Patterns of fruit production in tropical forests are shifting with negative outnumbering positive trends

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Summary

The impacts of climate change and anthropogenic disturbance are increasingly evident in the structure and demographics of tropical forests, yet the response of tree reproduction remains poorly understood. As fruit and seed production is the first step in forest recruitment, this gap is critical to understanding tropical forest resilience. Tropical fruits are important in diets of numerous frugivores and are essential resources for local human communities, thus changes in fruit quantity and composition could have cascading effects on ecosystems and the people who depend on them. In this study, we demonstrate that forest fruit production is shifting across tropical sites, with negative species-level trends occurring four times more frequently than positive ones across a network of 17 sites. Nevertheless, trends in fruit production are diverse across sites. While major spatial and temporal gaps in data coverage remain, by leveraging the expanding network of long-term monitoring, collaborative research has the potential to identify current trends in tropical fruit production and their drivers. This will enable robust predictions of future trends and advance our understanding of tropical forest vulnerability to environmental change.

Introduction

Tropical forests are under increasing pressure, with growing evidence of widespread changes in the structure and demographics of tropical forests, driven by climate change, logging and other land use change [1-3]. Syntheses have revealed pan-tropical forest trends, but these are strongly skewed to focus on growth, disturbance, and mortality dynamics [4-6]. However, tree reproduction—crucial as the first step to recruitment and determining the future composition and resilience of tropical forests—remains underexplored. Understanding how reproductive processes are changing, and the consequences for recruitment and forest dynamics is now an urgent priority.

Analysis of long-term phenology datasets has enabled substantial advances in understanding of the reproductive phenology of tropical forests, revealing the strong coupling of phenology and weather [7, 8]. Such links between weather and intra- and inter-annual variation in tree reproduction imply potential sensitivity of fruit production to climate change [9]. Direct mechanisms include weather-cued flowering and fruit maturation processes, while indirect drivers influence reproduction via underlying resource constraints [10]. For example, Numata et al. [11] showed that changes in the frequency of low-temperature flowering cues resulted in declines in flowering and fruiting in recent decades in Malaysia. Meanwhile, climate-driven changes in photosynthesis and productivity are proposed as mechanistic drivers explaining reported increases in flower production at Barro Colorado Island (BCI) in Panama [12, 13] and declines in flower production at Yasuní in Ecuador [10]. Despite wide recognition that these direct and indirect effects on flowering and fruit production are likely to affect tree reproduction in the tropics, no consistent picture has yet emerged of the response of forest tree reproduction.

Long-term shifts in fruit production will have important implications for regeneration dynamics in forests, to the extent that tree regeneration is limited by the production and dispersal of seeds [14-17]. Effects are likely to be particularly important in the recovery of disturbed forests [18, 19]. Changes in fruit production will also have wider cascading effects, as tree fruits are also a crucial food resource for forest food webs [20] and local human communities [21]. For example, when forest fruit production declines, the cascading effects on frugivores can be dramatic; an 81% long-term reduction in fruit production was linked with an 11% decline in forest elephant body condition in Lopé National Park [22]. Changes in fruit supply, both at the forest community level and via shifts associated with specific plant species, can also change frugivore behaviour, including foraging range or diet [20, 23]. They may also increase the risk of negative human-wildlife interactions where conflicts increase over fluctuating or declining resources [24-26].

Several studies have reported temporal trends in tropical forest reproduction (summarised in Table 1), often linking these trends to climate change. The effects, while species- and location-specific, consistently demonstrate strong associations between weather patterns and fruit production. For instance, numerous studies have linked long-term declines in fruit production with concurrent changes in climate. Bush et al. [22] and Lai et al. [27] documented declining fruit production over three decades in Gabon and Nigeria, which coincided with long-term warming and drying. Increases in fruit production were reported in Kibale National Park (Uganda), linked to increasing precipitation [28] although in Taï National Park (Côte d'Ivoire) an increase in community-level fruit production occurred alongside declining precipitation [29]. Similar declines in fruit or flower production have been observed in Puerto Rico [30] and Southeast Asia (Numata et al., 2022), and western Amazonia [10]. However, other studies indicate stable or gradually increasing trends in fruit or flower production [13, 31, 32]. While these findings suggest that declines in fruit production may be more common, particularly in response to climate change, it remains crucial to assess these trends on a larger scale to gain a clearer understanding of the broader impacts. A complementary focus on understanding the diversity in species-level trends will also shed light on the underlying drivers and likely consequences of changes in fruit production. For example, Zimmerman et al. [30] showed stronger declines in fruit production in large-stature trees in Puerto Rico and Potts et al. [33] linked shifts in fruit production to forest successional processes, while Bush et al. [22] showed fruit production declines were particularly steep in the species important in the diet of forest elephants.

