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ARTICLE

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Statistical power and the detection of global change responses: The case of leaf production in old-growth forests

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Abstract

Forests sequester a substantial portion of anthropogenic carbon emissions. Many open questions concern how. We address two of these questions. Has leaf and fine litter production changed? And what is the contribution of old-growth forests? We address these questions with long-term records (≥10 years) of total, reproductive, and especially foliar fine litter production from 32 old-growth forests. We expect increases in forest productivity associated with rising atmospheric carbon dioxide concentrations and, in cold climates, with rising temperatures. We evaluate the statistical power of our analysis using simulations of known temporal trends parameterized with sample sizes (in number of years) and levels of interannual variation observed for each record. Statistical power is inadequate to detect biologically plausible trends for records lasting less than 20 years. Modest interannual variation characterizes fine litter production, and more variable phenomena will require even longer records to evaluate global change responses with sufficient statistical power. Just four old-growth forests have records of fine litter production lasting longer than 20 years, and these four provide no evidence for increases. Three of the four forests are in central Panama, also have long-term records of wood production, and both components of aboveground production are unchanged over 21–38 years. The possibility that recent increases in forest productivity are limited for old-growth forests deserves more attention.

KEYWORDS

Barro Colorado Island, fine litter production, foliar litter production, global change responses, leaf production, long-term change, old-growth forest, Panama, reproductive litter production

INTRODUCTION

Until human behavior changes, atmospheric carbon dioxide concentrations ($_{atm}CO_2$), temperature, and climate extremes will rise globally, and precipitation will change regionally. These directional changes have profound effects on the biota that might mitigate or reinforce the underlying anthropogenic CO_2 emissions. For example, established forests sequestered 29% of anthropogenic CO_2 emissions between 1990 and 2007 (Pan et al., 2011) through a combination of secondary forest maturation and productivity increases associated with elevated $_{atm}CO_2$ and, in cooler regions, with rising temperature and longer growing seasons (reviewed by Ruehr et al., 2023; Walker et al., 2021). The future of this forest carbon sink is uncertain as nutrients become limiting, atmospheric vapor pressure deficits rise, drought and other disturbances become more frequent, and, in warmer regions, temperature and temperature-dependent respiration rise (reviewed by McDowell et al., 2020).

The land surface modules of Earth system models integrate these changing conditions to predict vegetation responses and the future terrestrial carbon sink. The leaf area index (LAI, in square meters of upper leaf surface per square meter of land surface) is a state variable and mediates the exchange of energy and mass, including carbon, between the vegetation and the atmosphere in all land models (Piao et al., 2020). Temporal trends in LAI are important given this central role in the global carbon cycle and Earth system models. Temporal trends in LAI are present in several time series of satellite-derived vegetation indices; however, the evidence is mixed, with temporal concordance among indices varying significantly among biomes and being lowest for forests and especially evergreen forests (Ding et al., 2020; Jiang et al., 2017; Qiu et al., 2021; Wang et al., 2022). Given this uncertainty, ground-based estimates of long-term trends in forest LAI are sorely needed. LAI equals specific leaf area (SLA, in square meters of upper leaf surface per gram of leaf dry mass) multiplied by the leaf production rate (in grams of leaf dry mass per square meter of land surface per year) and divided by the leaf turnover rate (per year). To our knowledge, ground-based measurements are yet to be explored for long-term trends in LAI, SLA, leaf turnover rates, or leaf production rates in old-growth forests.

We will present new long-term records of foliar, reproductive, and total fine litter production lasting 11, 21, 27, and 38 years for four old-growth forests in central Panama and compile similar long-term records for another 28 old-growth forests from the literature. Global foliar and total fine litter production average 22 and 31 Pg year^{-1}, respectively (Shen et al., 2019). Carbon comprises slightly less than half of fine litter production (Ma et al., 2018), making foliar litter production a key component of the global carbon cycle in addition to its contribution to LAI.

We evaluate temporal trends for each long-term record, with the expectation that fine litter production should increase as carbon stocks increase in intact tropical, temperate, and boreal forests (e.g., Fraser et al., 2023; Pan et al., 2011; Wang et al., 2023). We pay particular attention to the statistical power of our analyses, conducting a simulation study to identify the smallest linear increase that can be reliably detected given the length and variability observed for each long-term record. Statistical power turns out to be unacceptably low for all but the longest records of annual production (>20 years). This has broad implications for the study of global change responses because interannual variation is relatively modest for fine litter production and even longer records will be required to achieve sufficient statistical power to evaluate global change responses for more variable phenomena. Even the longest records of fine litter production with sufficient statistical power provide no evidence for directional temporal change. Rather, modest interannual variation around consistent mean values seems to be the rule.

