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Spatial and seasonal taxonomic patterns in moth communities of the central Congo peatlands

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Tropical insect communities are highly diverse but understudied, limiting understanding of tropical forest ecosystem functioning. This is especially true of the swamp forests of the central Congo peatlands, where peat occurs beneath two widespread forest types dominated by either hardwood trees or *Raphia laurentii* palms. Here, we describe taxonomic patterns in moth community composition, vertical stratification and seasonality in these two peat swamp forest types and the nearby *terra firme* forest. From 16 636 specimens, we identified 1110 species/morphospecies. Both swamp forest communities were distinctive and relatively species-poor: the palm swamp supported an estimated 637 species (46–52% of nearby *terra firme* forest), while the hardwood swamp supported an estimated 828 species (56–67%). Major taxonomic associations for each habitat suggest host plant availability shapes species distributions. Plant defences in the nutrient-limited swamps may further suppress moth abundance. Seasonal patterns of abundance and richness in the swamp forests diverge from the *terra firme* forest, decreasing rather than increasing in the wet season. This probably reflects different seasonal plant growth patterns in waterlogged ecosystems. Vertical stratification was most pronounced in the palm swamp, indicating particularly inhospitable understory conditions. Our results reveal that distinct ecological pressures shape swamp forest insect communities, highlighting general differences in insect herbivore-mediated ecosystem functioning. A French translation of this abstract is available in the supplementary material.

This article is part of the discussion meeting issue 'African tropical peatlands: function, value and vulnerability'.

1. Introduction

Identifying the drivers that generate and maintain species diversity is a long-standing challenge in evolutionary and ecological science [1]. Tropical forests host an unrivalled richness of species, a large proportion of which are arthropods, most of which are insects [2,3]. Yet, despite their ecological importance, insects have received proportionally little research attention in these systems [4]. Within the tropics, studies within Africa are particularly under-represented [4,5,6]. The Congo Basin supports the second-largest contiguous tract of tropical forest on Earth, with the region experiencing low deforestation rates historically; however, increasing forest loss over recent decades [7] places its insect fauna at risk of rapid, undocumented loss [5].

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Lepidoptera (butterflies and moths) comprise an estimated 10% of insect diversity [8] and fulfill a range of key functional roles in tropical ecosystems. Moths are integral components in tropical forest trophic networks, participating in both top-down and bottom-up interactions, and serving as pollinators for diverse plant taxa [9–11]. As herbivores, plant diversity is often described as a fundamental predictor of moth diversity, with richer floras argued to provide larval resources to a broader range of species [12–14]. This may be particularly evident in tropical systems, where dietary specialization of larval herbivores is believed to be greater than in temperate regions [15,16], contributing to high spatial turnover in tropical forest moth communities [17]. The influence of plant diversity on moth diversity may be less clear at the local community scale in tropical forests however; for instance, if adult mobility obscures local patterns [18–20], or where only a subset of the total moth community, interacting with a subset of the plant community, is considered [21,22]. Studies with wider taxonomic scope highlight the contributions of taxonomically obscure and ecologically distinctive moth lineages in community-wide responses to plant diversity [19,20]. Resultingly, moth diversity often more closely responds to the functional diversity and structural complexity of tropical forest plant communities rather than plant diversity alone [20,21,23]. Major differences in habitat structure and vegetative composition may therefore drive shifts in the functional contribution of moths to ecosystem processes.

Observed patterns of moth richness are further modulated by community responses to seasonality in the regional climate and resulting local ecosystem dynamics, with the wet and dry seasons in tropical forests marked by changes in precipitation, humidity and temperature [24]. Seasonality of insect herbivores enables species to capitalize on annual patterns of plant resource availability. Abundances of Lepidoptera in tropical forests are commonly correlated with host plant resource availability, as indicated by greenness of vegetation, producing peaks in richness and abundance during the wet season [25–27]. Similarly, seasonality of floral resources is known to influence patterns of pollinator abundance and richness [28,29]. Additionally, fluctuations in temperature and humidity can directly influence activity patterns via physiological mechanisms or drive movement along ecological gradients [30,31]. With seasonal shifts predicted for tropical regions [32], understanding insect phenology at the habitat scale is increasingly essential for understanding the trophic consequences for wider ecosystems.

Tropical forests, with their vertical and horizontal structural complexity, produce stratified plant communities containing a diversity of microclimates and microhabitats [33,34]. These provide some insect herbivores with larval or adult feeding resources in the canopy that are unavailable closer to the ground, and vice versa [35–38]. Evidence for vertical stratification of forest moth communities is widespread across the tropics, with canopy assemblages found to be different, and in some cases more diverse, than sub-canopy strata [39]. The extent and direction of stratification varies between moth taxa, meaning that the patterns described for each community depend on the taxonomic scope of the study [40,41]. Higher abundance or richness towards forest canopies has been found for Sphingidae [37,42,43], Arctiinae [44,45] and Noctuidae [23,40], whereas understory preferences have been found for Crambidae [23] and Geometridae [23,40,44,45]. As a result, studies of moth ecology that fail to capture canopy diversity risk biasing their findings towards understory processes. Respective data on moth stratification from the Afrotropics are scarce, beyond a recent study in Cameroonian forests, which found some support for patterns observed elsewhere [23]. This scarcity limits our ability to generalize both African and global patterns of vertical stratification.

Within Africa, the ecology of the Congo Basin is poorly understood, particularly the area of swamp forest in the central Basin depression. Within this swamp forest, the world's most extensive tropical peatland complex was recently mapped [46]. The peatland area spans an estimated 167 600 km^2 across the Republic of the Congo and the Democratic Republic of the Congo [47]. These peatlands largely comprise two distinctive classes of swamp forest, dominated by either hardwood trees or *Raphia laurentii* palms, both with varyingly reduced understory vegetation and canopy complexity [46,48]. The peatland-forming swamp forests are currently largely intact, but they are increasingly threatened by concessions for logging, oil and mining as well as by the currently still highly uncertain hydrological changes linked to climate-driven shifts in rainfall expected for the Congo Basin [48–50]. While these peat swamp forests are known to support important populations of forest elephants (*Loxodonta cyclotis*) and lowland gorillas (*Gorilla gorilla gorilla*), their wider ecology is poorly documented, and their insect diversity remains entirely unknown [48,51,52]. This data gap contributes to a relative paucity of insect diversity studies across the entire Congo Basin and wider Central African forests [4,53], with questions remaining over a potential undocumented hotspot of moth diversity in this region [6].

In this study, we use the first systematic sampling of any insect group in the central Congo peatlands to examine the following questions: (i) what diversity of moths do the peat swamp forests support, and how do they compare in richness and composition to non-peatland *terra firme* forest? (ii) do peatland insect communities undergo different seasonal dynamics as a result of the unique abiotic pressures in the swamp forest as compared to the *terra firme* forest? and (iii) what contribution does vertical stratification of moth communities make to overall diversity across these differently structured forest types? To address these questions, we employ light trapping across wet and dry seasons to assess the diversity of all macro-moths across three established vegetation plots in *terra firme* forest, hardwood-dominated peat swamp forest and palm-dominated peat swamp forest in the Republic of the Congo. We expect moth diversity to follow known broad patterns in plant diversity, with the palm swamp forest supporting the fewest species, and the hardwood swamp forest intermediate between that and the nearby *terra firme* forest. Seasonality of moth communities was expected to be similar across all forest types, with diversity and abundance peaking in the wet season as observed widely across tropical forest regions [25–27]. We finally expect vertical stratification to follow the same pattern as overall moth diversity, resulting in diversity peaks linked to the complex closed canopy in the *terra firme* forest, in contrast to the semi-open canopy in the hardwood-dominated swamp forest, and the lower and more open palm-dominated swamp canopy showing the least pronounced stratification.

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Table 1. Empirical physical characteristics of the forest in each permanent vegetation plot. (Canopy height estimates follow [57].)

	palm swamp (EKG-03)	hardwood swamp (EKG-02)	*terra firme* (EKG-01)
stem density[a]	85	382	378
tree species richness[a]	21	32	45
tree basal area (m^2) [a]	7.6	29.7	25.3
mean canopy height (m)	9.0[b]	18.2	26.5
maximum peat depth (m)	3.0	1.8	N/a

[a]Based on stems above 10 cm dbh recorded in most recent census (March 2021).
[b]Mean height of palm frond canopy.

2. Methods

(a) Study site and habitat description

This study was conducted in the Likouala department in the northeast Republic of the Congo. Mean annual rainfall is approximately 1700 mm and bimodally seasonal, with peaks in April–June and October–November (supplementary material, figure S1). The mean regional annual temperature is 25.6°C [54].

Sampling was carried out within three long-term 1 ha forest inventory plots established west of the Oubangui River, approximately 40 km south of Impfondo and closest to the village of Ekolongouma (supplementary material, figure S2). These plots represent three ecosystem types: (i) *R. laurentii* palm-dominated swamp forest, called EKG-03; (ii) hardwood-dominated swamp forest, called EKG-02; and (iii) non-peat-forming *terra firme* forest, called EKG-01, which provides a point of comparison to the two swamp forest ecosystems. Areas of palm- versus hardwood-domination form a patchy matrix at the local and interfluvial scale, while the *terra firme* forest is found adjacent to the swamps along the Oubangui River, but not within the peatland area [46,48,55]. The three inventory plots are located along a transect established by researchers from the CongoPeat research group in 2019, within forest areas matching habitat descriptions for the three ecosystem types described by Dargie [56]. The precise location of the inventory plots within respective habitat areas was selected randomly, by generating a random distance between 0 and 1000 m along the transect from the first transect interval matching habitat description, followed by a random compass bearing dictating the first clockwise boundary of a 100 x 100 m^2 plot (G. Dargie 2022, personal communication). Along the transect line, the palm swamp plot sits approximately 500 m from the nearest hardwood-dominated swamp forest area, 2000 m from the hardwood swamp plot and 3500 m from the nearest *terra firme* forest (supplementary material, figure S2).

EKG-03 is dominated by *R. laurentii*, a trunkless palm, forming an open canopy with a mean height of 9 m, with a low density of occasionally-emergent hardwood trees (mean height 17.6 m; estimates following [57]. As of 2021, the plot supported 85 stems at least 10 cm in trunk diameter, belonging to 21 species, with a maximum peat depth of 3.0 m (table 1). EKG-02 is dominated by dicot trees and has a mean canopy height of 18.2 m, supporting 382 stems (10 cm diameter at breast height (dbh)) representing 32 tree species as of 2021, with a maximum peat depth of 1.8 m. EKG-01 is characterized by a closed canopy forest on mineral soil, with no peat present. The mean canopy height is 26.5 m with emergent trees reaching 35 m. The 2021 census recorded 378 stems (10 cm dbh) of 45 tree species (table 1).