Despite the ongoing uncertainty surrounding fruit production trends across tropical forests, the emergence of long-term datasets [e.g., 34, 35, 36] is beginning to illuminate these patterns. In this study, we synthesise recent data on tropical forest fruit production, integrating publicly available datasets with evidence from the published literature. Our goal is to uncover emerging regional trends and emphasise the growing potential for global research collaboration, which will enhance our ability to predict future trends in tropical forest reproduction.

Methods

Data

The analysis relies on MASTREE+, an open-access database of annual records of population-level reproductive effort for perennial plants [37]. We updated MASTREE+ to incorporate newly accessible datasets, increasing representation of tropical data (https://github.com/JJFoest/MASTREEplus/). Time-series were selected with a minimum of ten years of data from tropical latitudes (within 23.44° of the equator). We retained only records of seed or fruit production (i.e., excluding records of flowering effort, or related measures). Time-series based on ordinal assessments were excluded. The number of species represented at each of 17 sites varied from 1 to 224. Species were rarely replicated across sites; 423 species were represented at a single site, 15 species at two sites, and four species at three sites (total of 442 species, 465 time-series, Supplementary Information 1). Each species-specific time-series was scaled between 0 and 1, to facilitate direct comparisons among data collected via different methods [38, 39].

Species-level trends in fruit production

We ran a beta regression, with a logit link, for each species-specific time series by using seed production as response and year as a covariate. The use of beta regression allows us to perform a regression with our response based on values in a standard unit interval (0,1) [40]. We extracted the slope from the fitted beta regression, and used the slope to classify the trend in reproduction over time, either positive or negative, and the significance of the trend based on a p-value <0.05. We tested whether species-level trends were related to phylogeny, and species-level traits.

Of the 423 species included on our dataset, we extracted the phylogeny for 224 species from Zanne et al. [41] and tested for a phylogenetic signal in fruit production trend using Pagel's lambda [42], with values close to 0 indicating low phylogenetic signal and values close to 1 suggesting a phylogenetic correlation. We estimated the Pagel's lambda using the *phylosig* function from the R package phytools (v1.5) [43], and we plotted the phylogenetic tree with the ggtree package (v3.8) [44]

We extracted plant height and wood density from Díaz et al. [45] for a total of 154 plant species. We ran a phylogenetic regression between fruit production trend and functional traits (plant height and wood density) to account for species relatedness [46]. Functional traits were log10 transformed. We ran phylogenetic regression using the package phylolm (v2.6.2). Linear regression without phylogeny provided similar trends (Supplementary Information 2).

Analysis of community-level trends, integrating MASTREE+ and other reports

To estimate community-level trends in reproductive effort from each MASTREE+ site we ran a beta regression model at a site level and extracted the slope. The response in that model was fruit production and year was used as a predictor, while species was included as a random intercept for sites including multiple species. We classified trends as significant if the p-value was less than 0.05, and the direction of the trend (positive or negative) according to the slope value. To enhance geographical representation of trends, we combined these assessments with community-level trends reported in the literature (Table 1). Community-level trends were classified as positive, negative, or non-significant, following the analysis presented in the original source. This enabled us to add 8 additional sites to the 17 sites analysed using data from MASTREE+.

