No evidence for consistent long-term growth stimulation of 13 tropical tree species: results from tree-ring analysis

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Abstract

The important role of tropical forests in the global carbon cycle makes it imperative to assess changes in their carbon dynamics for accurate projections of future climate–vegetation feedbacks. Forest monitoring studies conducted over the past decades have found evidence for both increasing and decreasing growth rates of tropical forest trees. The limited duration of these studies restrained analyses to decadal scales, and it is still unclear whether growth changes occurred over longer time scales, as would be expected if CO_2-fertilization stimulated tree growth. Furthermore, studies have so far dealt with changes in biomass gain at forest-stand level, but insights into species-specific growth changes – that ultimately determine community-level responses – are lacking. Here, we analyse species-specific growth changes on a centennial scale, using growth data from tree-ring analysis for 13 tree species (~1300 trees), from three sites distributed across the tropics. We used an established (regional curve standardization) and a new (size-class isolation) growth-trend detection method and explicitly assessed the influence of biases on the trend detection. In addition, we assessed whether aggregated trends were present within and across study sites. We found evidence for decreasing growth rates over time for 8–10 species, whereas increases were noted for two species and one showed no trend. Additionally, we found evidence for weak aggregated growth decreases at the site in Thailand and when analysing all sites simultaneously. The observed growth reductions suggest deteriorating growth conditions, perhaps due to warming. However, other causes cannot be excluded, such as recovery from large-scale disturbances or changing forest dynamics. Our findings contrast growth patterns that would be expected if elevated CO_2 would stimulate tree growth. These results suggest that commonly assumed growth increases of tropical forests may not occur, which could lead to erroneous predictions of carbon dynamics of tropical forest under climate change.

Keywords: climate change, dendrochronology, growth trends, tree growth, tree-ring analysis, tropical forests

Introduction

Tropical forests form an important element of the global carbon cycle. While covering only 7% of the Earth's terrestrial surface, they are responsible for one-third of the terrestrial net primary production and store approximately 40% of all carbon in terrestrial vegetation (Houghton, 2005). Due to their high storage and processing of carbon, changes in net uptake or loss of carbon has large implications for the global carbon cycle (Pan *et al.*, 2011). Shifts in climate, in atmospheric CO_2 levels, or in nutrient depositions may influence growth and mortality rates of trees and alter the dynamics of tropical forests (Lewis *et al.*, 2009a; Alvarez-Clare *et al.*, 2013). For instance, decreases in growth rates have been interpreted to reflect the limiting effect of increased temperature on growth (Feeley *et al.*, 2007), while growth increases interpreted to reflect the stimulating effect of increasing CO_2 concentrations (e.g. Phillips *et al.*, 2008; Lewis *et al.*, 2009a).

Monitoring studies of permanent sample plots (PSP) have provided valuable insights into the growth and dynamics of tropical forests at stand level. Evidence on the climate sensitivity of forest growth in these plots (Clark *et al.*, 2010) has been used to explain changes in growth rates, dynamics and biomass accumulation (e.g. Phillips *et al.*, 2008; Murphy *et al.*, 2013). Yet, such community-level changes are generated by the aggregate responses of the tree species that make up the community. Species-specific responses may potentially change the tree community, and understanding stand-level changes thus requires knowledge on species-specific shifts in dynamics. The high species diversity of tropical forests has prevented species-level analyses to be

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conducted in the generally small-sized plots (Phillips *et al.*, 2008; Lewis *et al.*, 2009b). As a consequence, studies on species-level responses are sparse in the tropics (Feeley *et al.*, 2007).

Although PSP studies have provided valuable insights into changes in tropical forests, these studies are limited by their relative short duration compared with the time span of the changes that are assessed: gradual climatic changes or recovery of forests from disturbances (e.g. forest fires, hurricanes, wind blowdowns, etc.; Vlam, 2014) take place at the scale of multiple decades up to centuries. Growth trends detected from plot studies over relatively short time spans may thus reflect decadal fluctuations in climatic factors (e.g. temperature; Feeley *et al.*, 2007) or forest disturbance cycles (if plots are small; Chambers *et al.*, 2013). To improve the understanding of tropical forests' responses to climate change, there is a need for long-term approaches analysing growth changes.

Tree-ring analysis offers the opportunity to extend insights into growth changes of individual tree species to the scale of multiple decades to centuries. In temperate regions, tree-ring analysis has widely been used to assess effects of climate on tree growth and to analyse historical growth changes (e.g. Esper *et al.*, 2012; Villalba *et al.*, 2012). In the tropics, tree-ring analysis has only recently been applied to analyse changes in growth (Rozendaal *et al.*, 2010; Nock *et al.*, 2011). Tree-ring analysis usually provides growth data that go back to the establishment of trees and allows for species-level analyses of growth changes. It thus has a great potential to assess historical growth changes and to improve the understanding of how tropical forests react to climate change (Bowman *et al.*, 2013; Zuidema *et al.*, 2013). When working with tree-ring data, however, spurious growth trends may be induced by the chosen field sampling strategies (Nehrbass-Ahles *et al.*, 2014), by the choice of trend detection method (Peters *et al.*, 2015) or due to the nature of tree-ring data (cf. Brienen *et al.*, 2012a). It is thus imperative to use proper field sampling strategies in tree-ring studies, to choose a reliable trend detection method and to account for the possible influence of various biases on trend detection (Bowman *et al.*, 2013; Nehrbass-Ahles *et al.*, 2014) when evaluating long-term growth trends using tree rings.

Here, we use tree-ring analysis to assess long-term growth changes in tropical forest species. We sampled 1262 trees of 13 species from three tropical forests sites across the tropics: in Bolivia, Cameroon and Thailand. We addressed the following questions: (i) Are growth rates changing over time for our study species?; (ii) Is the detection of growth changes affected by biases?; and (iii) Do species from the same site and across sites show similar growth changes?

Growth data for the 13 species were obtained from tree-ring analysis, and growth trends were analysed for the last ~150 years. We applied a standardized sampling protocol in the three sites to avoid the influence of sampling strategy on the trend detection (Nehrbass-Ahles *et al.*, 2014). Additionally, to ensure robust trend detection, we applied two trend detection methods: an established and sensitive method and a new and rather conservative method (cf. Peters *et al.*, 2015). Finally, we explicitly evaluated the possible effects of trend detection biases (Brienen *et al.*, 2012a) on our results.

Material and methods

Study areas and sample collection

We sampled trees from undisturbed tropical forests located in the three continents: South America (in Bolivia), Africa (in Cameroon) and South-East Asia (in Thailand). In Bolivia, trees were collected in the 'La Chonta' logging concession, situated at 15.84°S, 62.85°W, ca. 300 km north-east of Santa Cruz de la Sierra. The vegetation at La Chonta consists of semi-deciduous moist forest, on the transition between dry-forest (Chiquitano) and moist Amazonian forests (Peña-Claros *et al.*, 2008). Precipitation in the region is unimodal, with an annual average of 1580 mm and a 4-month dry season (with <100 mm rainfall) from May to September. In Cameroon, samples were collected inside the Forest Management Unit 11.001 of the logging company Transformation REEF Cameroon (TRC, 2008). The area is situated at 5.23°N, 9.10°E, adjacent to the Korup National park in the south-west region. Vegetation consists of semi-deciduous lowland rainforest of the Guineo-Congolian type (Kenfack *et al.*, 2006). Precipitation is also unimodal, with average annual precipitation around 4100 mm (Nchanji & Plumptre, 2003) and a 3-month dry season from December to February. In Thailand, the study site was situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), situated at 15.60°N 99.20°E, around 250 km north-west of Bangkok. The vegetation in HKK consists of semi-deciduous moist forest (Bunyavejchewin *et al.*, 2009). Precipitation is unimodal, with an annual average of 1473 mm and a 4- to 6-month dry season from November to April.

