Can the competition dynamics of non-native invaders be reconstructed to reveal historical impact? The case of *Cecropia peltata* and *Musanga cecropioides* (Urticaceae) in Cameroon

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Abstract Measuring impacts of non-native species is challenging, particularly for long-established invasions in poorly characterised native ecosystems. Recreating historical population dynamics using dendrochronological methods is a popular approach for addressing conservation and forest management questions. However, these tools are rarely applied for addressing questions of invasion. Classical dendrochronology is also not well suited to many tropical tree species as they do not produce growth rings. Here we test the validity of an alternative approach, based on the analysis of multiple morphological markers, that could allow for both the recreation of historical invasion dynamics as well as quantify the impacts of invasion on the recipient native ecosystem. We validate this method on the *Cecropia peltata* invasion in Cameroon and its potential impacts on a native tree, *Musanga cecropioides*. We were able to compare architectural development over time in a mixed secondary forest where the two species co-occur and revealed differences in performance (growth, branching and flower production) between the two tree species. Our results revealed more sustained growth during early establishment and an early sexual maturity for the non-native *C. peltata*, compared to its native counterpart. A lower density of *M. cecropioides* was observed in the region of co-occurrence, supporting a hypothesis of competitive exclusion of the native species at the juvenile stage. Our work provides a novel way to understand the impacts of plant invasions via retrospective analysis that could well be applied to other invasions globally, opening up more opportunities to prioritise management on an impact-focused basis.

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Introduction

Biological invasions by non-native species are recognised as a major cause of decline in biodiversity worldwide (Mollot et al. 2017), second only to land use change (Murphy and Romanuk 2014). These invasions by non-native species have been shown in some cases to lead to population decline or even competitive exclusion of native species in recipient ecosystems (Mollot et al. 2017), with cascading impacts that can include altering ecosystems functions and services (Hulme et al. 2013; Kumschick et al. 2015). Assessing and managing the threats from non-native species to ecosystems is therefore fundamental to preserve biodiversity and ecosystem integrity (Cardinale et al. 2012). Yet progress on management is particularly slow in the tropical regions of South America, Africa and Asia, often impeded by a lack of knowledge or financial resources (Pyšek et al. 2008; van Wilgen and Wilson 2018; Makoni 2020).

Prioritizing management to mitigate the threats posed by non-native species requires a deeper understanding of the impacts that they might cause, moving beyond management choices based on subjective observations of invasiveness (i.e. rapid range expansion) or abundance (Hulme et al. 2013; Kumschick et al. 2015). Unfortunately, measuring impacts from non-native species, whether positive or negative, has proved to be particularly challenging. This is in part because there is almost never longitudinal data for the species as it progresses along the invasion curve (*sensu* Blackburn et al. 2011), from introduction to establishment and then on to spread (Pergl et al. 2020). Moreover, impacts to the recipient ecosystem have generally happened decades in the past for long-established introductions, making it challenging to tease out impacts on native communities from a current snapshot of natural heterogeneity across the landscape. Some of the most useful insight on invasion impacts happens earlier on in the invasion process (Dawson et al. 2009; Drenovsky et al. 2012; Wilsey

et al. 2015), creating a demand for studies that can reveal these dynamics for past and current invasions.

Long-term field manipulation studies can provide insight on invasion impacts, but they are time consuming and require a robust baseline knowledge of the recipient ecosystem. However, alternative methods are now being applied to reconstruct past population dynamics, such as remote sensing, isotopic and genetic analyses, and dendrochronology (McCarroll and Loader 2004; Scott et al. 2019; Byrne et al. 2022). If such methods can also be applied to both the introduced species as well as potentially impacted native species, then there is also a chance to generate insights on historical impacts via a hierarchical approach to understanding past growth rates of individuals. That is, understanding how these traits impact on population dynamics and, in turn, how the fingerprint of past impacts can be inferred from interspecies demographic trends.

A technique that is starting to be applied more frequently to understanding past invasion demographics is the dendrochronological approach (Kasson et al. 2013; Siegert et al. 2014; Scott et al. 2019). Traditionally, the term 'dendrochronology' is used for the analysis of growth rings in wood to determine plant age and reconstruct its past diametric growth (Schweingruber 1993, 2007). Dendrochronology based on growth rings generally requires a large sampling effort, and some plant species are not well suited for this method because they do not produce rings in a temporally consistent manner, such as many tree species from tropical rain forests (but see Xavier et al. 2021). However, some plant species also have morphological scars (e.g. abscission points for dropped leaves, branches or flowers) that make it possible to understand how the processes of past primary growth, branching, and flowering occurred, and therefore to retrospectively deduce the architectural development and space occupancy of a particular individual (Rayback and Henry 2005; Heuret et al. 2006; Zalamea et al. 2008; Nicolini et al. 2012; Dolezal et al. 2020).

Applied to multiple trees within a community, this technique shows considerable promise for establishing invasion impacts, as it can be applied to both native and non-native components of an invaded community, revealing changes in localised abundance between species over time (i.e. inter-specific

competition). Moreover, it is a method that is also particularly well suited for applying in less developed regions, where access to expensive technology is often limited, where persistent high cloud cover in tropical regions interferes with remote sensing methods, and where accessing capability is less likely to be a rate limiting step for resourcing projects (Visser et al. 2014; Nazarova et al. 2020). It is also in these regions that a significant proportion of the world's plant invasions have occurred, meaning that there is a disproportionate need to improve understanding on the dynamics of these invasions to guide management (Sitzia et al. 2021).

Many of the world's most problematic non-native invasive plants today were first redistributed by the global botanical gardens network, particularly from the Neotropics towards Europe and then subsequently to what are now less developed regions of Africa and Asia (Alpern 2008; Dawson et al. 2008; Hulme 2011). This has been the case for several species from the genus *Cecropia*, which have been introduced into countries across Africa, Asia, the Pacific and Bermuda Islands (McKey 1988; Meyer 2004; Berg et al. 2005; Asner et al. 2008; Lok et al. 2010; Conn et al. 2012; Neuba et al. 2014; Raphael et al. 2015). Yet, despite *Cecropia peltata* being listed among the "100 of the World's Worst Invasive Alien Species" (Lowe et al. 2000), there remains considerable uncertainty about exactly which *Cecropia* species has been introduced where (Webber et al. 2011) and little robust evidence that introduced *Cecropia* populations have significant negative impacts in their non-native range. This absence of evidence for impacts, however, more likely reflects the fact that introductions have mostly been into less developed countries, where understanding invasive species impacts is more limited, than the alternative explanation that there are few impacts from *Cecropia* invasions.

One of the advantages of understanding the invasion ecology of *Cecropia* species is that they are well suited to morphological methods to reconstruct past growth trajectories (i.e. fluctuation and accumulation of growth over time; Heuret et al. 2003; Zalamea et al. 2008; Levionnois et al. 2023). While this method works well across multiple *Cecropia* species in their native range, it remains unknown if the species display the same growth characteristics (i.e. if a retrospective growth analysis method would work)

in regions where they have been introduced, as the approach has never been validated on *Cecropia* species outside of their native range.

Several studies have reported the introduction and the naturalization of a phenotype related to *Cecropia peltata* L. in West Africa, at least in Cameroon (McKey 1988), Ivory Coast (Neuba et al. 2014), and Senegal (Berg et al. 2005). *Cecropia peltata* was reported as being introduced into Cameroon via the Victoria Botanical Garden in Limbé, and has since spread rapidly through the surrounding coastal region (Berg et al. 1985, 2005; McKey 1988). *Prima facie* evidence suggests that *C. peltata* appears to be replacing a native congener, *Musanga cecropioides* R. Br., based on observations of the abundance and progression of the species in the coastal region around Limbé (McKey 1988). Belonging to the same tribe, *C. peltata* and *M. cecropioides* display many morphological and ecological similarities. They both grow in relatively open habitat, typically recently disturbed environments in humid tropical areas (*C. peltata*: Oldeman 1974; Van Der Meer et al. 1998; Vester 1998; Berg et al. 2005. *M. cecropioides*: Deval 1967; De Ruiter 1976; Gourley-Fleury 2013). The ecological and morphological similarities between the two species, as well as their similar role in forest succession, suggest that there is likely to be a strong overlap in their ecological niche, and therefore a greater risk of competitive exclusion during invasion.

