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

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Abstract

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 a key 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 production 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 declining species-level trends occurring four times more frequently than increasing ones across a network of 17 sites. At two sites in west Africa, community-level fruit production has declined by 25% and 52% in recent decades, and fruit production is declining several sites in the Neotropics. Nevertheless, trends in fruit production are diverse across sites, and drivers of changes remain unidentified. While major spatial and temporal gaps in data coverage remain, by leveraging the expanding network of long-term monitoring, collaborative research can 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. If the trends reported persist, they could induce important alteration in forest dynamics, impacting structural integrity, ecosystem functioning and species composition.

Key Words

Reproduction
Seed production
Climate change
Forest demography
Plant reproduction
Long-term data
Fruit availability
Phenology

Introduction

Tropical forests are under increasing pressure, with growing evidence of widespread changes in composition, structure and demographics driven by climate change, logging and other land use change (Lewis et al., 2004, Pisl et al., 2024, Hartmann et al., 2022). Syntheses have revealed pan-tropical forest trends in demography, but these are strongly skewed to focus on growth, disturbance, and mortality dynamics (McDowell et al., 2020, Bauman et al., 2022, Hubau et al., 2020). However, tree reproduction—crucial as the first step to recruitment and determining the future composition and resilience of tropical forests—remains underexplored (Vleminckx et al., 2025). Understanding how reproductive processes are changing, their drivers, 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 strong coupling with weather (Sullivan et al., 2024, Mendoza et al., 2017). Such links between weather and intra- and inter-annual variation in tree reproduction imply potential sensitivity of fruit production to climate change (Bogdziewicz et al., 2024). Direct mechanisms include weather-cued flowering and fruit maturation processes, while indirect drivers influence reproduction via underlying resource constraints (Vleminckx et al., 2024). For example, Numata et al. (2022) 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 (Pau et al., 2013, Pau et al., 2018) and declines in flower production at Yasuní in Ecuador (Vleminckx et al., 2024). 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. Such response will reflect species-specific climate sensitivities, forest composition, underlying climate limitations and regional climate trends (Vleminckx et al., 2025), plus the effects of forest successional change and other long-term forest dynamics (Potts et al., 2020).

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 (De Steven and Wright, 2002, Connell and Green, 2000, Wright et al., 2005, Norden et al., 2007). Effects are likely to be particularly important in the recovery of disturbed or degraded forests (Qiu et al., 2022, Wijdeven and Kuzee, 2000). Forest restoration is a global priority, and high potential for natural regeneration in the tropics was recently identified (Williams et al., 2024) but this requires sufficient seed supply (Chazdon and Guariguata, 2016, Ferragutti et al., 2025). Changes in fruit production will also have wider cascading effects, as tree fruits are also a crucial resource for forest food webs (Matthews et al., 2019) and local human communities (Staggemeier et al., 2017). 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 (Bush et al., 2020). 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 (Matthews et al., 2019, Reyna-Hurtado et al., 2018). They may also increase the risk of negative human-wildlife interactions where conflicts increase over fluctuating or declining resources (Memiaghe, 2023, Naughton-Treves et al., 1998, Ngama et al., 2019).