At each study site, we sampled trees of four to five species (Fig. 1 and Table 1), selected based on the possession of clear annual growth rings and on their local abundance (i.e. relatively common species). Trees were sampled using a stratified random approach inside large areas (144–297 ha) of undisturbed forest, that is where no previous logging activities had taken place and not showing signs of major anthropogenic disturbances. At each large study area, we created a virtual grid of several 300 × 300 m cells, and at random coordinates inside each cell, we installed circular plots of ca. 1 ha (radius of ~56 m) that were located using a GPS device (Garmin GPS-map 60CSx). Inside these plots, all trees >5 cm diameter at breast height (dbh, at 130 cm height) of our target species were sampled. We installed 16–25 plots per study site, distributed across the entire area, to ensure sample sizes of around
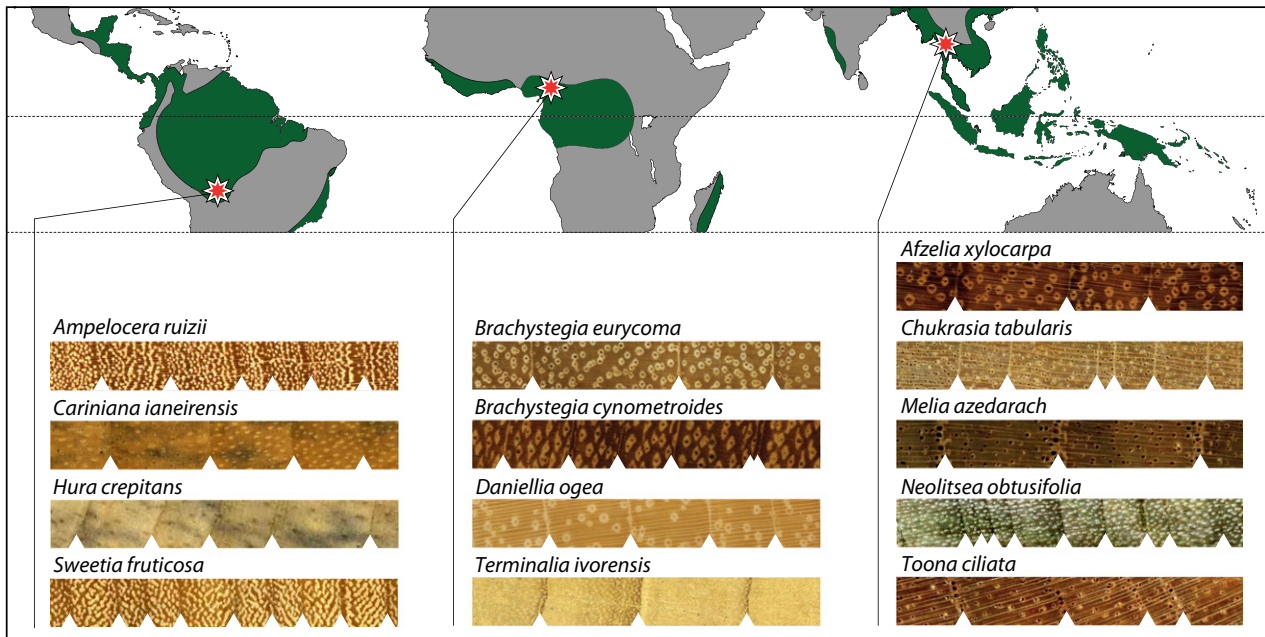
Fig. 1 Location of study areas and ring structures for the species studied. Wood samples were collected in wet tropical forests (green area; precipitation >1500 mm yr^{-1}) in three locations (red stars): in Bolivia at the La Chonta forest concession; in Cameroon in the TRC 11.001 logging concession, adjacent to Korup National park; and in Thailand in the Huai Kha Khaeng Wildlife Sanctuary. Growth-ring boundaries in the wood are indicated with white triangles.

Table 1 Characteristics of the 13 species studied, included are family, shade-tolerance guild (ST = shade-tolerant; PST = partial shade-tolerant; LLP = long-lived pioneer, definitions cf. Poorter *et al.* (2006); and leaf phenology (E, evergreen; D = deciduous; BD = brevi-deciduous)

County	Species	Family	Guild*	# Trees	Leaf phenology†	Annual rings
Bolivia	*Ampelocera ruizii*	Ulmaceae	ST	91	E	Lopez *et al.* (2012)
	Cariniana ianeirensis	Lecythidaceae	PST	102	D	Lopez *et al.* (2012)
	Hura crepitans	Euphorbiaceae	PST	95	D	Lopez *et al.* (2012)
	Sweetia fruticosa	Fabaceae	LLP	105	BD	Brienen & Zuidema (2003)
Cameroon	*Brachystegia cynometroides*	Fabaceae	PST	122	BD	Groenendijk *et al.* (2014)
	Brachystegia eurycoma	Fabaceae	PST	124	BD	Groenendijk *et al.* (2014)
	Daniellia ogea	Fabaceae	LLP	104	BD	Groenendijk *et al.* (2014)
	Terminalia ivorensis	Combretaceae	LLP	62	D	Détienne *et al.* (1998)
Thailand	*Afzelia xylocarpa*	Fabaceae	LLP	100	D	Vlam *et al.* (2014b)
	Chukrasia tabularis	Meliaceae	PST	104	BD	Vlam *et al.* (2014b)
	Melia azedarach	Meliaceae	LLP	89	D	Vlam *et al.* (2014b)
	Neolitsea obtusifolia	Lauraceae	ST	104	E	Vlam *et al.* (2014b)
	Toona ciliata	Meliaceae	LLP	61	D	Vlam *et al.* (2014b)

*Ecological Guilds: Bolivia (Peña-Claros *et al.*, 2008), Cameroon (Hawthorne, 1995), Thailand (Baker *et al.*, 2005); definitions cf. Poorter *et al.* (2006).
†Phenology: Bolivia (Mostacedo *et al.*, 2003), Cameroon (Hawthorne, 1995; Lemmens *et al.*, 2012), Thailand (Williams *et al.*, 2008).

100 trees per species (Table 1). We also collected samples outside the circular plots for some of the species, to include some large (and presumably old) trees or to ensure sample sizes, were reached. For two species in Cameroon – *Daniellia ogea* and *Terminalia ivorensis* – we also sampled trees outside the large study area to increase sample sizes.

In Bolivia and Cameroon, samples were collected inside logging concessions, allowing for the collection of stem discs for ~30% of the sampled trees. The remaining samples in Bolivia and Cameroon, and all samples from Thailand, were collected using 5-mm-diameter increment borers of different lengths (Suunto, Finland and Haglöf, Sweden) in three to four

directions per tree. All samples were taken at 1 m height or above buttresses or anomalies when present.

