

Rainforest conversion to plantations fundamentally alters energy fluxes and functions in canopy arthropod food webs

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Abstract

Tropical rainforests around the world are rapidly converted into cash crop agricultural systems. The associated massive losses of plant and animal species lead to changes in arthropod food webs and the energy fluxes therein. These changes are poorly understood, in particular in the extremely biodiverse canopies of tropical ecosystems. Using canopy fogging followed by stable isotope and energy flux analyses, we show that land-use conversion from rainforest to rubber and oil palm plantations not only causes a drastic reduction in energy fluxes of up to 75%, but also shifts fluxes among trophic groups. While rainforest featured high levels of both herbivory and algae-microbivory, and a balanced ratio of herbivory to predation, relative fluxes were shifted towards predation in rubber and towards herbivory in oil palm plantations, indicating profound shifts in ecosystem functioning. Our results highlight that the ongoing loss of animal biodiversity and biomass in tropical canopies degrades animal-driven functions and restructures canopy food webs.

Introduction

Conversion of tropical rainforest into cash crops is escalating due to the pressure to increase food and biofuel production (Laurance *et al.* 2014). Indonesia has experienced particularly high rates of deforestation and forest degradation within the last decades (Hansen *et al.* 2013; Margono *et al.* 2014). Conversion of rainforest into rubber and oil palm plantations, which are among the major cash-crops in Indonesia (Juniyanti *et al.* 2021), is not only accompanied by vast deforestation and above- and belowground carbon losses, but also by substantial inputs of fertilizers, herbicides and pesticides (Guillaume *et al.* 2018; Darras *et al.* 2019). Together, this has resulted in decreases in floral and faunal abundance and diversity in multiple taxonomic groups (Fitzherbert *et al.* 2008; Gibson *et al.* 2011; Chaudhary *et al.* 2016). However, functional consequences of biodiversity losses remain little understood. Biodiversity across trophic levels is of pivotal importance for maintaining ecosystem multifunctionality (Hunt & Wall 2002; Bardgett & van der Putten 2014; Tilman *et al.* 2014). Decreases in abundance and diversity of invertebrates may critically impact energy fluxes in food webs and ultimately lead to losses of ecosystem functions (Cardinale *et al.* 2006; Barnes *et al.* 2014, 2016; Clough *et al.* 2016; Drescher *et al.* 2016). However, until today we do not know how energy fluxes in tropical canopies, which are one of the most biodiverse habitats on Earth, are affected by land-use change (Erwin 1983; Ellwood & Foster 2004; Nakamura *et al.* 2017).

Studies on canopy arthropod groups such as ants, beetles, spiders and parasitoid wasps suggest substantial decline in species diversity, density and biomass if rainforest is converted into rubber and oil palm plantations (Nazarreta *et al.* 2020; Azhar *et al.* 2022; Kasmiatun *et al.* 2022; Ramos *et al.* 2022). Evaluating associated changes in energy fluxes may help to understand functional consequences of this decline (Barnes *et al.* 2014;

Zhou *et al.* 2022). Ecosystem functioning crucially depends on fluxes of energy and matter, which are closely linked to food web dynamics via trophic interactions (Reiss *et al.* 2009). Manning *et al.* (2018) argue that ecosystem functioning should ideally be defined via process rates involving fluxes of energy and matter between trophic levels and the environment. This calls for a holistic food web approach, focussing not only on individual trophic groups, but on energy fluxes through multiple trophic levels and entire communities (Soliveres *et al.* 2016; Barnes *et al.* 2018; Wan *et al.* 2022). Energy fluxes through food web nodes, characterizing the energy consumption of different trophic groups, can be used to infer ecosystem functions such as predation, herbivory and detritivory, that are closely related to ecosystem services, such as pest control, decomposition and carbon sequestration (Barnes *et al.* 2018; Gauzens *et al.* 2019).

Application of the energy flux approach to invertebrate communities in tropical canopies is challenging, because the trophic structure of arthropod communities in this habitat is poorly explored (Nakamura *et al.* 2017). Given the central role of food web topology for the correct estimation of energy fluxes (Jochum *et al.* 2021), it is crucial to obtain precise information on trophic positions and trophic interactions of multiple trophic groups in the food web (O’Neill 1969; Seibold *et al.* 2018). Thus, in-situ assessment of trophic positions of taxa and their potential shifts among tropical land-use systems is needed, but rarely done (Zhou *et al.* 2022). To the best of our knowledge, the trophic structure of arthropod communities in tropical canopies and land-use associated changes in energy fluxes therein have not been investigated in a comprehensive way until today.

Here, using canopy fogging, we collected arthropods in rainforest, and in three major transformation systems in Southeast Asia, i.e. jungle rubber (rubber agroforest system), rubber and oil palm plantations, replicated in two landscapes in Jambi Province, Sumatra. Sampling was conducted once in the dry and once in the rainy season. For all major arthropod taxa (12 orders and 5 families, representing consistent trophic groups) on each site, we recorded abundance and biomass, and used stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values) to estimate site-specific trophic positions from primary consumers to top predators and to assess the use of basal resources such as plants and epiphytic microorganisms. Stable isotope analysis allowed us to reconstruct realistic trophic positions of major taxa for calculating energy fluxes and to assess ecological functions such as herbivory, algae-microbivory and predation. We compared fluxes and functions among rainforest transformation systems and hypothesized that (1) due to decline in resource diversity, and density and biomass of canopy arthropods under anthropogenic disturbance, land use simplifies the trophic structure and decreases trophic redundancy; and (2) land use results in a strong reduction of the total energy flux in canopy food webs and leads to changes in proportions of key arthropod-driven trophic functions, such as herbivory, predation and microbivory.