Here we take advantage of this unique context of introduction and invasion of *C. peltata* in Cameroon to test the applicability of using morphological markers to quantify architectural development over time. If successful, this method could, in turn, recreate historical invasion context and establish evidence for invasion impacts on native biodiversity. Achieving this goal first requires proving that the architectural method developed for *Cecropia* in its native range can be applied to *C. peltata* and the closely related *M. cecropioides* in Cameroon. As Cameroon seasonality is similar to that of the Neotropics, with well-marked but relatively short dry seasons, it seems likely that this technique remains applicable for *C. peltata* in its area of introduction. In addition, the method has great potential for application to *M. cecropioides* since this species has the same architectural and growth markers as *Cecropia* species and could, therefore, allow

for a comparison of performance (in terms of growth and reproduction) in the same environment and to understand competition between these two species.

More specifically, we will address three primary questions:

(i) Does introduced *C. peltata* in Cameroon have predictable architectural development comparable to *Cecropia* taxa in their native range, which would enable the reconstruction of past invasion histories?

(ii) Can this method of quantifying architectural development over time, established for Neotropical *Cecropia* species, be applied to native *M. cecropioides* in Cameroon?

(iii) If so, does the comparison of developmental variation for individuals in mixed stands of *C. peltata* and *M. cecropioides* reveal differences in their relative performance that could reveal past competition dynamics?

Materials and methods

Study species

Cecropia peltata as delimited by Berg et al. (2005) is morphologically very variable in the Neotropics, so much so that it is still unclear if it is one or several species. In Cameroon, this species has a simple architecture, following the model of Rauh (Hallé and Oldman 1970), and morphology falling within the range of variability of *C. peltata* characters as defined by Berg and Franco Rosselli (2005; Online Resource 2). Despite this taxonomic uncertainty, for clarity we assumed hereafter that the *Cecropia* found in Cameroon belongs to *C. peltata sensu lato*. Representative specimens are deposited in the herbaria MPU and P (Bonnepoupa II, Cameroon, 4 Jul 2018 (♀ fl), Heuret 256 (MPU, P); Bonnepoupa II, Cameroon, 6 Jul 2018 (♂ fl), Heuret 257 (MPU, P); Bonnepoupa II, Cameroon, 14 Jul 2018 (♀ fl), Heuret 258 (P)). For detailed pictures of this species see Online Resource 2.

Musanga cecropioides trees can grow up to 45 m and develop stilt roots when they reach larger sizes (Coombe and Hadfield 1962). They form an open umbrella-like crown (Coombe and Hadfield 1962;

De Ruiter 1976) and also have an architecture following the model of Rauh (Hallé and Oldman 1970). *Musanga cecropioides* is a dioecious species, thought to flower throughout the year (De Ruiter 1976). For detailed pictures of this species see Online Resource 2.

Study site and tree sampling

The study site was located in the west coastal region of Cameroon (Texier et al. 2018), characterized by a dry season from November to March, with December to February as the driest months, and a rainy season from April to October, with a drop in temperature around August (Molua and Lambi 2006; Tingem et al. 2008; Texier et al. 2018; Online Resource 1). The study site consisted of fallow land close to the village of Bonepoupa II, about 50 km from Douala (4° 10′ N, 10° 02′ E, WGS84), in the Nkam department of Cameroon. The climate is tropical with abundant annual rainfall (up to 3702 mm/year nearby Douala). *Cecropia peltata* and *M. cecropioides* trees constituted a mixed stand and were the only two species that formed the canopy layer of this even aged stand.

Plant material and measurements

The fallow study site was formed by natural regeneration after a manual anthropogenic clearing event less than 10 years ago, according to local villagers. The *C. peltata* and *M. cecropioides* trees were around 12 m tall. These two species formed the canopy of the stand with crown in contact, so that they were in competition for space and light. In the absence of knowledge on the exact age of the trees and their growth rate, all the trees on the site were sampled randomly regardless of their size or social status (dominant vs. dominated). *Cecropia peltata* were however at higher densities than *M. cecropioides* and we studied 16 and 6 individuals of these two species, respectively. To complete the sampling for *M. cecropioides*, two close sub-adult individuals with comparable dimensions were studied in a fallow area immediately adjoining the study site.

The trunk girth at breast height (1.30 m; GBH) was measured on the standing trees before felling. The height of the tree was measured with a decameter

on the felled tree. Once on the ground, the successive internodes from the apex to the base for each axis were numbered. The limits of internodes are well defined by the ring-shaped scars left by the stipules. The trunk constitutes the A1 axis, the branches emerging directly from the trunk are the A2 axis, the branches emerging from the A2 are A3 axis and so on, up to order 4. Each axis was thus identified within the tree architecture by assigning it a label corresponding to its branching order and the rank of the node that carries it. Thus A2-110 is the branch (order 2) carried on the 110th node from the apex of the main axis (A1). A3-50–110 is the twig (A3) carried on the 50th node of the branch (A2) which is itself carried by the 110th node of the main axis (A1) and so on. The main axis is simply numbered A1. For each axis, we measured (i) the length, (ii) the basal diameter and (iii) its number of nodes.

The methodology used to reconstruct the past development of sampled trees along the axes follows that developed by Heuret et al. (2002), Zalamea et al. (2008) and Levionnois et al. (2023). For the successive phytomers constituting the axes we measured (i) the length of the internodes and (ii) the presence/absence of inflorescences, branches and leaves. The observations on each internode were coded as follows; (i) for the productions of lateral buds: (0) no inflorescence, (1) scars of developed inflorescences and (2) developed inflorescences; and (ii) for the production of the central bud: (0) no branch, (1) pruned branch and (2) branch present.
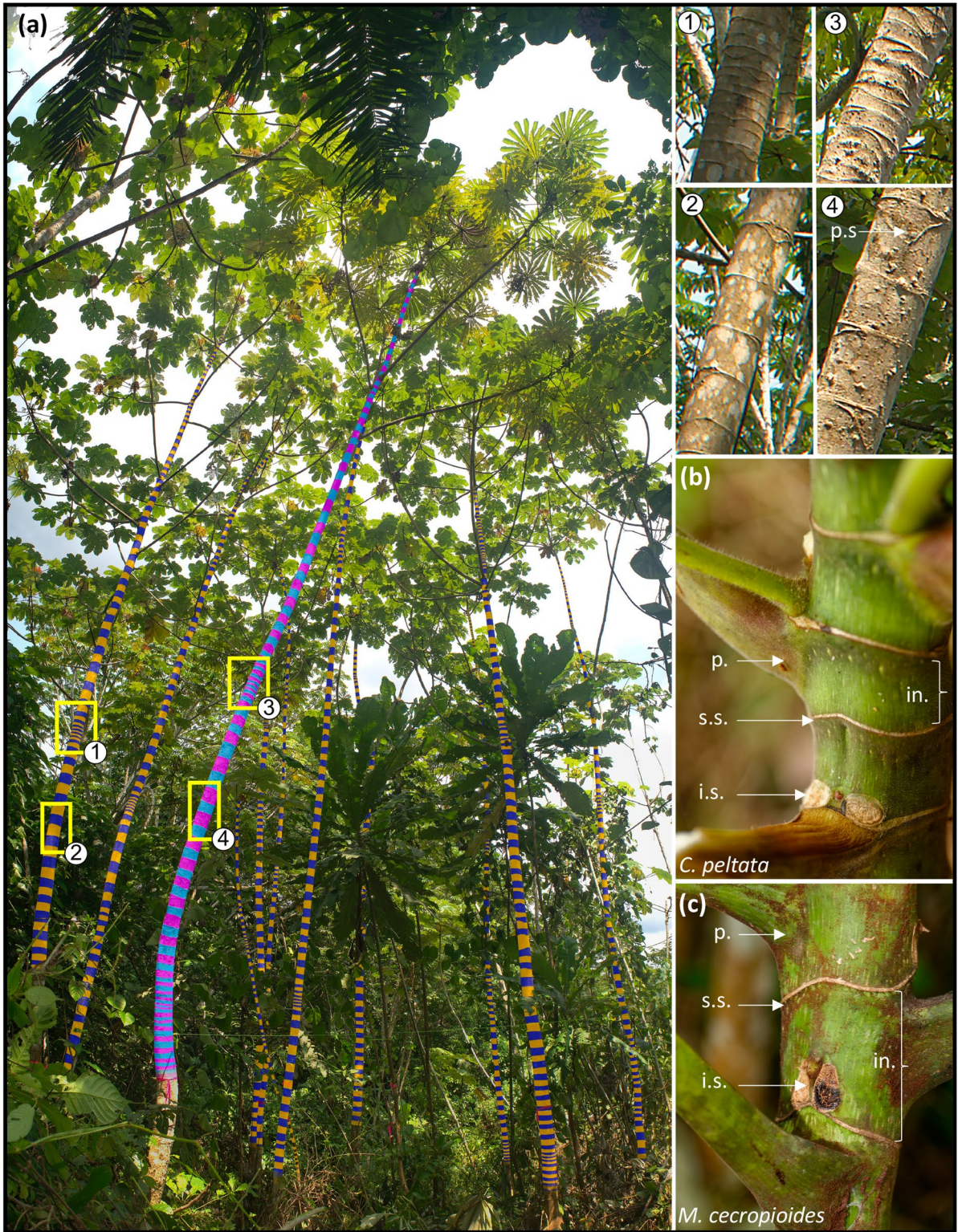
All six individuals of *M. cecropioides* were described completely for all their axes as well as seven *C. peltata* individuals. The remaining nine *C. peltata* were described precisely node to node only on the main axis. The topology, *i.e.* the relative position of the different botanical units described (axis, phytomers), was coded in Multi-scale Tree Graph format (MTG; Godin and Caraglio 1998).

