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Arthropod rain in a lowland tropical forest

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Abstract

1. In lowland tropical forests, "arthropod rain" (i.e., arthropods falling from the canopy to the understory), represents a potentially important terrestrial nutrient flux.
2. We investigated the composition, abundance, biomass and environmental drivers of arthropod rain on Barro Colorado Island, Panama. Pairs of traps (pan traps and pole traps) placed 1 m above the ground, respectively, collected fallen arthropods and arthropods potentially climbing to the canopy.
3. Average (±SE) arthropod biomass in pan traps was dominated by Hymenoptera (primarily ants; 0.501 ± 0.023 mg dry mass m^{-2} day^{-1}) and Lepidoptera larvae (0.228 ± 0.001 mg m^{-2} day^{-1}). Total dry biomass in pan traps was 0.891 ± 0.033 mg m^{-2} day^{-1}; thus, ca. 27 kg of arthropod biomass rains into the understory per km^2 per month during the wet season in this forest. This equates to ca. 3 million mid-sized ants falling from the canopy per day on BCI as a whole.
4. Arthropod abundance in pan traps, especially ants and spiders, increased marginally with the increasing number of high-wind events. By contrast, arthropod biomass showed no relationship with wind or rain.
5. Arthropod abundance was higher in pole traps than in pan traps and was dominated by Collembola and Acari. Compositional overlap between pan and pole trap contents suggests that some fallen arboreal arthropods regularly return to the canopy.
6. These findings illustrate an understudied pathway linking canopy and understory food webs within tropical forests, and the complex interactions between environmental conditions and arthropod rain.

KEYWORDS
abundance, ants, biomass, forest canopy, Formicidae, nutrient flux, Panama

INTRODUCTION

The vertical structure of forests leads to strong spatial partitioning (i.e., stratification) of habitats and communities (e.g., Lowman & Nadkarni, 1995). "Green" canopy food webs are distinct from "brown" understory litter food webs (Yanoviak & Kaspari, 2000); however, these components are fundamentally and unavoidably connected through gravity. For example, fallen plant litter is the main energy source for detrital food webs in the forest understory (Goncharov et al., 2016; Potapov et al., 2016). Similarly, honeydew produced by arboreal sap-sucking insects rains into the understory, where it provides large amounts of biologically available carbon as soluble sugar (Beggs et al., 2005). Finally, faeces (frass) falling from herbivores in the canopy contains more decomposable (labile) carbon per gram than leaf litter (Lovett et al., 2002), and can stimulate microbial growth (Clay et al., 2013; Frost & Hunter, 2004). Although such cross-compartment subsidies (e.g., Anderson & Polis, 1999; Polis et al., 1997; Rozanova et al., 2022) integrate the forest canopy and understory into a cohesive system, they are rarely quantified (e.g., Allen & Wesner, 2016; Marczak et al., 2007).

Arthropods falling from the forest canopy to the understory (i.e., "arthropod rain") represent another potentially important link between physically disconnected food webs. Arthropod rain is a high-quality food source for understory predators and saprophages (Goncharov et al., 2016; Haemig, 1997; Pringle & Fox-Dobbs, 2008; Rozanova et al., 2019, 2022). Although less abundant than litterfall, animal-derived inputs such as arthropod rain offer higher nutritional value per unit mass due to their lower C:N and C:P ratios (Bartels et al., 2012; Moyo et al., 2017). Thus, spatiotemporal variation in arthropod rain mediated by factors such as precipitation, wind and population dynamics (Hollinger, 1986) potentially affects understory food webs.

Precipitation (i.e., rainfall) likely influences arthropod rain by directly dislodging arthropods from vegetation and altering their adhesion to surfaces, as indicated by data from Japanese cedar forests (Yoshida et al., 2021). The adhesive performance of insect tarsi tends to be lower on wet surfaces (Stark & Yanoviak, 2018; Thomas et al., 2023), suggesting that even light precipitation can increase the probability of a fall and reduce landing success on leaves during a fall (Seiler, Stark, & Yanoviak, 2025a). However, many insects sense approaching rainfall (e.g., Fournier et al., 2005; Rousse et al., 2009) and avoid the risk of dislodgement from wet surfaces by seeking shelter (e.g., Corn, 1976). Thus, the positive or negative effect of rainfall on arthropod rain likely is influenced by the magnitude and timing of precipitation.

Wind also presumably causes arboreal arthropods to become dislodged from tree surfaces, although the ability of arboreal arthropods to resist the direct forces of wind remains unknown. Indirectly, wind-induced leaf movement reduces herbivory rates and decreases the diversity of invertebrates on leaves (Warren, 2015; Yamazaki, 2011), similar to the leaf movements caused by mammal activity in trees (Seiler, Schleff, et al., 2025). By contrast, many arthropods use wind to facilitate dispersal or escape (Cho et al., 2018; Logghe et al., 2024), suggesting that they sometimes drop from tree surfaces voluntarily.