Materials and Methods

Study region and experimental design

Canopy arthropods were collected from research plots ($n = 32$) of the EForTS (**E**cological and Socioeconomic **F**unctions of Tropical Lowland Rainforest **T**ransformation **S**ystems) project in the lowlands of Jambi Province, Sumatra, Indonesia (Supplementary Fig. S1; Drescher *et al.* 2016), a region dominated by smallholder cash crop agriculture (Clough *et al.* 2016). Eight 50 m \times 50 m plots each were established in three of the most dominant agricultural land-use systems in Jambi Province, i.e. monocultures of rubber (*Hevea brasiliensis*), oil palm (*Elaeis guineensis*), and jungle rubber (rubber agroforest system in gradually degrading rainforest remnants; Rembold *et al.* 2017), as well as in lowland rainforest as control. The 32 research plots were located within and around two lowland rainforest reserves, i.e. the Bukit Duabelas National Park and the Harapan Rainforest, which are covered by degraded primary rainforest (Margono *et al.* 2014). The plots inside and near Bukit Duabelas National Park are referred to as belonging to the “Bukit Duabelas landscape”, while the research plots inside and near Harapan rainforest are affiliated to the “Harapan landscape” (Drescher *et al.* 2016).

Sampling and analyses of canopy arthropods and leaves

Arthropods were collected by canopy fogging, i.e. the application of an insecticide to tree and palm canopies,

in three target canopies per 50 m × 50 m plot (Fig. 1). Canopy fogging was conducted twice: Once in dry season 2013 and once in the following rainy season 2013/14. Target canopies were randomly located in the plot, and consisted of interlocking canopies of ca 5 trees in rainforest and jungle rubber, two trees in rubber monocultures and one palm in oil palm plantations. Fallen trees and canopy gaps were avoided. A mixture of 50 mL DECIS 25 EC® (Bayer Crop Science, deltamethrine 25g/L) and four litres petroleum white oil was applied to each target canopy, taking approx. 20 min per fogging event. Underneath each target canopy, 16 square 1 m × 1 m collection funnels were hung from suspended ropes, each funnel was fitted with a 250 mL plastic bottle containing 100 mL 96% EtOH. Two hours after the application of the insecticide, stunned or dead arthropods were collected, cleaned from debris, the EtOH was exchanged and the samples stored at -20degC until further analysis.

To calibrate stable isotope measurements of the canopy arthropod community to the potential basal resource, five randomly selected leaves per plot were collected at head height near the plot centre. In rainforest, the leaves were from five different tree species; in jungle rubber, two of the leaves were from two different rubber trees, and three leaves from three different tree species in the plot or from as many tree species as present. In rubber, the leaves were from the five nearest rubber trees closest to the plot centre. In oil palm, we collected ca. 40 cm² leaf material from the five different oil palm trees closest to the plot centre.

Collected canopy arthropods were sorted to 12 orders: Acarina, Araneae, Blattodea, Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, Psocoptera and Thysanoptera. As large flying taxa such as Apoidea and Vespoidea in part actively evaded the insecticide fog at the time of application (J. Drescher, pers. obs.), the order Hymenoptera in this study is represented by Formicidae (ants) and Braconidae (a family of parasitoid wasps), both of which were highly abundant in the samples (Nazarreta et al. 2020; Azhar et al. 2022). Additionally, four abundant beetle families with contrasting feeding strategies were separately analysed from the rest of the order Coleoptera (henceforth termed ‘other Coleoptera’), i.e. Chrysomelidae, Curculionidae, Elateridae and Staphylinidae (for details see Kasmiatun *et al.* 2022). Average body length and width were measured for 15 (or if <15 in the sample as many as present) randomly selected individuals from each order/family at plot-level in the dry and rainy season. Biomasses (fresh weight) per square metre were calculated using taxon-specific regressions (Supplementary Table S1).

Stable isotope ratios of carbon and nitrogen (¹³C/¹²C and ¹⁵N/¹⁴N) and C-to-N ratios were measured for pooled leaves from each plot and for 15 (or if <15 in the sample as many as present) randomly selected and pooled individuals per plot for each order/family both in the dry and rainy season, resulting in 1073 measured samples of canopy arthropods and 32 measured samples of canopy leaves. Samples were measured with a coupled system of an elemental analyser and a mass spectrometer (Reineking et al. 1993). Isotopic signatures were expressed using the δ notation, with δX (R_{standard}/R_{standard} × 1000; X represents the target isotope, and R_{sample} and R_{standard} represent ¹³C/¹²C and ¹⁵N/¹⁴N ratios of samples and standard, respectively. PD belemnite (PDB) and atmospheric nitrogen served as the primary standard for δ¹³C and δ¹⁵N, respectively. Acetanilide (C₈H₉NO, Merck, Darmstadt) was used for internal calibration.

Statistical analyses

All statistical analyses were conducted with R version 4.1.0 (2021-05-18) ”Camp Pontanezen”. To account for different isotopic baselines among different land-use types, bulk isotope values (δ¹³C and δ¹⁵N) of canopy arthropod orders were normalized to trees or oil palms representing primary producers by subtracting the isotopic signatures of leaves from the respective plots. These leaf-calibrated isotope data are denoted as Δ¹³C and Δ¹⁵N. To calculate mean, minimum and maximum of Δ¹³C and Δ¹⁵N for each land-use system in the two landscapes, Δ¹³C and Δ¹⁵N values of canopy arthropod orders were weighted by biomass and scaled between 0 and 1 for each community in a plot (Cucherousset & Villéger 2015). To estimate biomass distribution among trophic levels, we assigned ‘Δ¹⁵N classes’ from the highest to the lowest Δ¹⁵N values, each with a span of 3 the biomass of taxa in each class for each plot. To test for differences in abundance, biomass and isotopic composition between canopy arthropod orders, land-use systems, landscapes and seasons, and for differences in biomass distribution among trophic levels and land-use systems, landscapes and seasons, we constructed linear mixed effects models in R using the packages ‘lme4’ (Bates et al. 2015) and ‘lmerTest’

(Kuznetsova et al. 2017). ‘Plot’ was included in the models as random effect. Non-significant effects were eliminated from full models using the ‘step’ function, but without reducing random effects. To test for differences among mean, minimum and maximum of $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$, we used the R packages ‘nlme’ (Pinheiro et al. 2021) and ‘mass’ (Ripley et al. 2019) to construct linear models with landscape, land-use and season as fixed factors.

