



# Transformation of dry dipterocarp to dry evergreen forests alters food webs of web-building spiders and their prey

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## Abstract

Anthropogenic habitat modification is a major contributor to global change. While the modification of natural habitats to agroecosystems attracts most of the attention, little is known about the conversion of one natural ecosystem to another. Dry dipterocarp forest is the key dry forest type across Southeast Asia. Moderate fire disturbance is essential for its regeneration, but humans often prevent fire in these forests. Consequently, dry dipterocarps can change to dry evergreen forests through succession. The consequences of this conversion on food webs are unknown. Using the network approach, we compared the food webs of web-building spiders and their prey in the understory between dry dipterocarp (open canopy, uniform understory) and dry evergreen forests (closed canopy, heterogeneous understory) in north-eastern Thailand. Overall, we collected 560 individual web-building spiders belonging to 37 genera. Further, we collected 1139 prey items from spider webs belonging to 16 arthropod orders. The composition of captured prey and the network structure differed between the forest types. Specifically, the web-building spiders were more specialized and their niches overlapped less in dry dipterocarps than in dry evergreens. The differences in food-web structure were driven mostly by trophic groups turnover rather than interaction rewiring. Implications for insect conservation: The transformation of dry dipterocarp to dry evergreen forests from the prevention of fire disturbance may lead to an altered ecological function of web-building spiders in forest understories. As trophic links and their strength are rewired, habitat modification may also lead to changes in nutrient and energy flow in forest understories.

**Keywords** Araneae · Habitat modification · Land-use change · Network · Predator–prey interaction

## Introduction

Habitat modification (i.e., conversion of one type to another) is one of the most significant drivers of global change (Sala et al. 2000) with pronounced effects on biodiversity (Liebke et al. 2021), trophic interactions (Tylianakis et al. 2007), and ecosystem functioning (Potapov et al. 2020). Most research has focused on the conversion of (semi)natural ecosystems to agroecosystems (e.g., Tylianakis et al. 2007; Birkhofer et al. 2018; Potapov et al. 2020); limited attention has been paid to the conversion of one natural ecosystem to another due to anthropogenic activities preventing natural disturbances. Natural disturbances such as fire, flooding, and insect outbreaks usually affect forest regeneration and the maintenance of biodiversity and ecosystem functioning (Swanson et al. 2011; Thom & Seidl 2016; Viljur et al. 2022).

The ecological impact of habitat modification is frequently evaluated by changes in taxonomic diversity (Hill

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& Hamer 2004; Liebke et al. 2021). However, a community is not only an array of species but also includes interactions among species such as predator–prey interactions (Begon et al. 2006). The maintenance of trophic interactions should be included in the key elements for conservation management because these interactions impact ecosystem functioning and services such as biocontrol of pests and nutrient and energy cycling (Vander et al. 2016). Moreover, the analysis of trophic interactions can be an even more powerful tool to detect changes in community structure than taxonomic composition (Tylianakis et al. 2007; Edwards et al. 2013) because trophic interactions change faster than the rate at which a species is lost from a community (Ebenman et al. 2018). Trophic interactions within a community can be analyzed using the network approach, where individual (trophic) species represent nodes, interactions between species represent links, and the weight of the links indicates the strength of the interaction between species (Dormann & Bluthgen 2018).

When studying the impact of habitat modification on trophic interactions, it is important to determine whether the changes in food webs are related mostly to differences in species composition (i.e., species turnover) or whether the change is caused by flexible adaptation of consumer diets (i.e., interaction rewiring; Poisot et al. 2012; Ceron et al. 2022). Different environments can select different species based on particular traits (e.g., body size, hunting strategy); these traits can consequently affect prey selection (Michalko et al. 2021a). In cases like this, species turnover is an important driver of variation in species interactions between habitats (Ceron et al. 2022). On the other hand, generalist predators can have wide environmental niches and can occur across a variety of habitats (Entling et al. 2007). Generalist predators can then adapt their diets depending on the relative availability of prey species in different habitats (Baudrot et al. 2016) to balance needs such as nutritional intake (Schmidt et al. 2012). Diet adaptation by generalist predators can rewire the interaction strengths between interacting species across space and time. When this happens, interaction rewiring is an important driver of variation of food-web composition among habitats (Ceron et al. 2022).