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. (2020) and Lai et al. (2025) 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 (Chapman et al., 2005) although in Taï National Park (Côte d'Ivoire) an increase in community-level fruit production occurred alongside declining precipitation (Polansky and Boesch, 2013). Declines in fruit or flower production have been observed in Puerto Rico (Zimmerman et al., 2018) and Southeast Asia (Numata et al., 2022), and western Amazonia (Vleminckx et al., 2024). However, other studies indicate stable or gradually increasing trends in fruit or flower production (Clark et al., 2013a, Pau et al., 2018, Pak et al., 2023). 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. (2018) showed stronger declines in fruit production in large-stature trees in Puerto Rico and Potts et al. (2020) linked shifts in fruit production to forest successional processes, while Bush et al. (2020) 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., Adamescu et al., 2018, Detto et al., 2018, Okimat et al., 2024) is beginning to illuminate these patterns. In this study, we assess 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 (Hacket-Pain et al., 2022). Most species in MASTREE+ are trees, but shrubs and lianas are included. We updated MASTREE+ to incorporate newly accessible datasets, increasing representation of tropical data. Time-series were selected with a minimum of ten years of data, from tropical latitudes (within 23.44° of the equator), and we only retained records of seed or fruit production (i.e., excluding records of flowering effort, or related measures). 17 sites were selected, represented by 1 to 224 species (Table 1). In a small number of cases data was recorded at the genus level. Data was collected using a diverse range of monitoring methods, including litter traps to quantify fruit production (number, mass), ground-based fruit counts, and fruit phenological monitoring observations (Table 1). The number of monitored individuals of each species also varied, but only species with >5 recorded individuals were retained in MASTREE+. Each species-specific time-series was scaled between 0 and 1, to facilitate direct comparisons among data collected via different methods (Journé et al., 2023, Journe et al., 2024). Consequently, analysis was focused on temporal trends in fruit production, as the diverse collection methods did not allow comparison of fruit productivity among species or sites (Journe et al., 2022).

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 (as our response had values in a standard unit interval (0,1)) (Cribari-Neto and Zeileis, 2010) with a logit link. 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 extracted site-level trends, and classified them as significant if the p-value was less than 0.05. 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+. Given the lack of replication across sites, in this analysis we were unable to control for the effects of varied tree reproduction monitoring methods (Table 1).

Species-level trends in fruit production

To investigate species-level trends, we also 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. We extracted the slope from the fitted beta regression and used the slope to classify the trend in reproduction over time, 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. (2014) and tested for a phylogenetic signal in fruit production trend using Pagel's lambda (Pagel, 1999), 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) (Revell, 2012), and plotted the phylogenetic tree with the ggtree package (v3.8) (Xu et al., 2022). To test the generality of plant stature-dependent trends in fruit production reported at Luquillo (Zimmerman et al., 2018), we extracted plant height from Díaz et al. (2022) for 154 plant species. We also tested for association with wood density extracted from Díaz et al. (2022). We ran a phylogenetic regression between fruit production trend and functional traits (plant height and wood density) to account for species relatedness (Revell, 2010), using the package phylolm (v2.6.2). Functional traits were log10 transformed. Linear regression without phylogeny provided similar trends (Supplementary Information 2).

Results

Community-level fruit production trends reveal a complex regional pattern of decline and variability. We found negative community-level trends at Lopé and Ngel Nyaki in West Africa, indicating a significant decline in fruit production in recent decades (Figure 1). In Lopé, community-level fruit production declined by 26% from 1980 to 2018, while at Ngel Nyaki it declined by 52% from 2003 to 2021 (Figure 1). 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, but multidecadal records from BCI, Luquillo and Yasuní all showed negative trends, while positive trends were found in the 34-year record from Altos de Pipe and the shorter record from La Selva. Other sites in the Neotropics exhibited non-significant trends, mostly based on shorter time-series (Figure 1). In Indomalaya, the multidecadal record from the Forest Research Institute Malaysia (FRIM) in 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.