METHODS

Litter traps in central Panama

We operate litter traps in four old-growth forests in Panama. Traps include a square PVC frame that holds an open 1-mm mesh bag 80–100 cm above the ground. At our Barro Colorado Island Inceptisol site (henceforth BCI Inceptisol), we randomly located 59 0.25-m^2 traps in four 1.44-ha forest plots in November 1985. In the Bosque Protector San Lorenzo (BPSL), we randomly located 40 0.5-m^2 traps in a 6-ha forest plot in May 1997. At Gigante on the mainland in the Barro Colorado Nature Monument, we randomly located 12 0.58-m^2 traps in four 0.16-ha plots distributed across a 38.4-ha plot in June 1998 and increased the number of traps to 20 in February 2007. In the BCI 50-ha Forest Dynamics Plot (BCI FDP), we randomly selected 64 of 250 0.5-m^2 traps and added all fine litter fractions to an ongoing census of flower, fruit, and seed production in May 2013 (Puerta-Pinero et al., 2013). Gigante traps are in control plots of a factorial nitrogen-phosphorus-potassium addition experiment (Wright et al., 2018). At the BCI Inceptisol site, a stand-level water addition experiment conducted between 1985 and 1989 did not alter fine litter production (Cavelier et al., 1999; Wright & Cornejo, 1990; Wright, Mulkey, et al., 2024), results of the current analyses are virtually identical for traps in control plots and for all traps, and we present data for all traps. Muller-Landau and Wright (2024) describe these forests.

We census BCI and BPSL traps weekly and Gigante traps monthly and oven dry captured material to constant mass at 60°C. For Gigante, we separate oven-dried material to standard foliar, reproductive, fine wood (<2 cm diameter), and dust fractions following Proctor (1984); however, only total mass was determined for the first four censuses in 1998 and the final four censuses before the covid-19 pandemic. For both BCI sites and BPSL, we separate fine wood (<2 cm diameter) and dust fractions and identify leaves and reproductive material to species before weighing. The pandemic interrupted the continuity of the Gigante census, which ends in February 2020 for present purposes. For detailed site descriptions, see

Appendix S1: Tables S1 and S2. The Panama data are publicly available (Wright & Calderón, 2024b).

Literature search

We conducted two literature searches for long-term records of total, foliar, and/or reproductive fine litter production that meet the following criteria: (1) collected with five or more litter traps at monthly or shorter intervals (2) for 10 or more years (3) from an unmanipulated old-growth forest. Old growth at higher latitudes was at least 100 years without human intervention and, for fire-adapted jack pine (*Pinus banksiana*) dominated boreal forests, at least 70 years without fire. Tropical forests were much older (Appendix S1: Table S2).

We first searched compilations of fine litter production (Chave et al., 2010; Holland et al., 2015; Proctor, 1984) for data sets that fulfilled our criteria without success. We then searched all databases at the Thomson WEB of Science for the following combination of keywords: “litter producti*” AND forest AND (“long term” OR long-term OR “time series” OR “interannual variation”). This identified 135 publications, whose references we also searched, producing eight publications that fulfilled our criteria (Bhatti & Jassal, 2014; Guo et al., 2022; Kitayama et al., 2021; Li et al., 2010; Marod et al., 2023; Martinez-Alonso et al., 2007; Nakagawa et al., 2019; Pereira et al., 2023). At the suggestion of an anonymous reviewer, we substituted “fine litter” for “litter producti*” and conducted a final search with Google Scholar. We sorted the results by relevance and examined the top 200 articles producing two additional publications that fulfilled our criteria (Tang et al., 2010, 2011). An anonymous reviewer identified a final article (Rowland et al., 2018). These 11 publications reported fine litter production for 28 independent old-growth stands dominated by different species or growing at different elevations or on different bedrocks. For detailed site descriptions, see Appendix S1: Table S2. We used Web Plot Digitizer to extract data from figures (Rohatgi, 2019). Data compiled from the literature are publicly available (Wright & Calderón, 2024a).

Analyses

Fine litter production is an annual phenomenon. Annual periodicity is enforced by freezing temperatures at higher latitudes and by species-specific responses to seasonal variation in moisture and light availability at lower latitudes. We perform all analyses for annual values, with sample size equal to the number of complete years available.

We evaluated monotonic trend for continuous records with rank-based Mann–Kendall tests and sieve bootstrapping. The sieve bootstrap removes autocorrelation from time series data by bootstrapping residuals from autoregressive models (Noguchi et al., 2011). We used the Akaike information criterion to select the order of the autoregressive filter, which was 0, 1, 2, 3, and 4 for 29, 5, 2, 4, and 2 data sets, respectively. This analysis requires continuous data to estimate autocorrelation and is invalid if years are missing.

Three studies and five long-term records include missing years (Table 1; Appendix S1: Table S2). For this reason, we also calculated Pearson correlation coefficients between year and litter amounts but note that Pearson correlation analyses assume independent observations and are compromised by the temporal dependence present in time series data. We present a meta-analysis of the Pearson correlation coefficients in Appendix S2 because, to the best of our knowledge, meta-analyses cannot accommodate temporally dependent time series data. Results of the meta-analysis are consistent with results of the Mann–Kendall analyses presented in the main text.