Results

Negative trends in reproduction were the most striking finding, occurring 4.2 times more frequently than positive trends in the species-level analysis, with 22% of species-site trends showing declines compared to just 5% showing increases (Figure 1). While species-level trends were variable within and among sites, the predominance of negative trends underscores a concerning pattern across the tropics. Negative trends dominated at two sites in West Africa: Lopé, Gabon (32/58 species, 55.2%) and Ngel Nyaki, Nigeria (20/37 species, 54.1%). Only a single species (*Massularia acuminata*) had a significantly positive trend at Lopé, and none at Ngel Nyaki. Negative trends were also more common than positive trends at BCI, Panama (20.1% v. 7.6%). Positive species-level trends did not dominate at any site represented by multiple species, but three well-replicated sites (Kanyawara, Uganda; Ranomafana, Madagascar; Mt Kinabalu, Malaysia) had approximately even proportions of positive and negative trends, and a dominance of non-significant trends.

Species-specific trends in reproduction were unrelated to phylogeny and did not correlate with plant height or wood density (Figure 2). It was notable that many species with the strongest declines in fruit production at Ngel Nyaki are associated with savannah habitats (e.g., *Maesa lanceolata*, *Psychotria succulenta,Trema orientalis*). These species have small fleshy fruits and are key species for passive restoration in these Afromontane forests [47]. Other species with declining fruit production include understory forest species (e.g., *Zanthoxylum leprieurii*, *Voacanga bracteata, Garcinia smeathmanii). G. smeathmanii* is the most abundant species in Ngel Nyaki forest (Abiem *et al*. 2020) and produces abundant large fleshy fruits. Another notable species with declining fruit production is *Anthonotha noldeae*, whose superabundant immature fruits are a key food of the primates tantalus (*Chlorocebus tantalus tantalus*) and putty-nosed monkey (*Cercopithecus nictitans*), and the Olive pigeon (*Columba arquatrix*). Similarly, at Lopé twelve out of twenty fruit trees identified as important in the forest elephant diet showed a significant decline at the species-level in our analysis, including highly favoured elephant foods such as *Sacoglottis gabonensis*, *Tetrapleura tetrapetra and Bobgunnia fistuloides* for which elephants are the major (or only) seed dispersers. Species with highly unusual fruiting patterns also feature in the list of significantly declining fruiting species at Lopé, such as *Duboscia macrocarpa* which on average exhibits an 18-month fruiting cycle at the individual-level [48].

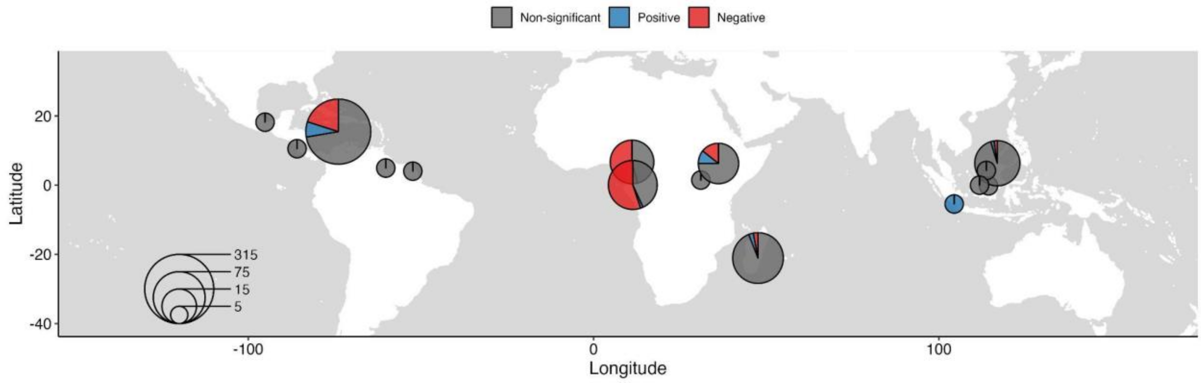

Figure 1: Species-level trends in tropical seed and fruit production. Each point represents a site in the MASTREE+ dataset (n = 17 sites), with point size proportional to the number of species. Wedges in the pie chart correspond to the distribution of non-significant, positive, and negative species-specific trends. The three sites on Mt Kinabalu, Malaysia have the same coordinates but different elevations; they are combined for this plot, but underlying data is reported in Supplementary Information 1.