Data analysis

The encoded field data were extracted and organized using the AmapMod software, now integrated as a Vplant package in the OpenAlea platform (Godin et al. 1997; Pradal et al. 2008). All graphs and statistical analysis were performed with the R software (http://CRAN-R-project.org).

To analyse fluctuations of internode length, classical methods of time series analysis relying on a decomposition principle of signal sows were performed. The trend in internode length changes over ontogeny (*i.e.*, over hundreds of internodes and several years) was modelled by a moving average. The symmetric smoothing filter was chosen, which corresponds to the probability mass function of binomial distributions with parameters $n = 100$ and $p = 0.5$. The fluctuations around this trend are calculated by dividing, for each node, its real length by the value calculated with the moving average (which we will call hereafter the standardized residuals). These variations reflect the seasonal effects of climate on growth, as work conducted in the Neotropics showed that shorter internodes series can be associated with slower growth occurring during the dry season (Zalamea et al. 2013). Qualitative analysis of the residuals variation patterns, coupled with the positioning of inflorescences and branches, allowed strong hypotheses to be made about annual boundaries along the axes (see Zalamea et al. 2008 or Levionnois et al. 2023 for more details). A complementary tool is the use of autocorrelation functions (correlograms) to assess if there is a relatively stable average return time (in terms of node number) between two successive events (e.g., two stages of branches or two successive series of short internodes separated by a series of long internodes; Guédon et al. 2007). This analysis allows us to explore the presence of patterns that could be interpreted as annual and to make hypotheses about the phyllochron (i.e. leaf production rates of the axes). We applied autocorrelation analysis to binary branching and flowering sequences as well as residual sequences obtained from filtered internode length sequences.

In addition, the study of the synchronism of internode production on the different axes of a tree was evaluated by calculating the ratios between the number of nodes on the lateral axes (order n) and the number of their bearing axes (order n-1) above their point of insertion. This relation was established for all the A2, A3 and A4 axes for 12 studied trees (7 *C. peltata* and 5 *M. cecropioides*). Mann–Whitney–Wilcoxon (MWW) non-parametric tests were used to compare tree height, diameter, first branch, and first inflorescence positions between the two populations because it allows distribution comparisons derived from relatively small samples (Saporta 1990).

Results

Architectural development of the non-native *C. peltata*

Morphological features

The morphological markers required for quantifying the architectural development of *C. peltata* in Cameroon were clearly visible and remained visible throughout the life of the trees. Based on a preliminary assessment of the felled individuals, *C. peltata* individuals had axes constituted by a succession of phytomers whose internode length fluctuated by alternating short and long internode series. This pattern is consistent with continuous growth with short internodes formed during dry periods and longer internodes formed during the rainy season (Fig. 1a). Branches were orthotropic by apposition (*sensu* Koriba 1958) and the branching was rhythmic (Fig. 1a). Nodes were marked by the scar left by the stipule that initially protected the terminal bud and the young leaf in formation. In the same way, the lateral production (inflorescences and branching) associated to each internode remained observable through the years by the scars they left (Fig. 1b, c). Each internode initially displayed three buds; a central bud which can produce a branch and two lateral buds, on each side of this central bud, which can produce inflorescences. After production and abscission of the inflorescences, two lateral scars remained visible throughout the life of the tree (Fig. 1b, c).

Synchronicity of node production between axes

The ratios between the number of nodes on a lateral branch (order n) and the number on its bearing branch (order n-1) above its point of insertion were calculated for seven *C. peltata*, for axes ranging from A1 to A4. Regardless of the order of the considered axis, the number of nodes per axis was positively correlated to the number of nodes of the bearing axis above its point of insertion. The slope of the regression line was very close to 1 ($R^2 = 0.95$), which indicates that new nodes were produced at approximately the same rate on the different axes of a given tree (Online Resource 3). However, as the axes order increased, a loss of this synchronicity was observed, with less internodes produced on the newly initiated axes compared to the bearing axes (A2-A1 R2 = 0.94; A3:A2 R2 = 0.98; A4:A3 R2 = 0.64). That is, a loss of synchronicity was observed on the oldest branches (*i.e.,* those composed of a higher number of internodes), which indicated asynchrony in the production of new nodes as the branches grow.

Periodicity in growth, branching and flowering

Considering internode length, the Spearman autocorrelation rank function calculated on the residual series did not reveal a clear periodic signal at the population level (Fig. 2a). Nevertheless, significantly positive coefficients were found for rank lags from 25 to 33 nodes, from 64 to 72 nodes, and then from 88 to 93 nodes. When considering the trees individually, some showed a clear sinusoidal signal (Fig. 2b). The rank lags for which the correlation coefficients were positive remained quite variable across individuals, which explains the flatter signal observed at the population level. On an individual scale, the rank lags that had the highest frequencies of significantly positive correlation coefficients values were around 32, 48, 65, 89.

At the population level, the Spearman autocorrelation rank function calculated on the series of branching events did not reveal a clear periodic signal (Fig. 2a). However, on an individual scale, periodic patterns were sometimes observed, as in the case of individual *C. peltata* C11 (Fig. 2b). For this individual, significantly positive coefficients were found for rank lags from 60 to 64 nodes and from 38 to 42 nodes, and a tendency towards positive values was observed for the rank lag from 18 to 25 nodes. On an individual scale, the rank lags that had the highest frequencies of significantly positive correlation coefficients values were around 61, 63, 70, 71, 72, 75.

Regarding the flowering process, no periodicity could be demonstrated at the population level (Fig. 2a), nor at the individual level (Fig. 2b).
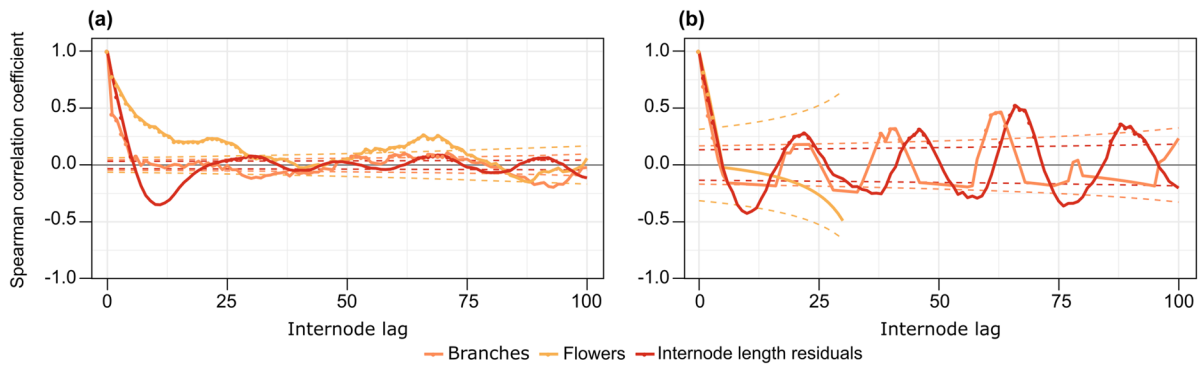
Fig. 2 Autocorrelation functions concerning internode length, flowering and branching occurrence for *Cecropia peltata*. **a** Autocorrelation functions for all individuals considered together **b** Autocorrelation functions for a single individual (C11). The dotted lines represent the randomness 95% confidence limits