Power analysis

We simulated linear increases in production to evaluate statistical power for each continuous long-term record. Each simulation starts with Y_{obs} normal distributions with the following record-specific parameterizations: $\mathcal{N}(\text{mean}_{\text{obs}}, \sigma_{\text{obs}})$, $\mathcal{N}(\text{mean}_{\text{obs}} \times (1 + X_i), \sigma_{\text{obs}})$, ..., $\mathcal{N}(\text{mean}_{\text{obs}} \cdot (1 + (Y_{\text{obs}} - 1) \times X_i), \sigma_{\text{obs}})$, where X_i is the fixed percentage annual increase to be detected and mean_{obs}, σ_{obs}, and Y_{obs} are the mean, standard deviation, and number of years, respectively, for an observed time series. We varied X_i 100-fold, taking the values 0.1%, 0.2%, ..., 0.9%, 1%, 2%, ..., 10%. To prevent a real temporal trend from inflating σ_{obs}, we quantified σ_{obs} as the SD of residuals from the best fit quadratic relationship between annual production and year. We drew one random number from each of the Y_{obs} normal distributions to simulate one long-term record and determined whether a Mann–Kendall test detected (at $p < 0.05$) the simulated linear increase. We repeated this process 1000 times for each simulated increase (X_i) for each observed time series (Y_{obs}, mean_{obs}, and σ_{obs}) and tallied the number of significant Mann–Kendall tests. A conventional threshold for sufficient statistical power is 0.8, meaning an effect of a given magnitude is detected 80% of the time (Gelman & Carlin, 2014; Kimmel et al., 2023). Thus, the minimum annual increase detectable with sufficient statistical power is the smallest value of X_i for which the Mann–Kendall test is significant (at $p < 0.05$) for 80% of simulations.

TABLE 1 Analyses of temporal trend for long-term (≥10 years) records of total, foliar, and reproductive fine litter production.

			Mann–Kendall test for monotonic trend[b]			Pearson correlation coefficient[c]	
Site (elevation, bedrock, or dominant plant)	**Years**	**CV[a]**	**Mann–Kendall tau**	**Nominal *p*-value[d]**	**Minimum detectable annual increase (%)[e]**	**Value**	**Nominal *p*-value[d]**
Foliar fine litter							
BCI Inceptisol, Panama	38	0.075	0.0327	0.789	0.4	0.145	0.386
Bosque Protector San Lorenzo, Panama	27	0.082	−0.0769	0.566	0.6	−0.204	0.309
BCI Forest Dynamics Plot, Panama	11	0.068	−0.309	0.223	2	−0.481	0.134
Gigante, Panama	19[f]	0.098	−0.0994	0.583	2	−0.161	0.510
Lambir Hills, Malaysia	16	0.157	0.544	0.140	2	**0.749**	**<0.001**
Mt. Kinabalu, Borneo (1700 m, quaternary)	16	0.138	−0.0167	0.947	3	−0.0802	0.768
Mt. Kinabalu, Borneo (1700 m, sedimentary)	16	0.130	−0.133	0.460	3	−0.225	0.401
Mt. Kinabalu, Borneo (700 m, sedimentary)	10	0.106	−0.778	<0.001	3	−0.853	0.00172
Guaratiba Reserve, Brazil (*Avicennia*)	11	0.166	0.346	0.165	4	0.548	0.0807
Guaratiba Reserve, Brazil (*Rhizophora*)	11	0.115	0.164	0.503	4	0.220	0.515
Xishuangbana, China	10	0.081	0.0222	0.964	4	0.0674	0.853
Candle Lake, Canada (*Picea mariana*)	10	0.108	0.0667	0.804	5	0.131	0.717
Mt. Kinabalu, Borneo (2700 m, ultrabasic)	10	0.139	−0.0667	0.838	6	−0.186	0.608
Segovia, Spain (1550 m, *Pinus sylvestris*)	11	0.178	0.127	0.615	6	0.0374	0.913
Candle Lake, Canada (*Pinus banksiana*)	10	0.156	0.0222	0.971	7	0.0354	0.923
Gillam, Canada (*Pinus banksiana*)	10	0.186	0.289	0.241	7	0.530	0.115
Gillam, Canada (*Picea mariana*)	10	0.213	0.244	0.336	7	0.457	0.185
Guaratiba Reserve, Brazil (*Laguncularia*)	11	0.429	0.600	0.157	7	0.608	0.0472
Mt. Kinabalu, Borneo (1700 m, ultrabasic)	10	0.209	−0.156	0.553	7	−0.266	0.458
Mt. Kinabalu, Borneo (2700 m, sedimentary)	10	0.218	−0.156	0.557	8	−0.273	0.445
Segovia, Spain (1300 m, *Pinus sylvestris*)	11	0.224	0.236	0.344	8	0.205	0.545
Thompson, Canada (*Pinus banksiana*)	10	0.185	0.135	0.417	8	0.0433	0.905
Thompson, Canada (*Picea mariana*)	10	0.237	0.244	0.338	8	0.314	0.377
Segovia, Spain (1450 m, *Pinus sylvestris*)	11	0.287	−0.200	0.411	10	−0.267	0.427
Mt. Kinabalu, Borneo (3100 m, granite)	10	0.312	0.156	0.643	>10	−0.164	0.650
Mt. Kinabalu, Borneo (3100 m, ultrabasic)	10	0.367	−0.467	0.063	>10	−0.564	0.0893
Caxiuanã National Forest Reserve, Brazil	10	0.146	…	…	…	−0.455	0.187
Reproductive fine litter							
BCI Inceptisol, Panama	38	0.157	−0.00711	0.963	0.7	−0.00149	0.993
Bosque Protector San Lorenzo, Panama	27	0.310	0.219	0.204	3	0.292	0.139
Gigante, Panama	19[f]	0.384	0.521	0.002	4	**0.724**	**0.000452**