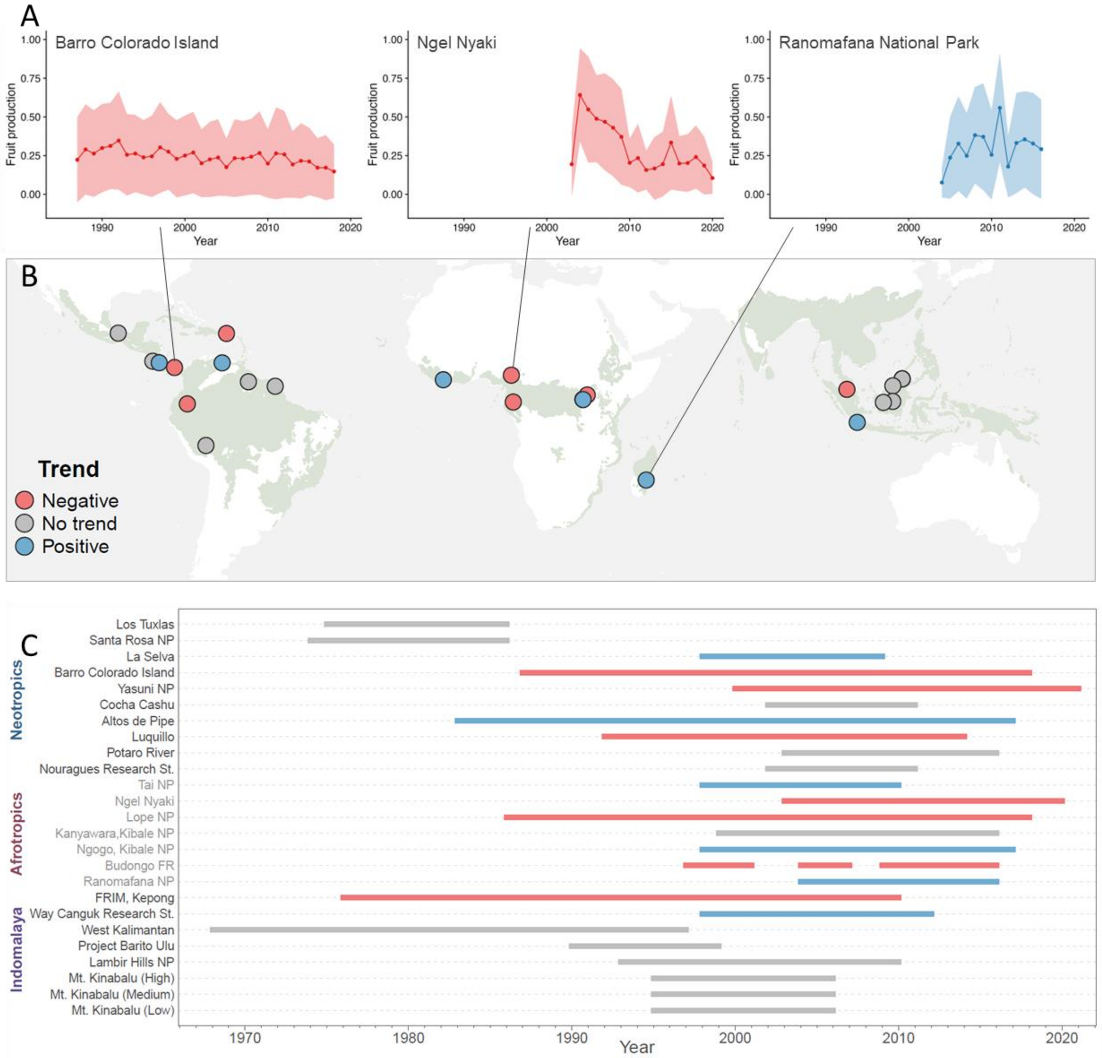

Figure 1. Trends in tropical community-level fruit or seed production. Site-specific fruit or seed trends are based on literature reports or community-level trends from the MASTREE+ database (see Table 1). The top panels show community-level trends in fruit production at three example sites. Middle panel 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. Information on the monitoring approach for each study and the trends in the original study (6) and in the analysis of MASTREE+ data (7) are report (+ = positive trend, 0 = no trend, -1 = negative trend). Sites are ordered by longitude.