Across both swamp forest types, the water level has been recorded from 0.74 m below the surface to 0.24 m above the surface (supplementary material, figure S1), and is typically below the surface from January to May and above the surface from June to December. Many swamp forest trees display adaptations to permanently waterlogged conditions, such as buttresses and stilt or aerial roots. The mean groundwater pH is 3.1–3.2 across both swamp forest plots. The *terra firme* plot has no open water within 500 m. Full physical and floristic descriptions of each can be found in the supplementary material, appendix SI.

(b) Moth sampling

Moth sampling was carried out over two periods: during the middle of the long dry season in January and February 2022, and during the short wet season in May–June 2023 (full dates and locations are detailed in the supplementary material, table S1). Sampling was carried out over four consecutive nights in each of the three forest plots in each season, unless stormy weather caused a delay, in which case sampling resumed on the next night without storms. This sampling protocol was conducted a second time in the *terra firme* forest in 2022 with three weeks' separation, with the intention to capture community changes following the arrival of rain after four weeks without precipitation. Controlling for ideal or similar weather or lunar phase conditions across all samples was not possible owing to constraints on sampling period and swamp plot access.

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On each sampling night, moths were sampled using light traps at two opposing corners of the 1 ha vegetation plots, with traps rotated through the four plot corners across sampling dates. One light trap was set in the understory with the lamp at 1.5 m above ground/water level, while the other was set in the canopy (14–16 m elevation in the hardwood swamp and *terra firme* forest plots; 10–12 m in the palm swamp). Moths were attracted using LepiLED *mini* UV lamps [58], captured using polypropylene funnel traps and euthanized in a 5 l holding bucket connected via a wick to a reserve of 99.0% chloroform. Lamps were illuminated from dusk until collection at 09.00 the following morning, a total of 15 h per trap per night.

Three dry season samples were incomplete owing to technical failure: one canopy trap in each of the *terra firme* forest and hardwood swamp, and one understory trap in the palm swamp experienced mid-sample power loss. In total, 53 complete and three incomplete moth trap samples were made across both seasons.

(c) Sample sorting and identification

All moth specimens were stored in glassine envelopes, dried using a firewood-heated drying oven and preserved with silica crystals. In the laboratory, dried specimens were sorted into familial groupings. Moths belonging to superfamilies within Macroheterocera as well as all members of Cossoidea, Pyraloidea, Sesioidea and Zygaenoidea were retained together with large and distinctive specimens of 'micro-moth' families, such as Tortricidae. Very small individuals from micro-moth families, and indistinct macro-moths lacking identifiable characteristics owing to damage in the trap or transit, were separated and excluded from further analyses.

Retained specimens were then sorted into morphospecies based on external morphology in consultation with taxonomic resources and museum collections (supplementary material, appendix SII). For each morphospecies, at least one best-preserved individual was pinned, spread, identified and retained in a reference collection. All remaining specimens were then re-sorted based on the finalized taxonomic classifications and counted for each trap sample. Identifications did not use genitalia dissection or genetic species determination owing to time and resource constraints. Accordingly, where positive identification was not possible, morphospecies delineations are conservative to minimize the overestimation of richness, although some highly variable or polymorphic species may still have been incorrectly separated [59,60]. Given the limited taxonomic resolution for some groups, underestimation of true species richness is more likely [61], but this is not expected to exert a significant influence on diversity patterns across habitats or seasons.

(d) Data analysis

All data analysis was conducted in R 4.4.1 [62]. Estimates for asymptotic species richness, and corresponding sampling completeness, were calculated using two estimators. Firstly, we calculated the bias-corrected (non-parametric) Chao1 estimator in the package *iNEXT* [63]. This indicator is suited to poorly-sampled communities with many singletons and doubletons and generates 'lower boundary' estimations of species richness. Secondly, the parametric 'total expected species' estimator based on species' abundance accumulation models developed by Zou *et al.* [64], which aims to estimate the *total* species richness of the sampled area, was computed. Their 'TES_{ab}' estimator, which takes the midpoint from two models with different assumptions and performs well in datasets with under 50% sampling completeness, was used for all sites based on recommendations by Zou *et al.* [64]. The package *vegan* [65] was used to estimate species richness at a constant rarefied sample size of 1000 individuals, enabling comparisons with prior publications, and to produce species accumulation curves.

Differences in abundance and species richness across forest types, sampling season and forest strata were assessed using negative binomial generalized linear models (NBGLMs) fitted to per-trap richness and abundance data, using the package *MASS* [66]. Models were fitted with forest type, season and trap height (understory/canopy) as interacting fixed effects, with the default log link function. These models were selected to account for overdispersion of the trap data and performed better, based on critical Akaike information criterion (cAIC) values, than standard generalized linear models using the Poisson distribution. To explore pairwise differences in samples between forest types and forest strata within seasons, and between those for each forest type between seasons, post hoc tests were performed using the *emmeans* package [67], applying the Tukey *p*-value adjustment to minimize type I errors. To provide insight into the contribution of sampled abundance to observed richness patterns, the package *vegan* was used to calculate mean per-trap values of Fisher's α diversity index [68]. Differences in Fisher's α across forest types and seasons were assessed using a generalized linear mixed-effect model (GLMM) with a Gamma error distribution and log link in the package *lme4* [69]. Site and season were included as non-interacting fixed effects and date as a random effect, selected based on cAIC and model diagnostics, with post hoc tests performed with *emmeans* with Tukey adjustment. Patterns of abundance and richness between forest strata for each major family were also examined using GLMMs, assuming Poisson-distributed data as they displayed suitable dispersion patterns.

Differences in taxonomic composition between samples were firstly described at the level of family. Families with fewer than 10 species or fewer than 50 individuals were pooled together into an 'other families' classification. The subfamily Arctiinae was separated from other Erebidae owing to the abundance and ecological distinctiveness of the group, with the Arctiinae tribe Lithosiini further separated from other Arctiinae for the same reasons. Overall, 14 taxonomic groupings were used for compositional analyses.

Assessments of distinctiveness of the moth communities in each forest type, and in each stratum for each forest type, were performed using non-parametric permutational multivariate analysis of variance (PERMANOVA) tests in the package *vegan*, using the Bray–Curtis dissimilarity index with 9999 permutations. The influence of individual trap samples on overall patterns

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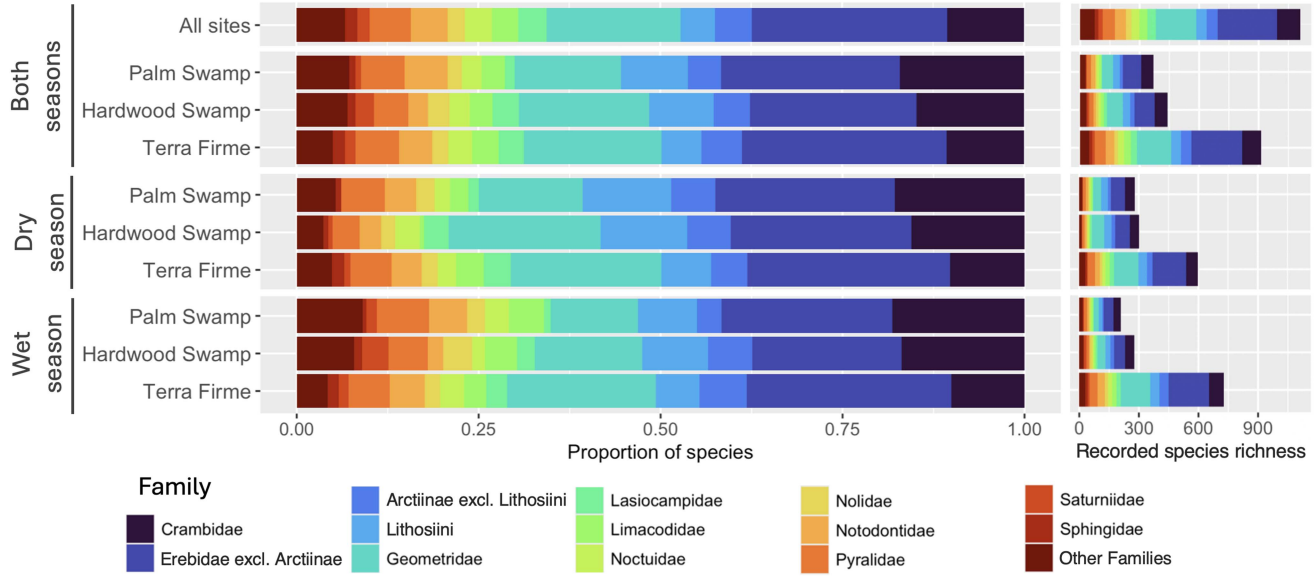


Figure 1. Familial proportions of moth species richness for data pooled across all sampling, data for each forest type and for each forest type split by season, plus a bar chart showing the overall recorded species richness in each subsample. For palm and hardwood swamp samples $n = 8$ for each season ($n = 16$ for combined seasonal data). For *terra firme* forest samples, $n = 16$ for dry season samples and $n = 8$ for wet season samples ($n = 24$ for combined seasonal data).

of community composition was assessed using non-metric multidimensional scaling (nMDS) ordination based on Bray–Curtis dissimilarities of family-level moth abundances, using the *MASS* package [66]. To identify habitat and stratum associations of higher taxonomic groups, indicator species analysis (indicator value (IndVal)) was performed using the package *indicspecies* [70]. The highly conservative Bonferroni correction was used to reduce the risk of type I errors, adjusting the significance threshold of p -values by dividing by the number of tests performed.

The chord-normalized expected shared species (CNESS) dissimilarity metric was used to characterize species turnover between forest types (beta diversity). Allowing dissimilarity between unequally sampled communities to be quantified, CNESS was calculated using the function described by Zou & Axmacher [71]. The CNESSa index, quantifying dissimilarity between 0 and 1, includes a sample size parameter (m) which calculates the probability that m specimens randomly drawn from both incomplete samples represent the same species, hence describing the (dis)similarity in dominant species for small m values or across the entire community for large m values. Here, pairwise CNESSa values between forest types were calculated for 30 logarithmically spaced values of m up to the maximum possible (the total sampled abundance in the forest type with the second highest abundance).

