Rainforest conversion to rubber and oil palm reduces abundances and diversity of canopy spiders

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ABSTRACT

Rainforest canopies, home to one of the most complex and diverse terrestrial arthropod communities, are threatened by conversion of rainforest into agricultural production systems. However, little is known about how predatory arthropod communities respond to such conversion. To address this, we compared canopy spider (Araneae) communities from lowland rainforest with those from three agricultural systems in Jambi Province, Sumatra, Indonesia, i.e., jungle rubber (rubber agroforest) and monoculture plantations of rubber or oil palm. Using canopy fogging, we collected 10,676 spider specimens belonging to 36 families and 445 morphospecies. The four most abundant families (Salticidae N = 2,043, Oonopidae N = 1,878, Theridiidae N = 1,533 and Clubionidae N = 1,188) together comprised 62.2 % of total individuals, while the four most ~~specious~~ speciose families, Salticidae (S = 87), Theridiidae (S = 83), Araneidae (S = 48) and Thomisidae (S = 39), contained 57.8 % of all morphospecies identified. In lowland rainforest, total abundance and species richness was at least twice as high as in rubber or oil palm plantations, with jungle rubber showing similar abundances as rainforest, and intermediate richness. Community composition of spiders was similar in rainforest and

jungle rubber, but differed from rubber and oil palm, which also differed from each other. Canonical Correspondence Analysis showed that canopy openness, aboveground tree biomass and tree density together explained 18.2 % of the variation in spider communities at family level. On a morphospecies level, vascular plant species richness and tree density significantly affected the data, but explained only 6.8% of the variance. While both abundance and diversity of spiders declined strongly with the conversion of rainforest into monoculture plantations of rubber and oil palm, we also found that a large proportion of the rainforest spider community can thrive in extensive agroforestry systems such as jungle rubber. Despite being very different from rainforest, the canopy spider communities in rubber and oil palm plantations may still play a vital role in the biological control of canopy herbivore species, thus contributing important ecosystem services. The components of tree and palm canopy structure identified as major determinants of canopy spider communities may aid~~e~~ in decision-making processes toward establishing cash-crop plantation management systems which foster herbivore control by spiders.

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INTRODUCTION

Tropical rainforests are among the most diverse terrestrial ecosystems and provide many ecosystem services, such as weather regulation and carbon storage at local, regional and global scales (Sodhi *et al.* 2010, Böhnert *et al.* 2016, Codato *et al.* 2019, Milheiras & Mace 2019). Worldwide, they are under threat due to extraction of timber and minerals, as well as conversion into agricultural land-use systems such as cattle farms and production of soy beans and oil palm (Rudel & Roper 1997, Sodhi *et al.* 2004, Grau *et al.* 2005, Renó *et al.* 2011, Barber *et al.* 2014, Vijay *et al.* 2016). Deforestation rates are very concerning in Southeast Asia (Koh & Wilcove 2008), particularly Indonesia, which in 2012 experienced the highest deforestation rates worldwide (Margono *et al.* 2014). Among the large islands of Indonesia, Sumatra has had the highest deforestation rates in the last decades (Miettinen *et al.* 2011, Margono *et al.* 2014) but has recently been surpassed by Kalimantan (BPS 2019). A potential cause is that the Sumatran lowlands are already largely converted to non-forest land-use systems, such as agriculture, settlements and mining, while this process is at an earlier stage in Kalimantan. In Jambi Province, Sumatra, plantations and non-forest shrub land (61.8%) cover more than twice the area of primary and secondary rainforest (29.7%) (Melati 2017).

Rubber and oil palm cash crops have become an increasingly dominant factor in overall Indonesian agricultural output over the last decades (BPS 2019). In Jambi Province, rubber and oil palm plantations covered almost 670,000 and 500,000 ha in 2017 (BPS 2018), equaling the area of remaining rainforest (BPS 2018). Most remnant rainforests are located in the mountainous west of the ~~Province~~province and in some mountainous national parks such as Bukit Duabelas and Bukit Tiga Puluh, with only small patches of rainforest in the lowlands.

Recent studies show that transformation of lowland rainforest into monocultures of rubber and oil palm leads to substantial losses in abundance, and functional and taxonomic diversity, as well as compositional shifts across a wide range of animal and plant groups (Barnes *et al.* 2014, Mumme *et al.* 2015, Böhnert *et al.* 2016, Prabowo *et al.* 2016, Rembold *et al.* 2017, Paoletti *et al.* 2018, Potapov *et al.* 2020). Large mammals iare~~s~~ the most conspicuous faunal~~a~~ group affected by rainforest loss (Nyhus & Tilson 2004), but the most severe consequences of rainforest transformation are associated with arthropods, which contribute the overwhelming majority of terrestrial animal species (Hamilton *et al.* 2010, May 2010) and biomass (Bar-On *et al.* 2018). Tropical rainforest canopies are inhabited by one of the most diverse arthropod faunas (Dial *et al.* 2006, Basset *et al.* 2012, Floren *et al.* 2014), which are particularly susceptible to the conversion into plantation systems such as rubber and oil palm due to direct habitat loss (Turner & Foster 2009, Fayle *et al.* 2010).

Spiders (Araneae) are among the top predators in the arthropod food web, feeding mainly on insects and occasionally other arthropods (Nelson & Jackson 2011). Some spiders are also known to consume larger prey, such as earthworms (Nyffeler *et al.* 2017), small skinks (Shine & Tamayo 2016), and even small amphibians, birds and mammals (Nyffeler & Vetter 2018, Babangenge *et al.* 2019). It is estimated that 400 – 800 million tons of prey are killed by the global spider community each year (Nyffeler & Birkhofer 2017). Many spiders are web-builders while others are free hunters, which sets them apart ecologically from other major arthropod predator groups such as centipedes and predatory beetles, and allows analysis of data according to basic ecological and biological characteristics. In addition to their role as predators, spiders are prey to a number of invertebrates and vertebrates, notably other spiders, parasitoid wasps, lizards and birds (Wise 1993). As such, spider abundance and diversity may have major effects on their environment, including the decomposer system (Wise *et al.* 1999, El-Nabawy *et al.* 2016) and agricultural pests (Suenaga & Hamamura 2015, Rana *et al.* 2016). Tropical rainforest conversion to rubber and oil palm plantations may thus have cascading top-down and bottom-up effects through the entire food web, and is likely to shape ecosystem functions and services of the converted ecosystems (Potapov *et al.* 2020).

Here, we studied canopy spider abundance, richness and community composition across a land-use gradient from tropical lowland rainforest via “jungle rubber” (rubber agroforest; Gouyon *et al.* 1993) to monocultures of rubber or oil palm in Jambi Province, Sumatra, Indonesia (Drescher *et al.* 2016). Based on previous studies on other taxa at our study sites (Clough *et al.* 2016, Grass *et al.* 2020), we hypothesized that (1) canopy spider abundance and richness declines from rainforest to jungle rubber to rubber to oil palm monocultures. We further hypothesized that (2) the community composition of canopy spiders differs among each of the land-use systems, with the exception of rainforest and jungle rubber, which we hypothesized to be similar due to comparable structural complexity of the canopies. Lastly, using a large dataset of environmental variables, we hypothesized that (3) changes in the structure of canopy spider communities are driven by changes in habitat structure and associated changes in climatic factors such as temperature and relative humidity.

