Ecosystems (2021) 24: 1962–1975
https://doi.org/10.1007/s10021-021-00627-7

ECOSYSTEMS

Reforestations of Tropical Forests Alter Interactions Between Web-Building Spiders and Their Prey

Radek Michalko,[1]* Ondřej Košulič,[2] Prasit Wongprom,[3]
Chaowalit Songsangchote,[3] Venus Saksongmuang,[4] and Yongyut Trisurat[3]

[1]Department of Forest Ecology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 3, Brno 613 00, Czech Republic; [2]Department of Forest Protection and Wildlife Management, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 3, Brno 613 00, Czech Republic; [3]Department of Forest Biology, Faculty of Forestry, Kasetsart University, Bangkok 10900, Thailand; [4]Department of Biology, Faculty of Science, Prince of Songkla University, Songkhla 90110, Thailand

ABSTRACT

Immense effort has been devoted to mitigating the negative effect of deforestation, one of the main factors causing global change. However, the effect of reforestation management on food-webs has been rarely studied and no study so far has investigated the effect on predator–prey interactions in forest understories. We studied predator–prey interactions in forest understories using web-building spiders in four forest types: dry evergreen forest representing a natural control and three 20–30-year-old reforestation types, namely secondary naturally regenerating dry evergreen forest, monoculture reforestation dominated by *Eucalyptus camaldulensis*, and mixture reforestation dominated by *Acacia mangium* and *E. camaldulensis*. We collected spiders with their prey and measured the availability of potential prey. We also measured different spider traits (web type, body size) that can be selected by various forest types and consequently affect the predator–prey interactions. The forest type influenced the predator–prey interaction in a complex way, interactively affecting spider density and prey-specific capture efficacy of spider community. The forest type also influenced the web-type and body-size distributions of spiders. Surprisingly, the prey composition caught by spider webs was related only to the web-type but not to the spider mean body size. None of the studied reforestations have yet restored the natural predator–prey interactions, which indicates that conservation management in the tropics should focus on establishing protected areas in pristine regions instead of relying on reforestation. Moreover, the food-web models need to incorporate not only body sizes but also hunting strategies of predators to improve their predictive abilities.

Key words: ecological function; *Eucalyptus*; food web; predator; restoration; trait.

HIGHLIGHTS

- Spider density and prey-specific capture efficacy differed among forest types.

Received 21 May 2020; accepted 27 February 2021;

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-021-00627-7.
The dataset can be found at https://zenodo.org/record/4312104; https://doi.org/10.5281/zenodo.4312104

Author Contributions RM conceived the idea; RM, OK, PW, YT designed the study; RM, OK, CS, VS, PW performed the experiments; RM, OK, PW determined the material; RM analyzed the data; RM, OK wrote the ms; All authors read, commented, and approved the ms.

**Corresponding author; e-mail:* radar.mi@seznam.cz

- Prey composition of spiders differed among forest types.
- None of the reforestation types have yet restored natural predator-prey interaction.

INTRODUCTION

Predator–prey interactions significantly affect ecosystem functioning but they are rarely used as a tool for evaluating the restoration success of ecosystems even though they provide a more precise measure of restored function than the often used patterns in diversity (Thompson and others 2012; Edwards and others 2013; Vander Zanden and others 2016). The elemental composition of prey can, for example, affect the paths of nutrient flows through ecosystems (Ludwig and others 2018; Perkins and others 2018) or influence the predator ecosystem services, such as pest control (Birkhofer and others 2016).

Deforestation and other forms of habitat loss are among the major factors causing global change (Tilman and others 2004; Brook and others 2008; Rosa and others 2016; Segan and others 2016). Awareness of the negative impacts of deforestation has led to immense global reforestation efforts to restore forest ecosystem functions but the restoration success of various reforestation types is mixed (Chazdon 2008; Hall and others 2011; Evans and others 2013; Menz and others 2013). The variability in restoration success partially arises due to our poor knowledge about how reforestations affect ecosystem processes such as predator–prey interactions (Hall and others 2011). In animals, the restoration success of reforestation practices has been mostly evaluated based on the changes in biodiversity of a certain model group(s) of organisms including birds, mammals, herpetofauna, and invertebrates (reviewed in Crouzeilles and others 2017).