3. Results

(a) Sampled and estimated richness and diversity

A total of 18 887 individual moths were recorded across all light trap samples ($n = 56$). Of these, 16 636 specimens were identified to the level of family or lower (88.1%), while 2251 individuals were either too small or too degraded to be identified (11.9%). Across all forest types, moths were identified as belonging to 1110 morphospecies in 30 families (supplementary material, figure S3). Of these morphospecies, 293 (26.4%) were confidently identified as recognized species, while a further 333 (30.0%) were assigned to recognized species but would require genetic identification or dissection for final confirmation. A further 353 (31.8%) morphospecies were identified to genus level only, while the remaining 131 morphospecies (11.8%; from here *species*) could only be assigned to their specific subfamily.

Erebidae, Geometridae and Crambidae were the most abundant families (46%, 17% and 13% of total identified samples, respectively), each being found in all 53 complete trap samples and together representing 76% of sampled individuals and 66% of all species (figure 1). Eleven families were present in all forest types and all seasons. Ten families were represented by fewer than 10 individuals. Thirty-one per cent of all recorded species were represented by only one specimen across all 56 trap samples ('singletons'; 347 individuals, 2% of identified individuals and 31% of species), with this proportion above 50% in several seasonal subsamples (supplementary material, figure S4). Fourteen per cent of sampled species were recorded just twice across all samples ('doubletons'; 2% of identified individuals, 14% of species).

Sampled moth species richness was highest in the *terra firme* forest at 914, intermediate in the hardwood swamp with 441 recorded species, and lowest in the palm swamp at 370 (figure 1 and table 2). Both Chao1 and TES_{ab} species richness estimators reproduced these patterns (table 2). Estimated moth richness in the palm swamp was 46–52% of the richness estimated for the *terra firme* forest, with hardwood swamp moth communities estimated to be 56–67% as rich as the *terra firme* forest. Both estimators

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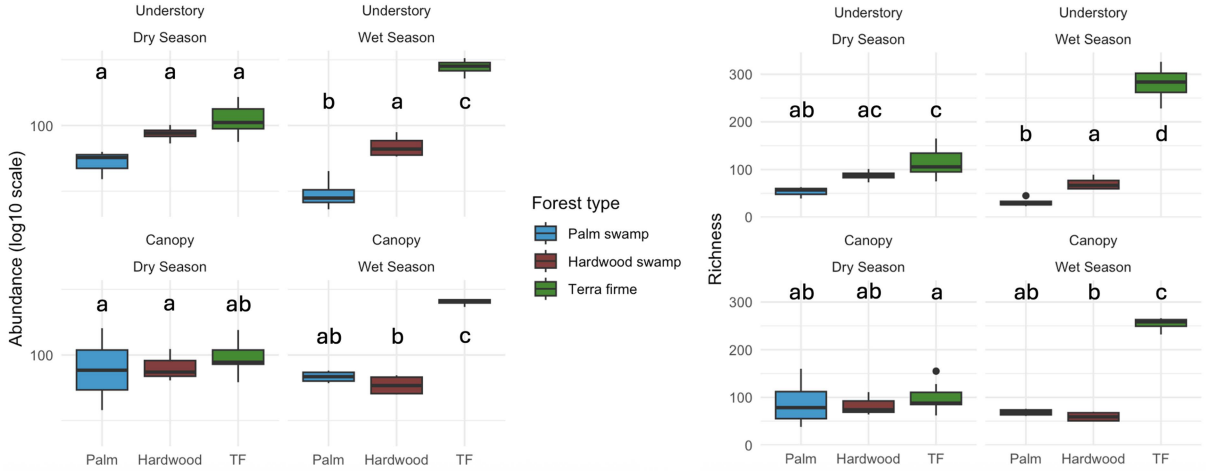


Figure 2. Boxplots representing medians and distributions of abundance and species richness per trapping event for each combination of sampling treatments. Letters indicate significant differences between subsamples across wet and dry seasons for each forest strata, as determined by post hoc pairwise comparisons based on NBGLMs for each dataset.

Table 2. Sampled abundance, richness and rarefied richness of macro-moths for each forest type and for pooled data, as well as two estimates of species richness and corresponding sampling completeness (%, bold) for each. (Note that Chao1 is a lower boundary richness estimator, whereas TES_{ab} attempts to estimate true richness [64]. Rarefied richness describes the expected number of species in a sample of 1000 individuals.)

	sampled abundance	sampled richness	rarefied richness	Chao1			TES_{ab}		
				estimate	%	s.e.	estimate	%	s.d.
palm swamp	2703	370	230	574.5	**64.4%**	44.2	637.4	**58.0%**	26.1
hardwood swamp	3098	441	249	691.6	**63.8%**	48.0	828.2	**53.2%**	102.3
terra firme	10835	914	339	1239.6	**73.7%**	51.0	1232.5	**74.2%**	107.9
all sites	16636	1110	346	1496.4	**74.2%**	55.6	1491.8	**74.4%**	134.1

show sampling completeness in each forest type above 50%, and above 70% for the *terra firme* forest, although species accumulation curves show no plateau for any forest type (supplementary material, figure S5).

Richness estimates for all three sampled areas combined suggest the palm swamp supports 38–43% of species across the three forest plots, while the hardwood swamp plot supports 46–56% of species, and the *terra firme* forest should support 83% of species when assuming 100% regional sampling completeness. Rarefaction to standardized samples of 1000 individuals also showed the swamp forest communities to be species-poor, with the *terra firme* forest 47% richer than the palm forest and 36% richer than the hardwood swamp forest. Eighty-five species were exclusively found in the palm swamp, 87 only in the hardwood swamp and 517 only in the *terra firme* forest.

(b) Patterns of richness, abundance and diversity

The NBGLMs fitted for abundance and species richness per trapping event indicated significant effects of forest type, season and forest strata, as well as complex interactions between each. Across treatments, pairwise Tukey-adjusted comparisons indicated that per-trap richness and abundance were each significantly higher in the *terra firme* forest than both swamp forest types, while richness alone was significantly lower in the palm swamp than the hardwood swamp. In the palm swamp, both richness (Est = 0.65, z-ratio = 4.91, $p < 0.0001$) and abundance (Est = 1.04, z-ratio = 5.14, $p < 0.0001$) were higher in the canopy than the understory, while no significant differences were found between strata for the hardwood swamp or *terra firme* forest.

Regarding seasonality, moth abundance was significantly lower in the wet season for both swamp forest types (palm swamp: Est = 0.97, z-ratio = 4.78, $p < 0.0001$; hardwood swamp: Est = 0.99, z-ratio = 4.92, $p < 0.0001$), but was significantly higher in the wet season for the *terra firme* forest (Est = 1.44, z-ratio = 8.59, $p < 0.0001$). Significant seasonal differences in species richness were found only for the *terra firme* forest, with higher richness in the wet season (Est = 0.92, z-ratio = −9.16, $p < 0.0001$).

Post hoc pairwise comparisons of richness and abundance between forest types and strata within each season (figure 2) reproduced some of these patterns, but the only statistically significant differences observed in the dry season were a product of the low richness of palm swamp understory traps. In the wet season, moth richness and abundance at both understory and canopy

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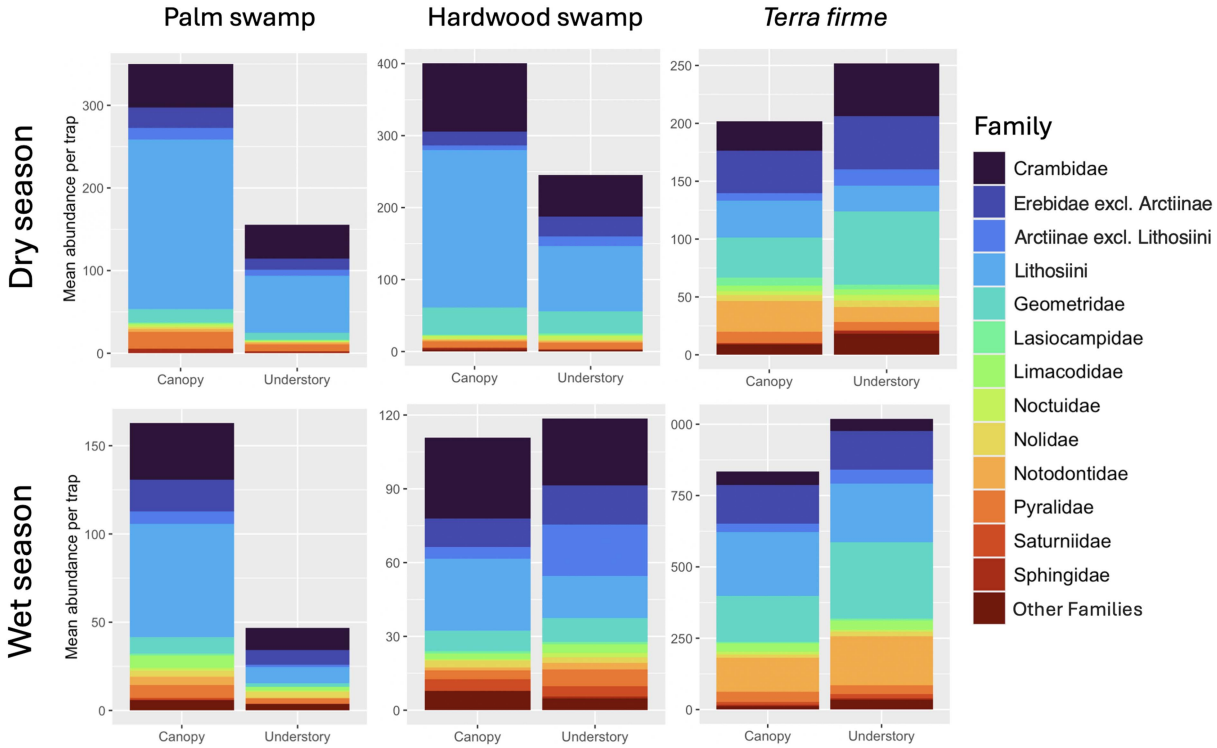


Figure 3. Mean familial abundances per complete trap across trap treatments, splitting by forest type, height and season. The scale of the *y*-axis differs between forest types and seasons, owing to the drastic differences in total per-trap mean abundances. Similar plots with uniform scales can be found in the supplementary material, figure S8.

terra firme traps were significantly higher than all other trap groups, while palm swamp understory trap samples again showed significantly lower values. The higher per-trap abundance (wet season) and richness (both seasons) in canopy versus understory traps in the palm swamp were the only significant differences between the two strata found across all forest types (not represented in figure 2).

In the dry season, per-trap values of Fisher's α (supplementary material, figure S6; all values mean ± s.d.) were lowest in the palm swamp ($\alpha = 36.6 \pm 13.3$), intermediate in the hardwood swamp ($\alpha = 43.9 \pm 10.4$), and highest in the *terra firme* forest ($\alpha = 95.8 \pm 14.6$; late dry season $\alpha = 83.9 \pm 16.8$). Fisher's α was significantly higher in the wet season for all three forest types, contrasting with the raw richness patterns for both swamp forest types, although this was more weakly pronounced in the palm swamp ($\alpha = 45.8 \pm 10.3$) and hardwood swamp ($\alpha = 65.3 \pm 23.2$) than in the *terra firme* forest ($\alpha = 128.0 \pm 7.2$).