For the reconstruction of the trophic structure of the studied taxa and the calculation of energy fluxes among them see Box 1. We additionally ran a sensitivity analysis to test if assumptions used for energy flux calculations will influence the conclusions of our study (Supplementary Text S1 and Fig. S2). To inspect differences between ecological functions depending on land-use, region and season, we again constructed linear mixed effects models with plot as random term (see above).

Results

Abundance and biomass

Average abundance of canopy arthropods differed significantly between land-use systems ($F_{3,27} = 28.35$, $p < 0.0001$), being only slightly lower in jungle rubber (221 ± 66 ind/m²) compared to rainforest (267 ± 118 ind/m²), but decreased by $\sim 70\%$ in rubber and oil palm plantations (83 ± 31 and 80 ± 28 ind/m², respectively). Average canopy arthropod biomass was also substantially lower in plantations, with a more severe decline in the Bukit Duabelas (up to 87%) than in the Harapan landscape (ca. 70%; significant landscape \times land-use interaction; $F_{3,56} = 3.47$, $p = 0.0221$); this was due to considerably higher arthropod biomass, mainly of large herbivorous/algae-microbivorous orthopterans and cockroaches/termites, in rainforest and to a lesser extent in jungle rubber in Bukit Duabelas (737 ± 335 and 381 ± 131 mg/m², respectively) than in Harapan (respective values of 252 ± 114 and 314 ± 225 mg/m²). By contrast, the biomass in rubber and oil palm plantations was generally low in both landscapes (ca. 90-100 mg/m²).

Similar to total arthropod abundance, differences in the abundance of individual taxonomic groups also depended on land use (significant taxon \times land use interaction; $F_{48,975} = 8.58$, $p < 0.0001$; Supplementary Fig. S3), with the biomass of individual taxa in addition varying with season (significant taxon \times land-use \times season interaction; $F_{51,902} = 1.48$, $p = 0.0182$; Supplementary Fig. S4). In decreasing order, the most abundant groups were Formicidae, Collembola and Diptera across all land-use systems except for oil palm, where Formicidae, Psocoptera and Diptera were most abundant (Supplementary Table S2). Taxa with the highest biomass, by contrast, comprised Orthoptera, Araneae and Blattodea in rainforest, jungle rubber and oil palm, whereas in rubber Araneae and Diptera featured the highest biomasses. Oil palm was dominated by Orthoptera and to a lesser extent by Araneae, but also featured high proportions of herbivorous Lepidoptera and Curculionidae (Fig. 2). The abundance and biomass of most arthropod groups decreased strongly from rainforest towards plantation systems; mean abundance of Collembola in oil palm plantations, for instance, was only one sixth of that in rainforest (5 ± 5 ind/m² in oil palm compared to 32 ± 19 ind/m² in rainforest and even 53 ± 31 ind/m² in jungle rubber). As an exception, compared to rainforest abundance and biomass of Lepidoptera and Curculionidae were only significantly lower in rubber plantations but not in oil palm plantations (Supplementary Table S2, Fig. 2). For details on variations in abundance and biomass of canopy arthropods with season and landscape, see Supplementary Chapter S1, Supplementary Figs. S4 and S5, and Supplementary Table S3.

Food web structure and functional composition

Land-use changes altered the trophic structure of canopy food webs. Biomass-weighted average leaf-normalized $\Delta^{15}\text{N}$ values of arthropods were significantly higher in rubber plantations (3.3 than in rainforest, jungle rubber and oil palm (ca. $2 F_{3,58} = 4.30$, $p = 0.0083$; Fig. 3). While the maximum of $\Delta^{15}\text{N}$ values were similar among land-use systems, minimum values were significantly lower in rubber and oil palm plantations than in rainforest ($F_{3,58} = 8.04$, $p = 0.0001$; Fig. 4). Similarly, biomass-weighted average, maximum and minimum $\Delta^{13}\text{C}$ values of canopy arthropods differed significantly among land-use systems ($F_{3,58} = 37.48$, $p < 0.001$, $F_{3,58} = 26.03$, $p < 0.0001$ and $F_{3,58} = 56.76$, $p < 0.0001$, respectively; Fig. 4), with significantly lower values in plantations, in particular in rubber, compared to rainforest and jungle rubber. Arthropods

from rainforest and jungle rubber were strongly enriched in ^{13}C compared to leaf material, with maximum $\Delta^{13}\text{C}$ values of 8.8 ± 1.6 respectively. Minimum $\Delta^{13}\text{C}$ values were still above 3 in arthropods from rainforest and jungle rubber, whereas minimum $\Delta^{13}\text{C}$ values were lower in oil palm and especially rubber (1.4 ± 1.2

$\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$ values also differed between canopy arthropod taxa depending on land-use system (Fig. 4, Supplementary Fig. S6; significant taxon \times land-use interaction; $F_{48,919} = 5.58$, $p < 0.0001$ and $F_{48, 869} = 3.37$, $p < 0.0001$ for $\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$, respectively). Taxa with the highest $\Delta^{15}\text{N}$ values across land-use systems were Diptera and Elateridae, followed by typical predators/parasitoids, such as Staphylinidae, Araneae and parasitoid wasps. Psocoptera, Collembola and Blattodea featured very low $\Delta^{15}\text{N}$ values, with minimum $\delta^{15}\text{N}$ values being in some cases more than 6 values of most taxa, in particular of those at higher trophic levels, such as Diptera, Staphylinidae and Araneae, were remarkably constant across land-use systems. $\Delta^{13}\text{C}$ values were generally lower in arthropod taxa from rubber and oil palm plantations than in those from rainforest and jungle rubber.