Ring measurements

Prior to measurements, samples were air-dried and either cut (Gärtner & Nievergelt, 2010) or polished to increase ring boundary visibility. Ring widths were measured using a LINTAB 6 measuring table and TSAPWin software (Rinntech, Heidelberg, Germany) or using high-resolution scans (1600–2400 dpi) and the WinDendro software (Regent Instruments, Quebec, Canada). Ring widths were measured in three to four different directions for each tree following standard dendrochronological approaches (for more details see Groenendijk et al., 2014; Vlam et al., 2014b). Finally, tree-ring width measurements were converted to cross-sectional area growth (basal area increment, BAI) as BAI is a meaningful expression of tree functioning, for example conducting xylem surface (e.g. Mendivelso et al., 2013; Sterck et al., 2014) and better represents a tree's biomass growth (henceforth the term tree growth refers to BAI).

The annual nature of ring formation has been previously demonstrated for the Bolivian species by Lopez et al. (2012). For the Cameroonian species, annuality of ring formation for T. ivorensis was established by Détienne et al. (1998) and for the remaining three species assessed through radiocarbon dating by Groenendijk et al. (2014). Two of the species – Brachystegia eurycoma and D. ogea – showed high-quality dating, while the third – Brachystegia cynometroides – showed some discrepancies in dating that lead to tree-age underestimations of about 10% (Groenendijk et al., 2014). For the species from Thailand, the annual character of ring formation was proven by Baker et al. (2005), and for the samples used here, Vlam et al. (2014b) confirmed annuality by building chronologies and analysing climate–growth relations (Table 1).

We checked the quality and dating of the tree-ring measurements by cross-dating the measured ring series within trees (i.e. among different radii) and among trees (i.e. among individuals). Cross-dating measurements within a tree ensure the same (amount of) rings are measured between the different radii of an individual and helps in identifying wedging rings (rings that merge on certain parts of the circumference of the tree) and 'false' ring structures (intra-annual growth variations). For nearly all 1262 measured trees, internal cross-dating proved successful, that is variation in ring width for the different radii within a tree-matched well, both visually and statistically. Successful cross-dating among individuals is a strong indication of the annual character of ring formation and provides a quality check of the measurements, for example by synchronizing individual measurements to the 'average' signal (i.e. the chronology). Cross-dating among individuals proved challenging, and we were only able to build chronologies for four Thai species (Vlam et al., 2014b) but not for the Bolivian and Cameroonian species (Groenendijk et al., 2014). Although dating mistakes were unavoidable, we believe that the quality of our measurements is high enough to address our (ecological) research questions (Van Der Sleen et al., 2015), as lacking chronologies does not mean dating accuracy is low (Fichtler et al., 2003; Groenendijk et al., 2014), and eventual

shifts in calendar year do not strongly affect trend detection (Van Der Sleen et al., 2015).

Growth trend detection methods

Detecting long-term growth changes in tree-ring data requires disentangling the age- or size-dependent trends in growth from long-term growth changes. Several methods have been developed for this purpose; however, the detection power and reliability of these methods vary (Peters et al., 2015) and method choice may affect the detection of trends. Here, we applied the well-established regional curve standardization (RCS) together with the less common size-class isolation (SCI) methods. The RCS was shown to have a high detection power and to be reliable when detecting long-term growth trends (Peters et al., 2015), whereas the SCI is a more conservative method when detecting trends (i.e. less sensitive), but analyses trends more directly using raw growth rates. These methods complement each other and combining them provides robust results when assessing growth changes (Peters et al., 2015).

In the RCS, an average ontogenetic growth trend for a species (the 'regional curve', the dashed line under 'Age/size correction'; Fig. 2) is calculated and individual tree-ring series are divided by this average curve (Briffa et al., 1992; Esper et al., 2003). The regional curve is usually calculated by aligning ring widths of all individuals to cambial age (i.e. age from the pith) and calculating the average expected growth for each age. For shade-tolerant species or for species showing periods of growth suppression (e.g. slow growth due to overshadowing), size rather than age is often a better indicator for an individual's ontogenetic stage (King et al., 2005; Nock et al., 2011). Several of our species were shade tolerant (Table 1) and all were present in closed canopy forests. Therefore, we calculated the regional curve using small diameter classes instead of age (the 'regional size curve'; cf. Bontemps & Esper, 2011). We used diameter classes of 0.5 cm and calculated average growth rates of all individuals in each class (with >10 individuals per class). To describe the relationship between tree size and growth rate (i.e. the 'regional curve'), we fitted nonlinear functions to the average growth rates per size class. For this purpose, we used four functions commonly applied to describe size-dependent growth of trees: Chapman-Richards, Hossfeld, Korf and Weibull (cf. Zeide, 1993). The function that best described the size – growth relationship for each species, that is the function with the lowest AIC value – was chosen to represent the regional curve. We then calculated residual growth rates for each individual tree by dividing each growth-year of an individual by the expected growth rate for its size. Finally, to ensure residuals were calculated for the same diameter classes as used for the calculation of the regional curve, we averaged (annual) residual growth rates within the same 0.5-cm-diameter classes.

In the size-class isolation, growth rates are compared inside the same size classes for extant small (and thus young) and extant large (thus old) trees (cf. Landis & Peart, 2005; Rozendaal et al., 2010). Growth rates of small trees are thus compared with growth rates of large trees when they were small (Fig. 2; and see Peters et al., 2015). The SCI assumes that
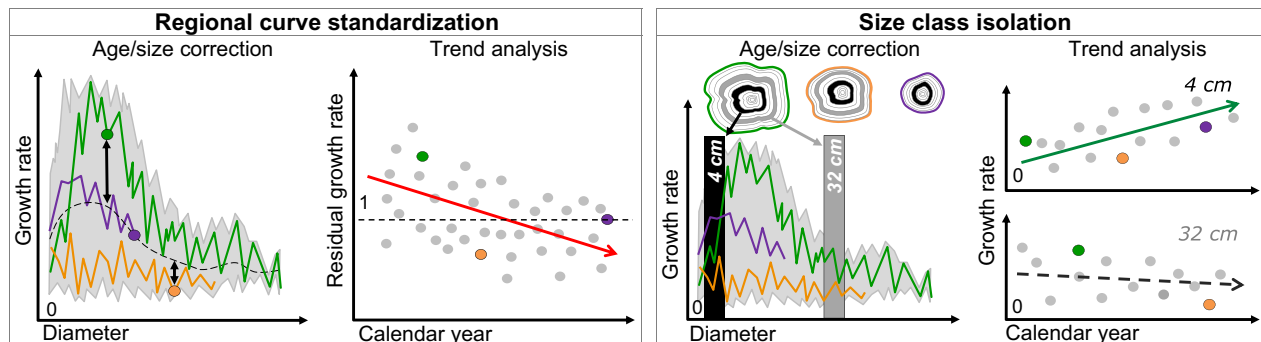
Fig. 2 Schematic overview of the application of the regional curve standardization (RCS) and size-class isolation (SCI) to disentangle age/size from long-term trends in tree growth. Left columns indicate how the age/size trend (i.e. the ontogenetic signal) is disentangled from long-term growth changes: for the RCS, by dividing individual growth curves by the average age/size trend (dashed line); for SCI, by analysing trends within size classes (e.g. in class 4 cm, black bar). The second column illustrates how trends are computed: on residual growth rates for the RCS and on raw rates for the SCI. See Material and methods section for more detailed explanation of the methods.

the age/size growth trend does not affect the detection of long-term trends if analysed within fixed size classes (i.e. within the same ontogenetic stage). We computed the SCI using 4-cm-diameter classes. To avoid the effect of single-year growth variation on the trend detection, we calculated growth rates as an average BAI of five rings: the year at which a tree reaches the diameter class (e.g. 4, 8, 12 cm; Fig. 2) and the two rings prior and after that year. Trends in the SCI are calculated over raw growth data (in BAI), making this method independent of decisions made during curve fitting procedures. However, due to its lower sample sizes (the unit of measurement is individual trees instead of individual rings), the power to detect trends using the SCI is lower than the RCS' (Peters *et al.*, 2015).