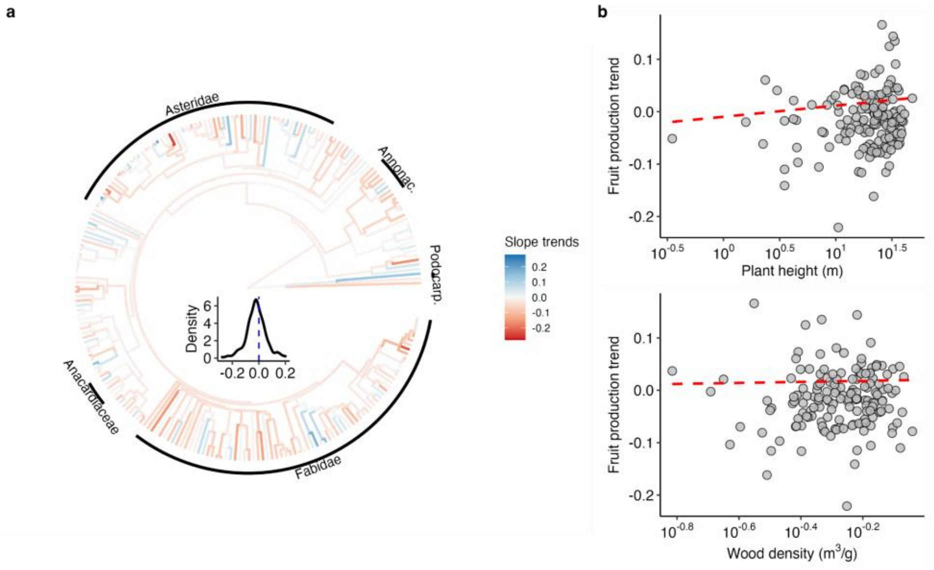

Figure 2: Species-specific trends in seed and fruit production according to phylogeny and traits. a) Absence of phylogenetic signal on seed production trends (Pagel's λ = 7.33e-05, p-value = 1, n = 224 species). b) Phylogenetic regression analysis includes fruit production trends as response and wood density and plant height as covariate (N = 154 species, adjusted R^2 = 0.002). The red dashed line represents non-significant relationships. Model coefficients and summary are reported in Supplementary Information 2. Regression without phylogeny provided similar results (see Supplementary Information 2).

Community-level fruit production trends reveal a complex regional pattern of decline and variability. The species-level trends at Lopé and Ngel Nyaki in West Africa translated into negative trends in community-level reproduction, indicating a significant decline in fruit production in recent decades (Figure 3). This contrasted with positive trends in fruit production reported at Taï National Park, Côte d'Ivoire, although this site had a shorter record. The Neotropics presented a diverse regional picture: multidecadal records from BCI and Luquillo (Puerto Rico) showed negative trends, while positive trends were found in the 34-year record from Altos de Pipe (Venezuela) and the shorter record from La Selva (Costa Rica). Other sites in the Neotropics exhibited non-significant trends, which were mostly based on shorter time-series (Figure 3). In Indomalaya, the multidecadal record from Forest Research Institute Malaysia (FRIM), Kepong (Malaysia) showed a long-term decline in fruit production, while a positive trend was found in the shorter record from Way Canguk (Indonesia). Other sites showed non-significant trends, including in the high, medium and low elevation plots at Mt. Kinabalu (Malaysia). It is important to note that data from Indomalaya did not extend into the most recent decade, leaving recent trends unexplored.