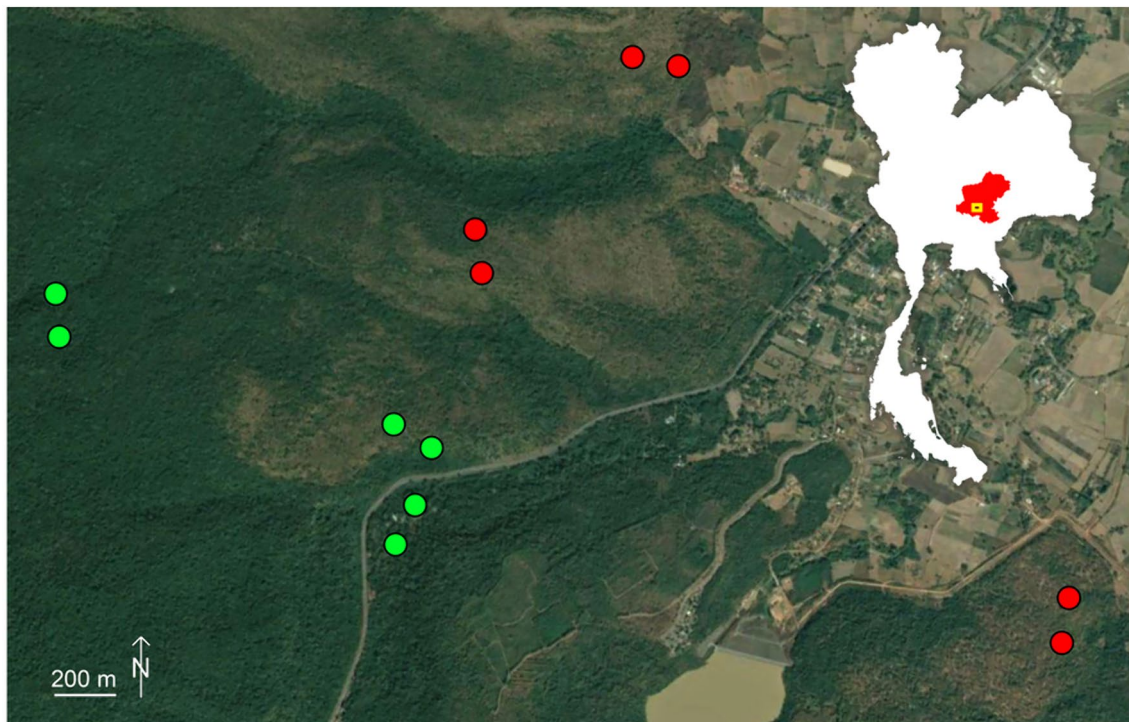
Dry dipterocarp forest is the key dry forest habitat type in Southeast Asia, the second most dominant forest type in Thailand, and supports high biodiversity (Sutthisrisinn & Noochdumrong 1998; Wohlfart et al. 2014). Even though dry dipterocarps are highly endangered, they have no legal protection (Hoekstra et al. 2005; Wohlfart et al. 2014). Dry dipterocarps are characterized by an open canopy and dense but uniform understory vegetation (Fig. 1A). Rare fire disturbance is essential for the natural regeneration of dry dipterocarps (Wanthongchai et al. 2014) but humans often prevent fires in these forests in Thailand. Consequently, the dry dipterocarps transform through natural

succession to dry evergreen forests. Dry evergreen forests are characterized by a closed canopy and relatively less dense but more heterogeneous understory vegetation (Fig. 1B). The consequences of the conversion from dry dipterocarps to dry evergreen forest on food webs are unknown.

The heterogeneous understory vegetation in dry evergreens (Fig. 1) may theoretically provide more types of spatial niches, thereby reducing negative intraguild interactions and ensuring coexistence of more species compared to dry dipterocarp forests (Langellotto & Denno 2004). This may result in larger food-webs in understories of dry evergreens (Swanson et al. 2011). Moreover, the reduced negative intraguild interactions may lead to a diet expansion among generalist predators (Staudacher et al. 2018). Consequently, this may lead to lower specialisation, higher connectance, larger niche overlap, and higher nestedness of food-webs in the understories of dry evergreen forests compared to dry dipterocarps.

Web-building spiders and their prey are an excellent model system to investigate the effect of environmental change on predator–prey food webs. Spiders are abundant and diverse arthropod predators in terrestrial ecosystems and affect ecosystem functioning (Nyffeler & Birkhofer 2017). Web-building spiders construct a variety of web types (Cardoso et al. 2011) that capture different prey types (Michalko & Pekar 2016). Habitat structure determines the web-type composition in local spider communities (Vasconcellos-Neto et al. 2017). The differences in web-type composition can affect prey composition captured by a local community of web-building spiders. Consequently, food-web properties can be affected (Diehl et al. 2013; Michalko et al. 2021a,b). The food web of web-building spiders and their prey may also be altered through intraspecific variation in prey selection; spiders can adapt their web architecture to maximize interception of the most abundant or their preferred prey (Sandoval 1994; Tso et al. 2007).