Trophic structure of canopy arthropod communities, i.e. biomass distribution within $\Delta^{15}\text{N}$ classes as an indication of trophic level, differed significantly between land-use systems, but the differences varied between landscapes (significant $\Delta^{15}\text{N}$ class \times landscape \times land-use interaction; $F_{3, 1051} = 3.89$, $p < 0.0088$; Fig. 4). Biomass distribution was close to normal among $\Delta^{15}\text{N}$ classes in rainforest, but shifted slightly towards lower trophic positions in Bukit Duabelas and towards higher trophic positions in Harapan. By contrast, rubber plantations featured high biomasses at high $\Delta^{15}\text{N}$ classes, and in case of Bukit Duabelas also at very low $\Delta^{15}\text{N}$ classes. Jungle rubber in Bukit Duabelas was similar to rainforest in the same region, but biomasses peaked at lower trophic levels compared to rainforest, whereas jungle rubber in Harapan was similar to rubber plantations, with higher biomasses at high trophic levels. Biomasses in oil palm plantations peaked at intermediate and low trophic levels.

Energy fluxes and ecological functions as influenced by land-use change

Land-use change influenced energy flux through canopy arthropod communities (for individual land-use systems see Supplementary Fig. S7). Total energy fluxes in tree canopies differed significantly between land-use systems ($F_{3,59} = 9.22$, $p < 0.0001$). They were highest in rainforest ($1160 \pm 1088 \text{ kJ ha}^{-1}\text{year}^{-1}$) and jungle rubber ($747 \pm 586 \text{ kJ ha}^{-1} \text{ year}^{-1}$), but significantly lower in rubber and oil palm plantations (293 ± 247 and $342 \pm 382 \text{ kJ ha}^{-1} \text{ year}^{-1}$, respectively). Importantly, energy fluxes within different trophic groups (algae-microbivores, herbivores and predators), as indicators of different ecological functions, also differed significantly between land-use systems (significant trophic group \times land-use interaction; $F_{6,116} = 6.14$, $p < 0.0001$; Fig. 5). In general, algae-microbivory and herbivory were the dominant feeding strategies in rainforest, jungle rubber and oil palm plantations. Algae-microbivory, indicated by low $\Delta^{15}\text{N}$ signatures, was highest in rainforest ($643 \pm 904 \text{ kJ ha}^{-1}\text{year}^{-1}$), even exceeding herbivory ($306 \pm 268 \text{ kJ ha}^{-1} \text{ year}^{-1}$). In jungle rubber, herbivory and algae-microbivory were of equal importance, whereas in oil palm plantations herbivory dominated. Interestingly, predation was dominant in rubber plantations, with similarly high fluxes as in jungle rubber, but considerably lower fluxes to herbivory and algae-microbivory. The ratio between herbivory and predation differed between the land-use systems ($F_{3,48} = 7.61$, $p = 0.0003$); it was significantly greater in oil palm (10.9 ± 20.2) than in rainforest, jungle rubber and rubber (3.5 ± 6.3 , 3.6 ± 6.3 and 1.9 ± 5.3 , respectively). For variations in energy fluxes with landscape and season see Supplementary Chapter S1 and Supplementary Fig. S8.

Discussion

Here, for the first time we quantitatively explored energy fluxes of canopy arthropod communities of tropical rainforest transformation systems. Conversion of rainforest into plantations drastically altered abundance, biomass and trophic structure of canopy arthropods, resulting not only in substantially decreased energy fluxes, but also in shifts in the relative importance of ecological functions such as algae-microbivory, herbivory and predation. The observed shifts may have far-reaching consequences for ecosystem functioning and underline the importance to counteract the rapidly accelerating land-use changes in tropical regions.

Total abundance and biomass of canopy arthropods strongly decreased from rainforest and jungle rubber

towards monoculture plantation systems of rubber and oil palm, as has been shown previously for ants, spiders and parasitoid wasps (Nazarreta *et al.* 2020; Azhar *et al.* 2022; Ramos *et al.* 2022). The decrease of combined average arthropod abundance across 12 major taxa by ca. 70 % from rainforest to monoculture plantations of rubber and oil palm was even more severe than reported for the abundance of soil invertebrates/arthropods at the same study sites of ca. 60 % (Potapov *et al.* 2019a), suggesting more pronounced effects of land-use changes on aboveground compared to belowground invertebrates, as has been shown for temperate ecosystems (Le Provost *et al.* 2021). Notably, differences in biomass of canopy arthropods varied between the two landscapes studied, with generally higher abundance and biomass in rainforests of Bukit Duabelas than in Harapan. This was mainly due to high biomasses of large herbivorous/algae-microbivorous Orthoptera and Blattodea in the former and resulted in a more drastic decrease in biomass of up to 87 % from rainforests to plantations in the Bukit Duabelas than the Harapan landscape (ca. 70 %). The regional differences are presumably due to differences in fertility and landscape heterogeneity, but in particular the longer history of rainforest transformation in the Harapan than the Bukit Duabelas landscape (Allen *et al.* 2015; Harrison & Swinfield 2015; Guillaume *et al.* 2018; Sibhatu *et al.* 2022). By contrast, rubber and oil palm plantations featured similarly low abundance and biomass of canopy arthropods in both regions, indicating that regional differences are levelled out by strong disturbance such as the conversion of rainforest into plantation systems. This highlights the importance of protecting intact tropical ecosystems at landscape scale.