1) Location	2) Study Period	3) Monitored organ	4) Monitoring method	5) Original unit of measurement	6) Trend reported in original study	7) Trend calculated from MASTREE+	8) Number of species	9) Reference
Los Tuxlas, Mexico	1975-1986	Fruit	Fruit count	Fruit/individual		0	1	(Martínez-Ramos et al., 1988)
Santa Rosa National Park, Costa Rica	1974-1986	Fruit	Fruit count	Fruit/individual		0	1	(Janzen, 1989)
La Selva, Costa Rica	1998-2009	Fruit + flower	Litter trap	Mg ha^{-1} y^{-1}	+1		>200	(Clark et al., 2013b)
Barro Colorado Island, Panama	1987-2003	Fruit	Litter trap	g m^{-2} y^{-1}	0	-1 (1988-2018)	289	(Wright and Calderón, 2006)
	1987-2014	Fruit	Litter trap	g m^{-2} y^{-1}	-1			(Alfaro-Sánchez et al., 2017)
Yasuní National Park, Ecuador	2000-2017	Seed	Litter trap	seeds m^{-2}	0*		1059	(Pak et al., 2023)
	2000-2021	Seed	Litter trap	seed mass m^{-2}	-1		203	(Vleminckx et al., 2025)
Cocha Cashu Biological Station, Peru	2002-2011	Seed	Litter trap	seeds m^{-2}	0*		654	(Pak et al., 2023)
Altos de Pipe, Venezuela	1983-2017	Fruit	Phenology scoring	Fraction of individuals fruiting	+1		15	(Flores et al., 2023)
Luquillo Experimental Forest, Puerto Rico	1992-2014	Seed	Litter traps	seeds m^{-2}	-1		76	(Zimmerman et al., 2018)
Potaro River, Guyana	2003-2016	Seed	Litter traps	kg ha^{-1} y^{-1}		0	1	(Henkel and Mayor, 2019)
Nouragues Research Station, French Guiana	2002-2010	Fruit	Litter traps	seeds m^{-2}		0	41	(Mendoza et al., 2018)
Taï National Park, Côte d'Ivoire	1998-2010	Fruit	Phenology scoring	Fraction of individuals fruiting	+1		44	(Polansky and Boesch, 2013)
Ngel Nyaki, Nigeria	2003-2021	Fruit	Phenology scoring	Fruit index	-1	-1	37	(Lai et al., 2025)
Lopé National Park, Gabon	1988-2018	Fruit	Phenology scoring	Fruit index	-1	-1	67	(Bush et al., 2020)
Kibale National Park, multiple sites, Uganda	1990-2002	Fruit	Phenology scoring	Fraction of individuals fruiting	+1	0 (1999-2016)	30	(Chapman et al., 2005)
Kanyawara,Kibale National Park, Uganda	1998-2013	Fruit	Phenology scoring	Fraction of individuals fruiting	0*			(Chapman et al., 2018)
Ngogo, Kibale National Park, Uganda	1998-2017	Fruit	Phenology scoring	Fraction of individuals fruiting	+1**		20	(Potts et al., 2020)
Budongo Forest Reserve, Uganda	1993-2016 (discontinuous)	Fruit	Phenology scoring	Fraction of species fruiting	-1		125	(Babweteera et al., 2018)
Ranomafana National Park, Madagascar	2004-2016	Fruit	Phenology scoring	Fruit index		+1	67	(Dunham et al., 2018)
Forest Research Institute Malaysia (FRIM) Arboretum, Kepong, Malaysia	1976-2010	Fruit	Phenology scoring	Fraction of species fruiting	-1		210	(Numata et al., 2022)
Way Canguk Research Station, Indonesia	1998-2012	Fruit[†]	Phenology scoring	Fraction of species fruiting		1	NA[†]	(Winarni et al., 2016)

West Kalimantan, Indonesia	1968-1997	Fruit[†]	Seed harvest	kg		0	NA[†]	(Curran and Leighton, 2000)
Project Barito Ulu, Indonesia	1990-1999	Fruit[†]	Phenology scoring	Fraction of individuals fruiting		0	NA[†]	(Brearley et al., 2007)
Lambir Hills National Park, CBP, Malaysia	1993-2010	Fruit[†]	Phenology scoring	Fraction of individuals fruiting		0	NA[†]	(Sakai and Itioka, 2016)
Mt. Kinabalu (Low), Malaysia	1995-2006	Fruit	Litter trap	g m^{-2} y^{-1}		0	19	(Tsujii et al., 2023)
Mt. Kinabalu (Medium), Malaysia	1995-2006	Fruit	Litter trap	g m^{-2} y^{-1}		0	13	(Tsujii et al., 2023)
Mt. Kinabalu (High), Malaysia	1995-2006	Fruit	Litter trap	g m^{-2} y^{-1}		0	10	(Tsujii et al., 2023)

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 7th column.