A limited number of studies have addressed the effect of reforestation and the shift in forest type on food-webs (Barnes and others 2014; Derhé and others 2016; Hu and others 2016; Klarner and others 2017; Potapov and others 2019). These studies indicate that the changes in forest stand characteristics lead to changes in the positions and widths of animal trophic niches and that the simplification and conversion of forests into monocultures steeply reduces ecosystem multifunctionality (Barnes and others 2014). What has not been considered is the change in multivariate diet composition in relation to prey availability. Moreover, the aforementioned studies focus on energy and matter fluxes in litter and soil but we are not aware of any study that investigates the effect of different reforestation practices on predator–prey interactions in the above-ground food-chain.

There are several types of reforestation management which can be divided into (a) spontaneous natural regeneration; (b) assisted natural regeneration; (c) agroforestry; and (d) commercial tree plantations (Chazdon 2013). The commercial forest plantations can be monocultures or polycultures of native and non-native tree species (Zhang and Stanturf 2008; Chazdon 2013). Different reforestation types are used for different purposes such as timber harvesting, water retention, carbon sequestration, or conservation restoration (Chazdon, 2008; Zhang and Stanturf 2008; Hall and others 2011). The reforestation types differ in various biotic, structural, and climatic conditions (Zhang and Stanturf 2008), which can alter predator–prey interactions in a plethora of complex ways by affecting the prey and predator densities and the per capita functional responses to prey densities (Denno and others 2005; Diehl and others 2013; Michalko and others 2019). The simplest and straightforward potential effect of different reforestation types on predator–prey interaction is the differential response of predator and prey densities to the different environmental conditions (Scheu and others 2003; Elek and others 2018).

Specific reforestation types may change the community-wide functional response of predators to prey density by altering the inter-specific composition of predator traits such as hunting strategy and body size that affect the utilization of various prey types (Michalko and Pekár 2016; Schmitz 2017; Perkins and others 2018). The reforestation type may also alter the community-wide functional response through the intraspecific changes in, for example, passive and active prey choice as a response to altered biotic (for example, intraguild predation, apparent competition) and abiotic conditions (Kruse and others 2008; Araújo and others 2011; Baudrot and others 2016; Schmitz 2017).

Web-building spiders represent an excellent model system to investigate the effect of management practices on predator–prey interactions (Diehl and others 2013; Birkhofer and others 2016; Arvidsson and others 2020). Spiders build various types of webs such as Orb webs, Space webs, and Sheet webs (Cardoso and others 2011), and cover a large gradient of body sizes (World Spider Catalogue 2019). The differences among forest types in bark texture of dominant trees, dry twig density, seedling density, and other features can affect the distribution of web-types and body sizes (Petcharad and others 2016; Vasconcellos-Neto and others 2017). The different web-types intercept similar prey types but in different proportions (Michalko and Pekár 2016), and differently sized spiders utilize differently sized prey (Nentwig and Wissel 1986). Variation in the composition of web-types and body sizes between communities of web-building spiders may therefore influence the food webs via web-type and body size specific predator–prey interactions (Nentwig and Wissel 1986; Sanders and others 2015; Michalko and Pekár 2016; Ludwig and others 2018).

Web-building spiders can also flexibly adapt their web architecture, mechanical properties, and prey handling behavior as a response to the changes in habitat structure and prey composition (Sandoval 1994; Tso and others 2007). The intraspecific variation in web-properties and handling behavior may be an additional (or a sole) source of variation in intercepted prey among communities of web-building spiders from different forest types (Staudaucher and others 2018).