TABLE 1 (Continued)

			Mann–Kendall test for monotonic trend[b]			Pearson correlation coefficient[c]	
Site (elevation, bedrock, or dominant plant)	Years	CV[a]	Mann–Kendall tau	Nominal *p*-value[d]	Minimum detectable annual increase (%)[e]	Value	Nominal *p*-value[d]
BCI Forest Dynamics Plot, Panama	11	0.175	−0.455	0.063	4	−0.724	0.0118
Caxiuanã National Forest Reserve, Brazil	10	0.344	…	…	…	−0.381	0.278
Total fine litter							
BCI Inceptisol, Panama	38	0.063	0.0811	0.496	0.3	0.179	0.282
Bosque Protector San Lorenzo, Panama	27	0.090	0.271	0.0640	0.7	0.378	0.0521
Gigante, Panama	21[f]	0.063	−0.0476	0.777	0.7	−0.0150	0.948
Mae Klong Watershed, Thailand	29	0.179	−0.462	0.042	1	**−0.628**	**0.000263**
BCI Forest Dynamics Plot, Panama	11	0.058	−0.527	0.026	2	−0.610	0.0465
Lambir Hills, Malaysia	16	0.191	0.310	0.385	3	0.479	0.0603
Tibet (*Abies*), China	10	0.249	0.556	0.239	6	0.774	0.00857
Tibet (*Juniperus*), China	10	0.207	0.333	0.210	7	0.480	0.160
Xishuangbana, China	10	0.182	−0.334	0.220	7	−0.384	0.274
Segovia, Spain (1300 m, *Pinus sylvestris*)	11	0.261	0.236	0.346	9	0.319	0.340
Segovia, Spain (1450 m, *Pinus sylvestris*)	11	0.276	0.164	0.516	9	0.236	0.484
Segovia, Spain (1550 m, *Pinus sylvestris*)	11	0.301	−0.0182	0.971	>10	0.196	0.563
Caxiuanã National Forest Reserve, Brazil	10	0.151	…	…	…	−0.371	0.291
Changbai Mountain Reserve, China	19	0.115	…	…	…	0.501	0.0290
Dinghushan Biosphere Reserve, China	21	0.161	…	…	…	−0.563	0.00782

Abbreviation: BCI, Barro Colorado Island.

[a] CV of annual litter production or SD/mean, where SD and mean are the standard deviation and mean of annual values, respectively.

[b] The Mann–Kendall test with sieve bootstrapping requires continuous records. Entries are missing values (…) for discontinuous records.

[c] Pearson correlation coefficients were calculated between year and litter amounts.

[d] Nominal *p*-values have not been corrected for the number of tests performed. Only bolded values are statistically significant after the Holm adjustment for multiple tests.

[e] The minimum detectable increase is the smallest percentage annual increase detected by the Mann–Kendall test (at $p < 0.05$) for 80% of simulated time series. Sites are ordered by this percentage within each fine litter fraction. *Methods* describes the simulations.

[f] For the Gigante site, foliar, reproductive, and total fine litter production were determined for 19, 19, and 21 consecutive years, respectively, because foliar and reproductive litter were not determined separately for the first and final four monthly censuses.

We used a multiple regression analysis to explore how number of years (Y_{obs}) and interannual variation affect statistical power. Levels of productivity varied widely among forests, so we standardized interannual variation as the CV ($\sigma_{\text{obs}}/\text{mean}_{\text{obs}}$). We quantified statistical power as the number of statistically significant records detected for a simulated increase of 0.3% year^{-1}. We chose 0.3% year^{-1} because the number of statistically significant simulations was not yet approaching its maximum value of 1000.

We performed all analyses in the R statistical language (R Core Team, 2023). We calculated 95% CIs over traps within years for each Panamanian forest with the "boot" package (Canty & Ripley, 2022). We implemented Mann–Kendall tests for observed data where autocorrelation might occur with the "funtimes" package and for simulated data where autocorrelation is absent with the "Kendall" package (Lyubchich et al., 2023; McLeod, 2022). R scripts to recreate all analyses are publicly available (Wright & Calderón, 2024a).