Analysis of species-level growth trends

We tested for long-term growth trends for each species using the RCS and the SCI. In the RCS, trends were analysed using linear and nonparametric tests. Linear trends were tested by computing Pearson's correlation coefficients (significance level $P < 0.05$) between log-transformed residual growth data and calendar year ('Trend analysis'; Fig. 2), whereas the nonparametric tests were performed using Spearman's rho on the untransformed RCS residuals (Appendix S1). In the SCI, for each species, we analysed trends for all size classes simultaneously using mixed-effect models, including 'calendar year' as fixed factor and 'size class' as random factor. We applied mixed-effect models with random intercept and with random intercept and slope and tested whether calendar year had a significant effect on the model. For each test, the most parsimonious model was chosen, that is the model yielding the lowest Akaike's information criteria (AIC), and we computed estimated *P*-values. For these analyses with mixed-effect models for SCI, we used the natural logarithm of the raw growth data, to normalize the data and stabilize residual variation.

For the species-specific analyses, we also calculated effect sizes of the detected trends. Effect sizes were expressed as the

relative linear growth change (expressed in % per decade). For the RCS trends, effect sizes were calculated as the slope of the residual growth data, and for the SCI trends, we calculated effect sizes per species as the average of all slopes detected for each size class divided by the average growth rate of that class (for more details see Appendix S2).

Testing for trend detection biases

When analysing growth trends using tree rings, it is imperative to account for several biases (Brienen *et al.*, 2012a; Nehrbass-Ahles *et al.*, 2014; Peters *et al.*, 2015). Two biases may have affected our results: the 'juvenile selection' bias (Rozendaal *et al.*, 2010; Van Der Sleen *et al.*, 2015) and the 'pre-death slow-growth' bias (Brienen *et al.*, 2012a), and we explicitly assessed the influence of these biases on the detection of trends in our data. The juvenile selection bias occurs if large canopy trees of today were relatively fast growing in the past, that is slow-growing juvenile trees have a lower chance to reach maturity than fast growers. This bias may lead to the detection of growth decreases over time, or may mask growth increases. To identify the presence of this bias, we performed the equivalent of a quantile regression on the 25% slowest and fastest growing juvenile trees (<20 cm dbh) for each species. The two quantiles, and their (differing) trends, provide additional information when interpreting the detected trends. The fastest growing juvenile trees in a population (i.e. the upper quantile) represent the (maximum) growth potential of a species, and a trend in this quantile may reflect changing growth conditions over time. The slowest growing juveniles (i.e. the lower quantile) can be used to assess the presence of the juvenile selection bias. A negative trend in the lower quantile indicates slow-growing individuals were selectively 'removed' from the population further back in time (see for more details Appendix S3).

To evaluate the effect of the predeath slow-growth bias, we re-analysed species-level trends after excluding the last 15 years of growth, that is the period over which we assume

this bias to take place (Wyckoff & Clark, 2002). If negative trends detected on all data disappear or become positive after the removal of the last 15 years, this indicates that the pre-death slow-growth bias may have influenced trend detection (see for more details Appendix S2).

Growth trends within and across sites

If growth changes are driven by a common external factor, we expect that all species of a site – or across sites – will show trends in the same direction. We used linear mixed-effect models to analyse aggregated trends in growth for all species from a site. In these models, we included 'calendar year' as fixed factor and 'species' as random factor. For the analysis of aggregated trends for all sites, we combined all data and analysed trends on a similar way as for the site-level analysis, but nested all random factors further inside 'site'. The natural logarithm of residual or raw growth data was used, to normalize data and stabilize variation. All linear mixed-effect models were tested with random intercept only and with random intercept and slope, and the most parsimonious model was chosen, that is the model yielding the lowest Akaike's information criteria (AIC). All analyses were performed in R (version 3.0.2; R Core Team, 2013), using the package NLME (Pinheiro *et al.*, 2015).

Results

Species-specific trends

We assessed long-term growth changes in tropical forests at three levels: at species level, site level and for all sites combined. In the species-level analysis using RCS, 12 of the 13 species showed significant changes in (log-transformed) growth rates over time and one species (*Afzelia xylocarpa*) showed no changes (Fig. 3). Two of these 12 species showed significant growth increases, whereas for 10 species growth rates decreased over time.

For the Bolivian species, we found growth decreases for three species (*Ampelocera ruizii, Cariniana ianeirensis* and *Sweetia fruticosa*) and an increase for one (*Hura crepitans*; Fig. 3). The Cameroonian species showed similar trends: growth decreases in three species (*B. eurycoma, B. cynometroides* and *T. ivorensis*) and a growth increases for one (*D. ogea*; Table 2). For the Thai species, growth decreases were found for four species (*Chukrasia tabularis, Melia azedarach, Neolitsea obtusifolia* and *Toona ciliata*) and no growth change for one (*A. xylocarpa*; Fig. 3). Results were similar when trends were computed on the raw residuals (i.e. not log transformed) using the nonparametric Spearman's rank correlation test (Fig. S1).

Detected trends using RCS ranged from significant to highly significant (*P*-values from ~0.02 to < 0.001, Table 2) and the period over which trends were assessed depended on the longevity of the species analysed and ranged from ~70 years (for e.g. *M. azedarach* and *A. ruizii*) up to ~250 years (e.g. for *D. ogea*, Table 2).

For the species-level analysis with SCI, we applied a linear mixed-effect model for each species with 'calendar year' as fixed and 'diameter category' as a random factor. SCI showed similar trends as the RCS, but with a lower detection power: trends detected for eight instead of 10 species (Table 2, Figs S2–S4). Only for one species – *A. ruizii* in Bolivia – did the detected trends not coincide: a growth decrease was found using RCS and an increase using SCI (Table 2).

Effect sizes of the detected trends (i.e. the % growth change per decade) varied among species and methods: using RCS, changes varied between a 8.8% growth reduction per decade and an increase of 2.2% (Table 2); and using SCI, changes varied between a 7.7% decrease and an increase of 7.3% per decade. For 12 of the 13 detected trends, effect size results were consistent between the two methods (Table 2; Fig. S5).

Analysis of biases

We assessed whether the juvenile selection bias affected the detection of trends by analysing trends on the slowest and fastest growth quantiles for juvenile trees (dbh <20 cm). For most species, the direction of the trends in the lower quantiles (Fig. 4; Table S1) was similar to those found when analysing all growth data (Table 2), indicating the juvenile selection bias does not have a strong effect on the trends detected. The only species that showed a possible effect of the juvenile selection bias was *A. xylocarpa* from Thailand. For this species, the lower quantile showed a negative trend, whereas trends were not significant in the upper quantile and in all data (Tables 2 and S1), indicating that slow-growing individuals were selectively removed from the data set further back in time. Additionally, for three species presenting growth reductions in the analysis of all data – *C. ianeirensis, T. ivorensis* and *Toona ciliata* – trends were not significant in the quantile analysis (Fig. 4).