Fig. 3 Example of an individual case of *Cecropia peltata* (C19), with representation of internodal lengths (black line), residual values of internodal lengths (red line), moving average (dotted black line), localization of branches (circles) and localization of inflorescences (triangles). The assumed annual limits are indicated with vertical dotted gray lines
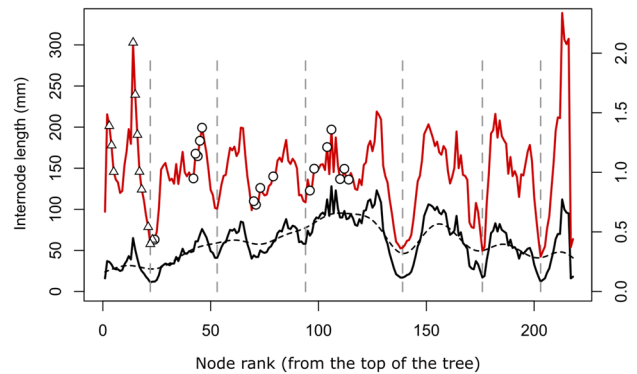
Annual delimitation and tree age

The assigning of annual limits on the internode series of individuals was based on an assessment that took several factors into account. First, these limits were placed on the zones with internodes that had a much shorter length than average (which can be attributed to the dry season). Indeed, when the series of internode lengths were plotted individually and with their residual values, alternating zones of short and long internodes were clearly visible. The size of the cycles delimited this way (in terms of number of internodes) was constrained at around 30 internodes, a value highlighted by the autocorrelation analyses (Fig. 2).

Second, the position of branches and inflorescences was also indicated on these series of internode lengths, in order to visualize the periodicity of branch production (branch tiers) in some individuals and the alternation of areas bearing inflorescences

(or inflorescence scars) with areas of sterile internodes. However, some individuals seemed to have continuous flowering. Nevertheless, direct field observations revealed that some series of inflorescence scars in these individuals were smaller, suggesting potential confusion with aborted structures.

Assigned annual delimitations were then compared between individuals to ensure that they were consistent with the entire dataset and with the results of previous studies on Neotropical *Cecropia* species.

Using these compiled factors, we were successfully able to assign age to all individuals in the study. For example, the *C. peltata* individual C19 was estimated to be 7 years old, producing branches during the 4th, 5th and 6th years, and flowers during the 7th year (Fig. 3). Branches were not produced at a specific time during the year, and two waves of flowering occurred during the 7th year (Fig. 3).

The majority of all *C. peltata* trees studied were estimated to be between 7 and 8 years old, with one

individual much older than the others (estimated to be 11 years old; Table 1 in the Online Resource 4) and one small individual that had resprouted from a severed main trunk estimated to be 4 years old.

Architectural development of the native species *M. cecropioides*

Morphological features

As for *C. peltata*, *M. cecropioides* trees had well-visible internodes (Fig. 1a, c), displaying the same bud's organisation and showing scars of past inflorescences and/or aborted branches (Fig. 1c).

Synchronicity in node production

As for *C. peltata,* the ratios between the number of nodes on a lateral branch (order n) and the number on its bearing branch (order n-1) above its point of insertion were calculated for 5 M. *cecropioides*, for axes ranging from A1 to A4. In a similar way, the slope of the regression line was close to 1 ($R^2 = 0.6$), which indicates that new nodes were produced at approximately the same rate on the different axes of a given tree (Online Resource 3).

However, as the axes order increased, a loss of this synchronicity was observed, with less internodes produced on the newly initiated axes compared to the bearing axes (A2-A1 R2 = 0.98; A3-A2 R2 = 0.42). This phenomenon was particularly marked in one *M. cecropioides* tree, where much less internodes were produced on the A3 axes

compared to the A2 axes (Online Resource 3). This considerable loss of synchronicity was observed only for one *M. cecropioides* individual, which featured highly branched architecture (a total of 19 branches).

Periodicity in growth, branching

As for *C. peltata*, the Spearman autocorrelation rank function calculated on the residual series of internode length did not reveal a clear periodic signal at the population level (Fig. 4a). Nevertheless, coefficients were significantly positive for rank lags from 30 to 34 nodes, from 48 to 53 nodes and from 76 to 84 nodes. When considering the trees individually, some of them showed a clear sinusoidal signal (e.g. individual M1; Fig. 4b). Regarding the branching events, no periodic pattern could be discerned, even at the individual level. For *M. cecropioides*, the periodicity of flowering could not be investigated as none of the individuals studied had yet produced flowers.

Annual delimitation and tree age

The age of the *M. cecropioides* trees studied could be evaluated with the method under consideration. All individuals studied were estimated to be between 6 and 9 years old, with one small individual that had resprouted from a severed trunk estimated to be 4 years old (Table 1 in Online Resource 4).
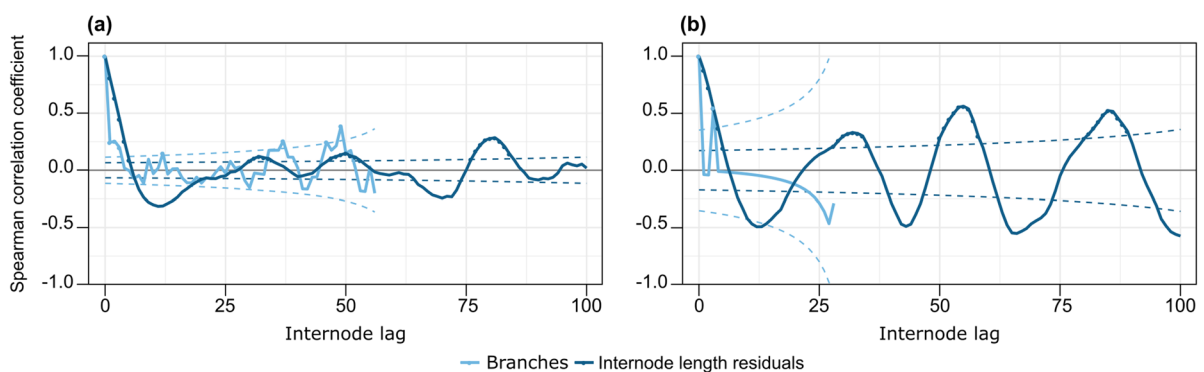
Fig. 4 Autocorrelation functions concerning internode length, flowering and branching occurrences for *Musanga cecropioides* (**a**) Autocorrelation functions for all individuals considered together (**b**) Autocorrelation functions for a single individual (M1). The dotted lines represent the randomness 95% confidence limits

Comparison of performance-related traits

*Height, diameter, number of leaves, branches,*
number of internodes

Most of the studied trees showed a similar height
and diameter ($\overline{H} = 11.72 \pm 1.8$ m $\overline{DBH} = 14 \pm 4$ cm),
with the exception of two individuals (one *C. peltata*
and one *M. cecropioides*) that had resprouted from
severed primary axes. These two individuals had a
smaller total height (around 8 m) and GBH (around
9 cm) than other studied trees (Fig. 5a). Indeed, by
longitudinally sectioning their trunk and observing
the structure of the pith, it could be confirmed that
the main axis for these two individuals originated
from a lateral bud after being cut at their base (i.e.
the pith structure of the primordial axis was bev-
elled and bearing on its side the pith structure of a
new secondary axis). At a similar comparative height,
C. peltata trees had a smaller diameter compared to
M. cecropioides (Fig. 5a). The two *M. cecropioides*
sampled immediately adjacent to the study site had
a larger diameter than those sampled within the site

(21.3 cm and 23.9 cm respectively), despite a compa-
rable height (11.9 m and 11.7 m, Fig. 5a).

At a similar comparative height, *C. peltata* trees
also had more branches compared to *M. cecropioides*
(Fig. 5b) but bore fewer leaves on each axis. On aver-
age, *C. peltata* axes had significantly less leaves per
axis than *M. cecropioides* (10.8 ± 3.8 and 17.1 ± 5.9
leaves, respectively; Wilcoxon $p = 6.1^{e-10}$). The
resprouting *C. peltata* individual was not included in
this calculation because its resprouting morphology
was abnormal, as 27 leaves were present on the main
axis. The total number of leaves per tree was posi-
tively related to their GBH, with larger diameter trees
carrying more leaves (Fig. 5d). In addition, it was
qualitatively observed in the field that the leaf blade
area of *M. cecropioides* was larger than that of *C. pel-
tata* (Online Resource 5).