RESULTS

The 32 old-growth forests with long-term records (≥10 years) of fine litter production span the global range of mean

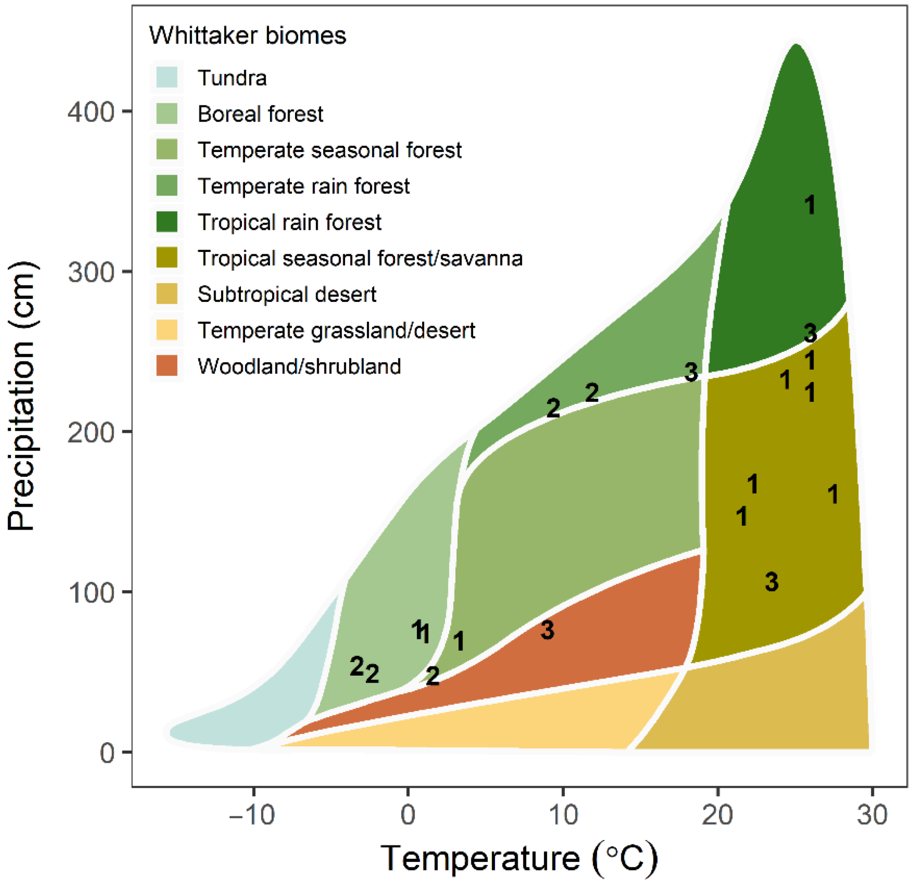

FIGURE 1 The 32 old-growth forests with long-term (≥10 years) litter production records span the global range of mean annual temperature (MAT) and precipitation (MAP) that supports forest. Values are numbers of continuous long-term records for forests with similar MAT and MAP. The seven forests whose MAT and MAP fall in the temperate rainforest biome are montane tropical forests growing at different elevations and on different bedrocks at Mount Kinabalu, Borneo. Appendix S1: Table S2 presents site descriptions.

annual temperature and precipitation that supports forest (Figure 1; Appendix S1: Tables S1 and S2). The 47 long-term records include 26, 4, and 12 continuous records and 1, 1, and 3 discontinuous records for foliar, reproductive, and total fine litter production, respectively (Table 1). Different hypotheses address these litter fractions (see *Discussion*). For this reason, we evaluate trend for every long-term record even though total fine litter includes leaves and reproductive parts.

Correlations between foliar litter production and year that control temporal dependence are negative for 11 forests and positive for 15 forests (see Mann–Kendall τ values in Table 1). Just 2, 1, and 2 of the continuous records have nominally significant ($p < 0.05$) Mann–Kendall tests for monotonic trend for foliar, reproductive, and total fine litter production, respectively (Table 1). Not one Mann–Kendall test is significant after implementing the Holm adjustment for multiple comparisons (Table 1).

Pearson correlation coefficients calculated between year and litter production are negative for 13 forests and positive for 14 forests (see Pearson correlation values in Table 1) and are nominally significant ($p < 0.05$) for the five records with nominally significant Mann–Kendall tests, three additional continuous records, and two of the five discontinuous records. Three Pearson correlation coefficients remain significant after implementing the Holm adjustment for multiple comparisons (Table 1). A meta-analysis of these Pearson correlation coefficients failed to detect any consistent trend in foliar fine litter production (Appendix S2).

Power analysis

An analysis with sufficient statistical power should detect an effect of a given magnitude 80% of the time (Kimmel et al., 2023). The sixth column of Table 1 presents the minimum annual percentage increase detected (at $p < 0.05$) by the Mann–Kendall test for 80% of simulations parameterized with the number of years and level of variation observed for each record. This minimum detectable annual increase varied between 0.3% year^{-1} and >10.0% year^{-1} across the 42 continuous records.