(c) Habitat-specific taxonomic differentiation

Significant differences in taxonomic composition were found between the three forest types at species, genus, subfamily and family level (PERMANOVA: $R^2 = 0.17$–0.19, $F_{2,53} = 5.45$–6.40, $p < 0.001$; supplementary material, table S2; figure 3). An nMDS ordination (supplementary material, figure S7) showed clear site-based clustering of trap samples, suggesting the observed differences in composition are not driven by single-trap outliers but instead reflect consistent assemblage differences among forest types. Three outliers observed in the nMDS comprise the incomplete samples where traps failed midway through the night, and these are excluded from the compositional analyses below, owing to expected taxonomic biases in flight timings between different groups [72].

IndVal indices identified several strong forest type associations at family and subfamily levels (table 3). Notodontidae and Sphingidae, as well as their major constituent subfamilies, were strongly associated with *terra firme* forest, along with the Erebid subfamilies Aganainae, Erebinae, Anobinae, Pangraptinae and Rivulinae, and the Arctiine tribes Arctiini and Amerilini. No families or subfamilies were specifically associated with either swamp forest type. However, several taxa were significantly associated jointly with *terra firme* and hardwood swamp forest, suggesting big differences in taxonomic composition between these forest types and the palm swamp forest. The taxa associated with both hardwood and terra firme forest types include the families Lasiocampidae and Saturniidae with their major constituent subfamilies, as well as the two largest Geometrid subfamilies Ennominae and Geometrinae (comprising 140 and 33 local species, respectively), plus the Erebidae subfamily Lymantriinae. No other families or subfamilies showed significant (Bonferroni-adjusted) habitat associations.

(d) Dissimilarity between forest communities

Overall, a high degree of dissimilarity existed across communities representing the different forest types, as indicated by the CNESS dissimilarity index (figure 4). CNESS calculates the probability that *m* specimens drawn from two incomplete samples

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Table 3. Significant family- and subfamily-level habitat associations, following Bonferroni correction for 30 families (threshold $p < 0.0017$) and 74 subfamilies (threshold $p < 0.0007$). (Habitat associations of the four tribes of the Erebid subfamily Arctiinae were also assessed, at the same significance threshold, owing to their high relative abundance and ecological distinctiveness.)

forest type(s)	family	subfamily	IndVal	*p*
terra firme	**Notodontidae**		0.977	0.0001
		Thaumetopoinae	0.997	0.0001
		Notodontinae	0.976	0.0001
		Pygaerinae	0.804	0.0001
	Sphingidae		0.808	0.0001
		Smerinthinae	0.771	0.0008
	Erebidae			
		Aganainae	0.901	0.0001
		Erebinae	0.889	0.0002
		Anobinae	0.850	0.0001
		Pangraptinae	0.730	0.0002
		Arctiinae: Arctiini	0.766	0.0001
		Rivulinae	0.724	0.0004
		Arctiinae: Amerilini	0.661	0.0006
terra firme and hardwood swamp	**Lasiocampidae**		0.870	0.0001
		Lasiocampinae	0.870	0.0004
	Saturniidae		0.818	0.0004
		Saturniinae	0.818	0.0002
	Geometridae			
		Ennominae	0.980	0.0001
		Geometrinae	0.933	0.0004
	Erebidae			
		Lymantriinae	0.969	0.0001

belong to the same species, thus describing the dissimilarity in dominant species (small m values) or across entire communities (large m values). Species compositions of the two swamp sites differed particularly strongly from communities in the *terra firme* plot, and this dissimilarity was most pronounced with respect to dominant species (i.e. $m < 10$). Increased weighting of rarer species (increasing m values) decreases this dissimilarity, reflecting a higher similarity of more completely sampled moth communities. By contrast, the two swamp forest types are at their most similar in relation to their dominant species (low m values), becoming increasingly dissimilar as the sample size widens.

(e) Vertical stratification

According to our PERMANOVA analysis (supplementary material, table S3), there were no detectable differences in the composition of canopy versus understory communities in the hardwood swamp and *terra firme* forests. By contrast, the moth community sampled in the canopy of the palm swamp was differently structured from understory communities at the family, subfamily and genus level in this habitat, while at the species level this difference is not significant ($p = 0.054$). No significant strata associations were found for families or subfamilies based on IndVal analysis, either when combining data across sites or when considering each forest type individually.

Patterns of stratification in abundance and richness were found to vary across families, other higher taxonomic ranks and forest types, as indicated by GLMMs (see the supplementary material, table S4). Of the three families with significant abundance

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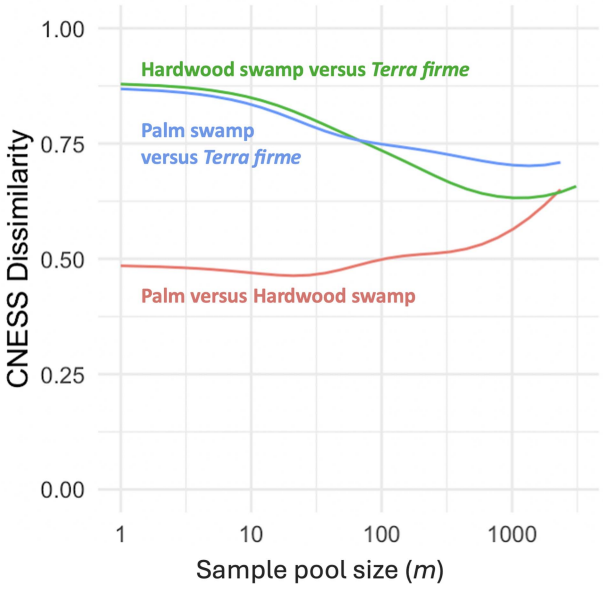


Figure 4. CNESS dissimilarity for each pairwise combination of species-level assemblages, across the possible range of values for *m* (sample size). Estimated dissimilarities are scaled between 1 (totally dissimilar) and 0 (identical).

distributions in all three forest types, only patterns for Lithosiini were consistent, with the tribe more abundant in the canopy across all sites. Crambidae were significantly more abundant in the canopy than in the understory for both swamp forest types, but the opposite pattern was found in the *terra firme* forest. Arctiinae (excluding Lithosiini) were more abundant in the understory of the hardwood swamp and *terra firme* forests, but showed a preference for the canopy of the palm swamp. Five families (Erebidae, Geometridae, Limacodidae, Notodondidae and Pyralidae) were more abundant in the canopy than in the understory of the palm swamp, with no families showing the opposite stratification pattern. This contrasted with higher abundance in the understory for Erebidae in the hardwood swamp forest, and for Geometridae and Notodontiidae in the *terra firme* forest. The pooled abundances from other families were also significantly higher in the understory of the *terra firme* forest.

The palm swamp canopy had a higher species richness of Crambidae, Erebidae (excluding Arctiinae), Lithosiini, Notodontidae and Geometridae than the understory. Only Arctiinae (excluding Lithosiini) had significant richness patterns in the hardwood swamp where they were richer in the understory. Significant richness stratification in the *terra firme* forest was found for Geometridae and non-Lithosiini Arctiinae, both of which were richer in the understory.

4. Discussion

(a) Diversity and composition of moths in peat swamp forests

The richness of moths we report from the *terra firme* forests of this newly sampled central Congo region is broadly comparable to similar forests in other tropical regions. For instance, a study using DNA barcoding to estimate macro-moth richness in lowland Gabonese rainforest produced 823 barcode index numbers (used as a proxy for species; [6]), whereas we found 914 (morpho)species in our *terra firme* forest. This would suggest the richness we found in the *terra firme* forest in Congo is broadly representative of wider Guineo-Congolian lowland forests. Elsewhere, a similar study of macro-moths in Malaysian rainforest sites found rarefied richness values standardized to 1000 individuals ranging from 290 to 475 [6,39], comparable to the rarefied richness estimate for the *terra firme* forest in Congo (339 species) reported here. By contrast, the swamp forests of the central Congo peatlands are found to support remarkably depauperate moth communities. This low richness stands not only in comparison to the nearby *terra firme* forest (best estimates of 52 and 67% of *terra firme* richness for palm and hardwood swamps, respectively), but also when comparing rarefied richness estimates (230 and 249 for palm and hardwood swamps, respectively) to Malaysian forest sites (290–475). Our results mirror the findings from a study of moth richness in a peatland forest in Kalimantan, Indonesia, where moth richness in the peat-swamp forest was just 36% of the richness of nearby secondary forest [73], although a deeper exploration of the Southeast Asian peatland moth fauna is required for further comparisons to be made.

The reported morphospecies richness in this time-limited study (1110 species caught across the 53 complete and three incomplete samples) clearly exceeds the entire number of species and subspecies of moths previously reported for the Republic of the Congo (1024; supplementary material, table S5). Combined with the high proportion of singletons (31%) and doubletons (14%), this highlights the prevailing extreme undersampling of these hyperdiverse Lepidoptera communities in the Congo Basin [74,75]. However, the rarefied richness estimates from our *terra firme* plot firmly refute the existence of a previously unknown hotspot of moth diversity in Central African forests. Rather, this suggestion from Delabye *et al.* [6] is a product of inflated Chao1 estimates owing to their selective sampling methodology.

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Beyond overall richness, Congo peatland swamp forest moth communities are highly compositionally distinct from those in nearby *terra firme* forest. Estimates of the total species richness and the incomplete overlap in the underlying species pools suggest that the swamp forests support unique species sets which are not mere filtered subsets of nearby non-swamp forest communities. This contrasts with the emerging view of the composition of the tree communities in this region, where swamp forest tree communities are composed of a subset of widespread tree species, rather than of peatland specialists [76]. The composition of the wider plant community is considerably less well described, however. Given that the central Congo peatlands are likely to have been ephemeral over evolutionary timescales [46,49], there may be few endemic plants. Any endemics present are more likely to be in the non-tree flora [77], which could allow suites of associated insect herbivores to persist. For instance, most caterpillars in the Crambid subfamily Acentropinae feed on aquatic macrophytes as larvae [78], but the group is very poorly known from Africa, with the 25 morphospecies identified in this study representing up to 43% of the entire known African fauna [79], and potentially representing a largely undescribed fauna specialized to the acidic swamp conditions.