In this study, we compared the food-web structure of web-building spiders and their prey in forest understories between dry dipterocarp forests and dry evergreen forests situated in one landscape in northeastern Thailand. For comparison, we used the network approach. Given the information detailed above, we expected that (i) the composition of captured prey would differ between the two forest types and would consequently lead to (ii) different network structures. Specifically, we expected that (iii) the understories of dry evergreen forest would host food-webs that are larger, more generalized, more connected, with larger niche overlaps, and more nested than understories of dry dipterocarp forests. We also expected that (iv) trophic group turnover would contribute more to the beta-diversity of species interactions than interaction rewiring.



### Forest type



● dry evergreen forest



● dry dipterocarp forest

**Fig. 1** Aerial photograph of the study area showing positions of the twelve sampling sites and illustrative examples of the two forest types studied. The map insert showing the position of the study area within Thailand (northeastern part, Nakhon Ratchasima province) was

downloaded from a free maps platform system (<http://www.freepik.com>) and modified in Adobe Photoshop CS6. Map background was created by Esri ArcMap 10.2

## Methods

### Study area and study design

The study took place in the northeastern part of Thailand, close to the Sakaerat Environmental Research Station and Sakaerat Silvicultural Research Station (14.51 N, 101.93 E, Nakhon Ratchasima Province in Thailand; Fig. 1). The study area was approximately 30 km<sup>2</sup> and formed one large forest complex without any disjointed forest patches (Fig. 1). A more detailed description of the study area can be found in

Michalko et al. (2021b). We established six sampling sites in each forest type (N = 12; Fig. 1).

The dry dipterocarp forests were characterized by high canopy openness values ranging from 51–59% of canopy cover and very dense vegetation coverage in undergrowth (81–90%), which were maintained mainly by the dominant grass species *Vietnamosasa pusilla* (A.Chev. & A.Camus). The tree layer was characterized by *Shorea obtusa* Wall. ex Blume, *Shorea siamensis* (Kurz), and *Dipterocarpus tuberculatus* Roxb. In the shrub layer, the dominant species were *Memecylon edule* Roxb. and *Catunaregam tomentosa*

(Blume ex DC). However, the coverage of shrub layer was quite low (22–34%). On the other hand, the dry evergreen forests were characterized by very dense canopy cover (78–88%) and moderately dense vegetation and shrub cover in the undergrowth (35–52% and 40–49%, respectively). The tree layer in dry evergreen forests was characterized by a dominant representation of *Shorea henryana* Pierre, *Hopea ferrea* Laness, and *Hopea odorata* Roxb. The shrub layer was dominated by *Croton cascarilloides* Raeusch and herb coverage was typically dominated by *Kaempferia* spp. (L.) and *Globba* spp. (L.).

### Sampling protocol and arthropod identification

Overall, we sampled 12 sites. Eleven sites were sampled twice, once during the wet season (20 October–1 November 2017) and once during the dry season (2–10 August 2018), to account for the species phenology and varying habitat (Diehl et al. 2013). One site was sampled only once during the dry season. We collected spiders and their prey according to established protocols (Diehl et al. 2013; Michalko et al. 2021b). Sampling followed a time-standardized protocol (Gotelli & Ellison 2004). Sampling consisted of a 20-min visual search for active webs (i.e., spider was using the web) by four arachnologists every time. When we found a web, we stopped the time counter and started again only when we finished the manipulation with the web and spider. We sampled web-building spiders from 10 a.m. to 5 p.m. from understory vegetation at heights from 30 to 170 cm. Spiders and prey were stored in 75% alcohol.

We identified the prey of spiders to the order or sub-order level. Formicidae were separated from other Hymenoptera. Larvae and adults of holometabolous insects represented separate categories because they greatly differ morphologically and ecologically. We used this rather broad determination because masticated prey were often impossible to identify to lower taxa. This level of identification is often used to study the trophic niches of spiders (reviewed in Michalko & Pekár 2016) and other predators (Hemprich-Bennett et al. 2021; Ceron et al. 2022). Spider individuals were identified to the genus level using identification keys (Deeleman-Reinhold 2001, Murphy & Murphy 2000, Jäger & Praxaysombath 2011). Many collected spiders were juveniles and could not be identified to the species level. This was deemed acceptable because sympatric congeneric spiders have very similar trophic niches (reviewed in Michalko & Pekár 2016) and genus diversity often closely correlates with species diversity (Cardoso et al. 2004).