For both species, there was a significant effect of
branching order on the number of leaves borne by
the axes, with higher order axes bearing fewer leaves.
Cecropia peltata bore an average of 14.2 leaves on
the A1 axes, 10.5 leaves on the A2 axes, 9.3 leaves on
the A3 axes and 7.7 leaves on the A4 axes (all signifi-
cantly different; Wilcoxon A1-A2 $p = 1.3^{e-5}$; A2-A3

Fig. 5 Relationships between tree diameter, number of axes, height (meters), number of nodes and the total number of leaves for the studied *Cecropia peltata* (red circles) and *Musanga cecropioides* (blue triangles) trees
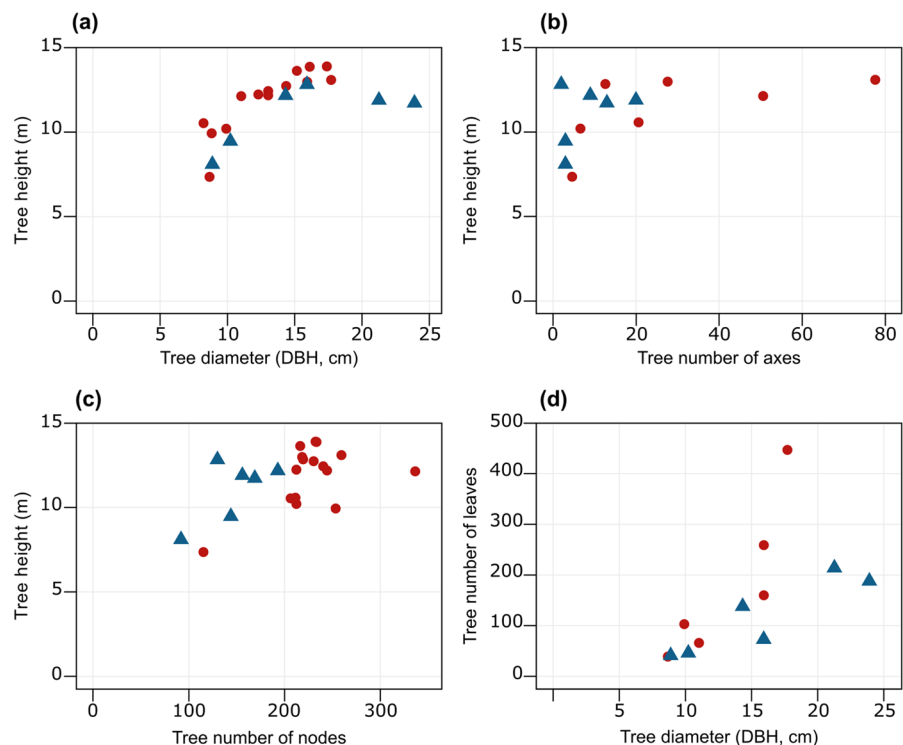
p = 5.2^{e-3}; A3-A4 p = 1.3^{e-2}; A2-A4 p = 1.5^{e-4}; A1-A3 p = 2.8^{e-7}; A1-A4 p = 2^{e-5}). In contrast, *M. cecropioides* bore an average of 24.0 leaves on the A1 axes, 15.7 leaves on the A2 axes, and the only A3 axis studied bore 10.0 leaves (means were not significantly different, except for the comparison of the A1 and A2 axes; Wilcoxon A1-A2 p = 4.5^{e-3}).

Regarding internodes, for a similar height, trunks of *M. cecropioides* had fewer internodes (Fig. 5c), which therefore indicates that this species produced on average longer internodes for a given height.

Variation in internode length

Considering internode length in relation to their rank from the base of the trees up to their apex, in both species internode length was highly variable (means for the A1 axes: *C. peltata*: 5.09 ± 2.5 cm; *M. cecropioides*: 5.47 ± 3.9 cm). It was also observed that the

trunks of *M. cecropioides* consisted of a lower number of internodes than those of *C. peltata* (Fig. 6a). Moreover, the superposition of an arithmetic mean on the data of each species highlighted a pattern where a succession of shorter internodes alternated with a succession of longer internodes (Fig. 6a).

Considering the length of the internodes as a function of tree height, the respective moving average for each species showed a gradual increase in internode size with a maximum at around 6 m high, followed by a gradual decrease in length towards the top of the tree (Fig. 6b). Internodes of *M. cecropioides* were longer than those of *C. peltata* (7.5 cm versus 5.5 cm respectively, at 6 m from the ground when elongation is at its maximum). Moreover, the decrease in internode length was more abrupt for *C. peltata*. Relatively long internodes up to 15–20 cm were produced in both species, yet much shorter internodes were also produced at certain heights, and these heights
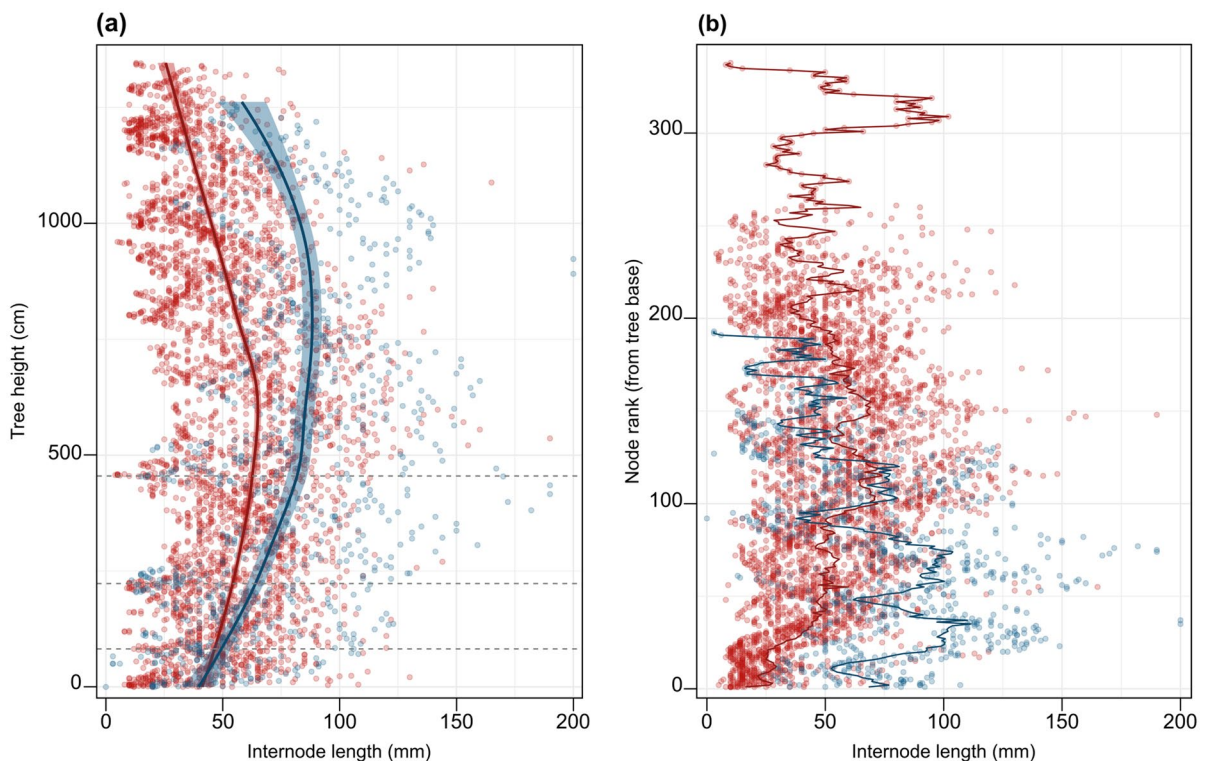
Fig. 6 Tree height and internode dynamics for *Cecropia peltata* (red) and *Musanga cecropioides* (blue) based on all studied individuals **a** Relationship between internode length (mm) and tree height (cm) with a moving average of internode length for each species and **b** Relationship between internode length (mm) and node ranks with average internode length per rank represented for each species

were similar in both species (e.g. at 75 cm, 2.4 m and 4.8 m; see dotted grey lines in Fig. 6b).

Height and age at first branch and first flower

In both species the first branch was produced before flowering, around node 100 ± 22 at a height of 7 ± 1.7 m for *M. cecropioides*, and node 116 ± 23 at a height of 6.6 ± 1.2 m for *C. peltata* (Table 2 in Online Resource 4). *Musanga cecropioides* therefore produced its first secondary branches after a lower number of nodes, but the corresponding height of these branches above the ground was not significantly different than for *C. peltata* (Wilcoxon, p=0.59). This corresponds to the production of their first branches between 4 and 5 years old.