Here we investigated the variation in prey composition intercepted by web-building spiders in a primary dry evergreen forest and three reforestation types: naturally regenerating secondary dry evergreen forest; monoculture active reforestation dominated by *Eucalyptus camaldulensis* Dehnh (Myrtaceae), and mixture reforestation dominated by *Acacia mangium* Wild. (Fabaceae) and *E. camaldulensis*. We hypothesized that the reforestation type will affect (i) the prey composition captured by web-building spiders. This will be caused by (ii) the altered density of prey and (iii) web-building spiders, and (iv) by altered trait composition of the web-building spider community (web type, body size). Finally, (v) The altered trait composition of the web-building spider community will then affect the prey-specific capture efficacy because web types differ in their effectiveness in capturing different prey types.

Materials and Methods

Study Area and Sampling Design

The twenty-four sampling sites were located around the Sakaerat Environmental Research Station (SERS) and Sakaerat Silvicultural Research Station in north-eastern Thailand (14.51 N, 101.93 E, Nakhon Ratchasima Province; Figure S1). The study area covered approximately 30 km^2 and formed one large forest complex without any disjointed forest patches (Figure S1). The forest area was dominated by dry evergreen forest, small clearings, dry dipterocarp forest, mixed deciduous forest, secondary growth, agroforestry, and forest plantations (Trisurat 2010). The mean annual temperature in the area is 26.8 °C and the mean annual precipitation is 1022 mm. The altitude of the sampling sites ranged between 309–565 m a.s.l. We collected the spiders from four forest types that represented a natural control and three 20–30-year-old reforestation types (Figure S2): a natural dry evergreen forest representing the control (herein evergreen; Figure S2A); naturally regenerating secondary dry evergreen forest (herein ‘secondary’; Figure S2B); monoculture reforestation dominated by *Eucalyptus camaldulensis* Dehnh (Myrtaceae) (herein ‘monoculture’; Figure S2C); and mixed reforestation dominated by *Acacia mangium* Wild. (Fabaceae) and *E. camaldulensis* (herein ‘mixture’; Figure S2D).

The natural dry evergreen forest was dominated by native trees from the Dipterocarpaceae family such as *Shorea henryana* Pierre, *Hopea ferrea* Laness and *Hopea odorata* Roxb. The shrub layer was dominated by of *Streblus asper* Lour, *Streblus ilicifolius* (Vidal) Corner and *Cleistanthus helferi* Hook.f.

Secondary forests (25–30 years old) were developed under spontaneous natural regeneration from previously logged primary dry evergreen forests. There was no silviculture treatment during its development. Secondary forest habitats were very dense and fully developed from dominant shrub species such as *Atalantia monophylla* (DC.) Correa, *Bauhinia saccocalyx* Pierr and *Memecylon scutellatum* Naudin.

Reforested habitats were artificially established 20–30 years ago from clear cut primary dry evergreen forest. After establishing, reforestation was maintained by spontaneous natural succession without any silviculture treatment. Except for the dominant representation of exotic trees (*Acacia*, *Eucalyptus*), native tree and shrub vegetation is mostly represented by *Cratoxylum formosum* (Jack) Dyer and *Croton poilanei* Gagnep.

We established six sites / plots per each forest type (Figure S1). We used all reforestations of the given age that occurred in the study area. To obtain a natural control with a minimum impact of human activity on the one hand and to minimize the impact of spatial distance on the other, the sampling plots in the dry evergreen forest were located closest as possible to the studied reforestations while still in the protected area. The monocultures and mixtures formed a mosaic of relatively small forest stands (5000 m^2) in comparison to the evergreen and secondary stands that covered large areas. This is a common limitation of studies that use natural forest stands as a control to a forest management (for example, Leidinger and others 2019). We therefore selected the sampling plots in the evergreen and secondary forest stands at such distance that approximately corresponded to the distance between a pair of monoculture and mixture (Figure S1). This was to prevent that some forest types would be more similar to each other due closer spatial proximity.

Data Collection

Due to space limitation, we provide only a basic description of the vegetation structure measurements, arthropod sampling, and statistical analyses. Detailed information is given in the Supplementary material. In each plot we quantified vegetation structure and collected potential and actual prey of web-building spiders. The vegetation structure was measured as canopy openness, shrub coverage, and herb coverage.