### Statistical analyses

All analyses were performed within the R environment (R Core Team, 2023). We analysed the data from the two

seasons separately as the network characteristics may vary between the seasons (Suzuki et al. 2023). We used negative binomial generalized linear models (GLM-nb) to compare the overall numbers of captured prey between the two forest types because the data were counts and overdispersed (Pekar & Brabec 2016a). We compared the prey community composition between the two forest types by PERMANOVA using Bray–Curtis distances and 999 permutations within the R package ‘vegan’ (Oksanen et al. 2018).

To compare the network structure between the two forest types, we computed five commonly used network characteristics using the R package ‘bipartite’ (Dormann et al. 2008), namely: network size (number of trophic groups), connectance (the percentage realized out of all possible interactions), weighted NODF (a measure of nestedness, i.e. the tendency of specialists to utilize a subset of resources utilized by generalists), network level specialization H2 (it calculates the overall level of specialisation of all interacting species in a bipartite web), and niche overlap among spiders (mean similarity in interaction pattern between species of the same level). As several indices are strongly related to network size and sampling intensity (Dormann et al. 2009), we z-transformed the indices (i.e., [observed value – mean value from null models] / SD of values from null models). We used the r2dtable algorithm to generate the null models and performed 1000 iterations.

To compare the network structure between the two forest types, we first ran the global multivariate linear model (many-LM) within the R package ‘mvabund’ to prevent p-value inflation (Wang et al. 2022). The response variables were the network characteristics while the explanatory variable was the habitat type. We then ran individual linear models (LMs) for each network characteristic except the network size. The network size during wet season was compared by GLM with Poisson error structure (GLM-p) because the data were counts. The network size during dry season was compared by GLM with quasipoisson distribution (GLM-qp) because the data were counts and underdispersed (Pekar & Brabec 2016a).

To compare the relative contribution of species turnover and interaction rewiring to the interaction beta-diversity between the two forest types. We computed the indices for species turnover (‘st’) and interaction rewiring (‘os’) using the command ‘betalinkr’ implemented within the R package ‘bipartite’ for each pair of sites belonging to dry dipterocarp and dry evergreen forests. We did not compute the beta-diversity between sites belonging to the same habitat type. As the measurements were not independent, we used permutational Generalized Least Squares (GLS) with the site as the grouping variable (Pekar & Brabec 2016b). GLS was run using the R package ‘nlme’ (Pinheiro et al. 2023). We used corCompSymm as the correlation structure because there were only two measurements within each group. To obtain

the p-value, we randomized the indices values across the species turnover and interaction rewiring and then compared the randomly obtained F-values to the observed F-value. We run 100 permutations.

## Results

Overall, we collected 560 individuals web-building spiders belonging to 37 genera. In addition, we collected 1139 prey items from spider webs belonging to 16 arthropod orders.

Spiders captured more prey in dry dipterocarp forests than in dry evergreen forests during wet season (GLM-nb;  $\chi^2_1=8.2$ ,  $P=0.004$ ; Fig. 2A) but during the dry season the difference was not significant (GLM-nb;  $\chi^2_1=2.6$ ,  $P=0.106$ ). The composition of captured prey differed between the forest types during wet season (PERMANOVA, 999 permutations,  $P=0.013$ ,  $R^2=0.32$ ; Fig. 3A) as well as dry season (PERMANOVA, 999 permutations,  $P=0.003$ ,  $R^2=0.39$ ; Fig. 3B). The web-building spiders in the two forest types captured similar prey but in different proportions. Spiders in the dipterocarps captured mostly Coleoptera, Diptera, Formicidae, and Auchenorrhyncha. Spiders in the dry evergreen forests captured mostly Diptera, Formicidae, and other Hymenoptera (Fig. 3).