Among the trees studied, almost all *C. peltata* individuals estimated to be 5 to 7 years old had already flowered. For *M. cecropioides*, only one individual studied had flowered on branches and was estimated to be 7 years old. For *C. peltata,* all but two had already produced flowers when measured (one of the non-flowering trees was the resprouting individual). In the fertile *C. peltata* individuals, first flowering was on the trunk, once the first branch stage had been established, at an average node rank of 171 ± 33 and an average height of 9.8 ± 2.2 m (Table 2 in Online Resource 4). This timing corresponds to flower production in their fifth year. The *C. peltata* individuals that flowered and had all axes described, had an average of 87.6 ± 10.7 nodes bearing inflorescences.

Leaf production rates (phyllochron)

The number of nodes produced each year was estimated to be 35.7 ± 7 for *C. peltata* and 25.4 ± 8 for *M. cecropioides.* On the reasonable assumption that growth is continuous in this species, this finding corresponds to one node produced every 10.2 days for *C. peltata* (with 7 days for the shorter phyllochron and 16 days for the longest) and every 14.4 days for *M. cecropioides* (with 9 days for the shorter phyllochron and 30 days for the longest). That is, *C. peltata* produces new leaves at a rate 40% faster than *M. cecropioides*.

Annual growth

Assessing comparative change in growth rate over time between the two species, as represented by tree height, the average increase per annual cycle (calculated by summing the internode lengths within a cycle) was 1.91 ± 0.8 m for *C. peltata* and 1.89 ± 0.9 m for *M. cecropioides*. For *C. peltata* the growth rate increased during the first three years until it reached a maximum during the fourth year (mean: 3.02 ± 0.9 m) when it was significantly higher than that of *M. cecropioides* (Fig. 7). For *M. cecropioides* the growth rate was more regular than that of *C. peltata* during the first years of growth and showed a decrease from the sixth year (Fig. 7).
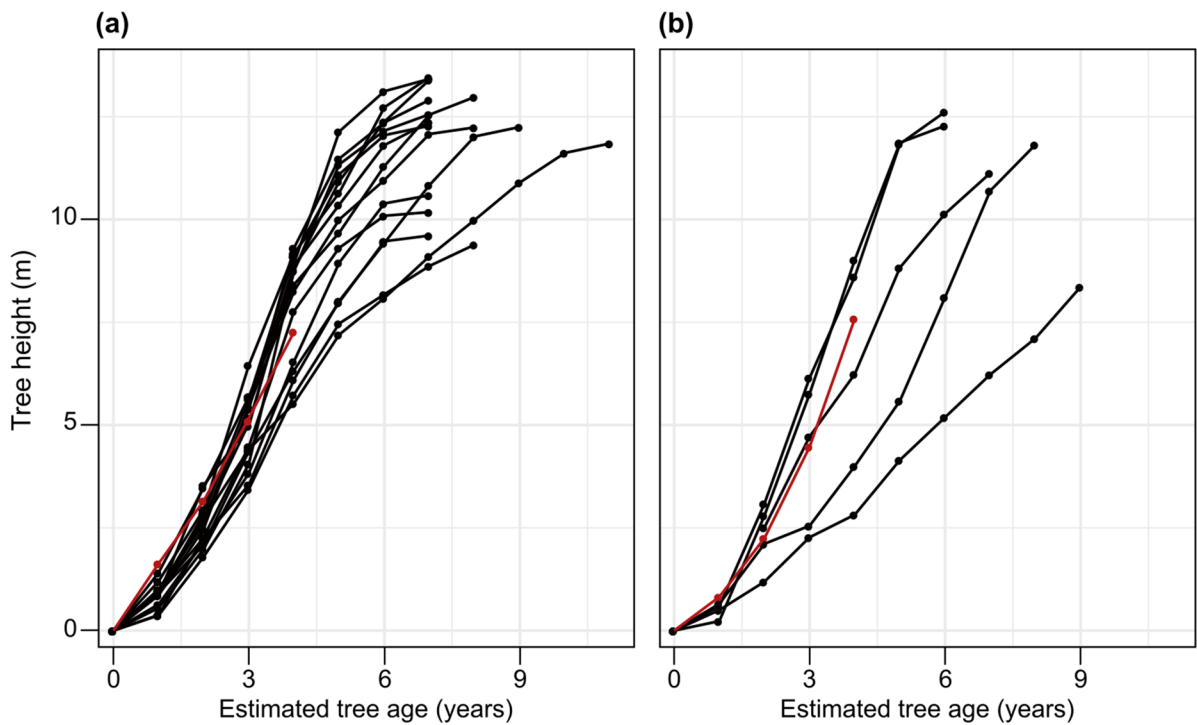
Growth trajectories

The annual estimation of growth permitted the reconstruction of growth trajectories for both species (Fig. 8). Growth curves for *C. peltata* individuals were very similar while those of *M. cecropioides* showed more inter-individual variability (Fig. 8). Although some *M. cecropioides* exhibited similar height growth dynamics to those of *C. peltata*, several of them presented flatter curves, reflecting a more moderate growth in the first years of life (Fig. 8).

The reconstruction of growth curves also allowed to compare growth strategies between trees that were direct neighbours and trees with similar characteristics. First, the two young resprouted individuals were estimated to have the same age (4 years) and their respective annual delimitations highlighted very similar growth curves, which supports the estimation of their age (Fig. 8; individuals in red). Second, the growth of three trees growing 1.3 to 1.6 m apart from each other was compared (Fig. 9). These three trees were estimated to have the same age, c. 7 years. The height growth of the two *C. peltata* individuals was very similar and did not seem to be reduced by their spatial proximity, since their growth dynamics were similar to those observed for other more distant *C. peltata* individuals (Fig. 9). During the first four years of development, the *M. cecropioides* tree was notably smaller than both of the *C. peltata* trees for the same age. However, later in development, during the fifth and the sixth year, the height gap between the trees narrowed. At the time of felling, all three trees were
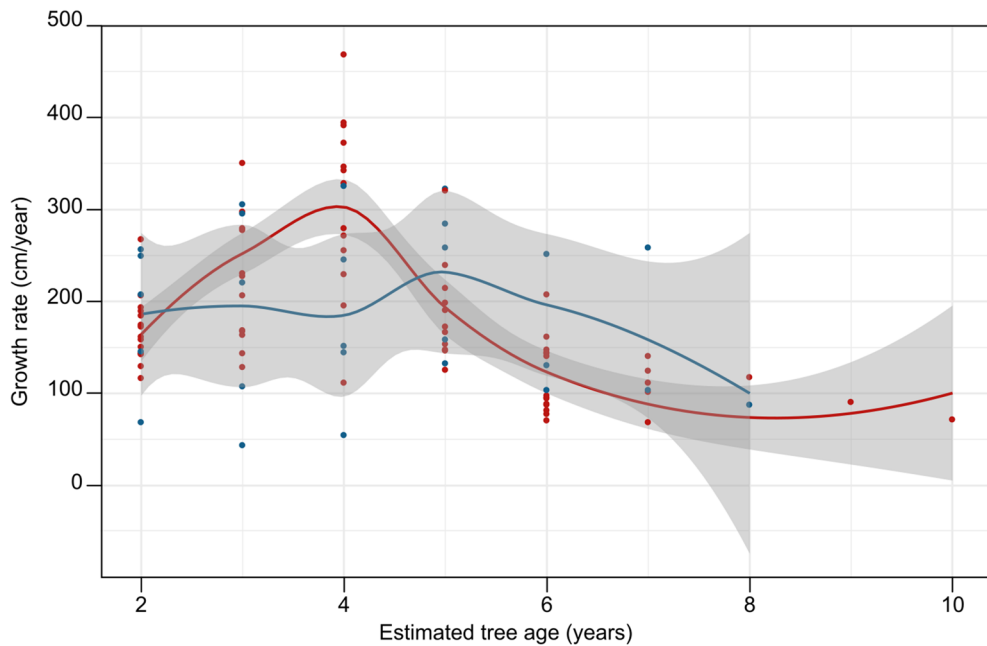
Fig. 7 Growth rates (cm per year) for *Cecropia peltata* (red) and *Musanga cecropioides* (blue) with their respective moving average. The shaded areas represent the 95% confidence intervals

Fig. 8 Cumulated trunk height through time for *Cecropia peltata* (a) and *Musanga cecropioides* (b) based on annual delimitations (previously defined for the estimation of the trees ages).