Regardless of the agent of dislodgement, arthropods frequently fall from trees, and the consequences of a fall presumably have favoured the evolution of aerial gliding and high-adhesive performance in some taxa (Stark et al., 2018; Stark & Yanoviak, 2018; Yanoviak et al., 2011; Zeng et al., 2024). Thus, the composition of arthropod rain is likely to be dominated by species that do not glide or have relatively low adhesive performance. Whereas aerial gliding behaviour occurs in a variety of tropical arthropods (Yanoviak et al., 2005, 2011), the adhesive performance of most arboreal arthropods is unknown.

The principal goal of this study was to measure the abundance, composition, and biomass of arthropod rain in a lowland, neotropical forest. We hypothesized that the amount and composition of arthropods falling from trees would be associated with variation in two conspicuous environmental variables in the forest canopy: wind and rain. We predicted that arthropod rain density (abundance and biomass per m^2 per day) would increase with an increasing number of high-intensity wind and rain events. We also expected that gliding species would be underrepresented in arthropod rain samples.

MATERIALS AND METHODS

Study area

Field work was conducted in the semideciduous, seasonally moist lowland tropical forest of Barro Colorado Island (BCI) in central Panama (9°10′ N, 79°51′ W). The mean annual temperature on BCI is 26°C, and the mean annual precipitation is ca. 2600 mm. Rainfall on BCI occurs mainly during the wet season from May to December (Leigh, 1999). The focal year of this study (2023) coincided with the onset of an El Niño warming event in the eastern equatorial Pacific Ocean, causing dry season conditions to continue late into the wet season. More information about BCI is provided elsewhere (Leigh, 1999; Leigh et al., 1996).

Pan and pole traps

Two different types of traps (pan traps and pole traps) were placed along one 150 m transect at each of three sites in late secondary forest (Dent & Elsy, 2024) on BCI (Table 1). We used pan traps to passively collect arthropods falling from the canopy to the understory. Pan traps were made from plastic wash basins (105 cm diameter) with drain holes ca. 15 cm above the bottom to prevent overflow during heavy rains. Each pan trap was filled to a depth of ca. 3 cm with a dilute soapy water solution (ca. 1 mL fragrance-free dish detergent in 250 mL water; Figure S1).

We used pole traps (inverted funnel traps) to collect arthropods that climb from the understory to the canopy via plant stems. Each pole trap consisted of an inverted funnel assembled from a 475 mL plastic bottle and secured 1 m above the ground on a PVC post (Figure S2). Each pole trap contained 20 mL of diluted soapy water (see above) and was positioned such that small arthropods ascending the post could easily enter. Pole traps provided a means to determine which fallen arthropods are likely to be lost in the understory versus those that fall and return to the canopy. They also provided a measure of general arthropod activity in the litter for comparison with arthropod rain.

Traps were arranged in pairs (one pan and one pole trap) at 15 stations approximately evenly distributed along the 150 m transect at each of the three sites on BCI (total $n = 45$ pan traps and 45 pole traps; 1 pair per station, 15 stations per site ×3 sites). One pan trap was suspended ca. 1 m above the forest floor at each station using fishing line tied to understory branches and lianas. Tangle-Trap (The Tanglefoot Company, Grand Rapids, Michigan, USA) applied to the fishing line prevented ants and other cursorial arthropods from wandering into the trap (Figure S1). One pole trap was inserted into the ground within 2 m of each pan trap. We measured canopy cover at each station using a spherical densiometer (model C; Forest Densiometers, Marianna, Florida, USA) on the first collection date. Four densiometer readings were recorded per station, one in each cardinal direction, and the average value was used as the datum for analysis.

TABLE 1 Transect sites on Barro Colorado Island, Panama.

Site code	Trail	Coordinates	Direction	Canopy cover (%)
W	W. M. Wheeler	9.16367° N, −79.84028° W	SW	97.3 (±2.3)
S	Snyder-Molino	9.15959° N, −79.83947° W	SW	97.0 (±2.1)
D	Donato	9.15885° N, −79.83543° W	SE	97.5 (±2.2)

Note: *Trail* = trail name. *Coordinates* = the latitude and longitude of the starting point for each transect. *Direction* = approximate ordinal direction of a transect from its starting point. *Canopy Cover* = average (±SD) percent canopy cover based on *n* = 15 densiometer readings per transect.

Traps were opened for two consecutive days each week for a total of 24 weeks distributed between 16 June and 22 November 2023. After each two-day trapping period, pan trap contents were poured through a 0.6 mm mesh sieve, and the arthropods and debris that were retained in the sieve were transferred to a plastic bag. Pans were then inverted to prevent capture until the beginning of the next two-day trapping period. The contents of each pole trap were poured into a plastic 50 mL centrifuge tube.

All collected trap contents were preserved in 90% ethanol and sorted in the laboratory. To avoid the confounding effects of insects flying into the traps or colonizing the trap water, all winged arthropods and larval Diptera were excluded from the trap data. Collected ants (Hymenoptera: Formicidae) were identified to species using various online and print resources (e.g., Bolton, 1994; Fernández & Guerrero, 2019; Ward, 2003) and reference collections from prior work at this site (e.g., Adams et al., 2017; Yanoviak & Kaspari, 2000); all other arthropods were identified to order. Arthropods collected in pan traps were grouped by taxon, dried at 60°C to a constant mass (>72 h), and weighed on an electronic balance to the nearest 0.1 mg.