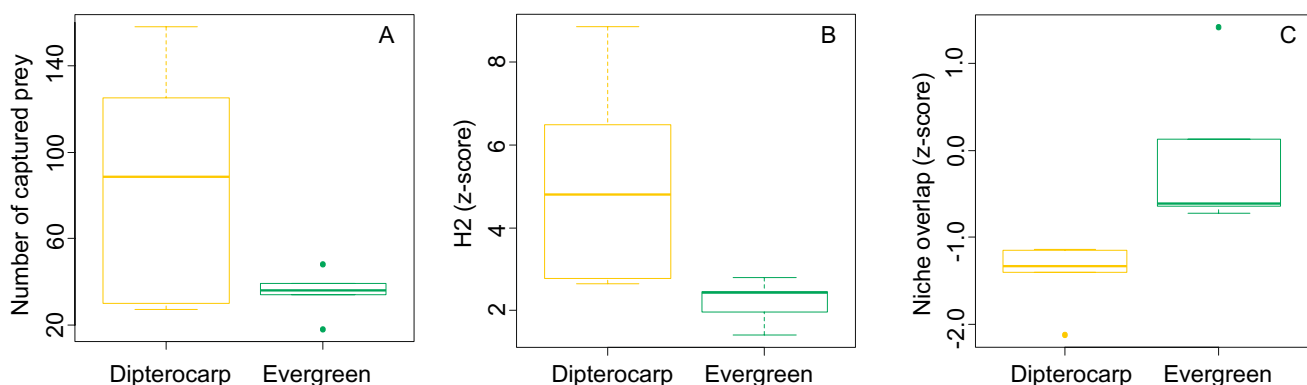
The network size at the forest stand level did not differ significantly between the two forest types during the dry season as well as during the wet season (Table 1). However, at the level of meta-web (i.e. composite food web across samples), more spider genera (dipterocarp forest: wet season  $N=15$ , dry season  $N=16$ ; evergreen forest: wet season  $N=25$ , dry season  $N=21$ ) but similar number of prey types (dipterocarp forest wet season  $N=19$ , dry season  $N=17$ ; evergreen forest: wet season  $N=17$ , dry season  $N=15$ ) were found in the dry evergreen forests and in the dipterocarps (Fig. 3).

When the network measures were z-standardized, the overall network structure of web-building spiders and their prey differed between the dry dipterocarps and dry evergreen forests during the wet season (many-LM,  $F_{1,9}=22.3$ ,  $P=0.008$ ; Fig. 2) but not during the dry season (many-LM,  $F_{1,10}=9.0$ ,  $P=0.145$ ). During the wet season, spiders in dry dipterocarps were more specialized (Table 1, Fig. 2B) than spiders in dry evergreen forests and their niches overlapped less (Table 1, Fig. 2C). Other network measures did not differ significantly (Table 1).

The differences in food webs were significantly more connected to trophic groups turnover than to interaction rewiring during both seasons (permutational GLSs,  $P<0.001$ ; Fig. 4). However, the interaction rewiring also contributed to the differences in food-web structure (Fig. 4).