Taxonomic groups responded differentially to land-use changes. The abundance and biomass of most arthropod groups decreased strongly from rainforest towards plantation systems; loss of Collembola abundance was most pronounced, with a loss of > 85 % from rainforest and jungle rubber to oil palm plantations. Abundance of Formicidae was also reduced by ca. 75 % from rainforest to plantations and biomass of Blattodea even decreased by > 90 %. The strong reduction in abundance and biomass of these taxa may be related to reduced habitat complexity, aboveground plant biomass and diversity, and available food sources (Novotny *et al.* 2006; Kotowska *et al.* 2015; Drescher *et al.* 2016; Zemp *et al.* 2019). On the other hand, abundance and biomass of some herbivorous taxa, such as Lepidoptera and Curculionidae, were not reduced in oil palm plantations. This is likely due to specialized herbivore species that thrive in oil palm plantations, such as red palm weevils, bagworms and nettle caterpillars, and to the introduced curculionid pollinator *Elaeidobius kamerunicus*, which is the dominating curculionid species in oil palm plantations in our study region (Greathead 1983; Kasmiatun *et al.* 2022).

Land-use changes also altered the trophic structure of canopy arthropod communities. Biomass-weighted mean of trophic positions as indicated by $\Delta^{15}\text{N}$ values were significantly higher in rubber plantations, indicating a higher proportion of predators. Low minimum $\Delta^{15}\text{N}$ values, with $\delta^{15}\text{N}$ values being in some cases more than 6 some canopy arthropod taxa, such as Psocoptera, Collembola and Blattodea, predominantly feed on algae or lichens which utilize atmospheric nitrogen and typically are depleted in $\delta^{15}\text{N}$ compared to vascular plants (Chahartaghi *et al.* 2005; Erdmann *et al.* 2007; Maraun *et al.* 2011). $\Delta^{15}\text{N}$ values of omnivores such as Hemiptera and Formicidae, but also of higher trophic level taxa such as Diptera, Staphylinidae and Araneae, were remarkably constant across land-use systems. This suggests that, despite high diversity within taxonomic groups (Basset 2001; Nazarreta *et al.* 2020; Ramos *et al.* 2022), overall trophic niches and therefore ecological functions of these supra-specific taxa bear phylogenetic signal, which was also postulated for belowground systems (Potapov *et al.* 2019b). In contrast to the relatively low $\Delta^{13}\text{C}$ values in plantation systems, in rainforest and jungle rubber canopy arthropods were on average 5-6 canopy leaves as potential basal resource; $\Delta^{13}\text{C}$ maxima in rainforest were even close to 9 the ^{13}C enrichment may be attributed to variations in ^{13}C signatures between leaves high and low in the canopy, with the latter used for calibration in this study (van der Merwe & Medina 1991; Hyodo *et al.* 2010). An additional cause may be selective utilization of only specific plant/leaf components, such as water-soluble amino acids and carbohydrates that are more easily accessible to digestion and are typically enriched in ^{13}C compared to bulk tissue of leaves. Tropical leaves feature high amounts of structural and hard-to-digest compounds, such as lignin and cuticular waxes, that are more depleted in ^{13}C than other less condensed carbon compounds (Pollierer *et al.* 2009). Given the diversity of herbivore feeding strategies, including leaf chewing and mining, fruit eating as well as xylem/phloem sucking (Novotny *et al.* 2010), selective utilization of specific components is likely.

Despite relatively constant trophic levels of taxonomic groups, the biomass distribution among trophic levels, as indicated by $\Delta^{15}\text{N}$ classes, differed significantly between land-use systems, but this also varied between landscapes. The shift from a close-to-normal biomass distribution in rainforests, in particular in Bukit Duabelas, to more uneven distributions in oil palm and rubber, suggests that, in line with our first hypothesis, land-use intensification decreases trophic redundancy and causes a more scattered distribution of trophic niches, possibly mitigated by reduced resource diversity (Krause *et al.* 2020). Low trophic redundancy may increase the vulnerability to the loss of trophic functions and to extinction cascades in intensively managed land-use systems (Sanders *et al.* 2018).

In line with our second hypothesis, energy fluxes were remarkably reduced by rainforest conversion into plantations. Total energy fluxes were reduced by up to 75 % in rubber and oil palm plantations compared to rainforest, and reduced by > 30 % compared to jungle rubber, mirroring the reductions in biomass. As energy fluxes can be used to infer ecosystem multifunctionality and stability (Barnes *et al.* 2018; Manning *et al.* 2018; Potapov 2022), the strong reduction in energy fluxes in plantation systems points to the loss of ecosystem functions and potentially to the deterioration of ecosystem stability. Significantly lower total energy fluxes in plantations compared to rainforests contrast findings from soil food webs at our study sites, where the presence of earthworms as large detritivores in plantations counterbalanced declined energy fluxes in other trophic groups (Potapov *et al.* 2019a). However, energy fluxes to canopy arthropods were not only just reduced, but shifted among different trophic groups, such as herbivores, algae-microbivores and predators, representing different ecosystem functions. Importantly, shifts in energy fluxes and respective functions were similar, but not congruent with shifts in biomass among trophic groups. This highlights that energy flux approaches go beyond biomass-based approaches by also considering metabolic rates and assimilation efficiencies of consumers, as well as trophic structure and preferred prey, thereby more realistically reflecting community functioning.