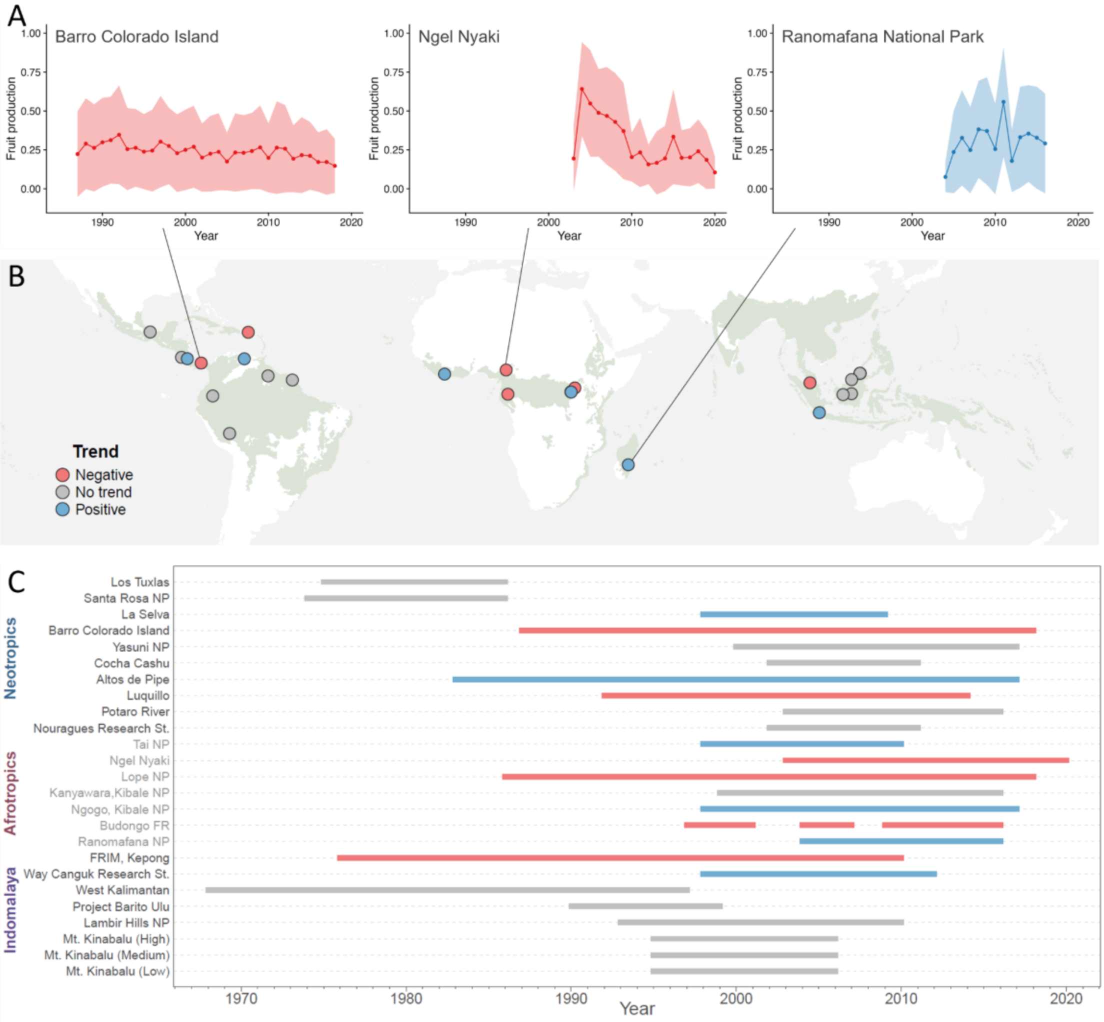

Figure 3. Trends in tropical community-level fruit or seed production. Site-specific fruit or seed trends are based on literature reports or community-level trends from the MASTREE+ database (see Table 1). The top panels show community-level trends in fruit production at three example sites. Middle panel shows the distribution of trends across tropical regions. The background map shows the spatial distribution of moist tropical or subtropical forest, from the WWF Terrestrial Ecoregions classification (based on Olson et al., 2001). The bottom panel shows the duration of each study and the trend, with sites ordered by longitude.

Table 1: Community-level tropical forest fruit & seed production trends.