Plant community composition is regarded as a strong ecological predictor of moth community composition [20,21,80], and while causal links have not been proven, we interpret the low moth species richness in the swamps to be a primary consequence of the low species richness of the plant communities. This is seen most distinctly in the near total absence of several important moth taxa from the compositionally and structurally simplified palm swamp, which can be linked to their larval ecologies. Lasiocampidae, Lymantriinae and the Geometrid subfamilies Ennominae and Geometrinae are frequently associated with trees and arborescent shrubs, aligning with their distribution being limited to the two hardwood-dominated forest types [11,81–83]. Notodontidae primarily feed on dicot angiosperm woody trees and shrubs [11], again explaining the strong association of this family with the *terra firme* forest and their relative rarity in the palm swamp. Host resource availability is also likely to produce the observed patterns in the CNESS dissimilarity metric, which shows that while many moth species may be supported across swamp and non-swamp forest types, few such species show high abundances in both. Species showing high abundances in one forest type may have individuals dispersing into other forest types, and many are likely to have caterpillar host taxa in sub-habitats analogous to the inverse forest type, such as the swamp plants found along *terra firme* blackwater streams.

The most abundant moth taxa in both swamp forest types were Lithosiini and Crambidae. Lithosiini are the largest clade of lichenivorous moths [11], and lichens are well-supported in the swamp forest, often heavily covering older *Raphia* palm fronds. Crambidae primarily feed on monocots as well as ferns and some non-vascular plants [84–86], plant groups consumed by few other Lepidoptera taxa, but which are again abundant in the swamp forests. Importantly, the high proportional abundance of these groups of generally very small species with unconventional larval hosts in the swamps, particularly in the palm swamp canopy, conceals much greater differences in moth biomass between swamp and non-swamp forests. The low abundance of larger taxa suggests a much weaker role of moth-mediated ecological functions in the swamp forest, with a smaller role of moths in provisioning a food resource to higher trophic consumers, as well as weaker top-down influence via herbivory.

Tropical peat swamp forest plant species are known to exhibit strong anti-herbivore defences, including a diversity of phenolic and antioxidant compounds, in response to the extreme nutrient limitation which characterizes these ecosystems [87]. While primarily studied for their contribution to organic matter accumulation owing to lower rates of litter decomposition, these plant anti-herbivore defences may provide an indirect causal link from peatland geochemistry to the low abundance and diversity of insect herbivores observed in this study [88,89]. Well-defended plant resources may impose stronger ecological filters on swamp forest moth communities, as well as limit moth abundance with lower rates of insect herbivory. Indeed, this is supported by a global study of the role of herbivores in biogeochemical processing, which includes data on herbivory pressure collected from the hardwood swamp and *terra firme* forest plots sampled here, finding 13.6% higher leaf herbivory in the *terra firme* forest [90]. However, other factors such as the thermal environment [91,92] or larval predation pressure [93] may also influence rates of herbivory across forest types, and analysis of swamp forest plant chemical composition is needed to better characterize the importance of this mechanism in structuring insect communities.

It is important to acknowledge the overall restrictions of the sampling design used in this study, which was limited to three 1 ha forest plots. This was necessitated in part by the extreme challenges in accessing and working in the swamp forest, as well as by the difficulty in characterizing any given locality within the swamps owing to the patchy and gradual gradients of hardwood versus palm domination that occur across their extent. With only approximately 100 m of separation between sampling locations within each plot, some degree of spatial autocorrelation within samples of each forest type can be expected. While the environmental gradients within the peat swamps are shallow, the studied forest types are known to vary in composition across their extent [48,56]. Along with other local factors such as topology, this compositional variation probably exerts influence over moth assemblage composition, which this study did not capture. However, the three forest plots studied here have been established, across a range of previous studies, to be representative of each forest type [57,90,94], as the key habitat elements of canopy composition and understory density are typical for the central Congo peatland region [48]. Resultingly, we are confident that the general patterns in richness and taxonomic composition we describe are likely to apply broadly to the rain-fed interfluvial sites that are common in the central Congo peatlands [46], particularly through the palm swamp with its near-monodominant *R. laurentii* palm canopy. However, the central Congo peatlands also feature geomorphologically distinct river-influenced and floodplain peatlands, which are common on the left bank tributaries of the Congo River [47,55]. These regions experience more extreme and river-influenced flooding, including sediment input, which can affect tree species composition [95], and support some tree species which appear not to be found in the interfluvial peatlands [96], probably altering moth community structure.

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(b) Seasonality

The abundance and richness of moths in the *terra firme* forest were higher in the wet season (314 and 149% higher, respectively), a pattern expected based on dry season limitations on larval resources [23,26,97,98]. By contrast, both swamp forests showed the exact opposite pattern for abundance (167 and 152% higher in the dry season for hardwood and palm swamps, respectively), with no significant trap-level richness differences. These divergent patterns are a product of lower wet season abundance in the swamps, rather than a lower diversity of active adult moths, as shown by higher values of Fisher's α in the wet season across all forest types (supplementary material, figure S6). Together, these findings point to fundamental differences in seasonal ecosystem dynamics in the swamp forests, which we hypothesize are owing to the impact of water availability and waterlogging on plant growth. Tropical Lepidoptera abundances are known to fluctuate in response to seasonal greening of vegetation [26], which has been observed to occur elsewhere in the Congo Basin in response to pronounced differences in water availability across wet and dry seasons [99]. In the *terra firme* forest, this should result in distinct periods of vegetation growth and larval resource availability following the onset of the wet season [26,27], which can be seen in the highly seasonal collection of edible Notodontidae caterpillars in the *terra firme* forest reported by local communities during March and April [100–102].

Conversely, swamp forest plant communities have a constant supply of water throughout the dry season as water levels rarely drop further than 50 cm below the soil surface [56], which should produce less distinct periods of seasonal plant growth. Such patterns have been observed in Amazonian forests, where seasonal fluctuations in productivity are less extreme in moist forests than seasonally dry forests [103]. Indeed, plant growth is impeded during flooded conditions owing to decreased oxygen availability for the plant roots [104], further contributing to inverse seasonal patterns of larval resource availability to the *terra firme* forest. Data on fine root production (FRP) in our study plots reflect these exact patterns, with FRP highest in the wet season for the *terra firme* plot but highest in the dry season for both swamp forest types [57]. The result is communities of swamp forest moths which are less seasonally variable, with population sizes instead reflecting the limited but relatively constant plant resource availability [24,105]. With population size less reliant on seasonal greening, other ecological factors may act to reduce abundances in the wet season, such as higher wet season mortality owing to extreme rainfall events [106–108], greater fungal pathogen growth [109] or higher predation rates [110]. These and other ecological factors will interact with moth larval ecology to produce different seasonal preferences across moth taxa, modulating the diversity patterns observed between forest types [25].

Tropical insect seasonality is expected to shift in response to direct climatic impacts and following shifts in plant phenology [24,105]. The future of rainfall in the Congo Basin region is uncertain, with some studies showing a drying trend, driven by lower wet season rainfall [50], and climate models showing a wide spread of potential future rainfall scenarios [32,111,112]. This snapshot description of insect seasonality in these forests suggests a lower sensitivity to climate change for insect communities in the swamp forest. However, potentially drastic consequences for peatland hydrology and ecosystem stability under drainage [113] or a decline in rainfall sufficient to dry the swamp, as appeared to happen several thousand years ago [49], would have severe impacts on swamp forest insect communities. Further longitudinal study of insect seasonality across Central African forests is required to better understand the impacts of current and future changes in climate and precipitation on insect-mediated processes in these ecosystems [25].

(c) Vertical stratification

The lack of clear compositional stratification in hardwood swamp and *terra firme* forest at any taxonomic level directly contradicts widely observed patterns of moth community stratification in hardwood forests across the tropics [23,39,45]. The notable exception of Lithosiini, which saw higher abundance in the canopy of hardwood swamp and *terra firme* forests, contrasts with the higher understory abundance for the remaining Arctiinae. The same opposite distributional patterns for these two groups have been observed in the Costa Rican rainforest [44], highlighting the importance of taxonomic resolution in stratification studies where opposing trends of related taxa can cancel out to preclude observation of higher-level patterns [40,41]. Significantly higher Geometridae richness in the understory of *terra firme* forest again matched observations from Costa Rica [44] as well as Cameroon [23], with both cases believed to be driven by the presence of larval hosts in lower forest strata. This may contribute to the observed association of Ennominae and Geometrinae with the tree-dominated forest types and their general absence from the palm swamp, where the open canopy produces a very sparse understory. Here, then, is clear support for the reduced structural complexity of the palm swamp being an important contributor to low habitat species diversity.

The absence of wider stratification patterns in our study may also represent an artefact of methodology, with maximum trap height logistically limited to < 16 m, hence representing the sub-canopy rather than the true canopy stratum in the hardwood swamp and *terra firme* forests. The sub-canopy has been found to support fewer moths than any other strata [40], and this may contribute to the lack of expected canopy-dominance for several taxa here. The lack of sampling of the highest part of the forest canopy may mean that total richness is underestimated in this study, as several families with upper canopy activity preferences are likely to have been missed. This may, for example, have contributed to the low recorded diversity of Sphingidae, a family known to be dominant in upper forest layers [37,42,43], as well as the remarkable paucity of Noctuidae, another canopy-associated family [23,40]. Notably, these two families contain the highest number of known flower-visiting moth species [114], with the abundance of floral resources in higher strata in tropical forests [115,116] considered a key factor in the stratification of pollinating taxa within and outside Lepidoptera [37,38,117]. Still, the presence of stratification patterns for Geometridae and Arctiinae in the hardwood-dominated forests demonstrates that although the results of this study may not capture fully canopy diversity, stratification of microclimate or resource availability probably contributes to the structuring of moth communities in these forests.

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Our finding that, contrary to prediction, only communities in the more structurally simple palm forest displayed clear evidence of vertical differentiation of moth communities may similarly be a product of methodological factors, such as a greater attractive radius of light traps in the open canopy than the denser understory [118], or attraction of moths dispersing from hardwood patches above the uniform palm canopy [119]. Alternatively, the observed stratification may be a product of reduced plant communities in the flooded palm swamp understory, with adult and larval feeding resources more abundant in the canopy [38,117]. Larger species of moths are known to be active in the canopy and avoid more open sub-canopy areas owing to greater predation pressure from bats where vegetation is minimal, and this may also contribute to the notable stratification of larger taxa in the palm swamp [118]. Regardless of the drivers, the very low richness and abundance in the palm swamp understory, even in the non-flooded dry season, suggest a very unfavourable environment for adult moths.