Environmental data

Weather data for BCI spanning the timeframe of this study were obtained from the Smithsonian Tropical Research Institute data portal (Smithsonian Physical Monitoring Program, 2025). Rainfall data were sourced from the BCI Clearing Rain Gauge dataset, which provides high-resolution precipitation measurements at five-minute intervals. Wind data were obtained from the BCI Lutz Tower dataset, which records maximum wind speed at 48 meters above the forest floor at five-minute intervals.

For each two-day trapping period, we extracted the number of high wind-speed events (recordings in the 95th percentile), and the number of high-precipitation events (rainfall amounts in the 90th percentile). We focused on these variables rather than cumulative precipitation or absolute wind speeds because they are most likely to affect arthropod rain. Specifically, ants and other canopy arthropods seek shelter at the onset of a major rain event and remain sheltered until conditions become favourable (Corn, 1976; SY personal observation). Thus, the number of extreme events is more relevant to this study than the total amount of rain that falls while the arthropods are sheltered. Similarly, we assume that arboreal arthropods are accustomed to wind exposure; thus, the number of extreme wind events should be a reliable indicator of the frequency of especially challenging environmental conditions in the forest canopy.

Statistical analyses

All analyses were performed in R version 4.4.3 (R Core Team, 2025). We used generalized linear mixed models (GLMM) with negative binomial distribution ("glmmTMB" package; Brooks et al., 2017) to analyse variation in arthropod abundance for each trap type (pan and pole traps) separately. The model included canopy cover, the number of high-wind events, and the number of high-precipitation events as main effects. Trap location (i.e., site; Table 1) and collection date were included as random effects. Full models included all interactions of predictors, and final models were selected via stepwise reduction of terms based on Akaike information criterion (AIC) values and biological relevance.

We used a GLMM with gamma distribution and log link function to analyse the biomass of arthropods collected in pan traps. The full model included taxon in addition to the main effects and interactions used in the abundance models. As stated above, the final reduced model was based on AIC selection procedure and biological relevance; it included canopy cover, the number of high wind events, and the number of high-precipitation events as fixed effects, with collection date as a random effect. Raw biomass data were pooled by taxon per day.

We used permutational multivariate analysis of variance (PERMANOVA) to evaluate variation in arthropod composition for each trap type using the *adonis2* function from the "vegan" package. Differences in arthropod composition were assessed using a Bray–Curtis dissimilarity matrix, and stratified permutations were used to account for site-level differences. PERMANOVAs for each trap type tested for effects of canopy cover, maximum wind speed, high-wind events, cumulative precipitation, and high-precipitation events, although with different matrices to reflect the distinct arthropod assemblage captured in each trap type. Variation in arthropod composition was visualized with non-metric multidimensional scaling (NMDS) ordination.

RESULTS

Collectively, the traps used in this study captured 7243 wingless arthropods; 1548 occurred as arthropod rain in pan traps.

TABLE 2 Relative abundance of invertebrates captured in pan and pole traps.

Class	Order	Pan trap	Pole trap
Arachnida		**31.5**	**18.8**
	Araneae	3.1	2.6
	Ixodida	0	<1
	Mesostigmata	<1	<1
	Oribatida	16.9	10.9
	Trombidiformes	11.3	4.7
	Pseudoscorpiones	<1	<1
	Scorpiones	<1	0
Insecta		**66.4**	**4.9**
	Archaeognatha	<1	<1
	Blattodea	3.1	<1
	Coleoptera[a]	2.9	<1
	Hymenoptera	56.4	3.7
	Lepidoptera[a]	2.0	<1
	Mantodea[a]	0	<1
	Neuroptera[a]	<1	<1
	Thysanoptera	1.6	<1
	Orthoptera[a]	0	<1
Entognatha		**1.4**	**76.0**
	Entomobryomorpha	<1	36.2
	Poduromorpha	<1	4.1
	Symphypleona	<1	35.6
Isopoda		**0**	**<1**
Diplopoda		**<1**	**<1**

Note: Values are percent abundance within a trap type (i.e., each column sums to 100% before rounding). Cumulative values for higher taxa within a trap type are in bold.

[a] Larvae/juveniles.

TABLE 3 The taxonomic distribution of cumulative invertebrate dry mass in the invertebrate rain (pan traps only) collected in this study.

Class	Order	Dry weight (mg m^{-2} day^{-1})
Arachnida	Araneae	0.060
	Oribatida	0.005
	Trombidiformes	0.003
	Scorpiones	0.002
Insecta	Archaeognatha	0.001
	Blattodea	0.083
	Coleoptera[a]	0.004
	Hymenoptera	0.501
	Lepidoptera[a]	0.228
Diplopoda		0.004
	Total	**0.891**

[a] Larvae.