In rainforests, algae-microbivory was the most important feeding strategy, followed by herbivory, while both of these feeding types were equally important in jungle rubber. Such high energy fluxes to algae-microbivores have not been demonstrated before for canopy arthropods and suggest that tropical canopy food webs more heavily rely on resources other than higher plants, with algae and microorganisms playing an even greater role than tissue of higher plants such as leaves. In contrast to vascular plant epiphytes, microbiota in tropical forest canopies are not well-studied (Nakamura *et al.* 2017). Microbial communities differ strongly with vertical stratification in tropical forests and are responsible for decomposition of suspended detrital substrates (Gora *et al.* 2019). Fungi, algae and lichens can significantly contribute to the diet of leaf litter and bark-inhabiting Oribatida and Collembola (Chahartaghi *et al.* 2005; Erdmann *et al.* 2007; Susanti *et al.* 2019). Potentially, due to the low resource quality and high lignin and wax contents of leaves of tropical trees, these resources are of particular relevance for arthropods in the canopy of tropical rainforests. This calls for further studies to disentangle microbial contributions from fungi, bacteria and algae to the diet of canopy arthropods and how they are influenced by land-use change.

While rainforest and jungle rubber were characterized by pronounced energy fluxes to algae-microbivores and herbivores, predation was the main feeding type in rubber. Food webs with pronounced energy fluxes to lower trophic levels, i.e. bottom heavy food webs, as in rainforest and jungle rubber, are assumed to be more stable than those with higher fluxes to high trophic levels (Rip & McCann 2011; Barnes *et al.* 2018). The strong reduction in energy fluxes to lower trophic levels and the concomitant shift to fluxes at higher trophic levels in rubber plantations are likely related to the conversion from evergreen to deciduous forest, causing temporal gaps in resource availability for herbivores and, due to faster replacement of leaves, lower algae-microbial colonization. As more energy is required to support high trophic levels, there is potentially an overall faster transfer and higher loss of energy along food chains in rubber plantations. This faster transfer may contribute to higher carbon and nutrient losses in rubber plantations (De Ruiter *et al.* 1993; Barnes *et al.* 2018; Guillaume *et al.* 2018). On the other hand, a significantly higher ratio of herbivory compared to predation, as in oil palm plantations, may indicate reduced pest control and concomitantly higher losses of oil palm tissue to herbivore pests, necessitating higher use of pesticides (Corley & Tinker 2015).

Here, for the first time we documented the dramatic impacts of tropical land-use change on abundance, biomass, trophic structure and functioning of canopy arthropod communities. We showed that the conversion of rainforest into rubber and oil palm plantations not only strongly reduces energy fluxes, but also alters ecological functions, shifting from stable systems with high energy fluxes at lower trophic levels and high trophic redundancy in rainforest to more contrasting trophic niches in plantation systems. While oil palm plantations were characterized by a high ratio of herbivory to predation suggesting reduced pest control, predation was dominant in rubber plantations, providing the risk of higher energy and nutrient losses. Together, our findings indicate that the conversion of rainforest into plantation systems compromises ecosystem multifunctionality and stability, and suggest high sensitivity of rainforests to even low levels of disturbance such as selective logging. A combined food web approach, not only considering changes in abundance and biomass, but also in trophic structure and energy fluxes is promising to comprehensively trace changes in ecological functions due to land-use change and may provide a reliable basis to foster informed management decisions.

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Competing interests

There are no competing interests to declare.

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Fig. 1 : Canopy fogging in rubber monoculture (Photo credit: Jochen Drescher)

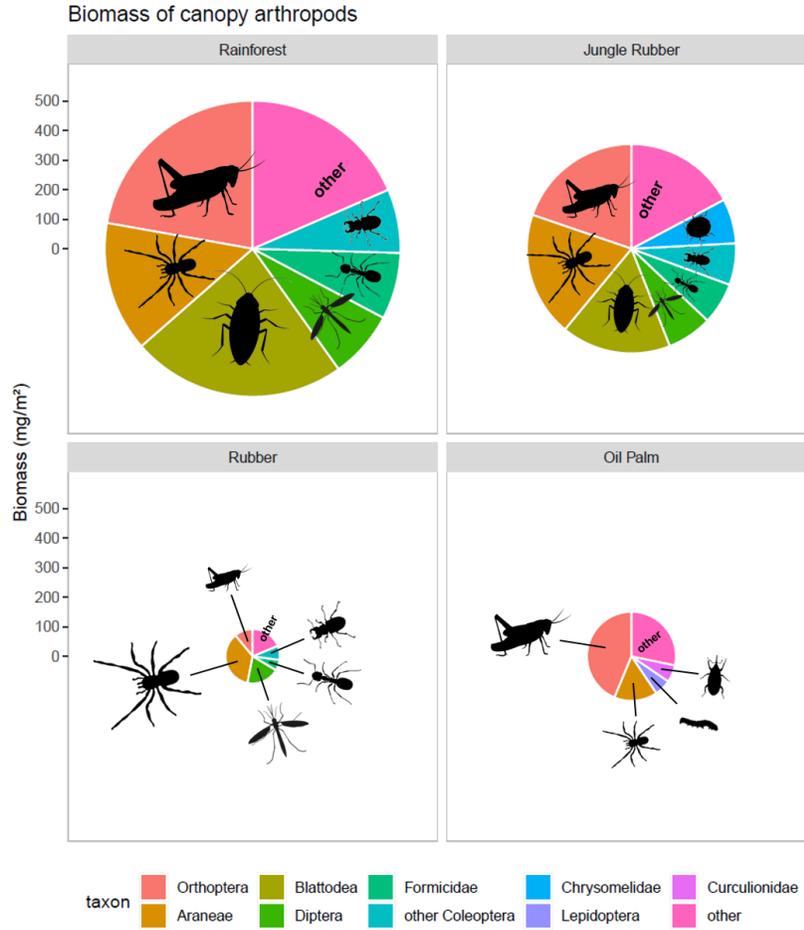


Fig. 2 : Total biomass (fresh weight, mg/m²), represented by the size of the pie charts, and relative biomass proportions (%) of canopy arthropod taxa in different land-use systems (rainforest, jungle rubber, rubber and oil palm plantations). Taxa with relative biomass contributions < 6 % were grouped as “other”.