A multiple regression analysis explored the relationship between the number of simulated increases of 0.3% year^{-1} detected (at $p < 0.05$) by the Mann–Kendall test, study length (Y_{obs}, in years), and interannual variation (CV) for the 26 continuous records of foliar litter production. With the response variable log-transformed, the explanatory variable years is statistically significant ($t_{23} = 11.5$, $p < 10^{-10}$), the explanatory variable CV is statistically insignificant ($t_{23} = -1.50$, $p = 0.147$), and residuals are well behaved (Appendix S1: Figure S2). Study length largely explains variation in statistical power among the long-term records (coefficient of determination or $r^2 = 0.875$).

DISCUSSION

Our analyses provide no evidence for long-term increases in litter production in old-growth forests (Table 1, Appendix S2). Modest levels of interannual variation characterize fine litter production, with coefficients of variation less than 0.25 for 79% of the data sets (Table 1). The evidence indicates that fine litter production has varied around consistent mean values on decadal time scales across 32 old-growth forests (Table 1, Figure 2; Appendix S1: Figure S1).

Caveats

A first caveat concerns statistical power. A biologically plausible response is required to evaluate statistical power. Long-term changes in aboveground carbon stocks documented for intact tropical forests provide a biologically plausible reference point for fine litter production. Aboveground carbon stocks increased by 0.47% year^{-1} to 0.59% year^{-1} between 1990 and 2007 for intact tropical forests in the Americas, Africa, and Asia (obtained by combining change estimates from Pan et al. (2011) with stock estimates from Sullivan et al. (2020)). Only the four longest records lasting 21 or more years have sufficient statistical power to detect a sustained increase of 1% year^{-1} (Table 1). More long records of fine litter production will be required to generalize with any confidence (see *Discussion*: *Research recommendations* and *Discussion*: *Implications of limited statistical power*).

A second caveat concerns the distribution of sites. Twenty-six of the 32 old-growth forests with long-term litter production records occur in six clusters of two to eight sites separated by tens to several hundred kilometers. Thus, even though the 32 forests span the range of mean annual temperature and precipitation that supports forest (Figure 1), just 12 widely separated sites are included (Appendix S1: Tables S1 and S2). Tropical America and Asia are represented by 20 forests including 15 in three clusters in central Panama, Mount Kinabalu, Borneo, and Brazil. The Temperate Zone is represented by six montane and alpine forests including five in two clusters in Spain and Tibet. The Boreal Zone is represented by just six forests in a single cluster along a 500-km transect in Canada. African and lowland Temperate Zone forests are not represented. Data from many more old-growth forests will be required to generalize with any confidence (see *Discussion*: *Research recommendations*).

A final caveat applies to all studies of fine litter production but is unlikely to affect temporal trend. Litter traps miss leaves consumed by herbivores, fruit consumed by frugivores, and decomposition before material falls and thereby underestimate production. This will only affect temporal trends if herbivory, frugivory, and/or decomposition rates have changed. Decomposition rates increase with temperature; however, the small temperature increases observed in the tropics and over the short records (10 or 11 years) available from higher latitudes are unlikely to have had a measurable impact. We recognize a consistent underestimate of production but, lacking evidence for change in herbivory, frugivory, or decomposition rates, discount the possibility that temporal trends are introduced or masked.

Research recommendations

Our analyses indicate that statistical power is sufficient to detect biologically reasonable temporal trends for just four old-growth forests with records of fine litter production lasting 21 or more years. Three of these forests are in central Panama. Without new data, the result that temporal trends in fine litter production are absent cannot be generalized beyond central Panama (Figure 2). Fortunately, there is a solution. There are many high-quality litter production records from the 1970s, 1980s, and 1990s (compiled by Chave et al., 2010; Holland et al., 2015; Proctor, 1984). New records collected 30–50 years later at the same sites would augment the global perspective on long-term trends in fine litter production. Until this happens, we are left with reasonably strong evidence that temporal trends in fine litter production are absent in central Panama (Figure 2).

Central Panama

We have shown that fine litter production has fluctuated around consistent mean values for up to 38 years in