MATERIALS & METHODS

Sampling

The study was carried out within and surrounding two rainforest reserves in Jambi Province, Sumatra: the Bukit Duabelas National Park (S 01°59'41.4", E 102°45'08.5") and Harapan Rainforest (S 02°09'52.9", E 103°22'04.0") (Fig. S1). The area surrounding these two reserves is dominated by agroforestry systems, predominantly cash crop monocultures of rubber and oil palm (Drescher *et al.* 2016), but also jungle rubber, an agroforestry system in rubber trees are planted in successively degrading rainforest (Gouyon *et al.* 1993, Rembold *et al.* 2017). Canopy arthropods were collected from three target canopies in each of eight research plots per land-use system, i.e. lowland rainforest, jungle rubber, rubber and oil palm (Drescher *et al.* 2016, Fig. S2). Using the Swingtec SN50 fogger, we applied 50 mL DECIS 25 (Bayer Crop Science; active ingredient deltamethrin~~e~~, 25 g/L) dissolved in four liters petroleum white oil to each of the target canopies within the first hour after sunrise, to avoid turbulence~~s~~ during the day. The three target canopies were randomly chosen to represent overall canopy structure in the plots, i.e. canopy gaps and fallen trees were avoided. Underneath each target canopy, 16 collection traps measuring 1 m * 1 m were suspended from ropes attached to height-adjustable tent poles; each trap was fitted with a plastic bottle containing 100 mL of 96% EtOH (Fig. S3). Two hour after fogging, the collection traps of each target canopy were collected and stored at -20°C for further use.

Arthropods were later determined to order~~s~~, and spiders from two target canopies per plot were identified to family and, if possible, to genus and morphospecies level using available literature (Jocqué and Dippenaar-Schoeman (2006), Murphy and Roberts (2015), Deeleman-Reinhold (2001), Koh and Bay (2019), the World Spider Catalog (https://wsc.nmbe.ch/) and the arachnological reference collections at the Zoological Museum in Hamburg (ZMH). All spider morphospecies are documented pictorially in “A guide to the spiders of Jambi (Sumatra, Indonesia)” (Ramos *et al.* 2019) and uploaded to the Ecotaxonomy database (http://ecotaxonomy.org).

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Environmental variables

A set of environmental variables measured in the EFForTS research plots was used to explain canopy spider community composition in the four land-use systems. These variables included mean canopy air temperature [°C] and mean relative humidity [%] (Meijide *et al.* 2018), canopy openness [%] (Drescher *et al.* 2016), aboveground tree biomass [Mg/ha] (Kotowska *et al.* 2015), vascular plant species richness and tree density [N/ha] (Rembold *et al.* 2017) and mean stand structural complexity index (SSC; Zemp *et al.* 2019). Canonical Correspondence Analysis (CCA) was used to visualize the influence of environmental variables on canopy spider communities, at both the morphospecies and family level. CCA was performed using vegan (Oksanen *et al.* 2019) in R (R Core Team 2020). The final model was constructed using forward selection (vegan::ordir2step, direction = forward, permutations = 999) from the above environmental variables and community data. R^2 and variance partitioning were adjusted (Borcard *et al.* 2018) for the number of explanatory variables (vegan::RsquareAdj). CCA and forward selection were done separately for family and morphospecies community matrices.

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Statistical analyses

Statistical analyses were performed using R (v. 3.6.2., R Core Team 2020) and visualized using ggplot2 (Wickham 2016). Rank abundance curves were compared (vegan::radrit) and plotted (Hartke 2020; https://github.com/tamarahartke/RankAbund.). An exploratory data analysis was also performed to ensure the data met underlying assumptions of the statistical tests (Zuur *et al.* 2010). The response variables total abundance, morphospecies richness and inverse Simpson Index 1/D (calculated using vegan::diversity; Oksanen *et al.* 2019) were analyzed using generalized linear models (glm) with the Gaussian family and log link function. Initial models included land use (forest, jungle rubber, rubber, oil palm), landscape (Bukit Duabelas, Harapan), and their interaction as fixed factors. Models were simplified using AIC to find the minimal adequate model for each response variable. Model fit was checked then multiple comparisons made using pairwise t-tests with Holm corrections (multcomp::glht; Hothorn *et al.* 2008). Beta diversity was partitioned into turnover, nestedness and overall beta diversity using Sørensen pairwise dissimilarities (Baselga *et al.* 2018). Each partition was used for non-metric multidimensional scaling (NMDS, vegan::metaMDS), and multivariate analysis of variance (MANOVA, Wilk’s lambda) was used to test how well land use and landscape predicted the variability in NMDS scores; pair-wise contrasts were FDR (False Discovery Rate) adjusted (Benjamini & Hochberg 1995).

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RESULTS

In total, we collected 10,676 spider individuals from 32 research plots across four land-use systems. Of these, we determined 7,786 adult and subadult individuals to 36 families and 445 morphospecies (images of canopy spider families in Fig. S4, 1-36). Not all samples could be assigned to a genus due to lack of relevant identification literature and a high proportion of presently undescribed species in putative new genera. Subadult individuals without fully developed sexual organs are usually not covered in identification keys, but we matched them with identified morphospecies based on general morphology whenever possible. The remaining 2,893 individuals could not be assigned to morphospecies because they were juveniles, however, they were determined to family based on general diagnostic features and thus included in the abundance analysis.

Overall, almost half of the specimens belonged to only four spider families (Salticidae, 2,043; Oonopidae, 1,878; Theridiidae, 1,533; Clubionidae, 1,188). Similarly, four families contributed 57.8 % of all morphospecies: (Salticidae, 87; Theridiidae, 83; Araneidae, 48, Thomisidae, 39). More than half of all spider families comprised less than five morphospecies and less than 10% of all specimens identified. Of the 445 morphospecies recorded, 72 were exclusively found in the Bukit Duabelas landscape and 100 exclusively in the Harapan landscape (Fig. S5 a). A total of 199 morphospecies (45 %) were exclusively found in lowland rainforest and jungle rubber, while only 54 morphospecies (12 %) were exclusively found in monoculture plantations of rubber or oil palm (Fig. S b).

Abundance and alpha diversity

The number of morphospecies of canopy spiders and their abundances were lower in monocultures of rubber and oil palm than in rainforest and jungle rubber (Fig. 1). The models describing the shapes of the curves in the Whittaker plots significantly differed between rainforest and jungle rubber on one hand, and monocultures of rubber and oil palm on the other (Tukey's HSD, all four $T < -2.6$, $P < 0.03$). On average, canopy spiders in rainforest and jungle rubber were almost twice as abundant as in rubber plantations, and almost three times as abundant as in oil palm plantations, with the effect of land use being highly significant (glm; $F_{3,27} = 14.8$, $P < 0.001$; Fig. 2). Landscape also significantly affected canopy spider abundance (glm; $F_{1,26} = 7.1$, $P = 0.01$), but there was no significant interaction between the factors land use and landscape.