5. Conclusion

Our results demonstrate that the distinctiveness of the moth communities in the central Congo peatland forests extends further than the patterns in diversity, which may be predicted based on plant community composition. While the low relative richness, as well as the uneven and unusual taxonomic composition of moths in these forests is notable, the abiotic pressures on plant communities appear to drastically alter insect community dynamics. The consequences for insect-mediated ecosystem processes in the swamp forests, including top-down and bottom-up effects as well as interactions such as pollination, warrant further investigation. This study also represents, to our knowledge, the first robust assessment of moth diversity for forests in the Republic of the Congo, highlighting the extensive work required to understand Central African moth diversity [6]. With accumulating and accelerating anthropogenic impacts threatening the central Congo peatlands [48], wider Congo Basin forests [7] and tropical insect diversity in general [5,120,121], closing the knowledge gap on insect diversity and their potentially highly complex functional roles is essential to understanding and safeguarding the future of these unique ecosystems.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data and code are available on the Zenodo repository. A CSV with the moth trap data is available at [122]. The code to reproduce all analysis and figures using said dataset is available at [123]. Both uploads will be fully indexed prior to paper publication.

Supplementary material is available online [124].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. C.H.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, validation, visualization, writing — original draft, writing – review and editing; S.L.: project administration, resources, supervision, writing — review and editing; A.T.: data curation, investigation, methodology; P.F.L.: data curation, investigation, methodology; J.C.A.: project administration, resources, supervision, writing — review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Agrawal AA *et al.* 2007 Filling key gaps in population and community ecology. *Front. Ecol. Environ.* **5**, 145–152. (doi:10.1890/1540-9295(2007)5[145:FKGIPA]2.0.CO;2)
2. Erwin TL. 1982 Tropical forests: their richness in coleoptera and other arthropod species. *Coleopt. Bull.* **36**, 74–75.
3. Stork NE. 2018 How many species of insects and other terrestrial arthropods are there on Earth? *Annu. Rev. Entomol.* **63**, 31–45. (doi:10.1146/annurev-ento-020117-043348)
4. Titley MA, Snaddon JL, Turner EC. 2017 Scientific research on animal biodiversity is systematically biased towards vertebrates and temperate regions. *PLoS ONE* **12**, e0189577. (doi:10.1371/journal.pone.0189577)
5. Boyle MJW *et al.* 2025 Causes and consequences of insect decline in tropical forests. *Nat. Rev. Biodivers.* **1**, 315–331. (doi:10.1038/s44358-025-00038-9)
6. Delabye S *et al.* 2019 Characterization and comparison of poorly known moth communities through DNA barcoding in two afrotropical environments in Gabon. *Genome* **62**, 96–107. (doi:10.1139/gen-2018-0063)
7. Hansen MC, Wang L, Song X-P, Tyukavina A, Turubanova S, Potapov PV, Stehman SV. 2020 The fate of tropical forest fragments. *Sci. Adv.* **6**, eaax8574. (doi:10.1126/sciadv.aax8574)
8. García-Robledo C, Kuprewicz EK, Baer CS, Clifton E, Hernández GG, Wagner DL. 2020 The Erwin equation of biodiversity: from little steps to quantum leaps in the discovery of tropical insect diversity. *Biotropica* **52**, 590–597. (doi:10.1111/btp.12811)
9. Novotny V *et al.* 2010 Guild-specific patterns of species richness and host specialization in plant–herbivore food webs from a tropical forest. *J. Anim. Ecol.* **79**, 1193–1203. (doi:10.1111/j.1365-2656.2010.01728.x)
10. Ollerton J. 2017 Pollinator diversity: distribution, ecological function, and conservation. *Annu. Rev. Ecol. Evol. Syst.* **48**, 353–376. (doi:10.1146/annurev-ecolsys-110316-022919)
11. Powell JA. 2009 Lepidoptera: moths, butterflies. In *Encyclopedia of insects* (eds VH Resh, RT Cardé), 3rd edn, pp. 559–587. San Diego, CA: Academic Press.
12. Basset Y *et al.* 2012 Arthropod diversity in a tropical forest. *Science* **338**, 1481–1484. (doi:10.1126/science.1226727)

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13. Lewinsohn TM, Novotny V, Basset Y. 2005 Insects on plants: diversity of herbivore assemblages revisited. *Annu. Rev. Ecol. Evol. Syst.* **36**, 597–620. (doi:10.1146/annurev.ecolsys.36.091704.175520)
14. Solis MA, Pogue MG. 1999 Lepidopteran biodiversity: patterns and estimators. *Am. Entomol.* **45**, 206–212. (doi:10.1093/ae/45.4.206)
15. Dyer LA *et al.* 2007 Host specificity of Lepidoptera in tropical and temperate forests. *Nature* **448**, 696–699. (doi:10.1038/nature05884)
16. Forister ML *et al.* 2015 The global distribution of diet breadth in insect herbivores. *Proc. Natl Acad. Sci. USA* **112**, 442–447. (doi:10.1073/pnas.1423042112)
17. Beck J, Holloway JD, Khen CV, Kitching IJ. 2012 Diversity partitioning confirms the importance of beta components in tropical rainforest Lepidoptera. *Am. Nat.* **180** E64–E74. (doi:10.1086/666982)
18. Rabl D, Alonso-Rodríguez AM, Brehm G, Fiedler K. 2020 Trait variation in moths mirrors small-scaled ecological gradients in a tropical forest landscape. *Insects* **11**, 612. (doi:10.3390/insects11090612)
19. Rabl D, Gottsberger B, Brehm G, Hofhansl F, Fiedler K. 2020 Moth assemblages in Costa Rica rain forest mirror small-scale topographic heterogeneity. *Biotropica* **52**, 288–301. (doi:10.1111/btp.12677)
20. Uhl B, Wölfling M, Fiedler K. 2022 Exploring the power of moth samples to reveal community patterns along shallow ecological gradients. *Ecol. Entomol.* **47**, 371–381. (doi:10.1111/een.13122)
21. Axmacher JC, Brehm G, Hemp A, Tünte H, Lyaruu HVM, Müller-Hohenstein K, Fiedler K. 2009 Determinants of diversity in Afrotropical herbivorous insects (Lepidoptera: Geometridae): plant diversity, vegetation structure or abiotic factors? *J. Biogeogr.* **36**, 337–349. (doi:10.1111/J.1365-2699.2008.01997.X)
22. Axmacher JC, Tünte H, Schrumpf M, Müller-Hohenstein K, Lyaruu HVM, Fiedler K. 2004 Diverging diversity patterns of vascular plants and geometrid moths during forest regeneration on Mt Kilimanjaro, Tanzania. *J. Biogeogr.* **31**, 895–904. (doi:10.1111/j.1365-2699.2004.00995.x)
23. Delabye S *et al.* 2021 Butterfly and moth communities differ in their response to habitat structure in rainforests of Mount Cameroon. *Biotropica* **53**, 567–580. (doi:10.1111/btp.12900)
24. Kishimoto-Yamada K, Itioka T. 2015 How much have we learned about seasonality in tropical insect abundance since Wolda 1988? *Entomol. Sci.* **18**, 407–419. (doi:10.1111/ens.12134)
25. Maicher V, Sáfián S, Murkwe M, Przybyłowicz Ł, Janeček Š, Fokam EB, Pyrcz T, Tropek R. 2018 Flying between raindrops: strong seasonal turnover of several Lepidoptera groups in lowland rainforests of Mount Cameroon. *Ecol. Evol.* **8**, 12761–12772. (doi:10.1002/ece3.4704)
26. Valtonen A, Molleman F, Chapman CA, Carey JR, Ayres MP, Roininen H. 2013 Tropical phenology: bi-annual rhythms and interannual variation in an Afrotropical butterfly assemblage. *Ecosphere* **4**, 1–28. (doi:10.1890/ES12-00338.1)
27. Grøtan V, Lande R, Chacon IA, DeVries PJ *et al.* 2014 Seasonal cycles of diversity and similarity in a Central American rainforest butterfly community. *Ecography* **37**, 509–516. (doi:10.1111/ecog.00635)
28. Abrahamczyk S, Kluge J, Gareca Y, Reichle S, Kessler M. 2011 The influence of climatic seasonality on the diversity of different tropical pollinator groups. *PLoS ONE* **6**, e27115. (doi:10.1371/journal.pone.0027115)
29. Souza CS, Maruyama PK, Aoki C, Sigrist MR, Raizer J, Gross CL, de Araujo AC. 2018 Temporal variation in plant–pollinator networks from seasonal tropical environments: higher specialization when resources are scarce. *J. Ecol.* **106**, 2409–2420. (doi:10.1111/1365-2745.12978)
30. Maicher V *et al.* 2020 Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. *J. Biogeogr.* **47**, 342–354. (doi:10.1111/jbi.13740)
31. Wardhaugh CW, Stone MJ, Stork NE. 2018 Seasonal variation in a diverse beetle assemblage along two elevational gradients in the Australian wet tropics. *Sci. Rep.* **8**, 8559. (doi:10.1038/s41598-018-26216-8)
32. Feng X, Porporato A, Rodriguez-Iturbe I. 2013 Changes in rainfall seasonality in the tropics. *Nat. Clim. Change* **3**, 811–815. (doi:10.1038/nclimate1907)
33. Dial RJ, Ellwood MDF, Turner EC, Foster WA. 2006 Arthropod abundance, canopy structure, and microclimate in a Bornean lowland tropical rain forest. *Biotropica* **38**, 643–652. (doi:10.1111/j.1744-7429.2006.00181.x)
34. Nakamura A *et al.* 2017 Forests and their canopies: achievements and horizons in canopy science. *Trends Ecol. Evol.* **32**, 438–451. (doi:10.1016/j.tree.2017.02.020)
35. Basset Y, Hammond P, Barrios HE, Holloway JD, Miller S. 2003 Vertical stratification of arthropod assemblages. In *Arthropods of tropical forests. Spatio-temporal dynamics and resource use in the canopy* (eds Y Basset, V Novotny, SE Miller, RL Kitching), pp. 17–27. Cambridge, UK: Cambridge University Press.
36. Ellwood MDF, Foster WA. 2004 Doubling the estimate of invertebrate biomass in a rainforest canopy. *Nature* **429**, 549–551. (doi:10.1038/nature02560)
37. Schulze C, Linsenmair KE, Fiedler K. 2001 Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecol.* **153**, 133–152. (doi:10.1023/A:1017589711553)
38. Wardhaugh CW, Stork NE, Edwards W, Grimbacher PS. 2012 The overlooked biodiversity of flower-visiting invertebrates. *PLoS ONE* **7**, e45796. (doi:10.1371/journal.pone.0045796)
39. Ashton LA, Barlow HS, Nakamura A, Kitching RL. 2015 Diversity in tropical ecosystems: the species richness and turnover of moths in Malaysian rainforests. *Insect Conserv. Divers.* **8**, 132–142. (doi:10.1111/icad.12090)
40. De Smedt P, Vangansbeke P, Bracke R, Schauwvliege W, Willems L, Mertens J, Verheyen K. 2019 Vertical stratification of moth communities in a deciduous forest in Belgium. *Insect Conserv. Divers.* **12**, 121–130. (doi:10.1111/icad.12320)
41. Intachat J, Holloway JD. 2000 Is there stratification in diversity or preferred flight height of geometroid moths in Malaysian lowland tropical forest? *Biodivers. Conserv.* **9**, 1417–1439. (doi:10.1023/A:1008926814229)
42. Lourido GM, Motta CS, Graça MB, Rafael JA. 2018 Diversity patterns of hawkmoths (Lepidoptera: Sphingidae) in the canopy of an ombrophilous forest in Central Amazon, Brazil. *Acta Amaz.* **48**, 117–125. (doi:10.1590/1809-4392201704721)
43. Valente DMP, Teston JA. 2024 Vertical stratification of sphingidae moths (Lepidoptera: Bombycoidea: Sphingidae) in the Tapajós National Forest, Pará, Brazil. *Zoologia (Curitiba)* **41**, e23008. (doi:10.1590/S1984-4689.v41.e23008)
44. Brehm G. 2007 Contrasting patterns of vertical stratification in two moth families in a Costa Rican lowland rain forest. *Basic Appl. Ecol.* **8**, 44–54. (doi:10.1016/j.baae.2006.02.002)
45. Brehm G, Axmacher JC. 2006 A comparison of manual and automatic moth sampling methods (Lepidoptera: Arctiidae, Geometridae) in a rain forest in Costa Rica. *Environ. Entomol.* **35**, 757–764. (doi:10.1603/0046-225X-35.3.757)
46. Dargie GC, Lewis SL, Lawson IT, Mitchard ET, Page SE, Bocko YE, Ifo SA. 2017 Age, extent and carbon storage of the central Congo basin peatland complex. *Nature* **542**, 86–90. (doi:10.1038/nature21048)