To assess whether the 'predeath slow-growth' bias has influenced the species-level results, we re-analysed all growth trends after removing the last 15 years of growth (i.e. on years prior to 1985). Removing these growth years affected the detected trends for four species. For two species – *H. crepitans* in *T. ciliata* – trends disappeared, that is, changed from significant to non-significant (Fig. S7 and Table S2). For another two species – *S. fruticosa* and *M. azedarach* – trends changed from negative to positive (Fig. S7, Table S2), indicating a possible predeath slow-growth bias.
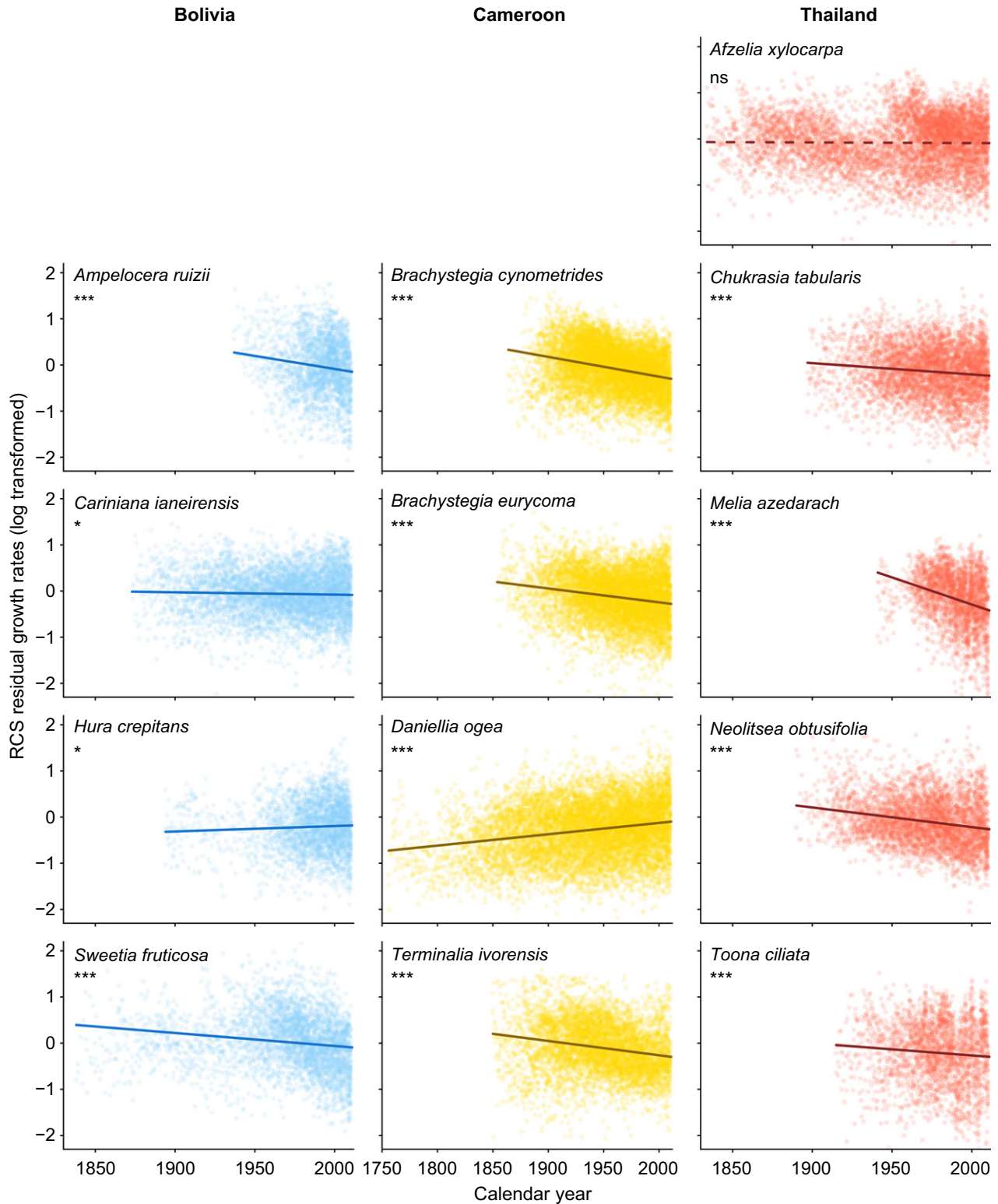
Fig. 3 Long-term trends in growth for 13 species from three tropical sites, using the regional curve standardization (RCS). Trends computed with Pearson's correlations between log-transformed standardized growth rates and against calendar year. Solid lines indicate significant trends in the quantiles, dashed lines nonsignificant trends. Significance levels: *$P < 0.05$; **$P < 0.01$; and ***$P < 0.001$. Note the varying *x*-axis. Nonparametric test of trends on the untransformed growth residuals is provided in Supplementary Materials, Appendix S1.

Table 2 Species-level analysis of long-term trends for the 13 tree species using regional curve standardization (RCS) and size-class isolation (SCI). Provided are the coefficient of the year effect in the linear (mixed-effect) models for each species, with significant trends highlighted in bold: red = growth decreases, green = growth increases; effect sizes for each species (as % growth change per decade); sample size (*n*); and period of analysis

Study site	Species	RCS year coefficient†	RCS effect size (%)	Sample size	Period of analysis	SCI year coefficient‡	SCI effect size (%)	Sample size	Period of analysis
Bolivia	*Ampelocera ruizii*	−0.134***	−7.2	2304	1937–2010	0.015***	7.3	341	1945–2009
	Cariniana ianeirensis	−0.033*	−0.5	5202	1874–2010	0.001	0.0	833	1876–2009
	Hura crepitans	0.049*	1.4	2725	1894–2010	0.002**	2.1	635	1856–2009
	Sweetia fruticosa	−0.160***	−3.2	3463	1838–2010	−0.001	−0.7	448	1802–2010
Cameroon	*Brachystegia cynometroides*	−0.269***	−4.9	8814	1864–2010	−0.008***	−7.7	1367	1870–2010
	Brachystegia eurycoma	−0.186***	−2.8	7761	1854–2010	−0.001*	1.7	1551	1857–2010
	Daniellia ogea	0.216***	2.2	9693	1756–2010	0.001***	1.4	1585	1749–2010
	Terminalia ivorensis	−0.205***	−3.8	5601	1850–2010	−0.003**	−3.3	1392	1838–2010
Thailand	*Afzelia xylocarpa*	−0.010	0.1	6427	1834–2010	0.000	0.0	1218	1826–2010
	Chukrasia tabularis	−0.109***	−2.1	4416	1897–2010	−0.001	−0.2	702	1835–2010
	Melia azedarach	−0.278***	−8.8	2619	1941–2010	−0.007***	−4.5	855	1894–2010
	Neolitsea obtusifolia	−0.214***	−4.2	3989	1890–2010	−0.002*	−1.9	515	1906–2010
	Toona ciliata	−0.081***	−1.6	2415	1915–2010	−0.001	−1.7	533	1864–2010

†RCS analysis: trends computed with Pearson's correlations of log-transformed standardized growth rates against calendar year. Nonparametric analysis of trends provided in Supporting Information.
‡SCI analysis: trends assessed with linear mixed-effect models on log-transformed basal area increment, with 'calendar year' as fixed factor and 'size class' as random factor. Significance of trends indicated as: *$P < 0.05$; **$P < 0.01$; and ***$P < 0.001$.