Growth trajectories shown in red are those of the two youngest trees (C7 and M3) issued from resprouting after being cut at their base

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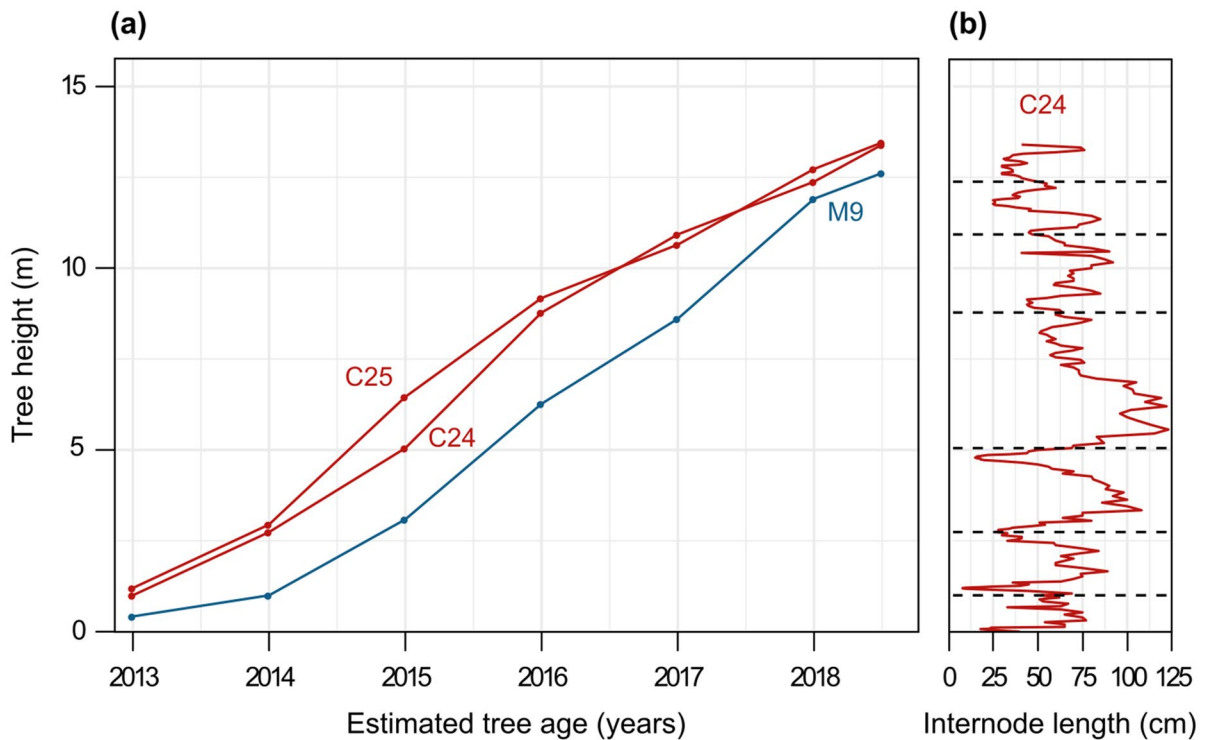
Fig. 9 **a** Accumulated trunk height on an annual basis for 3 individuals of *Cecropia peltata* (red) and *Musanga cecropioides* (blue) growing close to each other. **b** Residual sequence of internode length from the base to the top of the trunk for the *C. peltata* tree C24 with annual delimitation indicated by dotted black lines

at a similar height (12 m for *M. cecropioides* and about 13 m for the two *C. peltata*).

Discussion

In this study, we used plant architectural analysis to recreate past development histories for two co-occurring non-native and native tree species. This comparison provided insight into how specific life histories may influence outcomes of inter-species competition. The similarities between the two taxa (*C. peltata* and *M. cecropioides*), in terms of size, life form, life-history stages and taxonomic relatedness, offered a particularly interesting study model as it minimised the risk of bias in their response to competition (Vilà et al. 2004).

Quantifying the architectural development over time in *Cecropia* and *Musanga*

For Neotropical *Cecropia*, there are three interpretable morphological patterns (internode length, inflorescence scars, annual number of nodes) that can be used to delimit years of growth, and therefore, for understanding past development histories (Zalamea 2008, 2013, Levionnois et al. 2023). First, for *C. peltata* in Cameroon, only internode length, with short internodes corresponding to the dry season, was consistently informative. Second, and in contrast, inflorescence scars did not have a consistent pattern across individuals, suggesting both seasonal and continuous flowering. In other species of *Cecropia* in their native range, inflorescence scars are discretely located on a series of sequential internodes, separated by a series of internodes without scars, creating a distinct pattern of annual or biannual flowering (e.g. *C. obtusa*, *C. sciadophylla*; Heuret et al. 2002; Zalamea et al. 2008, 2011; Levionnois 2023). For other *Cecropia*

species, nodes bearing inflorescence scars are more or less continuous, suggesting year-round flowering (Zalamea et al. 2011). Third, the phyllochron was also variable within and between individuals, and therefore of diminished utility for understanding age. We were able to establish an annual node production rate of 35.7 ± 7 (corresponding to a phyllochron of 10.2 days), which is comparable to those observed in Amazonian *Cecropia* (c.10 days in *C. obtusa* and c.14 days in *C. sciadophylla*; Heuret et al. 2002; Zalamea et al. 2008, 2012; Levionnois 2023). Consequently, the age of an individual cannot be estimated as robustly as for other *Cecropia* species by simply counting the number of internodes on the trunk (Zalamea et al. 2012).

This greater variability in morphological patterns for non-native *C. peltata* in Cameroon may be explained by many factors. Environmental drivers, however, are known to influence growth patterns between regions (Zalamea et al. 2013). In the presumed native range of the *Cecropia* species introduced in Cameroon (supposed to be Jamaica, based on the absence of trichilia at the petiole base. For more information see Online Resource 2; Berg et al. 2005), there is a biennial pattern of precipitation (Zalamea et al. 2011). However, the region of invasion in Cameroon is known to be unimodal, corresponding to the African monsoon (Texier et al. 2018). The difference in rainfall patterns may explain the annual cycles of variation in internode length but does not explain the observed biennial pattern. Nevertheless, we successfully confirmed that the non-native *C. peltata* in Cameroon underwent predictable architectural development and highlighted the potential for broader applications of the retrospective developmental analysis method. Although it would be prudent to first test this method in other contexts, our findings suggest that the method could provide invaluable information for revealing the developmental histories of other *Cecropia* populations introduced to different parts of the world.

For the architecture of the native species, *M. cecropioides,* we found that it is similar to *C. peltata* in Cameroon and other *Cecropia* species in South America. The same three interpretable morphological patterns are present, but differ in their utility for reconstructing past architectural development. First, *M. cecropioides* still produces internodes of a predictably variable length that reflect seasonality,

which allowed for the estimation of growth over time. However, the nodes are fewer (but relatively longer) than *C. peltata*, meaning each node corresponds to a larger time unit, reducing the temporal resolution of this marker. Second, because *M. cecropioides* matures at a later stage, internode scars with flowers are absent during the early years of development and therefore cannot contribute to the understanding of annual growth cycles for younger individuals. Third, by using comparisons between interspecic pairs, we were able to show consistency in the annual node production among and between individuals (25.4 ± 8 nodes per year, corresponding to a phyllochron of 14.4 days). As with the non-native *C. peltata* individuals from this study, the phyllochron for *M. cecropioides* was more variable within and between individuals than is known for Amazonian *Cecropia* species (Heuret et al. 2002; Zalamea et al. 2008, 2012; Levionnois 2023). Taken together, the morphological patterns that can be interpreted for *M. cecropioides* have lower temporal resolution and ontogenetic coverage, making the identification of annual growth limits more challenging. For future work, we suggest that a focus on older individuals may help to generate more robust insight on morphological marker patterns for *M. cecropioides*.

In conclusion, our observations and analysis of native *M. cecropioides* in Cameroon revealed that this species exhibits morphological markers similar to those of *Cecropia* species (Zalamea 2008, 2013). This similarity not only enables the reconstruction of the historical developmental trajectory of *M. cecropioides* within its native habitat, but also allows a comparison of some performance aspects of its populations with those of non-native invasive populations, such as *C. peltata*. Nonetheless, it is worth noting that this species produces fewer internodes throughout its lifespan and exhibits later branching and flowering than *C. peltata* in Cameroon, making the analysis of growth markers for this species more challenging.