1) Location	2) Study Period	3) Monitored organ	4) Trend reported in original study	5) Trend calculated from MASTREE+	6) Reference
Los Tuxlas, Mexico	1975-1986	Fruit		0	[49]
Santa Rosa National Park, Costa Rica	1974-1986	Fruit		0	[50]
La Selva, Costa Rica	1998-2009	Fruit + flower	+1		[31]
Barro Colorado Island, Panama	1987-2003	Fruit	0	-1 (1988-2018)	[51]
	1987-2014	Fruit	-1		[52]
Yasuni National Park, Ecuador	2000-2017	Seed	0*		[32]
Cocha Cashu Biological Station, Peru	2002-2011	Seed	0*		[32]
Altos de Pipe, Venezuela	1983-2017	Fruit	+1		[53]
Luquillo Experimental Forest, Puerto Rico	1992-2014	Fruit	-1		[30]
Potaro River, Guyana	2003-2016	Seed		0	[54]
Nouragues Research Station, French Guiana	2002-2010	Fruit		0	[55]
Taï National Park, Côte d'Ivoire	1998-2010	Fruit	+1		[29]
Ngel Nyaki, Nigeria	2003-2021	Fruit	-1	-1	[27]
Lopé National Park, Gabon	1988-2018	Fruit	-1	-1	[22]
Kibale National Park, multiple sites, Uganda	1990-2002	Fruit	+1	0 (1999-2016)	[28]
Kanyawara,Kibale National Park, Uganda	1998-2013	Fruit	0*		[56]
Ngogo, Kibale National Park, Uganda	1998-2017	Fruit	+1**		[33]
Budongo Forest Reserve, Uganda	1993-2016 (discontinuous)	Fruit	-1		[57]
Ranomafana National Park, Madagascar	2004-2016	Fruit		+1	[58]
Forest Research Institute Malaysia (FRIM) Arboretum, Malaysia	1976-2010	Fruit	-1		[11]
Way Canguk Research Station, Indonesia	1998-2012	Fruit†		1	[59]
West Kalimantan, Indonesia	1968-1997	Fruit†		0	[60]
Project Barito Ulu, Indonesia	1990-1999	Fruit†		0	[61]
Lambir Hills National Park, CBP, Malaysia	1993-2010	Fruit†		0	[62]
Mt. Kinabalu (Low), Malaysia	1995-2006	Fruit		0	[63]
Mt. Kinabalu (Medium), Malaysia	1995-2006	Fruit		0	[63]
Mt. Kinabalu (High), Malaysia	1995-2006	Fruit		0	[63]

Where only the community-level trend from the original source is reported, data is not available in MASTREE+. Where community-level trends are available from the original study and from MASTREE+, both are reported. Where the timespan of data in MASTREE+ is different from the original study, years are given in parentheses in the 5th column.

*Based on the presented figure, no formal analysis reported

**Decline since 2008

†Data recorded in MASTREE+ at genus or family level only

Discussion

Pan-tropical and regional picture of trends in fruit production

The community-level fruit production trends across tropical sites are variable, yet a concerning pattern of decline emerges from several long-term monitoring datasets, including those from Lopé and Ngel Nyaki in West Africa, BCI and Luquillo in the Neotropics, and FRIM in Indomalaya. While shorter records (<20 years) predominantly show non-significant trends, these findings are limited by their duration, and many could be updated if ongoing monitoring data were incorporated. Notably, less than half of the 25 sites in our synthesis include data from the most recent decade, and this data gap is particularly evident in Indomalaya. There is an urgent need for collaborative efforts to update and integrate these records, as well as to expand monitoring to additional tropical locations [64]. The African Phenology Network offers a valuable model for achieving this [34], which would lead to substantial advances in our understanding of current trends in tropical fruit production, and the broader implications for tropical forest ecosystems.

Species-level trends in fruit production

Community-level trends provided a high-level perspective of trends in tropical fruit production and enabled us to expand the scope of our assessment by including trends from many study sites not included in the MASTREE+ database. Nevertheless, community-level analysis may mask important ecological changes represented by species-level shifts in reproductive performance. The record from Kanyawara (Kibale National Park, Uganda) showed no overall community-level trend, but this could hide ecologically important shifts given that equal numbers of species showed positive and negative trends at this site. For example, Zimmermann et al. [30] reported stronger declines in large-stature trees (a trend we did not detect in our analysis, Figure 2B), while Babweteera et al. [57] reported divergence in trends between species with different life-history strategies. Such analysis might help identify the drivers of changes in reproduction, e.g. the role of successional change [33]. Species-specific, rather than community-level trends may also dictate the wider impact of changes in seed and fruit production on frugivores [22]. At both Ngel Nyaki and Lopé, species known to be important food sources for frugivores showed significant declines in fruit production, and at Lopé these changes have already been identified as a likely cause of declining forest elephant body condition [22]. Impacts of declining fruit production on complex plant-frugivore interactions could be profound and have cascading effects on tropical forest functioning [65, 66].