*Based on the presented figure, no formal analysis reported. Yasuní results superseded by Vleminckx et al (2025) showing a decline in fruit production.

**Decline since 2008

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

For the subset of sites where species-level data was available in MASTREE+, significant negative trends in reproduction occurred 4.2 times more frequently than significant positive trends in the species-level analysis. 22% of species-site trends showed declines compared to 5% showing increases (Figure 2). Declines, estimated as percentage declines per decade, were ≥20% per decade for 13% species-sites, and ≥10% per decade for 31% species-sites. Positive trends were less common (increases ≥20% and ≥10% per decade occurred for 6% and 16% of species-sites, respectively) (Figure 2). While species-level trends were variable within and among sites, and majority of species had non-significant trends, declining trends predominated relative to increasing trends. Negative trends dominated among species at two sites in West Africa: Lopé, Gabon (32/58 species, 55.2% significantly negative) 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. Species-level negative trends were also more common than positive trends at BCI, Panama (20.1% v. 7.6%), where 13 species had fruit production declines equivalent to >20% per decade. 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. Across the dataset, species-specific trends in reproduction were unrelated to phylogeny and did not correlate with plant height or wood density (Figure 3).

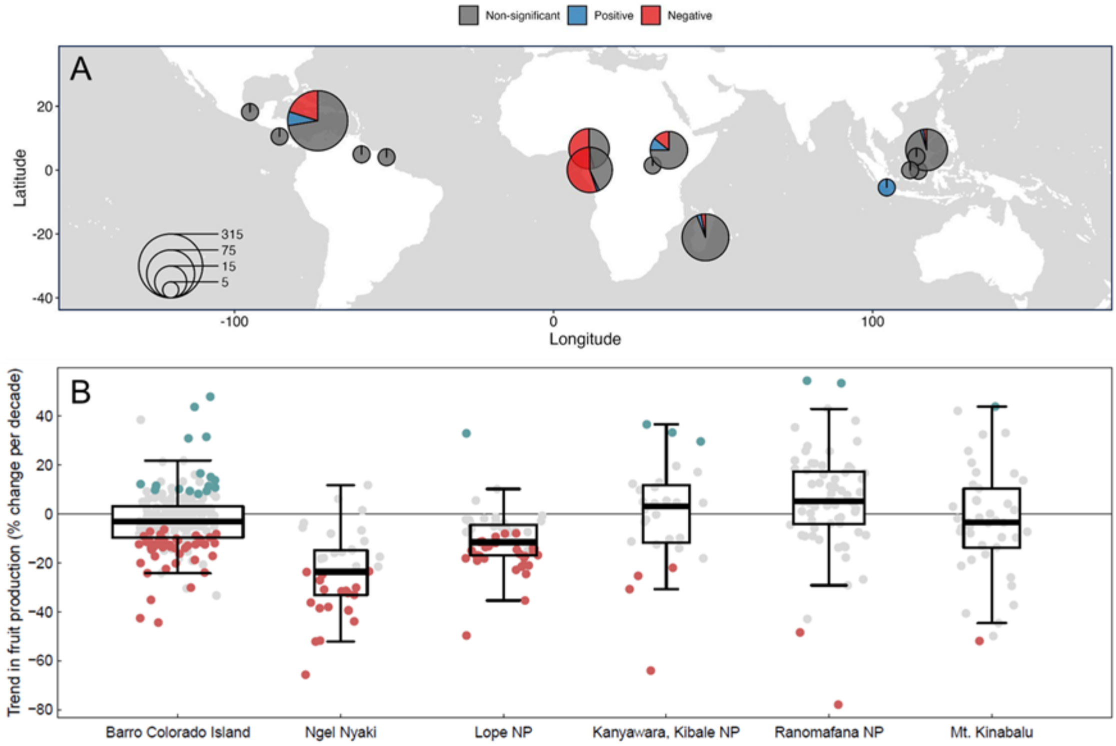

Figure 2: Species-level trends in tropical seed and fruit production. A) Each point represents a site in the MASTREE+ dataset (n = 17 sites), with point size proportional to the number of species (or in a small number of cases, genera, where species-level data was not available). Wedges in the pie chart 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. B) Species-specific trends for the six sites where data is available for multiple species, expressed as equivalent 10-year percentage change in reproduction. Significant positive and negative trends are coloured as for A).

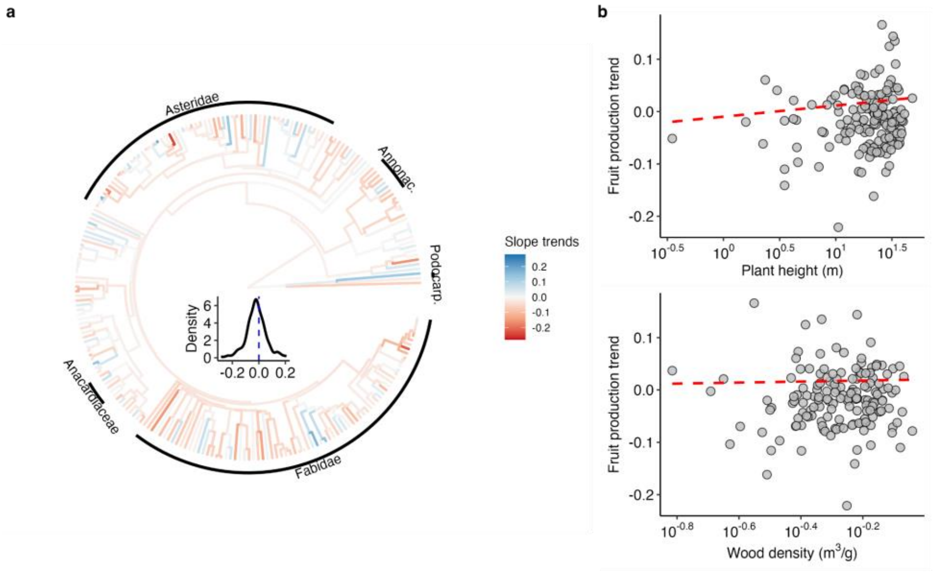

Figure 3: Species-specific trends in seed and fruit production according to phylogeny and traits. a) Absence of phylogenetic signal on seed production trends (Pagel's λ = 7.33e-05, p-value = 1, n = 224 species). b) Phylogenetic regression analysis includes fruit production trends as response and wood density and plant height as covariate (N = 154 species, adjusted R2 = 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).