Aggregated growth trends per site

To identify whether aggregated growth trends were present per site, we analysed trends for all species in each site simultaneously. In Bolivia, species-level increases and decreases in growth were both detected. However, when simultaneously analysing trends for all species, using both the RCS as the SCI, we found no evidence for aggregated changes in growth rates for the species of the Bolivian site (i.e. no significant 'calendar year' effect in the linear mixed-effect model). Results for Cameroon were similar to the Bolivian results: although species-level growth trends were present, no aggregated trends were detected among the species using both detection methods. For Thailand, in four of the five species, we detected growth decreases. When analysing for aggregated trends for all Thai, the mixed-effect model using RCS showed a weak growth decrease over time (year effect = −0.0041, $P = 0.033$, $n = 19\,860$; Table 3). Although significant ($P < 0.05$), the model that included the year effect only differed slightly from the no-trend model in Akaike's information criterion (ΔAIC = 1.83) and this difference is thus inconclusive (cf. Burnham *et al.*, 2011; Murtaugh, 2014). The mixed-effect models using SCI did not detect significant trends when analysing all species of the Thai site simultaneously (Table 3).

Growth trends across sites

To assess whether a common factor (e.g. increasing temperatures, or CO_2 fertilization) is driving growth changes over all three research sites, we analysed growth changes for all species from all sites simultaneously. Using RCS and the linear mixed-effect model for all sites, we found a weak reduction in growth over time (year effect = −0.0027, $P = 0.005$, df = 65 415; Table 3). Again, the model including the year effect differed slightly from the no-trend model (ΔAIC = 2.80), indicating that the detected trend was weak (cf. Burnham *et al.*, 2011; Murtaugh, 2014). Furthermore, no trends were detected in the SCI mixed-effect model for all sites (Table 3), confirming that the growth reduction detected using RCS is weak, if at all present.

Discussion

This is one of the first studies to assess species-specific long-term growth trends in tropical forest trees. We assessed these changes using tree-ring data from three sites across the tropics and two trend detection methods. Of the 13 species analysed, 10 showed growth decreases over time, two showed growth increases and for one species no growth changes were detected. When analysing trends on site level, an aggregated
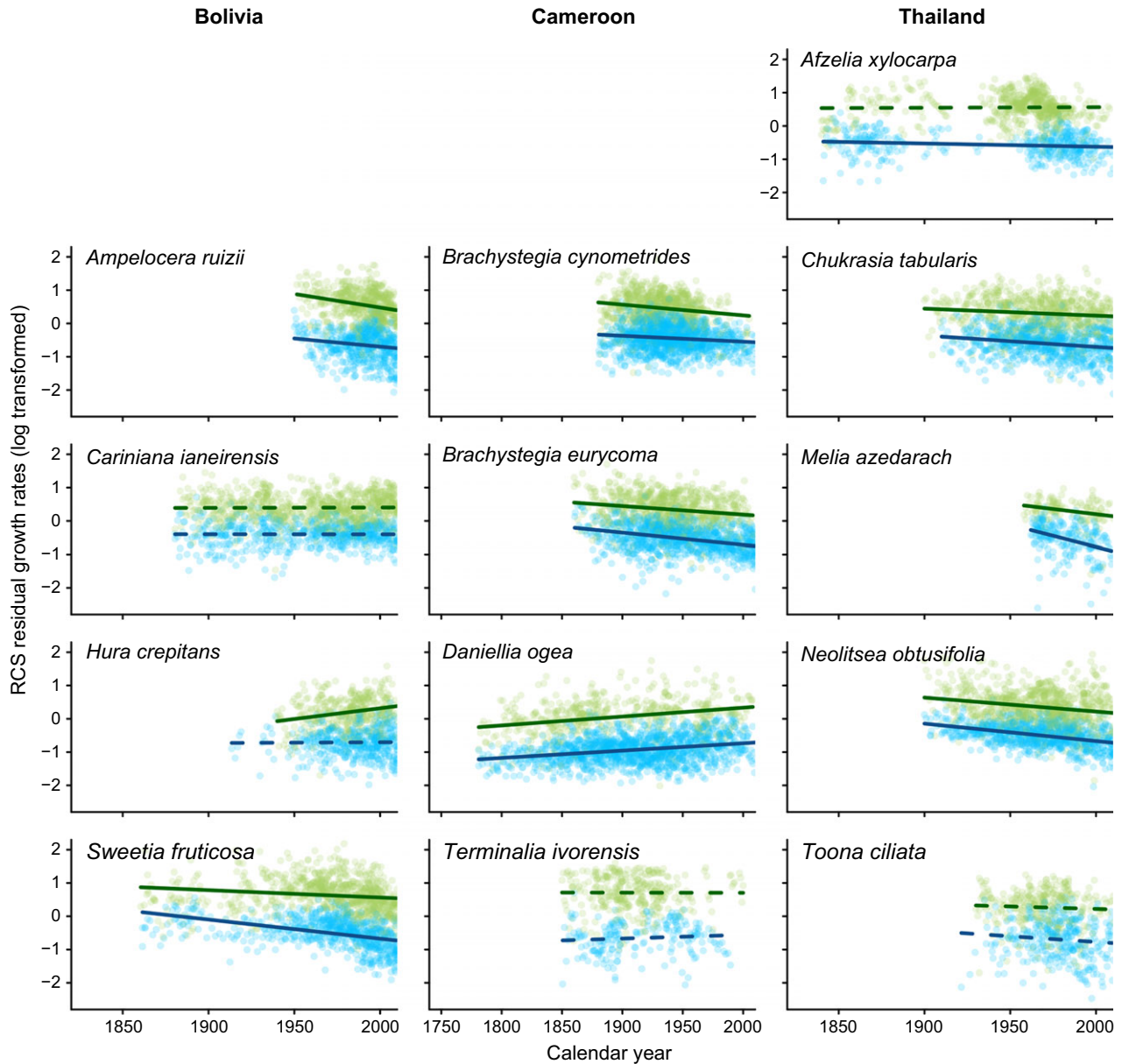
Fig. 4 Quantile regression of growth trends of juvenile individuals (< 20 cm dbh) for 13 tropical tree species from three tropical sites. Trends computed on the 25% fastest (green dots) and 25% slowest growers (blue dots) individuals to assess the effect of the juvenile selection bias (see Appendix S2). Trends computed using Pearson's correlations between growth rates (log transformed) and calendar year. Solid lines indicate significant trends in the quantiles (*P* < 0.05), and dashed lines nonsignificant trends. Evidence for a juvenile selection bias was only found for the Thai species *Afzelia xylocarpa*.

negative trend was found only for the trees from Thailand. Finally, we found an indication for a growth reduction over time when analysing trends for all species across the three sites.