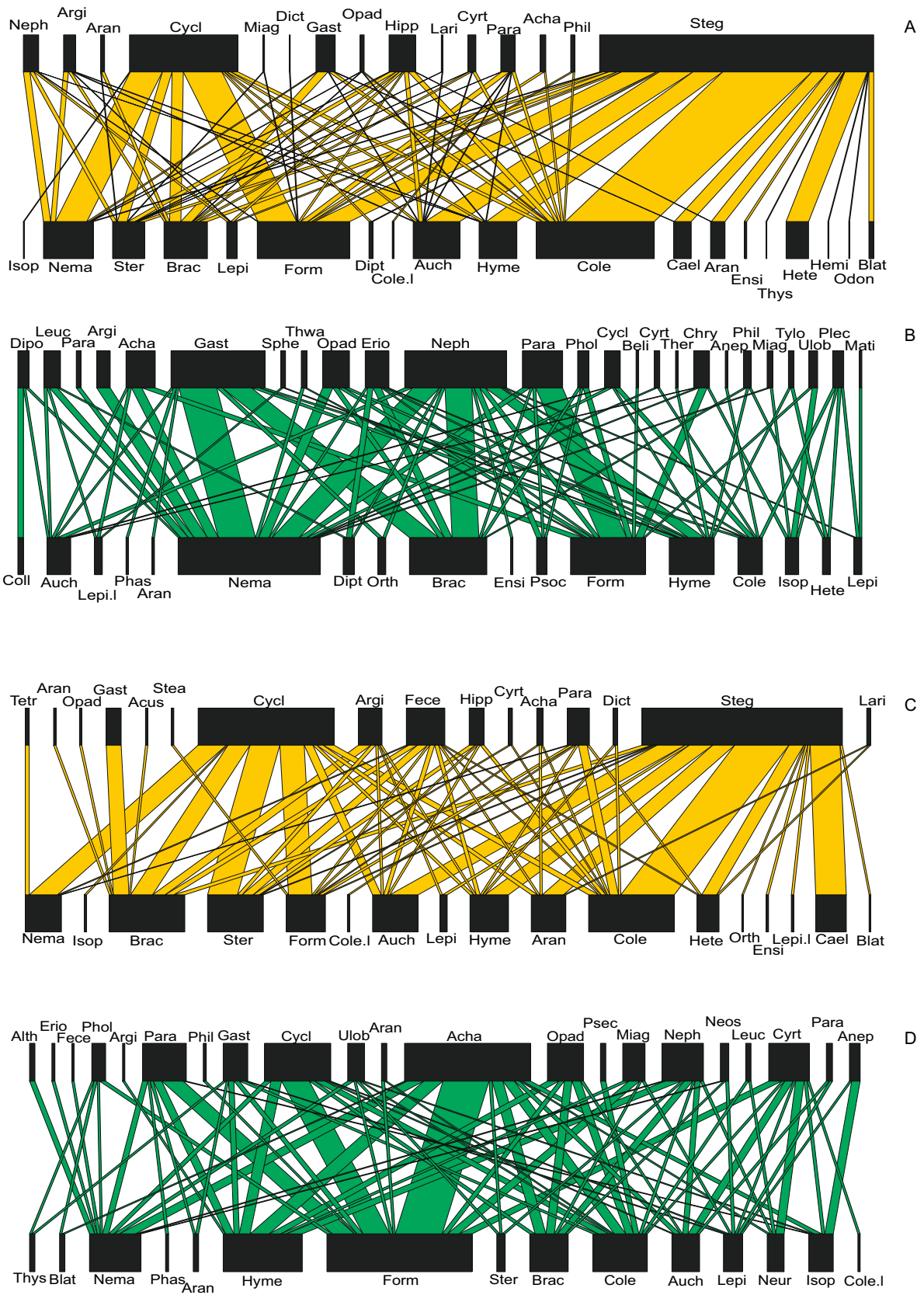
## Discussion

In our study, we compared the food webs of web-building spiders and their prey between understories in dry dipterocarp forests and dry evergreen forests to understand how the food-web structure changes when human activities prevent fire disturbance and the dipterocarps transform through succession to dry evergreen forests. In accordance with our first hypothesis, we found that the local spider communities in dry dipterocarps captured different prey than in evergreen forests. In accordance with our second hypothesis, the network structure differed between the two forest types, although only in two out of five measured characteristics and only during wet season. Specifically, spiders in dry dipterocarps were more specialized, and their niches were more separated compared to spiders in dry evergreen forests. We found mixed support for our third hypothesis, as the network size, connectance, and nestedness did not differ significantly between the two forest types. In accordance with our fourth



**Fig. 2** Comparison of number of captured prey **A**, z-standardized metric of network level specialisation **H2** **B**, and z-standardized metric of niche overlap **C** of web-building spiders and their prey between

dry dipterocarp forests and dry evergreen forests. The thick lines show mean values, boxes are quartiles, whiskers show 1.5 times interquartile range, and points are outliers



**Fig. 3** Composite food webs of web-building spiders and their prey in dry dipterocarp forests **A, C** and dry evergreen forests **B, D** during the wet **A, B** and dry **C, D** season. The individual spider genera are depicted by the upper rectangles and prey are depicted by the bottom rectangles. The width of upper rectangles shows the relative contribution of spider genera to the overall number of killed prey by the spider community. The width of the bottom rectangles shows the relative contribution of prey types to overall prey composition. The width of links connecting spiders and their prey corresponds with the relative interaction strength. Abbreviation of spider genera: Acha = Achaearanea ; Acus = Acusilas ; Alth = Altheopus ; Anep = Anepsion ; Aran = Araneus ; Argi = Argiope ; Beli = Belisana ; Chry = Chrysso ; Cycl = Cyclosa ; Cyrt = Cyrtophora ; Dict = Dictyna ; Dipo = Diploena ; Erio = Eriowixia ; Fece = Fecenia ; Gast = Gasteracantha ; Hipp = Hippasa ; Lari = Larinia ; Leuc = Leucocage ; Mati = Matidia ; Miag = Miagrammopes ; Neos = Neoscona ; Neph = Nephila ; Opad = Opadometa ; Para = Parasteatoda ; Phil = Philoponella ; Plec = Plectembolus ; Phol = Pholcus ; Psec = Psecchrus ; Sphe = Sphephanus ; Stea = Steatoda ; Steg = Stegodyphus ; Tetr = Tetragnatha ; Ther = Theridion ; Thwa = Thwaitesia ; Tylo = Tylorida ; Ulob = Uloborus . Abbreviation of prey types: Aran = Araneae ; Auch = Auchenorrhyncha ; Blat = Blattaria ; Brac = Brachycera ; Cael = Caelifera ; Cole = Coleoptera ; Cole.l = Coleoptera larvae ; Dipt = Diptera ; Ensi = Ensifera ; Form = Formicidae ; Hete = Heteroptera ; Hemi = Hemiptera ; Hyme = Hymenoptera without ants ; Isop = Isoptera ; Lepi = Lepidoptera ; Lepi.l = Lepidoptera larvae ; Nema = Nematocera ; Neur = Neuroptera ; Odon = Odonata ; Orth = Orthoptera ; Phas = Phasmatodea ; Ster = Sternorrhyncha ; Thys = Thysanoptera