In each plot we collected the potential and actual prey according to the standardized protocols (Diehl and others 2013; Arvidsson and others 2020). To account for species' phenology and varying habitat (Diehl and others 2013), we collected arthropods in each plot twice: dry season and wet season. Both sampling periods were then pooled to represent one sample. Two sticky traps (20 × 15 cm; one white and one yellow), were hung next to one other at a height of approximately 1.6 m above the ground for five days to collect potential prey (Wallis and Shaw 2008; Diehl and others 2013). We sampled the actual prey of web-building spiders in forest understories using a time-standardized protocol (Gotelli and Ellison 2012). The sampling of actual prey consisted of a 20 min straight time of visual search by four researchers in the near proximity to the sticky traps. We collected all the active spider webs (that is, spider was using the web) with the prey remnants and web-owners. We surveyed the actual prey between 10 a.m. and 5 p.m.

We identified the actual and potential prey to the order or sub-order level, and Formicidae were separated from other Hymenoptera. The spiders were identified to the lowest possible level according to Deeleman-Reinhold (2001), Murphy and Murphy (2000), and Jäger and Praxaysombath (2011). We then expressed the body size of each spider individual as a product of cephalothorax length and width. Each spider individual was also assigned to one of the three web-types as classified by Cardoso and others (2011), namely: Orb-web, Space-web, and Sheet-web. The voucher specimens are stored at the Forestry Faculty, Kasetsart University, Bangkok, Thailand.

Statistical Analyses

Here we describe only the ecological meaning of the analyses because of the space limitation. The detailed description and the statistical reasoning of the analyses are in the supplementary material. We ran four sets of analyses. We analyzed (1) the differences in vegetation structure among the forest types, (2) the factors that can affect the predator–prey interactions (for example, prey density, functional structure of spider community; see the following paragraph for details), (3) which part of the consumptive effect of predators on prey (density, capture efficacy [Solomon 1949]) is affected by forest type, and (4) whether the factors investigated in the first set can explain the pattern observed in the second set.

In the first set of analyses, we compared the environmental characteristics (canopy openness, shrub coverage, and herb coverage). In the second set, we compared the densities of potential prey and spiders, and the functional composition of spider communities (web-type, body size) among the forest types. In the third set, we first assessed whether the actual prey composition differs among the forest types. Then we investigated whether the differences in actual prey composition are caused not only by spider density but also by altered prey-specific capture efficacy. We investigated the prey-specific capture efficacy in two ways. First, we compared the per capita capture rate of all prey types without accounting for their availability. Second, for those groups for which we had measured prey availability (that is, Hemiptera, Coleoptera, Diptera, and Hymenoptera) we compared per capita capture rates with accounting for prey availability. This is because the per capita capture rate can be blurred by differences in prey density. In the fourth set, we examined the relationship between the trait composition of the web-building spider community and the actual prey composition. We also investigated whether the forest type explains residual variability if the effect of trait composition is filtered out, that is, whether it has some additional forest-type specific effect on predator–prey interactions besides affecting trait composition of web-building spiders.

All analyses were performed within the R environment (R Development Core Team 2019). Here we state only the names of models and the detailed descriptions are given in supplementary material.

We used a combination of multivariate and univariate linear models (LM), generalized linear models (GLM), and generalized additive models (GAM), and permutational GLMs (perm-GLMs). In GLMs, and GAMs, we used Gaussian, Poisson (GLM-p, GAM-p), negative binomial (GLM-nb, GAM-nb), gamma (GLM-g), and beta (GLM-beta) depending on which model fitted the data better (Zuur and others 2015). We used the R packages 'mvabund' (Wang and others 2012; Warton and others 2012) and 'mgcv' (Wood, 2011). We used such models that best fitted the data (Table 1; Statistical analyses in the Supplementary material).