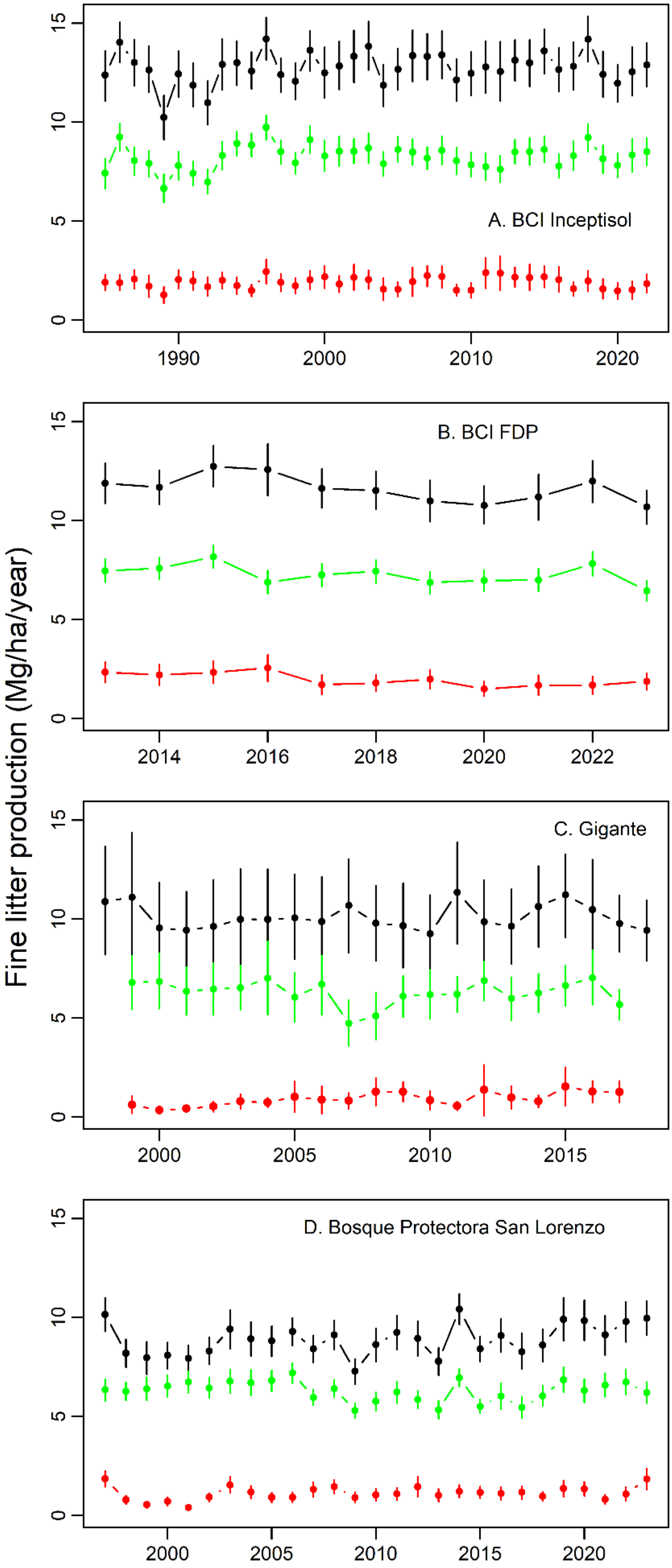

FIGURE 2 Legend on next page.

old-growth forests in central Panama (Figure 2, Table 1). Earlier studies produced similar results for wood production and aboveground biomass (AGB) stocks for the same forests and years (Condit et al., 2004, 2017; Rutishauser et al., 2020; Wright et al., 2018). The climate of central Panama lacks temporal trend over these decades, with precipitation, soil moisture content, solar inputs, and minimum and maximum temperatures fluctuating around consistent mean values at BCI (see fig. S18 in Rutishauser et al., 2020). In contrast, $_{\mathrm{atm}}CO_2$ rose 21.4% from 346 ppm in 1985 when our 38-year record began to 420 ppm in 2023 (https://keelingcurve.ucsd.edu/).

The long-term consistency of AGB and foliar production in central Panama contrasts with predicted increases in net primary production (NPP) associated with rising $_{\mathrm{atm}}CO_2$ in CMIP6 Earth system models (see section 5.4.5 in Canadell et al., 2021). This discrepancy could be reconciled for foliar production if decreases in allocation to foliage offset increases in NPP associated with rising $_{\mathrm{atm}}CO_2$. Exactly this happened in free-air CO_2 enrichment (FACE) experiments conducted in high-LAI forests in which NPP increased, allocation to foliage decreased, and LAI did not change in response to elevated CO_2 (De Kauwe et al., 2014; Norby et al., 2005, 2022, 2024; Norby & Zak, 2011).

Increased allocation belowground could also contribute to net NPP increases consistent with CMIP6 predictions. Nutrient limitation might constrain aboveground productivity and increase allocation belowground in response to rising $_{\mathrm{atm}}CO_2$ (e.g., Körner, 2022; Sigurdsson et al., 2013). Nutrient addition experiments provide overwhelming evidence that phosphorus and/or nitrogen limit productivity in most forests worldwide (Elser et al., 2007; LeBauer & Treseder, 2008; Ostertag & DiManno, 2016; Wright, 2019) and that phosphorus availability limits foliar and total fine litter production in central Panama (Wright et al., 2018). Plants exposed to 550–580-ppm CO_2 in FACE experiments consistently increased belowground productivity presumably to acquire limiting soil resources (reviewed by Norby & Zak, 2011). In the absence of long-term belowground NPP data, it is not possible to discount the possibility that belowground and total NPP have increased. In the meantime, the absence of evidence for long-term increases in aboveground NPP for old-growth forests in central Panama is consistent with reduced forest carbon sinks predicted when nutrient cycles and potential nutrient limitation are added to Earth system models (Walker et al., 2021; Wieder et al., 2015).