hypothesis, the changes in food webs between the two forest types were mostly caused by trophic groups turnover rather than interaction rewiring.

The web-building spiders in dry dipterocarps and dry evergreen forests captured similar prey types but in different proportions during both seasons (Fig. 3). Spiders in dipterocarps captured mostly Coleoptera, Diptera, Formicidae, and Auchenorrhyncha. Meanwhile, spiders in dry evergreens captured mostly Diptera, Formicidae, and other Hymenoptera. This pattern agrees with other studies showing that spiders capture similar prey types but in different proportions in different forest (Michalko et al. 2021a,b) and non-forest habitats such as agroecosystems (Diehl et al. 2013; Birkhofer et al. 2018; Arvidsson et al. 2020). The difference in the composition of captured prey can be explained, to some extent, by the availability of particular prey types (Birkhofer & Wolters 2012). However, web-building spiders show active as well as passive prey selection. Consequently, the composition of captured prey does not correspond to the proportional composition of available prey (e.g., Diehl et al. 2013; Arvidsson et al. 2020; Cuff et al. 2022).

Spiders in dry dipterocarps were more specialized and consequently their niches tended to be more separated than spiders in dry evergreen forests. These patterns can be explained by the ‘habitat heterogeneity hypothesis’ and is consistent with Staudacher et al. (2018), who showed that arthropod predators in agroecosystems are more specialized in structurally-simple environments than in heterogeneous

environments. Therefore, the higher generalisation of spider species and higher niche overlap in evergreens were likely caused by the more heterogeneous understories in dry evergreen forests that provide more types of spatial niches. The spatial separation of web-building spiders might relax competition, which consequently enables individual spider species to utilize a wider and similar spectrum of prey (Langelotto & Denno 2004; Staudacher et al. 2018).

Although the network size at the plot level did not differ significantly, at the composite meta-food web scale, we found more spider genera in dry evergreen forests than in dipterocarps. This may be explained again by more heterogeneous environment of the understories in dry evergreen forests that may provide more types of spatial niches for web-building spiders.

The differences in food webs between the two forest types were mostly due to the trophic groups turnover rather than interaction rewiring. The two forest types were dominated by spiders with different web types. The spider communities in dipterocarps were dominated by the Sheet web-builder *Stegodyphus tibialis* (O.Pickard-Cambridge, 1869) and by the Orb-web builder *Cyclosa* spp. The evergreen forest was dominated by various Orb-web builders (*Nephila*, *Gasteracantha*, *Cyclosa*) and various Space-web builders (*Achaearanea*, *Parasteatoda*). Different web types select different prey types (Michalko & Pekar 2016). Moreover, different genera can build their webs in different locations, which could also affect the type of captured prey (Sanders et al. 2015). Therefore, the differences in web-type composition and web locations between dipterocarps and evergreens most likely contributed to the differences in captured prey (Michalko et al. 2021a,b).

To a smaller extent, interaction rewiring also contributed to the differences in food-web structure, indicating that the same spider genera captured similar prey in the two forest types but in different proportions. The prey selection by web-building spiders is highly dynamic and depends on several internal and external factors affecting a spider (Michalko et al. 2019). For example, the differences in habitat structure or climatic conditions (e.g., temperature) between the two forest types might alter web architecture and silk properties resulting in differential prey capture (Yang et al. 2005; Cuff et al. 2023). Web-building spiders can adapt the properties of their webs to capture their preferable prey (Sandoval 1994; Tso et al. 2007). In addition, the prey preferences of web-building spiders can change along absolute and relative densities of particular prey types (Michalko et al. 2020). However, it is important to note that the contribution of interaction rewiring to the overall differences in food-webs may be still overestimated due to the lack of species-level identification for both spiders and prey. Overall, the rewired trophic links due to both the trophic group turnover and interaction rewiring may lead to changes