Unravelling the mechanisms that determine fruit production

Our results, in combination with recent efforts to synthesise tropical phenology records (e.g. African Phenology Network) show the potential for data synthesis to identify regional trends in tropical forest reproduction. For example, while we found negative trends in two West African tropical forests (Figure 1), these sites vary in climate and species composition, so simple extrapolation to infer regional trends is likely misleading. This risk is well illustrated by contrasting fruit production trends reported at Ngogo and Kanyawara, two sites in Kibale National Park, Uganda, separated by ~10km [discussed in 33]. Consequently, to understand the diversity within and between sites indicated in our analysis, and to enable prediction of future trends in tropical fruit production, we urgently need to improve understanding of the mechanisms that regulate tropical tree reproduction [7, 11, 56, 67]. These advances will come from fine-scale climate monitoring coupled with detailed phenological observations to identify the cues for flowering and fruit maturation, and the underlying drivers of allocation to reproduction. Advances will benefit from combining traditional visual phenology assessments with molecular phenology [67]. Ideally, this monitoring will be coupled with manipulation experiments [68]. A key objective will be distinguishing the roles of resource acquisition as a driver of reproduction [10, 13], and weather cues that regulate dynamic allocation to reproduction [7, 34]. The potential role of pollinator network disruption and other interactions also remains poorly understood [69].

Establishing species-specific mechanisms will enable the identification of species whose reproduction is most at risk from climate change [9], and may shed light on the diversity of species-level trends we found over recent decades [see also 27]. For example, species with strongly seasonal or supra-annual reproduction [e.g. 34], governed by weather cues, might show divergent climate-driven trends from species with less variable reproduction where fruit production responses might mirror productivity trends (i.e. resource matching). Where cues are important regulators of reproduction, the response of species will also vary depending on the nature of the cue [9]. For example, Numata et al [11] showed that across 98 Dipterocarp species, more than 50% may use cool temperature cues for flowering, making these species more vulnerable to climate warming compared to the species that use only drought for the initiation for reproduction.

Shortcomings of our analysis

The number of studies reporting long-term observations of tropical forest reproduction is growing but remains small. We attempted to synthesise available data and reported results, but important gaps and limitations remain, particularly due to the heterogeneity of fruit production monitoring methods. For example, our data is based on collection methods that include fruit counts on individual trees, assessments of the proportions of individual trees fruiting [e.g. 33], or fruit counts from litter traps. These methods may not be easily comparable [70]. Rare species are likely under-sampled, especially where estimates are based on litter traps, or where sampling has focused on species important to frugivore diets [33, 64]. In our analysis of community-trends, all species were equally weighted, but community-level trends may be determined by the response of dominant species. Wider ecosystem responses may also depend on trends in specific species, e.g., the response of palatable species [22]. Further, we used data on annual fruit or seed production, but the timing of fruit production is highly variable between and among tropical sites, and shifting in the timing of fruit production might have substantial ecological effects even in the absence of change in overall quantity [21, 71].

Conclusion

Detecting the drivers and long-term trends in tropical fruit production is challenging, but emerging data are beginning to shed light on these patterns [64]. Our findings reveal a concerning prevalence of negative trends in tropical forest reproduction, with 4.2-times more species showing declines than increases in fruit production, although negative species-level trends were unevenly distributed among sites. These changes could have profound ecosystem consequences, underscoring the urgency of expanding monitoring efforts. Including additional data from phenological studies will be important for identifying regional trends and understanding their underlying drivers. Enhancing our mechanistic understanding of fruit production is now a priority. This will aid in attributing current trends and in forecasting the potential impacts of climate change on tropical forests, including in forests where fruit production is not monitored. Progress requires a comprehensive analysis of flowering and fruiting phenology, including molecular approaches, to identify the cues that drive the timing and magnitude of reproductive efforts and the factors that influence the transition from flowers to ripe fruit. Given the evidence of climate-driven shifts in tropical forest productivity, disturbance, and mortality, understanding the response of seed and fruit reproduction must become central to studies of forest dynamics.