Species-specific trends

For the majority of the tree species analysed here (12 of 13), growth rates have changed in the past 70–260 years

and for 10 species growth has declined over time (Fig. 3). The growth reductions found for many species suggest that growth conditions have become less favourable over time. Growth reductions have also been found in other studies, though for much shorter periods of time (Feeley *et al.*, 2007), or analysed using much smaller sample sizes of trees and species (Nock *et al.*, 2011). In these two studies, growth decreases were linked to increasing temperatures, which for

Table 3 Results for the analysis of aggregated trends per site and across sites for the regional curve standardization (RCS) and the size-class isolation (SCI) methods. We analysed temporal trends in growth using linear mixed-effect models, with 'calendar year' as fixed factor (effect year). In the analysis per site, 'species' were included as random effects in the RCS and 'diameter category' nested in 'species' for the SCI. For the analysis for all sites, these random factors were further nested in 'site'. Growth data were log-transformed to normalize variance

Detection method	Study site	Intercept	Effect year	Sample size	Period of analysis
RCS	Bolivia	−0.0326	−0.0018	13 694	1838–2010
	Cameroon	−0.1444	−0.0019	31 869	1756–2010
	Thailand	−0.0513	−0.0041*	19 866	1834–2010
	All sites	−0.0743	−0.0027**	65 429	1756–2010
SCI	Bolivia	3.1328	0.0037	2257	1802–2010
	Cameroon	3.9786	−0.0027	5895	1749–2010
	Thailand	3.1136	−0.0020	3823	1826–2010
	All sites	3.5853	−0.0008	11 975	1749–2010

Two-tailed significance indicated with *$P < 0.05$ and **$P < 0.01$.

tropical species may already be reaching values limiting for tree growth, especially during the hottest periods of the day (Doughty & Goulden, 2008).

That growth conditions may become less favourable is supported by the results of the quantile regressions (Fig. 4) that suggest a reduction in the growth potential of most species (i.e. negative trend in the upper quantile). These growth decreases could reflect temperature increases noted for the study sites (Molua & Lambi, 2006; Seiler *et al.*, 2013). Additionally, several species in Thailand and Cameroon show weak regeneration (i.e. an establishment failure) in the last 20–80 years (Vlam, 2014), which also suggest deteriorating growth conditions. Weak or failing regeneration is common in tropical forests (e.g. Poorter *et al.*, 1996; Groenendijk *et al.*, 2012; Newbery *et al.*, 2013; Vlam, 2014) and may indeed reflect changing or fluctuating climatic conditions (Vlam *et al.*, 2014a). Alternatively, lacking regeneration may be caused by (reduction in) human-induced disturbances (Pourtier, 1989; Oslisly *et al.*, 2013), by defaunation due to bush meat hunting (Abernethy *et al.*, 2013), may be a particular life-history strategy of a species (Newbery *et al.*, 2013) or be caused by (lacking) large-scale disturbances (Baker *et al.*, 2005). Lacking regeneration – or regeneration in pulses – may have large consequences for the detection of trends in studies based on tree-ring data (Vlam, 2014) as well as in studies based on permanent sample plots (Chazdon, 2003; Chave *et al.*, 2008; Muller-Landau, 2009). In tree-ring data, such age clustering may cause apparent growth decreases (conditions in the past better than conditions now), whereas in plot studies, age clustering may induce apparent increases in biomass, while growth rates may decrease. If regeneration only occurs after large-scale disturbances – which are rare in time – trends in growth may be apparent in plot data that are induced by the recovery of forests from these disturbances (Wagner *et al.*, 2010; Chambers *et al.*, 2013). Disentangling trends caused by changing regeneration conditions from long-term trends induced by climatic changes are very challenging, for both tree ring- and PSP-based studies. However, tree-ring analysis provides the distribution of tree ages in time, and the clustering thereof is a strong indicator for sporadic or pulse-like regeneration (Tolera *et al.*, 2013). Also, lacking regeneration does not necessarily mean a growth reduction: *D. ogea* showed a growth increase (Table 2) while lacking regeneration (Vlam, 2014).

Robustness of growth trends results

Detecting trends in tree growth is challenging, irrespective of working with growth data obtained from PSPs or from tree-ring measurements (Bowman *et al.*, 2013), and several biases may erroneously induce the detection of or mask growth trends. In PSP studies, these biases may be induced if plots have not been installed at random locations (Phillips *et al.*, 2004) or by the relatively small size of plots (Chambers *et al.*, 2013). For tree-ring studies, biases may be induced by sampling design (Nehrbass-Ahles *et al.*, 2014), by the choice of trend detection method (Peters *et al.*, 2015) or due to the nature of growth data (Brienen *et al.*, 2012a; Bowman *et al.*, 2013). As we sampled trees randomly in space and following their size distribution in the forest, biases caused by sampling design probably did not affect our results. To avoid the effect of method choice on the detection of trends, we applied two complementary growth trend detection methods, for a robust trend analysis (Peters *et al.*, 2015). Next, we will discuss the two biases that may have influenced the detection of trends.

The 'juvenile selection bias' may induce the detection of growth decreases over time or mask growth increases. We expected this bias to be present mostly for light-demanding tree species (e.g. the long-lived pioneers *M. azedarach* and *T. ivorensis*; Table 1) as young individuals of these species require high light conditions and fast growth to reach maturity. Yet, only for one species – *A. xylocarpa* – evidence was found that slow-growing juveniles in the distant past were 'removed' from the data set, that is the lower quantile showed a growth reduction (Fig. 4). This species, however, shows a spatial and temporal pattern in regeneration (Vlam *et al.*, 2014a), with two clusters of juvenile trees back in time (Fig. 4). These regeneration clusters may hamper assessing the effect of the juvenile selection bias on the trends. For most of the remaining species, growth trends in the upper quantiles were similar to the trends detected on all data, reinforcing the suggestion that these overall trends were caused by changing growth conditions and not by the juvenile selection bias.

To assess the presence of the 'predeath slow-growth' bias, we tested whether the removal of the last 15 years of growth caused a change in the detected trend. For only two species – *M. azedarach* and *S. fruticosa* – did this removal result in a change in trend consistent with this bias: trends changed from negative to positive after removing the last 15 growth years (Table S2). For these species, the predeath slow-growth bias may thus have induced the growth decreases detected prior to the removal of the last 15 years. However, due to the rather short lifespan of for *M. azedarach* (maximum ~60 years), sample size reduced considerably after removing the last 15 years of growth data (from 2619 to 942, Tables 2 and S2). Whether this inversion in the trend for *M. azedarach* was thus caused by the predeath slow-growth bias or due to the exclusion of a large part of the 'population' is difficult to ascertain. Individuals of *S. fruticosa* may indeed be showing a growth reduction induced by the predeath slow-growth bias. It is important to ascertain whether this bias takes place and to quantify its effect. Doing so requires either long-term monitoring of tree growth and mortality or the sampling and analysis of tree rings on dead trees, which is difficult in the tropics due to high decomposition rates.