Canopy spider morphospecies richness was significantly affected by land use (glm; $F_{3,28} = 22.9$, $P < 0.001$) but not by landscape. On average, canopy spider morphospecies richness in rainforest (100.1 ± 21.4; mean ± *SD*) exceeded that in rubber (49.1 ± 11.4) and oil palm plantations (43.6 ± 10.7) by more than a factor of two, with jungle rubber being intermediate (87.9 ± 19.9; Fig. 3). By contrast, the inverse Simpson index was only marginally predicted by land use (glm; $F_{3,28} = 2.8$, $P = 0.06$) and not by landscape (glm; $F_{1,27} = 2.8$, $P > 0.09$).

Community composition and beta diversity

The interaction between land use and landscape explained 82.1 % of the total variance (Wilk's $\lambda = 0.179$, $F_{3,15} = 3.2$, $P < 0.001$) in canopy spider community composition, or overall beta diversity (land use: Wilk's $\lambda = 0.001$, $F_{3,15} = 40.8$, $P < 0.001$; landscape: Wilk's $\lambda = 0.163$, $F_{1,5} = 20.5$, $P < 0.001$). Overall, spider communities from rainforest and jungle rubber canopies were similar, but differed from communities in rubber and oil palm monocultures, which in turn differed significantly from each other (Fig. 4). The pattern for turnover (Fig. 5a) resembled that of overall beta diversity (interaction: Wilk's λ = 0.18, $F_{3,18}$ = 2.5, P = 0.005; land use: Wilk's λ = 0.01, $F_{3,18}$ = 16.0, $P < 0.001$; landscape: Wilk's λ = 0.14, $F_{1,6}$ = 18.3, $P < 0.001$). For turnover, however, jungle rubber in the Harapan landscape was more similar to rubber plantations in the Bukit Duabelas landscape. Nestedness, on the other hand, was only significantly influenced by land use (Wilk's λ = 0.18, $F_{3,15}$ = 3.2, $P < 0.001$). The ordination suggests overlapping nestedness between rainforest and jungle rubber on one hand, and rubber and oil palm on the other (Fig. 5b). Irrespective of landscape, turnover contributed most to overall beta diversity, while nestedness contributed little (Fig. S6).

Influence of environmental variables

At family level, only three of the seven environmental variables significantly contributed to the model, canopy openness (R^2_{adj} = 0.14, F = 5.95, P = 0.001), aboveground biomass (R^2_{adj} = 0.18, F = 2.63, P = 0.001) and number of tree species per hectare (R^2_{adj} = 0.21, F = 1.88, P = 0.012). Increased canopy openness was associated with rubber and oil palm plantations, while trees per hectare and aboveground biomass were associated with jungle rubber and rainforest. The first three CCA axes (CCA1: χ^2 = 0.12, F = 6.80, P = 0.001; CCA2: χ^2 = 0.05, F = 2.90, P = 0.003; CCA3: χ^2 = 0.02, F = 1.35, P = 0.14) together explained 20.8% of the variation in the data (CCA1 = 12.8%, CCA2 = 5.4%, CCA3 = 2.5%). Centroids of most canopy spider families clustered close to the center of the CCA graph and correlated little with the environmental variables, however Deinopidae and Selenopidae correlated closely with aboveground biomass and rainforest, and Liocranidae correlated closely with canopy openness and rubber and oil palm plantations (Fig. 6a,). At morphospecies level, only the environmental variables plant species richness (R^2_{adj} = 0.05, F = 2.64, P = 0.001) and number of tree species per hectare ($R^2_{\text{adj} =}$ 0.06, F

=1.54, $P = 0.002$) significantly contributed to the model. The two CCA axes (CCA1: $\chi^2 = 0.47$, $F = 2.73$, $P = 0.001$; CCA2: $\chi^2 = 0.25$, $F = 1.49$, $P = 0.002$) together explained 6.8 % of the variation in the data (CC1 = 4.4%, CCA2 = 2.4%). Similar to the family level CCA, most morphospecies clustered around the center of the ordination. The 39 morphospecies with scores > 1.5 along the first axis belonged to the families Theridiidae (8), Araneidae, Salticidae and Thomisidae (5 each), Corinnidae and Uloboridae (3 each), Gnaphosidae (2), and Clubionidae, Deinopidae, Linyphiidae, Liocranidae, Psechridae, Scytodidae, Sparassidae and Tetragnathidae (1 each) (Fig. 6b,). The greatest number of morphospecies was associated with rainforest and jungle rubber, few with rubber plantations, and none with oil palm plantations.

DISCUSSION

We investigated the effect of lowland rainforest conversion into jungle rubber, rubber and oil palm monoculture plantations on abundance, richness and community composition of canopy spiders in Sumatra, Indonesia. The study provided novel insight into the response of one of the most important invertebrate predators to the transformation of lowland rainforest into agroforest systems and intensively managed monoculture plantations in one of the least studied biodiversity hotspots on this planet, the tropical region of Southeast Asia (Myers *et al.* 2000).

Diversity

Abundance and morphospecies richness in plantations of rubber and oil palm were significantly lower than in rainforest and jungle rubber, confirming our first hypothesis and supporting previous studies on arthropod diversity in these land uses. The decrease in canopy spider abundance from rainforest to plantation systems also parallels findings of earlier studies on canopy spiders in other biomes, such as old vs. young forests in eastern Europe (Otto & Floren 2007) and secondary forest vs. rubber plantations in southwest China (Zheng *et al.* 2015). However, the average abundance of canopy spiders varies wildly between the few studies available. We collected 15.1 ind. m^{-2} (all individuals) and 10.8 ind. m^{-2} (identified individuals) in lowland rainforest in Sumatra. By comparison, between 0.97 and 14.6 ind. m^{-2} of canopy spiders were sampled in old-growth rainforests in Sulawesi (Russel-Smith & Stork 1994), 5.8 ind. m^{-2} in montane forests in Tanzania (Sørensen 2004) and ca. 30 ind. m^{-2} in secondary forests in southwest China (Zheng *et al.* 2015). The differences might be due to different fogging methods, but likely also reflect different densities of canopy spiders in various forests across the tropical / subtropical zone. The uniform decline in the abundance of canopy spiders with the conversion of forest into plantation systems reported by Zheng et al. (2015) and in our study indicates increased risk of local extinction of spider species in plantations (Ceballos *et al.* 2017, Hallmann *et al.* 2017, Sánchez-Bayo & Wyckhuys 2019). This may compromise the role of spiders as antagonists of herbivore prey species, ultimately threatening ecosystem functioning (Soliveres *et al.* 2016, Dislich *et al.* 2017).

Canopy spider morphospecies richness in rubber and oil palm plantations was less than half that of rainforest habitats. This loss in morphospecies richness with the conversion of rainforest into monoculture plantation systems is similar to patterns reported from southeast China, where rubber plantations had 42.6 – 50.0% fewer canopy spider morphospecies than secondary forest (Zheng *et al.* 2015). Similar differences have also been found between natural and young managed forests in Europe (Otto & Floren 2007). Overall, our data provide further support that conversion of natural or secondary forests into agricultural systems results in strong losses of species and overall biodiversity decline (Sala *et al.* 2000, Sodhi *et al.* 2004, Steffan-Dewenter *et al.* 2007, Mumme *et al.* 2015, Newbold *et al.* 2015, Grass *et al.* 2020, Potapov *et al.* 2020).