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47. Crezee B *et al.* 2022 Mapping peat thickness and carbon stocks of the central Congo basin using field data. *Nat. Geosci.* **15**, 639–644. (doi:10.1038/s41561-022-00966-7)
48. Dargie GC, Lawson IT, Rayden TJ, Miles L, Mitchard ET, Page SE, Bocko YE, Ifo SA, Lewis SL. 2019 Congo basin peatlands: threats and conservation priorities. *Mitig. Adapt. Strat. Glob. Change* **24**, 669–686. (doi:10.1007/s11027-017-9774-8)
49. Garcin Y *et al.* 2022 Hydroclimatic vulnerability of peat carbon in the central Congo basin. *Nature* **612**, 277–282. (doi:10.1038/s41586-022-05389-3)
50. Wongchuig S *et al.* 2025 Recent significant drying in central Congo basin linked to weakened Walker circulation and warmer Atlantic. *NPJ Clim. Atmos. Sci.* **8**, 344. (doi:10.1038/s41612-025-01225-3)
51. Poulsen JR, Clark CJ. 2004 Densities, distributions, and seasonal movements of gorillas and chimpanzees in swamp forest in northern Congo. *Int. J. Primatol.* **25**, 285–306. (doi:10.1023/B:IJOP.0000019153.50161.58)
52. Rainey HJ, Iyenguet FC, Malanda G-AF, Madzok ÉB, Santos DD, Stokes EJ, Maisels F, Strindberg S. 2010 Survey of *Raphia* swamp forest, Republic of Congo, indicates high densities of critically endangered western lowland gorillas *Gorilla gorilla gorilla*. *Oryx* **44**, 124–132. (doi:10.1017/S003060530999010X)
53. Miller SE, Rogo LM. 2001 Challenges and opportunities in understanding and utilisation of African insect diversity. *Cimbebasia* **17**, 197–218.
54. Samba G, Nganga D. 2012 Rainfall variability in Congo-Brazzaville: 19322007. *Int. J. Climatol* **32**, 854–873. (doi:10.1002/joc.2311)
55. Georgiou S *et al.* 2023 Mapping water levels across a region of the Cuvette Centrale peatland complex. *Rem. Sens.* **15**, 3099. (doi:10.3390/rs15123099)
56. Dargie GC. 2015 Quantifying and understanding the tropical peatlands of the central Congo basin. PhD thesis, University of Leeds, Leeds, UK.
57. Sciumbata M, Wenina YEM, Mbemba M, Dargie GC, Baird AJ, Morris PJ, Ifo SA, Aerts R, Lewis SL. 2023 First estimates of fine root production in tropical peat swamp and terra firme forests of the central Congo Basin. *Sci. Rep.* **13**, 12315. (doi:10.1038/s41598-023-38409-x)
58. Brehm G. 2017 A new led lamp for the collection of nocturnal Lepidoptera and a spectral comparison of light-trapping lamps. *Nota Lepidopterologica* **40**, 87–108. (doi:10.3897/nl.40.11887)
59. Moraes SDS, Cardoso LW, Silva-brandÃo KL, Duarte M. 2017 Extreme sexual dimorphism and polymorphism in two species of the tiger moth genus *Dysschema* (Lepidoptera: Erebidae): association between males and females, sexual mimicry and melanism revealed by integrative taxonomy. *Syst. Biodivers.* **15**, 259–273. (doi:10.1080/14772000.2016.1250835)
60. Zenker MM, Rougerie R, Teston JA, Laguerre M, Pie MR, Freitas AV. 2016 Fast census of moth diversity in the neotropics: a comparison of field-assigned morphospecies and DNA barcoding in tiger moths. *PLoS ONE* **11**, e0148423. (doi:10.1371/journal.pone.0148423)
61. Souto-Vilarós D *et al.* 2024 Illuminating arthropod diversity in a tropical forest: assessing biodiversity by automatic light trapping and DNA metabarcoding. *Environ. DNA* **6**, e540. (doi:10.1002/edn3.540)
62. R Core Team. 2020 *R: a language and environment for statistical computing (Version 4.0. 3)*. Vienna, Austria: R Foundation for Statistical Computing. (doi:10.1201/9780203738672-4)
63. Hsieh TC, Ma KH, Chao A. 2016 iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* **7**, 1451–1456. (doi:10.1111/2041-210X.12613)
64. Zou Y, Zhao P, Axmacher JC. 2023 Estimating total species richness: fitting rarefaction by asymptotic approximation. *Ecosphere* **14**, e4363. (doi:10.1002/ecs2.4363)
65. Oksanen J *et al.* 2013 vegan: ordination methods, diversity analysis and other functions for community and vegetation ecologists. *Community ecology package vegan, version 2.4*. See https://cran.r-project.org, https://github.com/vegandevs/vegan.
66. Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D, Ripley MB. 2013 Package 'mass'. *Cran R* **538**, 113–120.
67. Lenth R, Singman H, Love J, Buerkner P, Herve M. 2019 *Package emmeans*. R package version 1(3.2), 1199. See https://rdrr.io/cran/emmeans.
68. Magurran AE. 2003 *Measuring biological diversity*. Oxford, UK: John Wiley & Sons.
69. Bates D, Machler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1-48. (doi:10.18637/jss.v067.i01)
70. De Caceres M, Jansen F, Endicott S, Dell N. 2016 Indicspecies: relationship between species and groups of sites. R package version 1. See https://cran.r-project.org/web/packages/indicspecies/index.html.
71. Zou Y, Axmacher JC. 2020 the chord-normalized expected species shared (CNESS)-distance represents a superior measure of species turnover patterns. *Methods Ecol. Evol.* **11**, 273–280. (doi:10.1111/2041-210X.13333)
72. Lamarre GPA, Mendoza I, Rougerie R, Decaëns T, Hérault B, Bénéluz F. 2015 Stay out (almost) all night: contrasting responses in flight activity among tropical moth assemblages. *Neotrop. Entomol.* **44**, 109–115. (doi:10.1007/s13744-014-0264-3)
73. Sutrisno H. 2005 Moth diversity at Sebangau peat swamp and Busang river secondary rain forest, Central Kalimantan. *HAYATI J. Biosci.* **12**, 121–126. (doi:10.1016/S1978-3019(16)30338-2)
74. Novotný V, Basset Y. 2000 Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* **89**, 564–572. (doi:10.1034/j.1600-0706.2000.890316.x)
75. Coddington JA, Agnarsson I, Miller JA, Kuntner M, Hormiga G. 2009 Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *J. Anim. Ecol.* 573–584. (doi:10.1111/j.1365-2656.2009.01525.x)
76. Bocko Y, Dargie G, Suspense I, Yoka J, Loumeto J. 2016 Répartition spatiale de la richesse floristique des forêts marécageuses de la Likouala, Nord-Congo. *Afrique Sci.* **12**, 200–212.
77. Draper FC *et al.* 2018 Peatland forests are the least diverse tree communities documented in Amazonia, but contribute to high regional beta-diversity. *Ecography* **41**, 1256–1269. (doi:10.1111/ecog.03126)
78. Pabis K. 2018 What is a moth doing under water? ecology of aquatic and semi-aquatic Lepidoptera. *Knowl. Manag. Aquat. Ecosyst.* **419**, 42. (doi:10.1051/kmae/2018030)
79. Agassiz DJL. 2012 The acentropinae (Lepidoptera: Pyraloidea: Crambidae) of Africa. *Zootaxa* **3494**, 1–73. (doi:10.11646/zootaxa.3494.1.1)
80. Novotny V *et al.* 2007 Low beta diversity of herbivorous insects in tropical forests. *Nature* **448**, 692–695. (doi:10.1038/nature06021)
81. Brehm G. 2002 Diversity of geometrid moths in a montane rainforest in Ecuador. PhD thesis, University of Bayreuth, Bayreuth, Germany.
82. Holm S, Javoiš J, Molleman F, Davis RB, Õunap E, Roininen H, Tammaru T. 2019 No indication of high host-plant specificity in afrotropical geometrid moths. *J. Insect Sci.* **19**, 1. (doi:10.1093/jisesa/iez028)
83. Pitkin LM. 2002 Neotropical ennomine moths: a review of the genera (Lepidoptera: Geometridae). *Zool. J. Linn. Soc.* **135**, 121–401. (doi:10.1046/j.1096-3642.2002.00012.x)
84. Fuentes-Jacques LJ, Hanson-Snortum P, Hernández-Ortiz V, Díaz-Castelazo C, Mehltreter K. 2022 A global review and network analysis of phytophagous insect interactions with ferns and lycophytes. *Plant Ecol.* **223**, 27–40. (doi:10.1007/s11258-021-01187-5)