Discussion

Pan-tropical and regional picture of trends in fruit production

Community-level fruit production trends were variable across tropical sites, yet a concerning pattern of decline emerges from several long-term monitoring datasets, including at Lopé and Ngel Nyaki in West Africa, Barro Colorado Island (BCI), Luquillo and Yasuní in the Neotropics, and FRIM in Indomalaya. Recently, declines in tropical forest flower production have also been reported elsewhere in the Neotropics, supporting our reported declines in fruit production (Wright and Calderón, 2024, Vleminckx et al., 2024, Flores et al., 2023). Declining tree reproduction could have profound impacts for tropical forest dynamics (McDowell et al., 2020). Despite seed production in tropical forest exceeding high latitude forests by two orders of magnitude (Journe et al., 2022), seed limitation in considered common (Wright and Calderón, 2024), and seed addition experiments have indicated seeds limit seedling recruitment (Clark et al., 2013a). The impacts of declines in reproduction on seedling establishment might be strongest in rare species, or in species or environments where the seed to seedling transition is already a strong demographic bottleneck (Abiem et al., 2023, Muscarella et al., 2013). Our results indicate that tropical forest fruit and seed production is changing, and although the drivers remain unclear, neglecting to consider tree reproduction within a framework of ecological resilience (Flores et al., 2024) risks incomplete assessment of the ability of tropical forests to persist in a changing environment. For example, major ecosystem shifts in the tropics have almost exclusively been considered through the mechanism of elevated mortality, including via drought, land-use change or other disturbance (Flores et al., 2024, Cano et al., 2022, Bauman et al., 2022). However, our results highlight that changing reproduction could also shape future ecosystem change, driving composition shifts even where mortality-focused assessment indicate high resilience (Flores et al., 2024). Additionally, the response of reproduction could ultimately shape ecosystem resilience to elevated mortality, given that reproduction and subsequent recruitment shape recovery trajectories (Qiu et al., 2022).