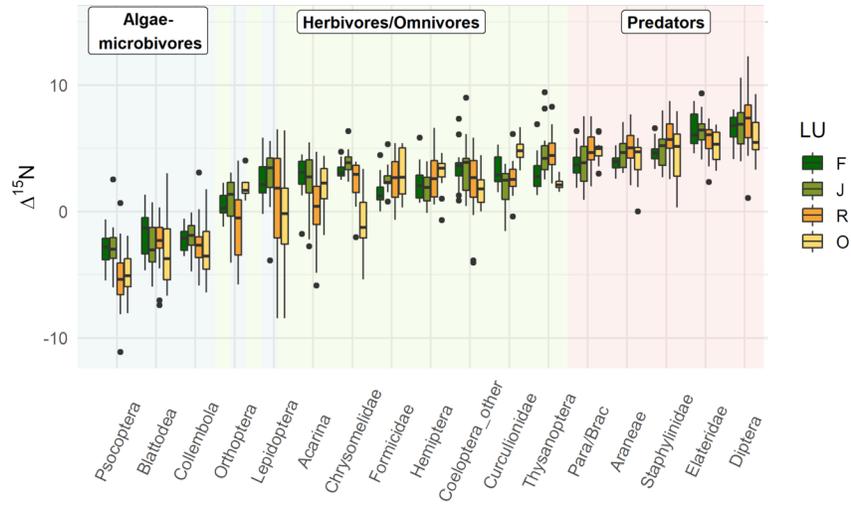


Fig. 3 : $\Delta^{15}\text{N}$ values (normalized to tree leaves) of canopy-living algae-microbivores (Psocoptera, Blattodea, Collembola), herbivores and omnivores (Orthoptera, Lepidoptera, Acarina, Chrysomelidae, Formicidae, Hemiptera, other Coleoptera, Curculionidae, Thysanoptera) and predators (parasitoid wasps/Braconidae – Para/Brac, Araneae, Staphylinidae, Elateridae, Diptera) in different land-use systems (LU: rainforest – F, jungle rubber – J, rubber – R and oil palm – O). Taxa are ordered by increasing mean $\Delta^{15}\text{N}$ values.

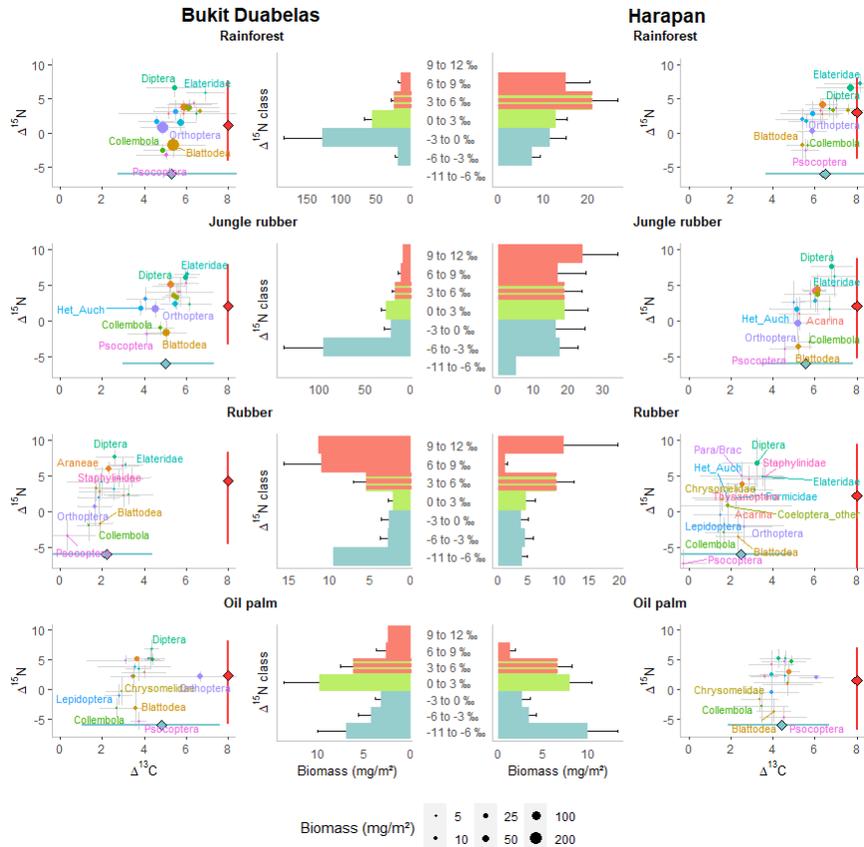


Fig. 4 : Biomass and trophic position of canopy arthropod taxa in different land-use systems (Rainforest, Jungle rubber, Rubber and Oil palm) in the landscapes Bukit Duabelas (left column) and Harapan (right column). The dot plots show mean (\pm SD) $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ values of arthropod taxa ($n = 4$ plots \times 2 seasons = 8 per taxon per landscape), with the size of dots representing their mean biomass. The light blue diamond and horizontal line, and the red diamond and vertical line represent the biomass-weighted mean and range of arthropod $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ values, respectively. The bar plots show mean (\pm SEM) biomass (mg/m^2) of arthropods grouped into $\Delta^{15}\text{N}$ classes as an indication of trophic level (turquoise - algae-microbivores, green - herbivores, red - predators, striped - omnivores); note the different scales for biomass.