Spider species in monoculture plantations were a subset of those found in rainforest, comprising species resilient against the transformation process and the changed environmental conditions in plantations. These findings are in line with earlier studies on other arthropod groups including canopy ants (Hymenoptera: Formicidae) (Nazarreta *et al.* 2020, Kreider *et al.* 2021), butterflies (Panjaitan *et al.* 2020), and parasitoid wasps (Fahri *et al.* 2016, Azhar et al. 2022). Nazarreta *et al.* (2020) found that the conversion of rainforest into jungle rubber results in moderate species loss, suggesting that the majority of canopy ant species are resilient against moderate changes in land use. Presumably, the same is true for certain spider families in this study, e.g. Salticidae, Theridiidae and Oonopidae reaching similar diversity in rainforest and jungle rubber (). The strong decline in the richness of spiders, as well as other canopy arthropod taxa such as ants (Nazarreta *et al.* 2020), with conversion of rainforest into monoculture plantations of rubber and oil palm suggests that intensification of land use may critically compromise ecosystem functions and services provided by canopy arthropod predators and omnivores (Power 2010, Junggebauer *et al.* 2021).

Community composition

Similar to abundance and species richness, canopy spider community composition was affected by land use and landscape. Rainforest and jungle rubber communities were similar, but differed strongly from those of oil palm and rubber plantations, confirming our second hypothesis. Shifts in community composition associated with land-use changes have been investigated in a wide range of tropical arthropods including ground spiders (Potapov *et al.* 2020), jumping spiders

(Junggebauer *et al.* 2021), ants (Rubiana *et al.* 2015, Nazarreta *et al.* 2020, Kreider *et al.* 2021), beetles (Fahri *et al.* 2016), butterflies (Dumbrell *et al.* 2008, Panjaitan *et al.* 2020) and pseudoscorpions (Liebke *et al.* 2021). Generally, within in each of these taxa, a number of generalist species tolerate increased disturbance and the harsher environmental conditions in plantations. For spiders this suggests that certain species tolerate disturbances in plantations as long as essential habitat requirements are met, such as structural elements to allow attachment of webs (Halaj *et al.* 2000, Jiménez-Valverde & Lobo 2007, Ávila *et al.* 2017, Ganser *et al.* 2017, Rao 2017).

By contrast, a range of spiders predominantly occur in tropical rainforests compared to a variety of disturbed habitats as shown for *Aporosa yunnanensis* forests compared to rubber-tea mixture and rubber plantations (Zheng *et al.* 2017), firewood plantations compared to grasslands and cultivated wetlands (Chen & Tso 2004), old growth forests compared to younger re-forested areas (Floren & Linsenmair 2001, Floren & Deeleman-Reinhold 2005) and rainforest compared to rubber and oil palm plantations (Potapov *et al.* 2019, 2020). Although sampling methodologies differed between these studies, only few families, including web-building Araneidae, Theridiidae and Tetragnathidae, and the free hunt~~er~~ing Corinnidae, Salticidae, Sparassidae and Thomisidae, contributed most to overall spider abundance and species richness (61 – 94%). Similarly, these families also contributed most to total abundance (57 %) and richness (59 %) of spiders in rainforest in our study, and even more to the overall abundance (63 % and 68 %) and richness (74 % and 72 %) in rubber and oil palm plantations. Differences in relative abundance and species richness between rainforest and plantations indicate different sensitivities of spider families to disturbance. A total of 14 families, including Anapidae, Ctenidae and Deinopidae, were present in our rainforest samples but absent in rubber and oil palm plantations, suggesting that species of these families are particularly sensitive to disturbance and the altered abiotic and biotic conditions in plantation systems.

Environmental variables

Three of the seven studied environmental variables affected the spider community structure at family or morphospecies level, supporting our third hypothesis. At the family level, changes in canopy openness, aboveground tree biomass and tree density contributed to the shift in spider communities from rainforest to monoculture plantations. Canopy structure and tree diversity have been identified previously as drivers of canopy spider communities. Floren & Deeleman-Reinhold (2005) found reduced spider diversity in disturbed isolated forest patches with more open canopies compared to less disturbed regenerated forest, while Jiménez-Valverde & Lobo (2007) found that richness of orb-weavers (Araneidae) and crab spiders (Thomisidae) correlate closely with shrub canopy and ground herb cover, i.e. vegetation complexity. In our study, canopy openness was closely associated with oil palm and rubber plantations, which are generally characterized by lower canopy complexity compared to rainforest and jungle rubber (Zheng *et al.* 2015, Drescher *et al.* 2016, Zemp *et al.* 2019). Our results indicate that reduced complexity detrimentally affected a wide range of spider taxa, but may also favor specialist species benefitting from associated increase in temperature and light, e.g. by facilitating hunting of prey via optical cues (Fayle *et al.* 2010, Ganser *et al.* 2017). In fact Liocranidae, predominantly comprising surface-hunting species known to prefer open habitats (Deeleman-Reinhold 2001), flourished in plantations.

Aboveground biomass, which increases with plant species richness, vegetation cover, height and age of trees (Vogel *et al.* 2019), was identified as predictor for spider community composition in our study. Similar studies have found spiders communities to be negatively affected by low tree density (Barton *et al.* 2017) and to benefit from high tree species richness and height (Schuldt *et al.* 2011)**.** Further, Floren *et al.* (2011) found spider communities in southeast Asia to benefit from tree age, suggesting that older trees support a wider range of spider species. Results of our study indicate that in particular the net-casting Deinopidae and the ambush hunting Selenopidae, which only occurred in rainforest, benefit from high aboveground biomass as also suggested by Deeleman-Reinhold (2001) and Floren *et al.* (2011). Potentially, the specific hunting technique used by these spiders combined with a greater degree of habitat specialization contributed to their high sensitivity to rainforest conversion.

At the morphospecies level, spider community structure only correlated closely with plant diversity-associated variables (plant species richness and number of tree species per hectare) and the variation in species distribution was not well explained by the studied environmental variables (combined explanatory power of first two CCA axes 6.9%, compared to 18.2 % at family level). Presumably, stochastic processes play a more pronounced role in structuring spider communities at morphospecies level than at the level of families. The close correlation with plant diversity-associated variables likely reflects the fact that habitat preferences at morphospecies level are more specific than at family level. Plant species richness is known to be an important driver of predator arthropods such as ants or spiders in both temperate and tropical forest ecosystems (Schuldt *et al.* 2011, Drescher *et al.* 2016, Matevski & Schuldt 2021). Samu *et al.* (2014) found 26 % of the variation in spider assemblages to be explained by tree species composition and showed certain spider species to be associated with specific tree species in temperate forests. Similarly, Schuldt *et al.* (2011) found certain spiders species to be associated with individual tree species even in forests with high tree diversity. Canopy spider diversity also has been found to closely correlate with vegetation complexity and other plant variables in tropical forests (Zheng et al. 2015). Despite being the most prominent variables explaining spider community composition at morphospecies level, plant diversity-associated variables only explained a small proportion of the variability in our spider communities suggesting that other factors are likely to be more important for structuring spider communities at species level. In addition to other environmental variables, interactions with other species, including prey and predators, inter-specific competition and intra-guild interactions, may contribute to the local assemblage of spider species (Sih *et al.* 1998, Mooney 2007, Mestre *et al.* 2013). Elucidating the role of these interactions for canopy spider community composition is difficult to infer and requires experimental studies in the field, which are difficult to establish in tropical forest ecosystems.