While shorter records (<20 years) predominantly show non-significant trends in fruit production, these findings are limited by their duration. Notably, less than half of the 25 sites in our synthesis include data from the most recent decade in our analysis, 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 (Abernethy et al., 2018, Morellato et al., 2018). The African Phenology Network offers a valuable model for achieving this (Adamescu et al., 2018), 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

Important species-level changes in reproduction might be masked by community-level trends. For example, 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 increasing and decreasing trends in fruit production at this site. Zimmermann et al. (2018) reported stronger decreases in large-stature trees (a trend we did not detect in our analysis, Figure 3B), while Babweteera et al. (2018) reported divergence in trends between species with different life-history strategies. While we did not detect effects of phylogeny, plant stature or wood density on fruit production trends, such analysis might help identify the drivers of changes in reproduction, e.g. the role of successional rather than climatic driver of changes in fruit production quantities and composition (Potts et al., 2020).

Species-specific, rather than community-level trends may also dictate the wider impact of changes in seed and fruit production on frugivores (Bush et al., 2020). 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* (-65% per decade), *Psychotria succulenta* (-52%), *Trema orientalis* (-52%)), and are key species for passive restoration in these Afromontane forests (Jaafar et al., 2021). Other species with declining fruit production included 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* (-36% per decade), whose superabundant immature fruits are a key food of the primates *Chlorocebus tantalus tantalus* and *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 significant declines in our analysis, including highly favoured elephant foods such as *Sacoglottis gabonensis* (-35% per decade), *Tetrapleura tetrapetra* (-50%) *and Bobgunnia fistuloides* (-18%), for which elephants are the major (or only) seed dispersers. Declining forest elephant body condition has already been associated with declining fruit production at this site (Bush et al. 2020). Wider impacts of declining fruit production on complex plant-frugivore interactions could be profound and have cascading effects on tropical forest functioning (Bascompte & Jordano 2007; Berzaghi et al. 2018).

Unravelling the mechanisms that determine fruit production

Our results, in combination with recent efforts to synthesise tropical phenology records (e.g. the 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 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 Potts et al., 2020). Consequently, to understand the diversity of signals 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 (Sullivan et al., 2024, Chapman et al., 2018, Numata et al., 2022, Satake et al., 2022, Wright and Calderón, 2024), including the effect of ontogeny (at the individual level) and successional and compositional dynamics (at the community level). Advances will come from fine-scale climate monitoring coupled with detailed phenological observations to identify the cues for flowering and fruit maturation (Morellato et al., 2016), including the factors that determine the flower-fruit transition (Vleminckx et al., 2025). Advances will benefit from combining traditional visual phenology assessments with molecular phenology (Satake et al., 2022). Ideally, monitoring will be coupled with manipulation experiments (Graham et al., 2003, Werkmeister et al., 2024). A key objective will be distinguishing the roles of resource acquisition as a driver of reproduction (Pau et al., 2018, Vleminckx et al., 2024), and weather cues that regulate dynamic allocation of those resources to reproduction (Sullivan et al., 2024, Adamescu et al., 2018, Bogdziewicz et al., 2024). The potential role of pollinator network disruption and other interactions also remains poorly understood (Ferreira et al., 2020, Morellato et al., 2016).