Comparison of performance-related traits

Given that both study species were suitable for quantifying architectural development over time, it was possible to use this method for understanding the dynamics of both native and non-native populations. Since the performance of a species in a particular ecological habitat is assessed by its ability

to grow, reproduce, and survive (Violle et al. 2007), we framed our assessment of competition dynamics between the two species, based on our architectural analysis, focusing on three components of individual performance.

Tree development and space occupation

Non-native species introduced to a new region can gain an inherent competitive advantage over native species arising from specific traits, such as a higher growth rate, a higher total height, or a greater lateral spread (Rejmanek and Richardson 1996; van Kleunen et al. 2010; Gioria and Osborne 2014). These traits can then provide the introduced species an advantage, such as a higher rate of resource acquisition or the ability to tolerate low resource availability (Gioria and Osborne 2014). Through reconstruction of historical tree growth, this study has shown that the non-native *C. peltata* shows a more sustained growth than *M. cecropioides* during its early years, and with a peak in growth rate occurring at a younger age. Together, these factors mean that *C. peltata* is taller than its native congener during the early stage of establishment and development. Moreover, it produces branches slightly before *M. cecropioides* (from four years old), leading to earlier crown formation and lateral expansion. These elements could provide the non-native species a superior ability to intercept light and, in turn, generate subsequent shading effects (Morris et al. 2002; Iponga et al. 2008; Hoyos et al. 2010; Gioria and Osborne 2014). Such overtopping would likely reduce the growth of shorter *M. cecropioides* individuals, owing to lower light levels and reduced space in which to establish a canopy.

Taking full advantage of a faster growth rate during seedling establishment would benefit from faster germination. While germination is known to be photoblastic in *Cecropia* (Vázquez-Yanes and Smith 1982; Baskin and Baskin 1998) and reasonably rapid in *C. peltata* (pers. obs.), not enough is known about germination rates for *M. cecropioides* to understand this component of inter-species competition. A final point worth noting is the significant difference in leaf production rates between the two species. Considering that the phyllochron is estimated to be 10.2 days for *C. peltata* and 14.4 days for *M. cecropioides*, new leaves are produced on a significantly more regular basis by the non-native species. Coupled with a higher branching intensity, this higher rate of leaf production could enable *C. peltata* to handle the impacts of leaf damage (e.g. foliar herbivory; Coley 1982) much better than the native species, providing an additional competitive advantage.

Reproduction

Our findings have shown, through the assumptions made about the annual delimitation of growth, that the non-native *C. peltata* reaches sexual maturity earlier than *M. cecropioides*, producing flowers from the age of five years. As for *M. cecropioides*, only one individual studied had flowered and was already seven years old. No other individual bore flowers, even those estimated to be eight and nine years old. Furthermore, because *C. peltata* has been shown to produce flowers on all its axes simultaneously once it is branched, the branching process directly affects the intensity of flowering. The earlier and more intense branching of *C. peltata*, in comparison to *M. cecropioides*, along with flowering occurring on all axes, provides it with the potential to produce significantly more fruits and seeds in a given period of time.

Compounding the competitive disadvantage of delayed maturity for *M. cecropioides* is the repeated and frequent clearing of vegetation to facilitate small-scale agriculture. In Cameroon, such clearings are becoming far more common and larger in size as closed forest canopy is degraded or cleared to make way for more managed landscapes. This disadvantage would worsen in these landscapes if the time between anthropogenic clearing decreases, because young trees will not have flowered before being cut again. In this context, *C. peltata* benefits from early flowering, allowing the production of seeds before the next clearing.

Taken together, this higher seed production for *C. peltata* could flood the surrounding landscape with increased propagule pressure, relative to the native *M. cecropioides*, enabling increases in abundance and range expansion. This outcome assumes dispersal vectors are foraging equally effectively on both species, which is likely to be the case, as fruits of both species are considered to be keystone food supply in the diet of many animals such as birds, bats and monkeys (McKey 1975; Berg et al. 2005). If our interpretation is correct, we predict that *C. peltata* should be able to replace *M. cecropioides* in rural and (sub)

urban areas but probably not in natural forest gaps, where achieving a large stature before reproduction may be more important for life-long reproductive success.

Mortality

With the architectural method used in this study we had access to only two aspects of tree performance: growth (including elongation of axes and branching) and reproduction. As the trees studied were adult individuals, having managed to survive a potential competitive pressure, we were not able to factor in any information on tree mortality at an early stage of development. A much lower relative density of *M. cecropioides* was observed across the study site, as well as on other disturbed roadside lands nearby (Fig. 1a). Taken together with the findings of our early year growth rates, these observations suggest that the establishment of *M. cecropioides* seedlings is not as successful as that of *C. peltata* in mixed stands and/or that mortality could have occurred among *M. cecropioides* seedlings, leading to the difference in density observed in larger trees.

Limitations and future directions

While the analysis of morphological markers has enabled us to make strong hypotheses on the growth, branching and reproductive phenology of the species studied, our findings stand to benefit considerably from four areas of further work. First, broader application of the morphological marker method in both species will no doubt reduce model uncertainty and enable a better understanding of intra-annual variability and the influence of seasonality on fluctuations in internode length (Zalamea et al. 2013). As our study was limited to a single site and on a relatively consistently aged stand, it would be valuable to undertake further work across sites with contrasting tree ages and a broader range of climates. Integrating stands of various ages would reveal how competition is expressed in the early stages of colonization and how mortality might differ within mixed age stands, while sites with contrasting climates would help to better understand the ontogenetic and phenotypic plasticity of these species and their interactions. It would be particularly interesting, for example, to study sites further south on the colonization front (e.g. towards

Déhané), which have a more pronounced seasonal climate (Texier et al. 2018).

Second, the germination and seedling stage is often critical for the success of invasive species. Early germination can significantly influence competitive interactions between native and non-native species (Wolkovich and Cleland 2011; Gioria and Pysek 2017) and non-native seedlings generally exhibit higher growth rates than co-occurring native species (Rejmánek and Richardson 1996; Raphael et al. 2015) and demonstrate a strong priority effect (Fukami 2015; Delory et al. 2019). Together, these traits could confer a competitive advantage. Because our study did not consider these early stages, confirmation of our hypotheses by growth monitoring is still necessary to tease out the competition dynamics from germination through to early-stage establishment to understand how *C. peltata* is apparently out-competing *M. cecropioides* in Cameroon (McKey 1988). Experimental plantings could also be used to assess competitive ability across a range of environmental conditions that reflect resource availability (Vilà and Weiner 2004; White et al. 2006).

Third, the formal identity of *Cecropia* populations introduced into Cameroon remains uncertain. While Limbe Botanic Gardens is mentioned as a likely introduction location (Berg et al. 1985), this material could have come from multiple sources, either directly or indirectly from the native range (Conn et al. 2012). A Jamaican provenance is mentioned because, like these native populations, the morphotypes from Cameroon lack trichilia (Berg et al. 2005), which is a key characteristic in species discrimination. Identifying the species identity and region of origin of introduced populations using a molecular approach would provide a better understanding of the fundamental ecology of the species, as well as its relationship to other introductions of *Cecropia* across western and central Africa.

Fourth, the fact that we were able to apply dendrochronological techniques developed in the native range for one genus to the non-native range and to another species bodes well for expanding this approach to recreating other invasion histories and past competition dynamics across the tropics and beyond in other tree species. Other studies have successfully used external morphological features to recreate growth histories for trees in both temperate and tropical environments (Martinez-Ramos

et al. 1988; Duarte et al. 1999; Charles-Dominique et al. 2009, 2012). Progress in this space would particularly benefit the management of invasions in less developed countries, where knowledge on the history of existing invasions is often limited, and where the resources and logistics to better understand them are even more constrained.

Conclusion

We have shown that dendrochronological techniques based on morphological markers are promising tools for evaluating the competition between co-occurring native *M. cecropioides* and non-native *C. peltata*. This method can highlight differences in performance, notably reproductive success and space occupation strategies, and therefore could help to disentangle the different mechanisms that determine performance, community assembly, and species coexistence across space and time (Barthélémy et Caraglio 2007; Charles-Dominique et al. 2009, 2012). Moreover, the approach does not rely on expensive equipment and can be used to recreate past insight that would otherwise be lost for poorly understood invasions. For Cameroon, a broader application of the technique across the currently invaded range of *C. peltata* may give insight into how to manipulate environments to tip the balance in favour of *M. cecropioides*. More broadly, with further application of the method to other invasions worldwide, we may have the ability to recreate tree invasion histories across many other ecosystems.

Declarations

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