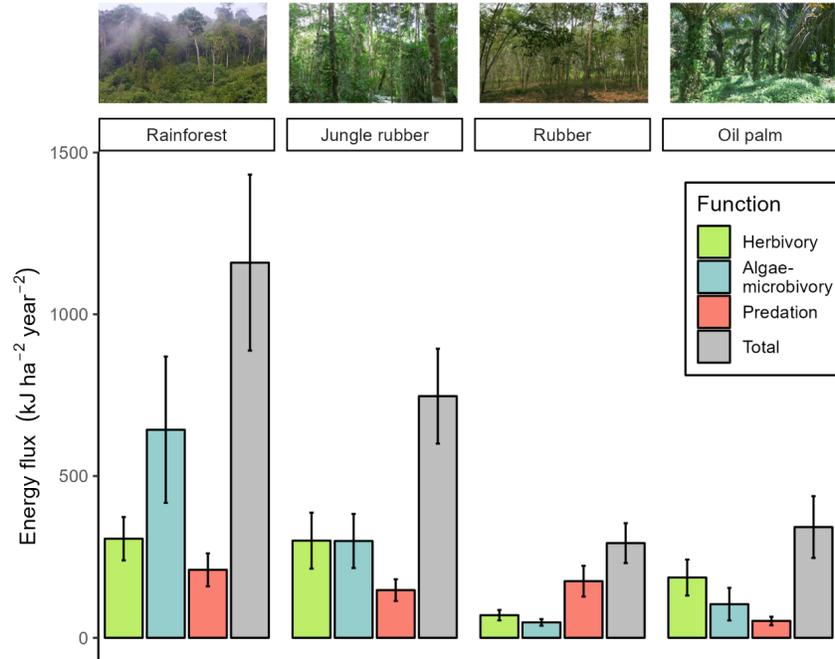


Fig. 5 : Canopy energy flux (mean \pm SE) within different feeding interaction types (algae-microbivory, herbivory, carnivory) and total energy flux in four land-use systems (rainforest, jungle rubber, rubber and oil palm) pooled for landscape and season.

Box 1: *Trophic structure and calculation of energy fluxes*

For reconstructing the trophic structure of the studied taxa and calculating energy fluxes among them, we generated predator-prey adjacency matrices for each plot in both the dry and rainy season based on (1) bulk stable isotope composition, (2) optimum predator-prey mass-ratios (PPMR) and (3) biomass-based preferences (Potapov 2022). Bulk isotope composition was used to calculate ‘optimum’ prey or food resource for each animal group by taking in account a trophic enrichment of $2.3 \delta^{13}\text{C}$ between prey and predator (Tiunov 2007). Taxa with $\delta^{15}\text{N}$ values below those of plant leaves were assumed to mainly feed on algae/microbes that have lower $\delta^{15}\text{N}$ values than plants (Potapov *et al.* 2019). PPMR was used as a characteristic that reflects size-based predation (i.e., small predator feeds on small prey and large predator can also feed on larger prey) and optimum foraging strategy (i.e., balancing the energetic profit and handling efforts; Brose *et al.* 2008), commonly used in food-web ecology (Brose *et al.* 2019). The optimum PPMR was set to 100, implying that typical prey has 100 times less mass than the predator (Brose *et al.* 2008). Since this value is derived from laboratory experiments and modelling, we allowed for a very broad range for “optimum” prey (PPMR width), i.e. body mass range of the optimum prey was set to be triple the body mass range of the predator, representing a large niche. Parasitoids (parasitoid wasps/Braconidae and Diptera) and ants were ‘allowed’ to feed on larger prey and the range for potential prey was set two times wider than for other groups due to parasitic lifestyle/pack hunting (Potapov 2022). Biomass-based preferences were set up assuming that prey preference scaled with available prey biomass (Gauzens *et al.* 2019). The three optimum prey (adjacency) matrices above were multiplied to obtain a final food web matrix for each plot in each season representing feeding preferences among food web nodes (taxa). The food web matrices were subsequently used to calculate energy fluxes per square metre at plot-level using the R package ‘Fluxweb’ (Gauzens *et al.* 2019). When applying the ‘fluxing’ function, biomass preferences were set to ‘false’ as they were already accounted for in the food web matrices. Biomass losses were set to ‘true’, as metabolic losses

of taxa were defined per unit of biomass. Per capita metabolic rates in W based on metabolic theory scaling (Brown 2004) were calculated assuming a constant temperature of 25.2 °C and using general coefficients for invertebrates (Jochum *et al.* 2021). The efficiency level was set to ‘predator’, i.e. the efficiencies with which the predator/consumer assimilates consumed prey were used. Temperature-corrected assimilation efficiencies of food for predators (0.915) and herbivores (0.573) were calculated using parameters from Lang *et al.* (2017) and the mean annual temperature measured by meteo-stations across all studied plots, i.e. 25.2 °C (Drescher *et al.* 2016). We assumed assimilation efficiencies of algae-microbivores to be similar to herbivores. To infer ecological functions, the fluxes to herbivores were summed up as herbivory, the fluxes to algae-microbivores were summed up as algae-microbivory and the fluxes to predators were summed up as predation.