees, only found in the Amazon and Atlantic Forest biomes, the growth rate is consistently higher in the last biome. Canopy height is usually lower at the Atlantic Forest when compared to the Amazon Forest (Simard et al 2011). It is possible that it takes longer to reach the canopy in the Amazon Forest than in the Atlantic Forest.

If trees emerge sooner at the Atlantic Forest, they will increase the growth rate afterwards as a result of the absence of aboveground competition.

Studies of age and growth rate of tropical species, including the *Hymenaea* species studied here, are relevant to understand the ecology, and therefore, to aid the conservation and management of these tropical biomes. For instance, the persistent growth reported in our study, and a few others in the tropics, strongly drive the population dynamics of tree species (Bullock et al. 2004) leading to distinct timber yield projections in future logging cycles (Brienen and Zuidema 2007). Based on our study, and previous ones, the life-time growth patterns are dependent on species and on sites of provenance and any generalization of it should be carefully done with the risk of taking inappropriate decisions for species conservation and management.

## 5 Conclusions

Both *H. courbaril* and *H. parvifolia* trees may be more than two-fold older than *H. stigonocarpa* trees and the presence of younger trees in the Cerrado could be related to the fire regime common in this biome. Out of these three species, *H. courbaril* trees showed the widest range of average growth rates with fast and slow growing trees reported within the same population, while the other two species showed a narrower range of growth rates. Overall, the studied populations presented pronounced lifetime growth patterns that are related to the environmental conditions of the biome of provenance. For instance, the reduced amount of light in the Amazon Forest understory results in a slow growth rate of smaller trees while the open vegetation found in the Cerrado favors a higher growth rate in similar trees. However, the growth rate of trees inhabiting the Cerrado is subsequently constrained by the environmental limitations and disturbances. In the Atlantic Forest, the growth rate of larger trees is higher than in the Amazon Forest, probably because they reach the canopy sooner. It is important to highlight that the lifetime growth patterns of trees reflect well the growth strategy of species and the growth conditions found in these biomes, which in turn are key information to understand the ecology of these tropical biomes and to aid their conservation and management.

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## Authors

Dr. Giuliano M. Locosselli
Prof. Dr. Gregório Ceccantini
Department of Botany
University of São Paulo
Rua do Matão, nº. 277
- Cidade Universitária - Butantã – SP
CEP 09715-030 São Paulo
Brazil
locosselli@yahoo.com.br

Stefan Krottenthaler
Philipp Pitsch
Prof. Dr. Dieter Anhuf
Department of Physical Geography
University of Passau
Innstraße 40
94032 Passau
Germany