Hymenoptera (mostly ants; Formicidae) dominated the abundance of fallen arthropods, followed by oribatid mites and trombidiform mites (Table 2). The five most common ant species in pan traps were *Crematogaster acuta*, *C. limata*, *Technomyrmex albipes*, *Azteca trigona/chartifex*, and *Dolichoderus bispinosus* (Table S1). None of these species exhibits directed aerial descent (i.e., gliding) behaviour when falling.

The cumulative dry biomass of wingless arthropods collected in pan traps (pooled) was ca. 0.9 mg m^{-2} day^{-1} (Table 3). By extrapolation, an estimated 27 kg of arthropod biomass falls into the BCI understory per square kilometre per month during the wet season (9×10^{-7} kg $\times$ 1×10^6 m^2 $\times$ 30 days). This equates to 13.5 kg or ca. 3 million mid-sized ants (e.g., *D. bispinosus*; Stark et al., 2017) per day for BCI as a whole (1500 ha). Hymenoptera were the largest contributors, with ants representing over half of the arthropod rain biomass, followed by Lepidoptera (Table 3). The mass of individual ant workers spans five orders of magnitude among species (Kaspari & Weiser, 1999), and the majority of collected ant biomass was contributed by genera with medium to large-sized workers, specifically *Neoponera*, *Dolichoderus*, *Ectatomma* and *Paraponera* (Table S2). Although some *Neoponera* and *Dolichoderus* will spin (autorotate) when falling (Yanoviak et al., 2011), to our knowledge none of these genera includes gliding species.

EFFECTS OF ENVIRONMENTAL VARIABLES

Precipitation values for each 2-day trapping period recorded over the course of this study ranged from 0.00 to 54.72 mm (mean ± SD = 8.53 ± 13.03 mm), and maximum wind speeds ranged from 5.33 to 15.50 km h^{-1} (8.56 ± 2.29 km h^{-1}). Canopy cover at the trap locations was consistently high (mean: ~97%; range: 93%–99%) and did not differ among sites (one-way ANOVA: $F_{2,42} = 0.63$, $p = 0.54$; Table 1).

Arthropod abundance in pan traps marginally increased with the number of high-wind events ($\beta = 0.056$, $z = 1.879$, $p = 0.060$; Figure 1); however, the abundance of arthropod rain showed no relationship with the number of high-precipitation events (Table S3). The composition of arthropods in pan traps was consistent among sites (Figure 2), but changed with the number of high-wind events (pseudo-$F = 2.99$, $p = 0.002$; Figure 2, Table S4). Specifically, the abundance of ants and spiders occurring in pan traps over each two-day collection period increased with increasing frequency of strong winds (Figure S3). By contrast, the number of high-precipitation events had no significant effects on the composition of arthropod rain (Table S4). Finally, the dry biomass of arthropod rain collected in pan traps was not associated with collection date, canopy cover, or the number of high wind and rain events (Table S5).

COMPARISON WITH POLE TRAPS

Overall, pole traps captured more wingless arthropods than pan traps (Figure 3). Pole trap contents were dominated by small (<5 mm body

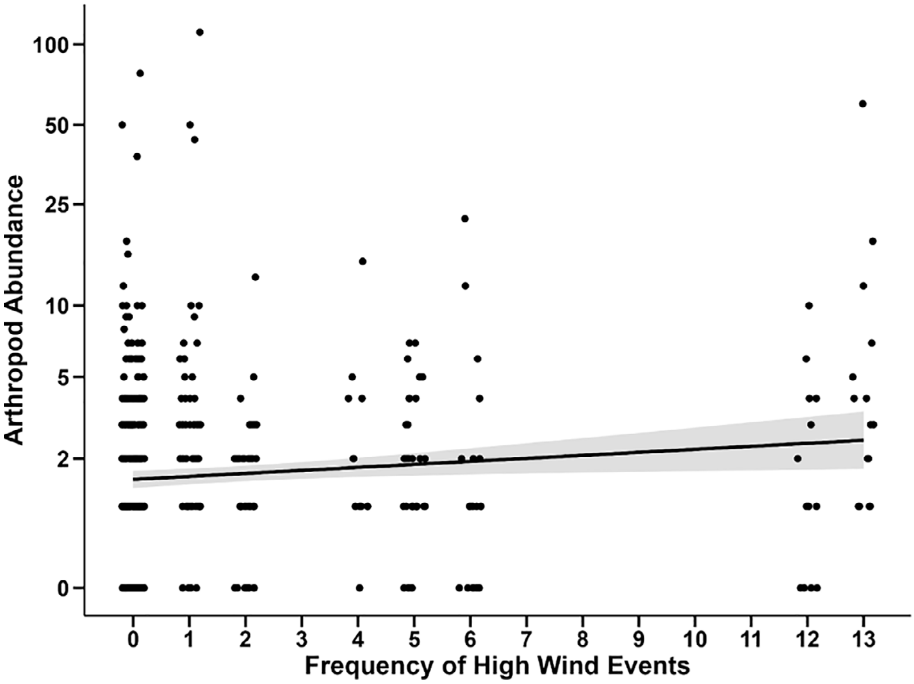

FIGURE 1 The relationship between the number of high-wind events and arthropod abundance in pan traps for each two-day trapping period. Shading indicates the 95% confidence interval. Some points are obscured by overlap. Regression line: Abundance = 0.787 + 0.056 × high-wind events.