Conclusions

Overall, the results showed that canopy spider communities in oil palm and rubber plantations are less abundant and less diverse compared to the more natural ecosystems rainforest and jungle rubber. Notably, species composition of spider communities was similar in rainforest and jungle rubber and differed strongly from that in oil palm or rubber plantations, with the latter also differing from one other. At family level, aboveground biomass, number of trees per hectare and canopy openness were identified as major environmental factors determining spider community composition, while at species level the most important factors were plant richness and number of trees per hectare. The results highlight the importance of rainforest for the conservation of canopy spider communities, as only a subset of the community can tolerate the harsh environmental conditions and disturbances in monoculture plantations. Similar diversity and community composition in rainforest and jungle rubber highlights that the majority of spiders tolerates moderate disturbances and decline in trees species indicating that agroforest systems may contribute substantially to the conservation of tropical canopy spider communities.

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REFERENCES

ÁVILA, A. C., C. STENERT, E. N. L. RODRIGUES, and L. MALTCHIK. 2017. Habitat structure determines spider diversity in highland ponds. Ecol. Res. 32: 359–367.

BABANGENGE, G. B., R. JOCQUÉ, F. M. MASUDI, M. O. RÖDEL, M. BURGER, V. GVOŽDÍK, and O.

S. G. PAUWELS. 2019. Frog-eating spiders in the Afrotropics: An analysis of published and new cases. Bull. Chicago Herpetol. Soc. 54: 57–63.

BAR-ON, Y. M., R. PHILLIPS, and R. MILO. 2018. The biomass distribution on Earth. Proc. Natl. Acad. Sci. 115: 6506–6511. Available at: https://www.pnas.org/content/115/25/6506.

BARBER, C. P., M. A. COCHRANE, C. M. SOUZA, and W. F. LAURANCE. 2014. Roads, deforestation, and the mitigating effect of protected areas in the Amazon. Biol. Conserv. 177: 203–209.

BARNES, A. D. ET AL. 2017. Direct and cascading impacts of tropical land-use change on multi-trophic biodiversity. Nat. Ecol. Evol. 1: 1511–1519. Available at: https://doi.org/10.1038/s41559-017-0275-7.

BARNES, A. D., M. JOCHUM, S. MUMME, N. F. HANEDA, A. FARAJALLAH, T. H. WIDARTO, and U. BROSE. 2014. Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. Nat. Commun. 5: 1–7.

BARTON, P. S., M. J. EVANS, C. N. FOSTER, S. A. CUNNINGHAM, and A. D. MANNING. 2017. Environmental and spatial drivers of spider diversity at contrasting microhabitats. Austral Ecol. 42: 700–710.

BASELGA, A., D. ORME, S. VILLEGER, J. DE BORTOLI, and F. LEPRIEUR. 2018. betapart: partitioning beta diversity into turnover and nestedness components. R package version 1.5.1. https://cran.r-project.org/package=betapart. Available at: https://cran.r-project.org/package=betapart.

BASSET, Y. ET AL. 2012. Arthropod diversity in a tropical forest. Science (80-.). 338: 1481–1484. Available at: http://www.sciencemag.org/content/338/6113/1481.abstract.

BENJAMINI, Y., and Y. HOCHBERG. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. Ser. B 57: 289–300. Available at: https://rss.onlinelibrary.wiley.com/doi/abs/10.1111/j.2517-6161.1995.tb02031.x.

BÖHNERT, T., A. WENZEL, C. ALTENHÖVEL, L. BEERETZ, S. S. TJITROSOEDIRDJO, A. MEIJIDE, K. REMBOLD, and H. KREFT. 2016. Effects of land-use change on vascular epiphyte diversity in Sumatra (Indonesia). Biol. Conserv. 202: 20–29.

BORCARD, D., F. GILLET, and P. LEGENDRE. 2018. Numerical Ecology with R. Springer International Publishing.

BPS. 2018. Provinsi Jambi Dalam Angka 2018. Badan Pus. Stat. Pemerintah Provinsi Jambi 650 pp; available at https://jambi.bps.go.id/. Available at: http://jambiprov.go.id.

BPS. 2019. Statistical Yearbook of Indonesia. Badan Pus. Stat. Indones. 738 pp; available at https://www.bps.go.id/. Available at: https://www.bps.go.id/.

CEBALLOS, G., P. R. EHRLICH, and R. DIRZO. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc. Natl. Acad. Sci. 114: E6089--E6096. Available at: https://www.pnas.org/content/114/30/E6089.

CHEN, K., and I. TSO. 2004. Spider diversity on Orchid Island, Taiwan: A comparison between habitats receiving different degrees of human disturbance. Zool. Stud. 43: 598–611.

CLOUGH, Y. ET AL. 2016. Land-use choices follow profitability at the expense of ecological functions in Indonesian smallholder landscapes. Nat. Commun. 7: e:13137. Available at: https://www.nature.com/articles/ncomms13137#citeas.

CODATO, D., S. E. PAPPALARDO, A. DIANTINI, F. FERRARESE, F. GIANOLI, and M. DE MARCHI. 2019. Oil production, biodiversity conservation and indigenous territories: Towards geographical criteria for unburnable carbon areas in the Amazon rainforest. Appl. Geogr. 102: 28–38.

DEELEMAN-REINHOLD, C. L. 2001. Forest spiders of South East Asia : with a revision of the sac and ground spiders (Araneae: Clubionidae, Corinnidae, Liocranidae, Gnaphosidae, Prodidomidae, and Trochanterriidae). Koninklijke Brill NV, Leiden, Netherlands.

DIAL, R. J., M. D. F. ELLWOOD, E. C. TURNER, and W. A. FOSTER. 2006. Arthropod abundance, canopy structure, and microclimate in a Bornean lowland tropical rain forest. Biotropica 38: 643–652. Available at: https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1744-7429.2006.00181.x.

DISLICH, C. ET AL. 2017. A review of the ecosystem functions in oil palm plantations, using forests as a reference system. Biol. Rev. 92.

DRESCHER, J. ET AL. 2016. Ecological and socio-economic functions across tropical land use systems after rainforest conversion. Philos. Trans. R. Soc. B Biol. Sci. 371: 20150275. Available at: https://doi.org/10.1098/rstb.2015.0275.

DUMBRELL, A. J., E. J. CLARK, G. A. FROST, T. E. RANDELL, J. W. PITCHFORD, and J. K. HILL. 2008. Changes in species diversity following habitat disturbance are dependent on spatial scale: Theoretical and empirical evidence. J. Appl. Ecol. 45: 1531–1539.