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85. Munroe E, Solis MA. 2013 The Pyraloidea. In *Teilband/Part 35, volume 1: evolution, systematics, and biogeography* (ed. W Kükenthal), pp. 233–256. Berlin, Germany: Walter de Gruyter GmbH. (doi:10.1515/9783110804744.233)
86. Poltavsky AN *et al.* 2018 The Pyraloidea (Lepidoptera) fauna of the woody savannah belt in Mali, West Africa. *Zootaxa* **4457**, 39–69. (doi:10.11646/zootaxa.4457.1.2)
87. Yule CM, Gomez LN. 2009 Leaf litter decomposition in a tropical peat swamp forest in peninsular Malaysia. *Wetl. Ecol. Manag.* **17**, 231–241. (doi:10.1007/s11273-008-9103-9)
88. Becerra JX. 2007 The impact of herbivore–plant coevolution on plant community structure. *Proc. Natl Acad. Sci. USA* **104** 7483–7488. (doi:10.1073/pnas.0608253104)
89. Descombes P, Marchon J, Pradervand J-N, Bilat J, Guisan A, Rasmann S, Pellissier L. 2017 Community-level plant palatability increases with elevation as insect herbivore abundance declines. *J. Ecol.* **105**, 142–151. (doi:10.1111/1365-2745.12664)
90. Hwang BC *et al.* 2024 The impact of insect herbivory on biogeochemical cycling in broadleaved forests varies with temperature. *Nat. Commun.* **15**, 6011. (doi:10.1038/s41467-024-50245-9)
91. Ashe-Jepson E *et al.* 2023 Tropical butterflies use thermal buffering and thermal tolerance as alternative strategies to cope with temperature increase. *J. Anim. Ecol.* **92**, 1759. (doi:10.1111/1365-2656.13970)
92. Ashe-Jepson E, Hayes MP, Hitchcock GE, Wingader K, Turner EC, Bladon AJ. 2023 Day-flying Lepidoptera larvae have a poorer ability to thermoregulate than adults. *Ecol. Evol.* **13**, e10623.866. (doi:10.1002/ece3.10623)
93. Anttonen P, Perles-Garcia M, Kunz M, von Oheimb G, Li Y, Bruelheide H, Ma K-P, Zhu C-D, Schuldt A. 2023 Predation pressure by arthropods, birds, and rodents is interactively shaped by tree species richness, vegetation structure, and season. *Front. Ecol. Evol.* **11**, 1199670. (doi:10.3389/fevo.2023.1199670)
94. Bocko YE, Panzou GJL, Dargie GC, Mampouya YEW, Mbemba M, Loumeto JJ, Lewis SL. 2023 Allometric equation for *Raphia laurentii* De Wild, the commonest palm in the Central Congo peatlands. *PLoS ONE* **18**, e0273591. (doi:10.1371/journal.pone.0273591)
95. Kanyama TJ, Dargie G, Hawthorne D, Crezee B, Girkin N, Emba Botuli O, Bola P, Ewango CEN, Lewis SL *et al.* 2026 Plant diversity and composition of peatlands adjacent to the white- and blackwater rivers in the central Congo Basin. *Phil. Trans. R. Soc. B.* **381**, 20240479. (doi:10.1098/rstb.2024.0479)
96. Crezee BJ. 2022 Spatial distribution, carbon stocks and diversity of peat swamp forests in the central Congo basin. PhD thesis, University of Leeds, Leeds, UK.
97. Hopkins GW, Memmott J. 2003 Seasonality of a tropical leaf-mining moth: leaf availability versus enemy-free space. *Ecol. Entomol.* **28**, 687–693. (doi:10.1111/j.1365-2311.2003.00552.x)
98. Kato M, Inoue T, Hamid AA, Nagamitsu T, Merdek MB, Nona AR, Itino T, Yamane S, Yumoto T. 1995 Seasonality and vertical structure of light-attracted insect communities in a Dipterocarp forest in Sarawak. *Popul. Ecol.* **37**, 59. (doi:10.1007/BF02515762)
99. Sun Y, Knyazikhin Y, She X, Ni X, Chen C, Ren H, Myneni RB. 2022 Seasonal and long-term variations in leaf area of Congolese rainforest. *Remote Sens. Environ.* **268**, 112762. (doi:10.1016/j.rse.2021.112762)
100. Bomolo O, Niassy S, Tanga CM, Chocha A, Tartibu L, Shutcha MN, Longanza B, Ekesi S, Bugeme DM. 2019 The value chain of the edible caterpillar *Elaphrodes lactea* Gaede (Lepidoptera: Notodontidae) in the Miombo forest of the Democratic Republic of the Congo. *J. Ethnobiol. Ethnomed.* **15** 1–11. (doi:10.1186/s13002-019-0319-y)
101. Mabossy-Mobouna G, Ombeni J, Bouyer T, Latham P, Bocquet E, Mbuta A, Tabi PP, Malaisse F. 2022 Diversity of edible caterpillars and their host plants in the Republic of the Congo *Afr. J. Trop. Entomol. Res.* **1**, 3–27. (doi:10.5281/zenodo.6351855)
102. Numbi Muya GM, Mutiaka BK, Bindelle J, Francis F, Caparros Megido R. 2022 Human consumption of insects in Sub-Saharan Africa: Lepidoptera and potential species for breeding. *Insects* **13**, 10. (doi:10.3390/insects13100886)
103. Girardin CAJ *et al.* 2016 Seasonal trends of Amazonian rainforest phenology, net primary productivity, and carbon allocation. *Glob. Biogeochem. Cycles* **30**, 700–715. (doi:10.1002/2015GB005270)
104. Melling L, Tan CY, Goh KJ, Hatano R. 2013 Soil microbial and root respirations from three ecosystems in tropical peatland of Sarawak, Malaysia. *J. Oil Palm Res.* **25**, 44–57. https://www.webofscience.com/wos/woscc/full-record/WOS:000317873400005.
105. van Dijk LJA *et al.* 2024 Temperature and water availability drive insect seasonality across a temperate and a tropical region. *Proc. R. Soc. B* **291**, 20240090. (doi:10.1098/rspb.2024.0090)
106. Intachat J, Holloway JD, Staines H. 2001 Effects of weather and phenology on the abundance and diversity of geometroid moths in a natural Malaysian tropical rain forest. *J. Trop. Ecol.* **17**, 411–429. (doi:10.1017/S0266467401001286)
107. Lawson DA, Rands SA. 2019 The effects of rainfall on plant–pollinator interactions. *Arthropod-Plant Interact.* **13**, 561–569. (doi:10.1007/s11829-019-09686-z)
108. Wainwright CE, Volponi SN, Stepanian PM, Reynolds DR, Richter DH. 2023 Using cloud radar to investigate the effect of rainfall on migratory insect flight. *Methods Ecol. Evol.* **14**, 655–668. (doi:10.1111/2041-210X.14023)
109. Leger RJS. 2021 Insects and their pathogens in a changing climate. *J. Invertebr. Pathol.* **184**, 107644. (doi:10.1016/j.jip.2021.107644)
110. Molleman F, Remmel T, Sam K. 2016 Phenology of predation on insects in a tropical forest: temporal variation in attack rate on dummy caterpillars. *Biotropica* **48**, 229–236. (doi:10.1111/btp.12268)
111. Cook KH, Vizy EK, Andrews PC, Zhao S. 2024 Temperature increases threaten the Congo basin rainforest in the twenty-first century more than precipitation changes. *J. Climate* **38**, 369–386. (doi:10.1175/JCLI-D-24-0289.1)
112. IPCC. 2022 *Climate change 2022: impacts, adaptation and vunerability. Contribution of working group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
113. Young *et al.* 2026 Land-use change causes rapid carbon losses in Congo Basin peatlands across climate scenarios, whereas the effects of climate change alone are uncertain. *Phil. Trans. R. Soc. B* **381**, 20240486. (doi:10.1098/rstb.2024.0486)
114. Hahn M, Brühl CA. 2016 The secret pollinators: an overview of moth pollination with a focus on Europe and North America. *Arthropod-Plant Interact.* **10**, 21–28. (doi:10.1007/s11829-016-9414-3)
115. Bawa KS. 1990 Plant-pollinator interactions in tropical rain forests. *Annu. Rev. Ecol. Syst.* **21** 399–422. (doi:10.1146/annurev.es.21.110190.002151)
116. Mertens JE, Janeček Š, Foryuy FD, Chmelová E, Fokam EB, Tropek R. 2020 Changes in pollinator community of *Scadoxus cinnabarinus* (Amaryllidaceae) along its elevational range on Mount Cameroon. *Arthropod-Plant Interact.* **14**, 1–12. (doi:10.1007/s11829-020-09741-0)
117. Nice CC, Fordyce JA, Bell KL, Forister ML, Gompert Z, DeVries PJ. 2019 Vertical differentiation in tropical forest butterflies: a novel mechanism generating insect diversity? *Biol. Lett.* **15**, 20180723. (doi:10.1098/rsbl.2018.0723)

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118. Cava SL, Rijllo G, Zucco G, Innocenti S, Guasti M, Puletti N, Ferrara C, Scalercio S. 2024 Moths in space: the below-canopy structure of forest drives abundance and mobility-related traits of moth communities. *Sci. Total Environ.* **921**, 171056. (doi:10.1016/j.scitotenv.2024.171056)
119. Beck J, Linsenmair KE. 2006 Feasibility of light-trapping in community research on moths: attraction radius of light, completeness of samples, nightly flight times and seasonality of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae). *J. Res. Lepidoptera* **39**, 18–36. (doi:10.5962/p.266537)
120. Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672. (doi:10.1073/pnas.0709472105)
121. Outhwaite CL, McCann P, Newbold T. 2022 Agriculture and climate change are reshaping insect biodiversity worldwide. *Nature* **605**, 97–102. (doi:10.1038/s41586-022-04644-x)
122. Hackforth C, Tsoumou A. 2026 Moth abundance and composition dataset for: Spatial and seasonal taxonomic patterns in moth communities of the Central Congo peatlands. *Zenodo*. (https://doi.org/10.5281/zenodo.15557772)
123. Hackforth C. 2026 R code for: Spatial and seasonal taxonomic patterns in moth communities of the Central Congo peatlands. *Zenodo*. (doi:10.5281/zenodo.15557776)
124. Hackforth C, Lewis S, Tsoumou A, Loubaki PF, Axmacher JC. 2026 Supplementary material from: Spatial and seasonal taxonomic patterns in moth communities of the central Congo peatlands. Figshare. (doi:10.6084/m9.figshare.c.8574381)

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