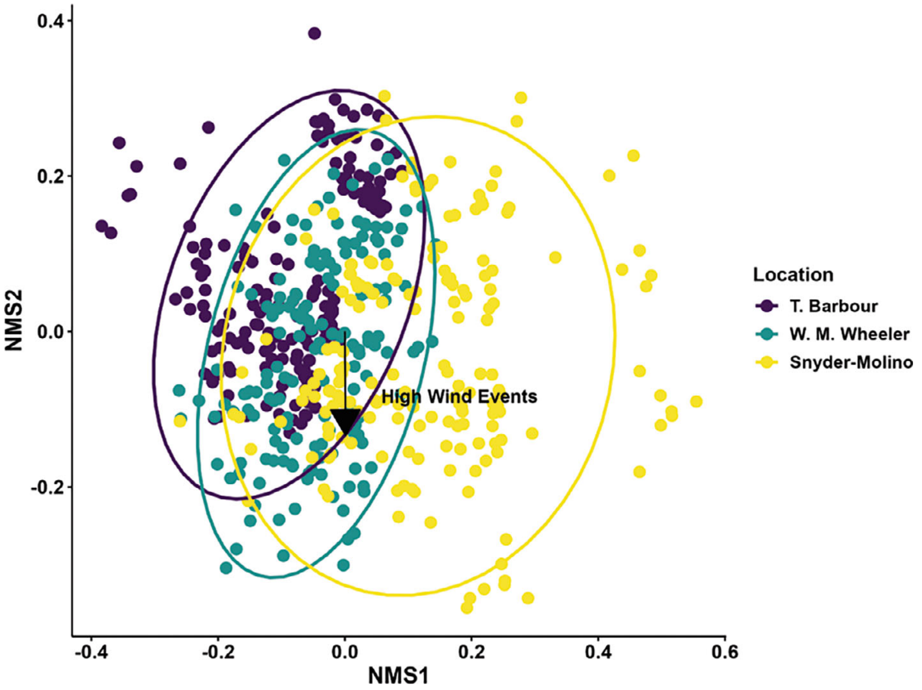

FIGURE 2 Non-metric multidimensional scaling (NMDS) ordination of arthropod composition in pan traps among the three collection sites (see Table 1). Points represent individual samples; ellipses indicate 95% confidence intervals around site centroids. The ordination is based on Bray–Curtis dissimilarity. The *High-Wind Events* vector illustrates the effect of the frequency of strong winds on arthropod composition (Table S4). Stress = 0.239.

length) ground- and litter-dwelling taxa, especially collembola and oribatid mites. Ants occurred in pole traps with relatively low abundance, but almost all ant genera occurring in pole traps also occurred in pan traps (*Paraponera* and *Acromyrmex* are the two exceptions that were absent from pole traps; Table S1). Three of the five most abundant ant species in pan traps (*Crematogaster acuta*, *C. limata* and

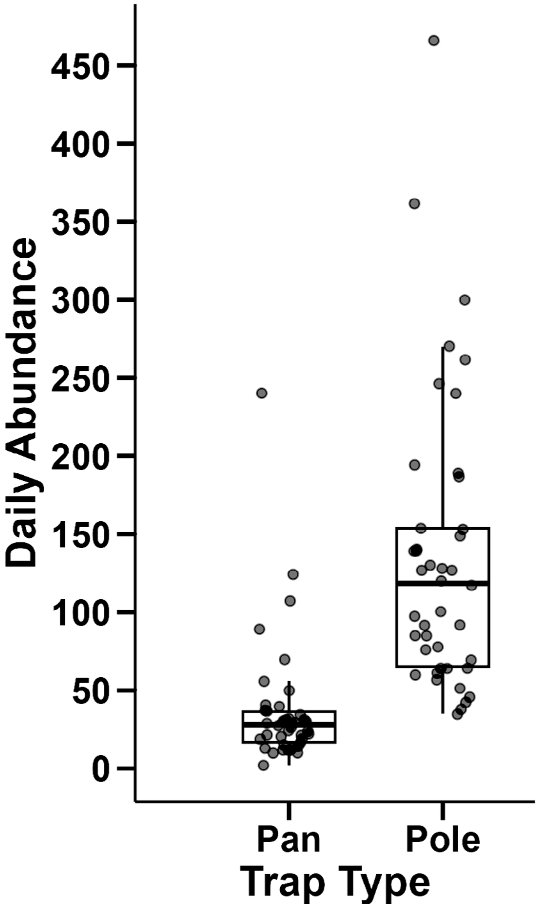

FIGURE 3 Box-and-whisker plots of the daily abundance of arthropods in the two trap types. Darker points indicate overlapping data.