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Author contribution statement

Conceptualization: AH-P
Methodology: all authors
Formal Analysis: AH-P, VJ
Writing – Original Draft: all authors
Writing – Review & Editing: all authors
Visualization: AH-P, VJ

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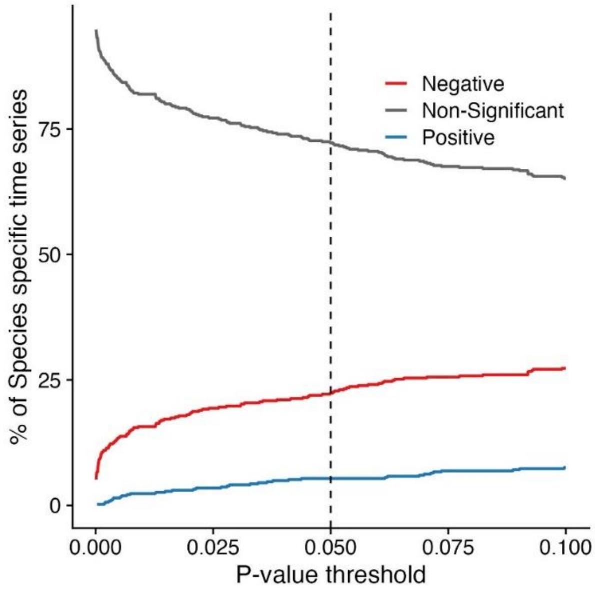
Supplementary Information

Supplementary Information 1: Site and species information, including species-specific trends in annual fruit production. Hacket-Pain_species_trends_tropical_fruit_production.csv

Supplementary Information 2: Phylogenetic and linear regression with fruit production trends as the response (ie the slope) and plant height and wood density as covariates. Plant height and wood density were log10 transformed in the analysis.

	Phylogenetic regression			Linear regression		
Coefficient	Estimates	Conf. Int (95%)	P-Value	Estimates	Conf. Int (95%)	P-Value
Intercept	-0.01	-0.09 – 0.08	0.871	-0.04	-0.08 – -0.00	0.043
Plant height	0.02	-0.01 – 0.05	0.132	0.02	-0.01 – 0.05	0.126
Wood density	0.01	-0.06 – 0.08	0.791	0.02	-0.05 – 0.08	0.588
Nb. of species	154			182		
R^2 / R^2 adjusted	0.015 / 0.002			0.014 / 0.003		

Supplementary Information 3: Proportion changes in the classification of trends of species specific-time series related to the p-value threshold used to assess statistical significance. In the main text we reported trends based on a p-value threshold at 0.05 (dashed line).



Supplementary Information 4. A list of 20 important fruiting tree species for forest elephants at Lopé National Park (Memiaghe, 2023)

Fruiting tree species	Families
Baillonella toxisperma	Sapotaceae
Bobgunnia fistuloides	Fabaceae
Detarium macrocarpum	Fabaceae
Duboscia macrocarpa	Malvaceae
Irvingia gabonensis	Irvigiaceae
Nauclea diderrichii	Rubiaceae
Sacoglottis gabonensis	Humiriaceae
Uapaca guineensis	Phyllanthaceae
Antidesma vogelianum	Euphorbiaceae
Chrysophyllus africanum	Sapotaceae
Klainedoxa gabonensis	Irvigiaceae
Mammea africana	Calophyllaceae
Massularia acuminata	Rubiceae
Myrianthus arboreus	Urticaceae
Omphalocarpum procerum	Sapotaceae
Panda oleosa	Pandaceae
Pentadesma butyracea	Clusiaceae
Psidium guineense	Myrtaceae
Tetrapleura tetraptera	Fabaceae
Uvariastrum pierreanum	Annonaceae