Establishing species-specific mechanisms will enable the identification of species whose reproduction is most at risk from climate change (Bogdziewicz et al., 2024), and may shed light on the diversity of species-level trends we found over recent decades (see also Lai et al., 2025). For example, species with strongly seasonal or supra-annual reproduction (e.g. Adamescu et al., 2018), 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, response will vary depending on the nature of the cue (Bogdziewicz et al., 2024). For example, Numata et al. (2022) showed that more than 50% of 98 Dipterocarp species 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. Similarly, minimum temperatures are important cues for the reproduction of Africa species, and warming temperatures is predicted to result in less frequent cueing and declining in fruit production (Tutin and Fernandez, 1993).

Shortcomings of our analysis

The number of studies reporting long-term observations of tropical forest reproduction is growing but remains small. We attempted to assess available data and reported results, but important gaps and limitations remain. Given that tree reproduction is typically characterised by high interannual variability (Clark et al., 2021, Bogdziewicz et al., 2024), it was unsurprising that shorter time-series tended to show non-significant temporal trends. Consequently, while declining species-level trends outweighed increasing trends by a factor of four, almost three-quarters of trends were non-significant. It remains unclear whether these represent ecological stability or limitations in statistical power. Additional uncertainty originates from heterogeneity (and limited replication) of fruit production monitoring methods. For example, collection methods included fruit counts on individual trees, assessments of the proportions of individual trees fruiting (e.g. Potts et al., 2020), or fruit counts from litter traps (Wright and Calderón, 2024). These methods may not be easily comparable (Parrado-Rosselli et al., 2006). Fruit counts from litter traps provide quantification of fruit dispersal, but the effects of changes in fruit production or pre-dispersal predation cannot be separated. Conversely, estimates based on fruit counts in the canopy enable estimates of production (including at the individual-tree level), but these may not reflect fruit (and seed) dispersal to the forest floor. 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 (Potts et al., 2020, Abernethy et al., 2018). 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 (Bush et al., 2020). 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 (Staggemeier et al., 2017, Butt et al., 2015). Our analysis highlights that tropical fruit production is changing and identifies this as a priority for further research, but additional work is required to expand the network of data and develop methods to identify and account for the effects of heterogeneity in monitoring methods.

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. Our findings reveal a concerning prevalence of declining 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 to enable more complete assessment of ecosystem resilience. Including additional data from phenological studies will be important for identifying regional trends and understanding their underlying drivers, which remain unclear. Enhancing our mechanistic understanding of fruit production is now a priority because it 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.

Acknowledgements

Funding

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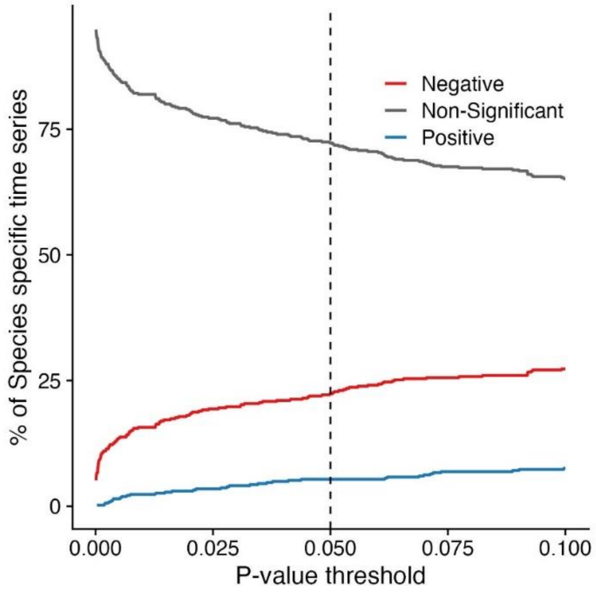
Supplementary Information

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

Supplementary Information 2: Phylogenetic and linear regression with fruit production trends as the response (i.e. 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