Technomyrmex albipes) also were among the five most abundant ant species in pole traps (Table S1). The other relatively common ant species in pole traps were *Ectatomma ruidum* and *Pseudomyrmex oculatus* (Table S1).

As observed in the pan traps, the abundance of arthropods collected in pole traps was marginally affected by the number of strong wind events (Table S6). However, in this case, the trend was reversed: arthropod abundance in pole traps tended to decline with increasing frequency of strong winds ($\beta = -0.053$, $z = -1.722$, $p = 0.085$; Figure 4). Similar to the arthropods raining into pan traps, the composition of arthropods in pole traps was consistent among sites (Figure 5) and changed with the number of high-wind events (Table S7). This outcome was driven by the tendency for a decrease in the abundance of collembola (specifically Entomobryomorpha and Symphypleona) with increasing frequency of strong winds (Figure S4).

DISCUSSION

Although it is common to encounter a fallen canopy ant on one's shoulder while walking through lowland tropical forest, the results of this study suggest that the potential contribution of arthropod rain to litter food webs in these systems is quite small. For comparison, the arthropod rain biomass reported in this study is three orders of magnitude less than annual plant-derived litterfall in tropical forests (e.g., Wood et al., 2009). Similar to Yoshida et al. (2021), we found an abundance of mites and collembola moving toward the canopy. Although their collective mass is very small, this movement illustrates the complexity of vertical energy and biomass transfer in tropical forests.

The results of this study strongly suggest that arboreal arthropods are not commonly dislodged by strong rain events. Most canopy ants and other cursorial arboreal arthropods tend to seek shelter at the onset of rain (e.g., Corn, 1976), and suspend foraging for long periods following a rain event (SY personal observation). Under such circumstances, the intensity of precipitation becomes irrelevant. The results of this study also align with the findings of Yoshida et al. (2021), ultimately suggesting that rainfall has a limited role in directly dislodging arthropods from the forest canopy.

In contrast to heavy rainfall, strong wind events marginally enhance the abundance of arthropod rain (specifically ants and spiders). Presumably this is due to individuals becoming dislodged from leaves that are rapidly and unpredictably moved by gusts (Warren, 2015; Yamazaki, 2011). This is a likely scenario given that ants and other arthropods commonly take shelter on the undersides of leaves during storms (Corn, 1976; SY personal observation). Moreover, when strong winds co-occur with rain, a dislodged arthropod is unlikely to successfully land on and adhere to a wet leaf during a fall (Seiler, Stark, & Yanoviak, 2025a; Stark & Yanoviak, 2018).

The negative relationship between strong winds and arthropod (especially Collembola) abundance in pole traps seems anomalous given that the understory is largely sheltered from the effects of wind. However, the combined effects of breezy conditions and rain in the understory likely would suppress the activity of litter arthropods, reducing their abundance in pole traps (e.g., Cuff et al., 2023; but see Lensing et al., 2005). Regardless, experimental studies of the effects of strong winds (sustained or as gusts, with or without associated rainfall) on arboreal arthropods are needed to improve our understanding of this relationship.

The high abundance of ants in the arthropod rain collections was expected given that they are among the most abundant arthropods in lowland tropical forest canopies (e.g., Davidson et al., 2003). Gliding arboreal arthropods including certain species of ants (Yanoviak et al., 2005), spiders (Yanoviak et al., 2015), and jumping bristletails (Yanoviak et al., 2009), were underrepresented in the arthropod rain collected in this study. Gliding species are common in the BCI forest canopy (e.g., Adams et al., 2017; Yanoviak et al., 2005), but are unlikely to land in the understory following a fall. By contrast, the relatively high abundance of *Technomyrmex albipes* in both pan and pole traps was unexpected. This species was not found in prior ant surveys on BCI and nearby secondary forests (e.g., Adams et al., 2017; Adams, Gora, et al., 2019; Adams, Schnitzer, & Yanoviak, 2019; Yanoviak & Kaspari, 2000), suggesting that it recently invaded this site. The high abundance of *Crematogaster* ants in pan traps was somewhat