Reproduction increased in response to elevated CO_2 in two forest FACE experiments that included reproductive trees (reviewed by Norby & Zak, 2011). Wright and Calderón (2006) speculated that rising $_{\mathrm{atm}}CO_2$ contributed to a highly statistically significant, one-standard-deviation increase in flowering activity across 17 years for 81 tree and liana species at BCI (see fig. 3 in Wright & Calderón, 2006). In contrast, there is no long-term increase in the dry mass of reproductive material captured by the same BCI traps (the BCI Inceptisol and FDP sites in Figure 2 and Table 1). These contrasting results can be reconciled. Wright and Calderón (2006) analyzed the numbers of flower presences in traps, not reproductive dry mass. The numbers of flower presences rose steadily from 1987 through 2003, were sustained at 2003 levels through 2009, and then fell steadily from 2010 through 2021, returning to levels not observed since 1987 (see fig. 2B in Wright, Calderón, et al., 2024). We have no explanation for the sustained and dramatic changes in flowering activity. We conclude that community-level reproductive effort expressed as dry mass production has not changed at BCI (Figure 2, Table 1).

The constancy of AGB and fine litter production contrasts with dramatic changes in forest dynamics and species composition over the same years in the same central Panama forests. Changes in forest dynamics include large, nondirectional temporal variation in growth and mortality rates of many tree species (Condit et al., 2017; Rutishauser et al., 2020; Wright et al., 2018). Species compositional changes include large increases in the importance of vines and lianas (Ingwell et al., 2010; Schnitzer et al., 2021; Wright et al., 2004) and large fluctuations in the abundances of many tree species (Chisholm et al., 2014; Condit et al., 2017). The causes of these dramatic species-level changes are largely unknown. Given dramatic species-level change with unknown causes, we fear that the consistent levels of AGB and fine litter production observed since the early 1980s could end at any time for the old-growth forests of central Panama.

The long-term consistency of litter production and woody biomass stocks in Panama contrasts with strong increases in woody biomass stocks estimated from repeated censuses of large numbers of small tree plots (mostly 1 ha) elsewhere in the tropics (e.g., Pan et al., 2011). The

FIGURE 2 Total (black), leaf (green), and reproductive (red) fine litter production for four forests from central Panama. Symbols represent means and 95% CIs. Panel labels include site names. Soil fertility and fine litter production decreases from panels A through D. The number of traps (and the area of one trap) are 59 (0.25 m^2), 64 (0.5 m^2), 12/20 (0.58 m^2), and 40 (0.5 m^2) for panels A through D, respectively, where 12/20 indicates 12 traps through 2006 and 20 traps thereafter. Table 1 presents results for analyses of temporal trend for each time series. Appendix S1: Table S1 presents site descriptions. BCI, Barro Colorado Island; FDP, Forest Dynamics Plot.

interpretation of these estimates is controversial in part because the disturbance history of the small plots is rarely known (e.g., Clark, 2002; Wright, 2013), many are likely to have been disturbed by humans (e.g., McMichael et al., 2017), and recovery from past human disturbance could contribute to increasing woody biomass stocks. Chave et al. (2008) found much smaller increases in AGB stocks for larger tropical tree plots (16–52 ha) with known, minimal past human disturbance. Thus, Chave et al. (2008) might provide a more accurate estimate of change in woody biomass stocks for old-growth tropical forests.

Implications of limited statistical power

Underpowered studies can mislead because, as statistical power declines, estimated effect sizes become less reliable (Gelman & Carlin, 2014; Kimmel et al., 2023). As statistical power falls to 50%, the magnitude of statistically significant effects becomes exaggerated because increasing numbers of effect sizes are overestimated and thereby become statistically significant. As statistical power falls to 10%, estimated effect sizes become so unreliable that badly underestimated effect sizes with the wrong sign become statistically significant. In our analyses, statistical power to detect a sustained increase in fine litter production of 1% year^{-1} was <10% for 22 of 28 records lasting 10 or 11 years, between 14% and 64% for five records lasting 16 and 19 years, and >80% for seven of eight records lasting 21 or more years, where 80% is the conventional level accepted for sufficient statistical power. Studies of fine litter production lasting <20 years are likely to exaggerate temporal trends and studies lasting ≤11 years might identify misleading trends.

Kimmel et al. (2023) demonstrate that underpowered studies are pervasive in ecology and inflate the perceived importance of ecological interactions. The problem might be particularly acute for studies that attribute temporal trends to diffuse global change responses. Modest levels of interannual variation characterize foliar and total fine litter production (CVs < 0.25 for 83% of long-term records, Table 1). Even longer records will be required to document temporal trends for more variable annual phenomena. Unfortunately, very few ecological studies last even 20 years. For these reasons, statistical power should be documented whenever temporal trends are attributed to global change.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data collected from four old-growth forest in central Panama (Wright & Calderón, 2024b) are available in Dryad at https://doi.org/10.5061/dryad.z8w9ghxk2. Additional data compiled from the literature and R scripts (Wright & Calderón, 2024a) are available in the Smithsonian Research Data Repository at https://doi.org/10.60635/C3RG6V.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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