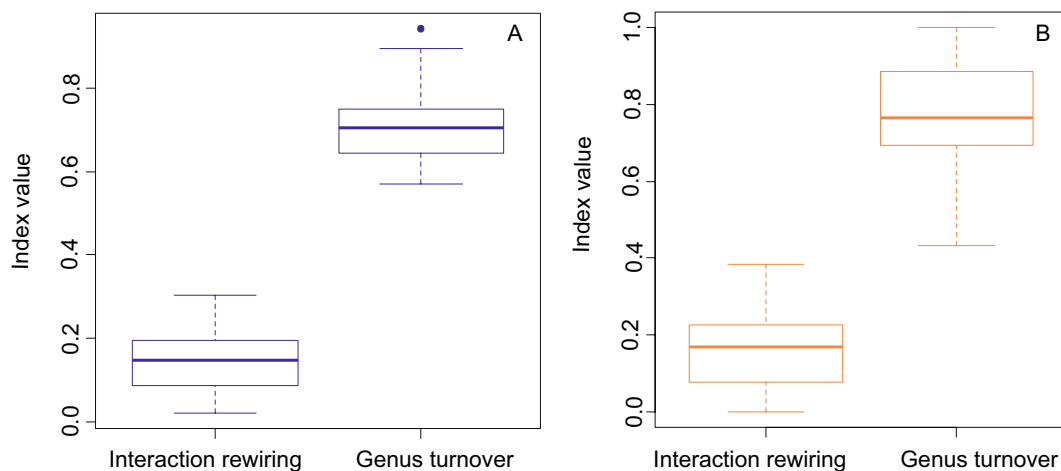
**Table 1** The results of individual general (LM) and generalized linear models (GLM) comparing the network size and z-standardized indicators of network structure during wet season between dry dipterocarp forests and dry evergreen forests

Network characteristic	Model	Test statistic	p-value
network size during wet season	GLM-p	$X^2_1=0.4$	0.511
network size during dry season	GLM-qp	$F_{1,10}=0.7$	0.430
connectance during wet season	LM	$F_{1,9}=1.7$	0.227
weighted NODF during wet season	LM	$F_{1,9}=3.0$	0.118
H2 during wet season	LM	$F_{1,9}=6.7$	0.029
niche overlap during wet season	LM	$F_{1,9}=11.0$	0.009

in energy and nutrient flows through ecosystems (Perkins et al. 2018; Ludwig et al. 2018; Bartley et al. 2019). As both forest types hosted unique interactions, the conversion of dry dipterocarps to dry evergreen forests might theoretically lead to the loss of interaction diversity at the landscape scale. Interaction diversity is an important facet of biodiversity that is necessary to conserve (Pugh & Field 2022).

In conclusion, the web-building spiders captured similar prey but in different proportions in the dry dipterocarp forests and the dry evergreen forests, which led to differences in food-web structure. During the wet season, spiders in the dry dipterocarp forests were more specialized than those in the dry evergreen forests, resulting in more separated niches. The higher specialisation of web-building spiders and lower niche overlap in dry dipterocarps than in dry evergreen forests was probably caused by the higher heterogeneity of understory vegetation in evergreens. The higher habitat heterogeneity enabled the spatial separation of individual spider species and enabled the utilization of a

wider and similar spectrum of prey (Staudacher et al. 2018). The differences in food-web structure were driven mostly by trophic groups turnover rather than interaction rewiring. As trophic links and their strength are rewired, habitat modification from dry dipterocarp forests to dry evergreen forests may lead to changes in nutrient and energy flow through ecosystems in forest understories (Perkins et al. 2018; Ludwig et al. 2018; Bartley et al. 2019). As both forest types hosted unique interactions, the conversion of dry dipterocarps to dry evergreen forests may lead to the reduction of interaction diversity at the landscape scale.



**Fig. 4** The comparison of the relative contribution of trophic groups turnover and interaction rewiring to the overall interaction beta-diversity between dry dipterocarp forests and dry evergreen forests during

wet **A** and dry **B** season. The thick lines show mean values, boxes are quartiles, whiskers show 1.5 times interquartile range, and points are outliers



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**Author contributions** RM conceived the idea; RM, OK, YT, PW designed the study; OK, RM, CS, VS, PW performed the experiments; RM performed the statistical analyses and wrote the manuscript; All authors read and critically commented the manuscript.

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**Data availability** The data will be made available upon request.

## Declarations

**Competing interests** The authors declare no competing interests.

**Ethical Approval** Not applicable.

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