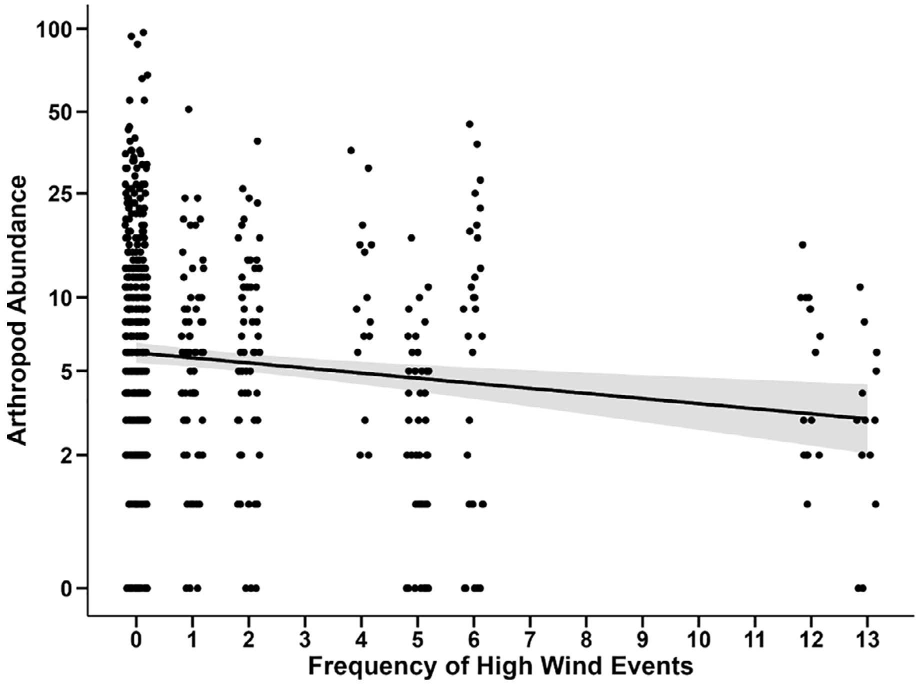

FIGURE 4 The relationship between the number of high-wind events and arthropod abundance in pole traps for each two-day trapping period. Shading indicates the 95% confidence interval. Some points are obscured by overlap. Regression line: Abundance = 2.124–0.052 × high-wind events.

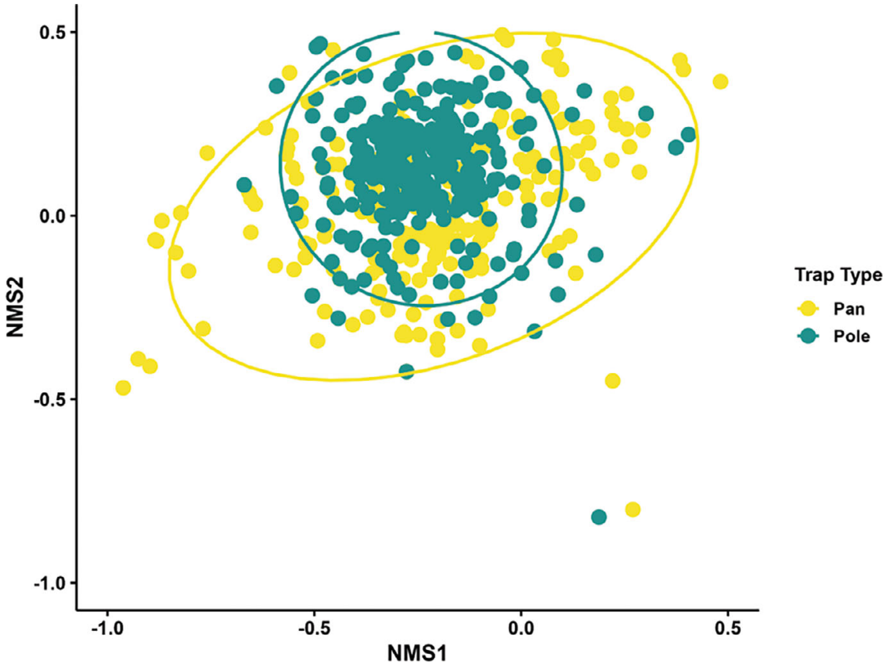

FIGURE 5 Non-metric multidimensional scaling (NMDS) ordination comparing arthropod composition in pan and pole traps. Points represent individual samples, with ellipses indicating 95% confidence intervals around the centroids for each trap type. The analysis was based on Bray–Curtis dissimilarity. The *high-wind events* vector illustrates the effect of the frequency of strong winds on arthropod composition (Table S7). Stress = 0.0016.

unexpected because they exhibit relatively strong tarsal adhesion (Stark et al., 2018), suggesting that they rarely fall from the canopy. Regardless, their abundance in pole traps indicates that living fallen workers readily return to the canopy.

The abundance of arthropods collected in pan traps in this study is comparable to the arthropod rain abundance reported for a Japanese cedar forest (Yoshida et al., 2021); however, the biomass of arthropod rain measured here is lower than that of other studies

(Chan et al., 2008; Rozanova et al., 2019; Small et al., 2013; Yoshida et al., 2021). We attribute this difference to at least three factors. First, this study focused exclusively on wingless arthropods, whereas other studies included winged individuals potentially attracted to traps. This difference is consequential because the presence of a single mid-sized adult beetle would increase the biomass value for a given trap by an order of magnitude. Second, the study took place during an El Niño event, which likely reduced overall arthropod activity by extending dry season conditions into the wet season (Newell et al., 2023). In particular, arboreal ants tend to shift their foraging to the understory during the dry season (Hahn & Wheeler, 2002), thus, it is possible that ant activity in the canopy during this study was lower than would occur during a typical wet season. Third, tropical ants demonstrate strong tarsal adhesion and versatility in locomotion over a broad range of substrates and conditions (Clay et al., 2010; Stark et al., 2017, 2018; Stark & Yanoviak, 2018, 2020; Yanoviak et al., 2017). As noted above, many tropical arboreal arthropods also glide during a fall. Thus, arthropod rain could be less abundant in tropical forests simply because tropical species tend to have enhanced fall-prevention and gliding traits relative to temperate species, although this remains to be studied.