EL-NABAWY, E.-S. M., K. TSUDA, Y. SAKAMAKI, A. ODA, and Y. USHIJIMA. 2016. The effect of organic fertilizers and flowering plants on sheet-web and wolf spider populations (Araneae: Lycosidae and Linyphiidae) and its importance for pest control. J. Insect Sci. 16.

FAHRI, T. ATMOWIDI, and W. A. NOERDJITO. 2016. Diversity and abundance of cerambycid beetles in the four major land-use fypes found in Jambi Province, Indonesia. HAYATI J. Biosci. 23: 56–61.

FAYLE, T. M., E. C. TURNER, J. L. SNADDON, V. K. CHEY, A. Y. C. CHUNG, P. EGGLETON, and W. A. FOSTER. 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. Basic Appl. Ecol. 11: 337–345.

FLOREN, A., and C. DEELEMAN-REINHOLD. 2005. Diversity of arboreal spiders in primary and disturbed tropical forests. J. Arachnol. 33: 323–333. Available at: http://dx.doi.org/10.1636/05-22.1.

FLOREN, A., and K. E. LINSENMAIR. 2001. The influence of anthropogenic disturbances on the structure of arboreal arthropod communities. Plant Ecol. 153: 153–167.

FLOREN, A., T. MÜLLER, C. DEELEMAN-REINHOLD, and K. E. LINSENMAIR. 2011. Effects of forest fragmentation on canopy spider communities in SE-Asian rain forests. Ecotropica 17: 15–26.

FLOREN, A., W. WETZEL, and M. STAAB. 2014. The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. Myrmecological News 19: 65–74.

GANSER, D., L. H. DENMEAD, Y. CLOUGH, D. BUCHORI, and T. TSCHARNTKE. 2017. Local and landscape drivers of arthropod diversity and decomposition processes in oil palm leaf axils. Agric. For. Entomol. 19: 60–69.

GOUYON, A., H. DE FORESTA, and P. LEVANG. 1993. Does “jungle rubber” deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. Agrofor. Syst. 22: 181–206.

GRASS, I. ET AL. 2020. Trade-offs between multifunctionality and profit in tropical smallholder landscapes. Nat. Commun. 11: 1186. Available at: https://www.nature.com/articles/s41467-020-15013-5#citeas.

GRAU, H., N. GASPARRI, and T. AIDE. 2005. Agriculture expansion and deforestation in seasonally dry forests of north-west Argentina. Environ. Conserv. 32: 140–148.

HALAJ, J., D. W. ROSS, and A. R. MOLDENKE. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos 90: 139–152. Available at: http://dx.doi.org/10.1034/j.1600-0706.2000.900114.x.

HALLMANN, C. A., M. SORG, E. JONGEJANS, H. SIEPEL, N. HOFLAND, H. SCHWAN, W. STENMANS, A. MÜLLER, H. SUMSER, T. HÖRREN, D. GOULSON, and H. DE KROON. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12: 1–21. Available at: https://doi.org/10.1371/journal.pone.0185809.

HAMILTON, A. J., Y. BASSET, K. K. BENKE, P. S. GRIMBACHER, S. E. MILLER, V. NOVOTNÝ, G. A. SAMUELSON, N. E. STORK, G. D. WEIBLEN, and J. D. L. YEN. 2010. Quantifying uncertainty in estimation of tropical arthropod species richness. Am. Nat. 176: 90–95. Available at: https://doi.org/10.1086/652998.

HARTKE, T. 2020. RankAbund: Calculate rank abundances and plot rank abundance curves. R package version 0.2.0. https://github.com/tamarahartke/RankAbund. Available at: https://github.com/tamarahartke/RankAbund.

HOTHORN, T., F. BRETZ, and P. WESTFALL. 2008. Simultaneous inference in general parametric models. Biometrical J. 50: 346–363. Available at: https://onlinelibrary.wiley.com/doi/abs/10.1002/bimj.200810425.

JIMÉNEZ-VALVERDE, A., and J. M. LOBO. 2007. Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: Climate and altitude vs. habitat structure. Ecol. Entomol. 32: 113–122.

JOCQUÉ, R., and A. S. DIPPENAAR-SCHOEMAN. 2007. Spider families of the world. Royal Museum for Central Africa, Tervuren, Belgium Available at: www.africamuseum.be.

JUNGGEBAUER, A., T. R. HARTKE, D. RAMOS, I. SCHAEFER, D. BUCHORI, P. HIDAYAT, S. SCHEU, and J. DRESCHER. 2021. Changes in diversity and community assembly of jumping spiders

(Araneae: Salticidae) after rainforest conversion to rubber and oil palm plantations. PeerJ 9: e11012. Available at: https://doi.org/10.7717/peerj.11012.

KOH, J., and N. BAY. 2019. Borneo Spiders, a Photographic Field Guide. Sabah Foresty Department, Sandakan, Malaysia.

KOH, L. P., and D. S. WILCOVE. 2008. Is oil palm agriculture really destroying tropical biodiversity? Conserv. Lett. 1: 60–64. Available at: https://conbio.onlinelibrary.wiley.com/doi/abs/10.1111/j.1755-263X.2008.00011.x.

KOTOWSKA, M. M., C. LEUSCHNER, T. TRIADIATI, S. MERIEM, and D. HERTEL. 2015. Quantifying above- and belowground biomass carbon loss with forest conversion in tropical lowlands of Sumatra (Indonesia). Glob. Chang. Biol. 21: 3620–3634.

KREIDER, J. J., T.-W. CHEN, T. R. HARTKE, D. BUCHORI, P. HIDAYAT, R. NAZARRETA, S. SCHEU, and J. DRESCHER. 2021. Rainforest conversion to monocultures favors generalist ants with large colonies. Ecosphere 12: e03717. Available at: https://doi.org/10.1002/ecs2.3717.

LIEBKE, D. F., D. HARMS, R. WIDYASTUTI, S. SCHEU, and A. M. POTAPOV. 2021. Impact of rainforest conversion into monoculture plantation systems on pseudoscorpion density, diversity and trophic niches. Soil Org. 93: 83–96. Available at: http://www.soil-organisms.org/index.php/SO/article/view/147.

MARGONO, B. A., P. V POTAPOV, S. TURUBANOVA, F. STOLLE, and M. C. HANSEN. 2014. Primary forest cover loss in Indonesia over 2000-2012. Nat. Clim. Chang. 4: 730–735.

MATEVSKI, D., and A. SCHULDT. 2021. Tree species richness, tree identity and non-native tree proportion affect arboreal spider diversity, abundance and biomass. For. Ecol. Manage. 483: 118775.

MAY, R. M. 2010. Tropical arthropod species, more or less? Science (80-.). 329: 41–42.

Available at: https://science.sciencemag.org/content/329/5987/41.

MEIJIDE, A., C. S. BADU, F. MOYANO, N. TIRALLA, D. GUNAWAN, and A. KNOHL. 2018. Impact of forest conversion to oil palm and rubber plantations on microclimate and the role of the 2015 ENSO event. Agric. For. Meteorol. 252: 208–219. Available at: http://www.sciencedirect.com/science/article/pii/S0168192318300133.