Growth trends within and across sites

In the analysis of aggregated trends per site, only for the Thai site, we found evidence for consistent growth changes among different species. The lack in aggregated growth trends in Bolivia and Cameroon suggests that the growth changes detected for several species in these sites are not driven by a singular external factor. On the other hand, the aggregated negative trend found in the Thai site suggests declining growth conditions for all species. Such growth reductions were also found in a large-scale (50 ha) monitoring plot adjacent to our study site (Dong *et al.*, 2012) and using tree-ring analysis for three of the species also studied here: *Chukrasia tabularis*, *M. azedarach* and *T. ciliata* (Nock *et al.*, 2011), though for much smaller sample sizes (from 14 to 36 trees). These growth changes could be caused by an external factor (e.g. changing climate) or be driven by internal dynamics (e.g. disturbances). Growth of most Thai species analysed here is positively related to precipitation amount and negatively to temperature (Vlam *et al.*, 2014b). Rising temperatures and respiration costs, and more frequent El Niño-induced droughts may thus have caused the detected growth declines (Nock *et al.*, 2011). The hump-shaped age distributions found for many of the Thai species (Vlam, 2014) support the suggestion of deteriorating growth conditions in the more recent past (Vlam, 2014). On the other hand, there is evidence for large-scale disturbances in the study site ~250 years ago (Baker *et al.*, 2005). Forest recovery from such (large-scale) disturbances may thus still be driving the (aggregated) growth reduction detected, perhaps in combination with climatic changes. Unravelling the causes for these growth changes and assessing whether growth conditions have indeed changed is challenging and is hampered by the rather short time span covered by the measurements of tree growth in monitoring plots and by the short local climate record.

We found evidence for a growth reduction across all study sites. Although suggesting tropical forests tree growth has reduced in the past ~150 years, a significant trend was detected only by one of the methods (i.e. the RCS) and this trend was weak (ΔAIC = 2.8; cf. Burnham *et al.*, 2011). Irrespective of detecting a negative trend – or no trend at all – these results contrast strongly with the growth increases expected under a strong CO_2 fertilization effect (Lloyd & Farquhar, 2008), and with several studies that found decadal-scale increases in forest biomass (Phillips *et al.*, 2008; Lewis *et al.*, 2009b) and growth rates (Laurance *et al.*, 2004). Surprisingly, growth did not increase in spite of increases in intrinsic water-use efficiency over time being found in trees of 12 of our study species (Nock *et al.*, 2011; Van Der Sleen *et al.*, 2015a), suggesting that growth decreased while the photosynthetic efficiency of trees increased over time. On the other hand, tropical tree growth is sensitive to temperature (Clark *et al.*, 2010; Vlam *et al.*, 2014b) and increasing temperatures may have induced the detected growth decreases (Feeley *et al.*, 2007; Nock *et al.*, 2011). The effects of rising CO_2 concentrations and rising temperatures on growth could thus cancel each other out. Furthermore, the

suggested gains in photosynthesis due to the higher CO_2 levels may not be invested in stem growth, as diameter growth is low on the carbon allocation hierarchy of trees (Sala *et al.*, 2012; Richardson *et al.*, 2013). Alternatively, tree growth might not be carbon limited in tropical forests, with other nutrients limiting growth (e.g. phosphorus Lloyd *et al.*, 2001).

Implications and outlook

Tropical forests are as complex as the combination of all species and their interactions. Understanding how growth changes occur on the species level thus forms the basis to understand whether site or forest changes are taking place. We found species-level growth changes for most of the species analysed, but we also found that these changes were not necessarily reflected in the aggregated trends for the sites. That these results vary illustrates the importance of assessing trends on both the levels of species and communities.

Our results showed decreasing growth rates for most of the species analysed. These growth decreases may lead to shifts in competition between species, which may in turn lead to species shifts and to the dominance of more drought adapted species (e.g. if temperatures increase; Feeley *et al.*, 2011). These shifts may be already happening in tropical forests (Laurance *et al.*, 2004) as suggested by the lacking regeneration for many our study species (Vlam, 2014). When analysed for all species together, however, these trends were less pronounced, with only weak (i.e. nonconclusive) aggregated trends being detected. Still, these results contrast strongly with the increases in growth of tropical forest trees found in several studies (Laurance *et al.*, 2004; Lewis *et al.*, 2009a) and expected under CO_2 fertilization (Lloyd & Farquhar, 2008). If growth of tropical forest trees is indeed decreasing – or at least not changing – this will have large consequences for the projections of the carbon dynamics of tropical forests under increasing ambient CO_2 (Huntingford *et al.*, 2013). Currently, models used to predict vegetation development under changing climate (e.g. dynamic global vegetation models) usually assume a CO_2 fertilization on the growth of tropical forests (Sitch *et al.*, 2008; Huntingford *et al.*, 2013), with tropical forests predicted to act as carbon sinks in the coming century. This widespread assumption of CO_2 fertilization is controversial (Körner, 2009) and may not be valid for the species studied here (Van Der Sleen *et al.*, 2015a). Our results support the assumption that elevated ambient CO_2 does not directly lead to higher tree growth.

Detecting whether changes have or are taking place in tropical forest growth is challenging (Bowman *et al.*, 2013), and every method used to assess these changes – tree-ring analysis, monitoring plots, etc. – has limitations and biases (Phillips *et al.*, 2004; Brienen *et al.*, 2012a; Chambers *et al.*, 2013). Understanding the drivers of these changes is possibly even more challenging – and arguably even more important – than only detecting them. We argue that to know whether and why tropical forests are changing requires an integrative approach (Zuidema *et al.*, 2013) combining long-term growth data (from tree rings) with field measurements from monitoring plots; (e.g. Lewis *et al.*, 2009b), carbon flux estimates (e.g. Saleska *et al.*, 2003), and large-scale experimental studies (e.g. Nepstad *et al.*, 2007; Tollefson, 2013). Monitoring plots provide the most complete data on the dynamics and changes in tropical forests as they include growth, mortality and regeneration rates, and allow to assess changes in species composition (Laurance *et al.*, 2004). Carbon flux measurements provide large-scale estimates of the carbon dynamics and net primary productivity of forests (e.g. Saleska *et al.*, 2003; Gatti *et al.*, 2014), while large-scale experimental approaches allow to directly quantify the effects of (predicted) climatic changes on plant processes and growth (e.g. Nepstad *et al.*, 2007; Cavaleri *et al.*, 2015). The foreseen CO_2-enrichment experiment in the Amazon (Tollefson, 2013) will fulfil an important knowledge gap on topical forest responses to higher CO_2 concentrations. Tree-ring analysis can provide a long-term perspective to extrapolate results from these short-term measurements and experiments to the scale of centuries. Such integrative approaches have been applied in temperate forests (Girardin *et al.*, 2008; Babst *et al.*, 2014; Belmecheri *et al.*, 2014), but are still lacking in the tropics.

More tree-ring studies are needed in the tropics and many species throughout the tropics produce annual rings (Zuidema *et al.*, 2012). Tree-ring analysis provides the species-specific and long-term growth data necessary to assess changes in tree growth on relevant time scales. Standardized sampling protocols, analogous to the existing protocols for sampling plots (e.g. RAINFOR, AfriTRON, CTFS), would greatly increase the potential of using tree rings to detect and compare growth changes in forest trees worldwide. In the tropics, further studies should focus on widespread or dominant species (e.g. 'hyperdominant' species; Ter Steege *et al.*, 2013), of which many produce rings and that can be sampled in large numbers over large areas. Additionally, the analysis of stable isotopes in the tree rings provides additional information on both environmental (Fichtler *et al.*, 2010; Brienen *et al.*, 2012b; Van Der Sleen *et al.*, 2015b), and physiological processes (Nock *et al.*, 2011; Van Der Sleen *et al.*, 2015a) that drive tree growth. Integrated with other methods and combined with the analysis of stable isotopes, well-

designed tree-ring sampling can provide the missing and important long-term contextual information that is needed understand the effect of climatic changes on tropical tree growth.

Acknowledgements

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