Finally, variation in canopy cover within a forest is potentially relevant to arthropod rain. A denser canopy can increase the local abundance of arboreal arthropods, but it also increases the abundance of surfaces that can intercept or slow their descent. Precise vegetation measurements (e.g., LAI; Fang et al., 2019; Jennings et al., 1999), and vertical stratification of traps within the forest (e.g., Yoshida et al., 2021) would improve our understanding of the potential relationship between vegetation structure and arthropod rain.

CONCLUSIONS

Here, we provide the first quantification of arthropod rain for a lowland tropical forest—specifically, the mass of ca. 3 million mid-sized ants falls to the forest floor per day on BCI (27 kg km^{-2} per month). The lack of strong association between arthropod rain and the frequency of strong wind and rain events suggests that tropical arboreal arthropods are resistant to these common perturbations. The results raise at least three potential avenues for future research. First, given that both canopy arthropod behaviours and environmental characteristics differ between the wet and dry seasons on BCI (Hahn & Wheeler, 2002; Leigh et al., 1996; Smithsonian Physical Monitoring Program, 2025), a seasonal comparison of arthropod rain density likely would be informative. Second, differentiation between dead and living fallen arthropods (e.g., Rozanova et al., 2019) would improve the biomass estimate by allowing the exclusion of individuals that potentially return to the canopy. Finally, chemical analysis of fallen arthropods (e.g., Rozanova et al., 2022) would clarify their role in nutrient cycling within tropical forests. Ultimately, characterizing arthropod rain on BCI and at other tropical sites will improve our understanding of the challenges faced by arthropods inhabiting the forest canopy.

AUTHOR CONTRIBUTIONS

Andrew R. Seiler: Investigation; writing – original draft; methodology; visualization; formal analysis; data curation. **Alyssa Y. Stark:** Funding acquisition; project administration; writing – review and editing. **Stephen P. Yanoviak:** Conceptualization; funding acquisition; writing – review and editing; supervision; project administration; methodology; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest, and no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

Data from this study (Seiler, Stark, & Yanoviak, 2025b) are available from the Dryad Data Repository (https://datadryad.org/) with DOI: https://doi.org/10.5061/dryad.1zcrjdg54.

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SUPPORTING INFORMATION

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

Figure S1. Diagram (A) and image (B) of the pan traps used in the study.

Figure S2. Diagram (A) and image (B) of the pole traps used in the study. Each pole trap consisted of a 470 mL plastic bottle cut transversely into three sections. The top section was inverted and secured inside the bottle midsection with clear silicone caulk. The bottom section of the bottle was reattached to the midsection with tape and wire to create a hinged removable cap. The trap received ca. 20 mL soapy water and was positioned on a 5 cm-diameter PVC tube such that climbing invertebrates could enter from below.

Figure S3. Abundance of the four most common taxa in pan traps vs. the number of high wind events (wind speeds in the 95% quantile for each two-day collection period). Darker points indicate overlapping data.

Figure S4. Abundance of the four most common taxa in pole traps vs. the number of high wind events (wind speeds in the 95% quantile for each two-day collection period). Darker points indicate overlapping data.

Table S1. Relative abundance of ants captured in pan and pole traps. Values are percent abundance within a trap type (i.e., each column sums to 100% before rounding).

Table S2. The taxonomic distribution of cumulative ant dry mass in arthropod rain (pan traps only) collected in this study.

Table S3. GLMM results for arthropod abundance in pan traps. *High Precipitation Events* and *High Wind Events* refer to the number of high rainfall amounts (within the 90% quantile) or high wind speeds (within the 95% quantile) recorded for each two-day collection period, respectively.

Table S4. PERMANOVA results for pan traps. *High Precipitation Events* and *High Wind Events* refer to the number of high rainfall amounts (within the 90% quantile) or high wind speeds (within the 95% quantile) recorded for each two-day collection period, respectively.

Table S5. GLMM results for arthropod biomass in pan traps. *High Precipitation Events* and *High Wind Events* refer to the number of high rainfall amounts (within the 90% quantile) or high wind speeds (within the 95% quantile) recorded for each two-day collection period, respectively.

Table S6. GLMM results for arthropod abundance in pole traps. *High Precipitation Events* and *High Wind Events* refer to the number of high rainfall amounts (within the 90% quantile) or high wind speeds (within the 95% quantile) recorded for each two-day collection period, respectively.

Table S7. PERMANOVA results for pole traps. *High Precipitation Events* and *High Wind Events* refer to the number of high rainfall amounts (within the 90% quantile) or high wind speeds (within the 95% quantile) recorded for each two-day collection period, respectively.

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