MELATI, D. N. 2017. The use of remote sensing data to monitor land use systems and forest variables of the tropical rainforest landscape under transformation in Jambi Province, Sumatra, Indonesia. Georg-August University of Goettingen. Available at: https://d-nb.info/1150960159/34.

MESTRE, L., J. PIÑOL, J. A. BARRIENTOS, X. ESPADALER, K. BREWITT, C. WERNER, and C. PLATNER. 2013. Trophic structure of the spider community of a Mediterranean citrus grove: A stable isotope analysis. Basic Appl. Ecol. 14: 413–422.

MIETTINEN, J., C. SHI, and S. C. LIEW. 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. Glob. Chang. Biol. 17: 2261–2270.

MILHEIRAS, S. G., and G. M. MACE. 2019. Assessing ecosystem service provision in a tropical region with high forest cover: Spatial overlap and the impact of land use change in Amapá Brazil. Ecol. Indic. 99: 12–18.

MOONEY, K. 2007. Tritrophic effects of birds and ants on a canopy food web, tree growth, and phytochemistry. Ecology 88: 889.

MUMME, S., M. JOCHUM, U. BROSE, N. F. HANEDA, and A. D. BARNES. 2015. Functional diversity and stability of litter-invertebrate communities following land-use change in Sumatra, Indonesia. Biol. Conserv. 191.

MURPHY, J. A., and M. J. ROBERTS. 2015. Spider families of the world and their spinnerets.

British Arachnological Society, Dorchester, United Kingdom.

MYERS, N., R. A. MITTERMEIER, C. G. MITTERLEIER, G. A. B. DA FONSECA, and J. KENT. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858. Available at: internal-pdf://201.15.121.170/Myers...2000.Nature - Biodiversity hotspots fo.pdf.

NAZARRETA, R., T. R. HARTKE, P. HIDAYAT, S. SCHEU, D. BUCHORI, and J. DRESCHER. 2020. Rainforest conversion to smallholder plantations of rubber or oil palm leads to species loss and community shifts in canopy ants (Hymenoptera: Formicidae). Myrmecological News 30: 175–186.

NELSON, X. J., and R. R. JACKSON. 2011. Flexibility in the foraging strategies of spiders. *In* M. E. Herberstein (Ed.) Spider Behaviour: Flexibility and Versatility. pp. 31–56, Cambridge University Press, Cambridge, United Kingdom.

NEWBOLD, T., L. N. HUDSON, S. L. L. HILL, S. CONTU, I. LYSENKO, R. A. SENIOR, L. BÖRGER, D. J. BENNETT, A. CHOIMES, and B. COLLEN. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520: 45–50.

NYFFELER, M., and K. BIRKHOFER. 2017. An estimated 400–800 million tons of prey are annually killed by the global spider community. Sci. Nat. 104.

NYFFELER, M., W. LAPINSKI, A. SNYDER, and K. BIRKHOFER. 2017. Spiders feeding on earthworms revisited: consumption of giant earthworms in the tropics. J. Arachnol. 45: 242–247. Available at: https://doi.org/10.1636/JoA-17-013.1.

NYFFELER, M., and R. S. VETTER. 2018. Black widow spiders, Latrodectus spp. (Araneae: Theridiidae), and other spiders feeding on mammals. J. Arachnol. 46: 541–548. Available at: https://doi.org/10.1636/JoA-S-18-026.1.

NYHUS, P., and R. TILSON. 2004. Agroforestry, elephants, and tigers: balancing conservation theory and practice in human-dominated landscapes of Southeast Asia. Agric. Ecosyst. Environ. 104: 87–97. Available at: http://www.sciencedirect.com/science/article/pii/S0167880904000349.

OKSANEN, J., G. BLANCHET, M. FRIENDLY, R. KINDT, P. LEGENDRE, D. MCGLINN, P. R. MINCHIN, R. B. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. H. H. STEVENS, E. SZOECS, and H. WAGNER. 2019. vegan: Community Ecology Package. R package version 2.5.6. https://cran.r-project.org/package=vegan. Available at: https://cran.r-project.org/package=vegan.

OTTO, S., and A. FLOREN. 2007. The spider fauna (Araneae) of tree canopies in the Bialowieza forest. Fragm. Faun. 50: 57–70.

PANJAITAN, R., J. DRESCHER, D. BUCHORI, D. PEGGIE, I. S. HARAHAP, S. SCHEU, and P. HIDAYAT. 2020. Diversity of butterflies (Lepidoptera) across rainforest transformation systems in Jambi, Sumatra, Indonesia. Biodiversitas 21: 5119–5127.

PAOLETTI, A., K. DARRAS, H. JAYANTO, I. GRASS, M. KUSRINI, and T. TSCHARNTKE. 2018. Amphibian and reptile communities of upland and riparian sites across Indonesian oil palm, rubber and forest. Glob. Ecol. Conserv. 16: e00492. Available at: http://www.sciencedirect.com/science/article/pii/S2351989418301033.

POTAPOV, A. M., N. DUPÉRRÉ, M. JOCHUM, K. DRECZKO, B. KLARNER, A. D. BARNES, V. KRASHEVSKA, K. REMBOLD, H. KREFT, U. BROSE, R. WIDYASTUTI, D. HARMS, and S. SCHEU. 2020. Functional losses in ground spider communities due to habitat structure degradation under tropical land-use change. Ecology 101: e02957. Available at: https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecy.2957.

POTAPOV, A. M., B. KLARNER, D. SANDMANN, R. WIDYASTUTI, and S. SCHEU. 2019. Linking size spectrum, energy flux and trophic multifunctionality in soil food webs of tropical land-use systems. J. Anim. Ecol. 88: 1845–1859.

POWER, A. G. 2010. Ecosystem services and agriculture: tradeoffs and synergies. Philos. Trans. R. Soc. B Biol. Sci. 365: 2959–2971. Available at: internal-pdf://99.45.172.54/Power.2010.PhilTransRSocB - Ecosystem services.pdf.

PRABOWO, W. E., K. DARRAS, Y. CLOUGH, M. TOLEDO-HERNANDEZ, R. ARLETTAZ, Y. MULYANI, and T. TSCHARNTKE. 2016. Bird responses to lowland rainforest conversion in Sumatran smallholder landscapes, Indonesia. PLoS One 11: e0154876.

R CORE TEAM. 2020. R: A language and environment for statistical computing. https://www.r-project.org/. Available at: https://www.r-project.org/.

RAMOS, D., M. LIA, S. SCHEU, and J. DRESCHER. 2019. A guide to the spiders of Jambi (Sumatra, Indonesia) - Identification key to common families and images of the EFForTS collection. Version 1.0, June 2019. https://www.uni-goettingen.de/de/handbooks+and+guides/605977.html.

RANA, M. A., M. SHABNAM, N. RANA, T. SULTANA, S. SULTANA, S. KANWAL, and M. BATOOL. 2016. Species richness and spatial diversity of spiders among fodder crops. J. Biodivers. Environ. Sci. 8: 168–178.

RAO, D. 2017. Habitat selection and dispersal. *In* C. Viera and M. O. Gonzaga (Eds.) Behaviour and ecology of spiders - contributions from the neotropical region. Springer International Publishing, Cham, Switzerland.

REMBOLD, K., H. MANGOPO, S. S. TJITROSOEDIRDJO, and H. KREFT. 2017. Plant diversity, forest dependency, and alien plant invasions in tropical agricultural landscapes. Biol. Conserv. 213: 234–242.

RENÓ, V. F., E. M. L. M. NOVO, C. SUEMITSU, C. D. RENNÓ, and T. S. F. SILVA. 2011. Assessment of deforestation in the Lower Amazon floodplain using historical landsat MSS/TM imagery. Remote Sens. Environ. 115: 3446–3456.

RUBIANA, R., A. RIZALI, L. H. DENMEAD, W. ALAMSARI, P. HIDAYAT, D. PUDJIANTO HINDAYANA, Y. CLOUGH, T. TSCHARNTKE, and D. BUCHORI. 2015. Agricultural land use alters species composition but not species richness of ant communities. Asian Myrmecology 7: 73–85.

RUDEL, T., and J. ROPER. 1997. The paths to rain forest destruction: crossnational patterns of tropical deforestation, 1975-90. World Dev. 25: 53–65.

RUSSEL-SMITH, A., and N. STORK. 1994. Abundance and diversity of spiders from the canopy of tropical rainforests with particular reference to Sulawesi, Indonesia. J. Trop. Ecol. 10: 545–558.

SALA, O. E., S. C. I. F., J. J. ARMESTO, E. BERLOW, J. BLOOMFIELD, R. DIRZO, E. HUBER-SANWALD, L. F. HUENNEKE, R. B. JACKSON, A. KINZIG, R. LEEMANS, D. M. LODGE, H. A. MOONEY, M. OESTERHELD, N. L. POFF, M. T. SYKES, B. H. WALKER, M. WALKER, and D. H. WALL. 2000. Global Biodiversity Scenarios for the Year 2100. Science (80-.). 287: 1770–1774. Available at: https://science.sciencemag.org/content/287/5459/1770.

SAMU, F., G. LENGYEL, É. SZITA, A. BIDLÓ, and P. ÓDOR. 2014. The effect of forest stand characteristics on spider diversity and species composition in deciduous-coniferous mixed forests. J. Arachnol. 42: 135–141.

SÁNCHEZ-BAYO, F., and K. A. G. WYCKHUYS. 2019. Worldwide decline of the entomofauna: A review of its drivers. Biol. Conserv. 232.

SCHULDT, A., S. BOTH, H. BRUELHEIDE, W. HÄRDTLE, B. SCHMID, H. ZHOU, and T. ASSMANN.

2011. Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. PLoS One 6.

SHINE, R., and B. TAMAYO. 2016. When predators become prey: The lizard-eating spiders of suburbia. Aust. Zool. 38: 212–213.

SIH, A., G. ENGLUND, and D. WOOSTER. 1998. Emergent impacts of multiple predators on prey. Trends Ecol. Evol. 13: 350–355.

SODHI, N. S., L. P. KOH, B. W. BROOK, and P. K. L. NG. 2004. Southeast Asian biodiversity: an impending disaster. Trends Ecol. Evol. 19: 654–660. Available at: internal-pdf://129.194.21.8/Sodhi...2004.TREE - SE Asian Biodiversity Impe.pdf.

SODHI, N. S., M. R. C. POSA, T. M. LEE, D. BLICKFPRD, L. P. KOH, and B. W. BROOK. 2010. The state and conservation of Southeast Asian biodiversity. Biodivers. Conserv. 19: 317–328. Available at: internal-pdf://97.59.12.19/Sodhi...2010.BiolConserv - Conserving Southeas.pdf.

SOLIVERES, S. ET AL. 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536: 456–459. Available at: https://doi.org/10.1038/nature19092.

SØRENSEN, L. L. 2004. Composition and diversity of the spider fauna in the canopy of a montane forest in Tanzania. Biodivers. Conserv. 13: 437–452. Available at: https://doi.org/10.1023/B:BIOC.0000006510.49496.1e.

STEFFAN-DEWENTER, I. ET AL. 2007. Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. Proc. Natl. Acad. Sci. U. S. A. 104: 4973–4978. Available at: internal-pdf://0176899169/Steffan-Dewenter...2007.PNAS - Biodiversity Ec.pdf.

SUENAGA, H., and T. HAMAMURA. 2015. Effects of manipulated density of the wolf spider, Pardosa astrigera (Araneae: Lycosidae), on pest populations and cabbage yield: a field enclosure experiment. Appl. Entomol. Zool. 50: 89–97. Available at: http://dx.doi.org/10.1007/s13355-014-0310-y.

TURNER, E. C., and W. A. FOSTER. 2009. The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. J. Trop. Ecol. 25: 23–30.

VIJAY, V., S. L. PIMM, C. N. JENKINS, and S. J. SMITH. 2016. The impacts of oil palm on recent deforestation and biodiversity loss. PLoS One 11.

VOGEL, A., A. EBELING, G. GLEIXNER, C. ROSCHER, S. SCHEU, M. CIOBANU, E. KOLLER-FRANCE, M. LANGE, A. LOCHNER, S. T. MEYER, Y. OELMANN, W. WILCKE, B. SCHMID, and N. EISENHAUER. 2019. A new experimental approach to test why biodiversity effects strengthen as ecosystems age. Adv. Ecol. Res. 61: 221–264.

WICKHAM, H. 2016. ggplot2 - Elegant graphics for data analysis (2nd edition). Springer International Publishing, Cham, Switzerland Available at: http://www.springer.com/gp/book/9783319242750.

WISE, D. H. 1993. How spiders avoid competition. *In* Spiders in ecological webs. pp. 97–140, Cambridge University Press, Cambridge, United Kingdom.

WISE, D. H., E. SNYDER, WILLIAM, P. TUNTIBUNPAKUL, and J. HALAJ. 1999. Spiders in decomposition food webs of agroecosystems: theory and evidence. J. Arachnol. 27: 363–370.

ZEMP, C. D., M. EHBRECHT, D. SEIDEL, C. AMMER, D. CRAVEN, J. ERKELENZ, B. IRAWAN, L. SUNDAWATI, D. HÖLSCHER, and H. KREFT. 2019. Mixed-species tree plantings enhance structural complexity in oil palm plantations. Agric. Ecosyst. Environ. 283: 106564.

ZHENG, G., S. LI, P. WU, S. LIU, R. L. KITCHING, and X. YANG. 2017. Diversity and assemblage structure of bark-dwelling spiders in tropical rainforest and plantations under different management intensities in Xishuangbanna, China. Insect Conserv. Divers. 10: 224–235.

ZHENG, G., S. LI, and X. YANG. 2015. Spider diversity in canopies of Xishuangbanna rainforest (China) indicates an alarming juggernaut effect of rubber plantations. For. Ecol. Manage. 338: 200–207. Available at: http://www.sciencedirect.com/science/article/pii/S0378112714006999.

ZUUR, A. F., E. N. IENO, and C. S. ELPHICK. 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1: 3–14. Available at: https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/j.2041-210X.2009.00001.x.