Results

Vegetation Structure

Vegetation structure differed among forest types in all measured characteristics ($P < 0.001$, Table S1). The forest canopy was most open in mixture and monoculture reforestations (Figure S3), the shrub layer was densest in the secondary forest (Figure S3), and the herb layer was densest in the mixture (Figure S3).

Table 1. Influence of Forest Type (Dry Evergreen Forest, Secondary Forest, Monoculture of *Eucalyptus camaldulensis*, and Mixture of *Acacia mangium* and *E. camaldulensis*) on the Abundance of Web-building Spiders, Trait Composition of Spider Community, Potential Prey (Hemiptera, Coleoptera, Diptera, and Hymenoptera) and Actual Prey Composition, and Prey-specific Per Capita Capture Rate

Context	Group / Trait	Method	Test statistic	*P* value
Abundance	Spiders	GLM-nb	$\chi^2_3 = 18.0$	< 0.001
Web-type composition	Overall	multiGLM-nb	999 permutations, $\chi^2_3 = 34.1$	0.003
	Orb-web	GLM-nb	$\chi^2_3 = 18.2$	< 0.001
	Sheet-web	GLM-nb	$\chi^2_3 = 5.0$	0.171
	Space-web	GLM-nb	$\chi^2_3 = 26.2$	< 0.001
Body size	Spiders	LM	$F_{3,20} = 6.0$	0.004
Potential prey composition	Overall	multiGLM-nb	999 permutations, $\chi^2_3 = 24.4$	0.161
Actual prey composition	Overall	multiGLM-nb	999 permutations, $\chi^2_3 = 146.2$	0.001
	Isoptera	GLM-nb	$\chi^2 = 20.0$	< 0.001
	Orthoptera	GLM-p	$\chi^2_3 = 4.5$	0.209
	Sternorrhyncha	GLM-p	$\chi^2_3 = 7.6$	0.054
	Auchenorrhyncha	GLM-nb	$\chi^2_3 = 11.8$	0.008
	Heteroptera	GLM-p	$\chi^2_3 = 4.5$	0.210
	Coleoptera	GLM-p	$\chi^2_3 = 8.2$	0.041
	Lepidoptera	GLM-p	$\chi^2_3 = 13.9$	0.003
	Diptera	GLM-nb	$\chi^2_3 = 12.4$	0.006
	Other Hymenoptera	GLM-nb	$\chi^2_3 = 29.8$	< 0.001
	Formicidae	GLM-nb	$\chi^2_3 = 19.2$	< 0.001
Per capita capture rate	Overall	multiLM	999 permutations, $F_{3,20} = 23.6$	0.005
	Isoptera	LM	$F_{3,20} = 3.6$	0.033
	Orthoptera	LM	$F_{3,20} = 0.5$	0.686
	Sternorrhyncha	LM	$F_{3,20} = 0.5$	0.669
	Auchenorrhyncha	LM	$F_{3,20} = 3.6$	0.032
	Heteroptera	LM	$F_{3,20} = 0.6$	0.622
	Coleoptera	LM	$F_{3,20} = 0.8$	0.517
	Lepidoptera	LM	$F_{3,20} = 3.8$	0.027
	Diptera	LM	$F_{3,20} = 3.1$	< 0.050
	Other Hymenoptera	LM	$F_{3,20} = 2.5$	0.091
	Formicidae	LM	$F_{3,20} = 5.2$	0.008

LM—Linear models; GLM—Generalized linear models; GLM-p—GLM with Poisson error structure and log link function; GLM-nb—negative binomial GLM with log link; manyGLM—extension of GLMs for multivariate data.

Overview of Collected Arthropods

Overall, we collected 878 spider individuals, 1341 actual (including all prey types) and 4387 potential (including only Hemiptera, Coleoptera, Diptera, Hymenoptera orders) prey individuals. Spiders belonged to 52 species or morphospecies in 41 genera and 10 families (Table S2). The actual prey belonged to 14 arthropod orders (Table S3).

The Effect of Forest Type on Spider Communities

The forest type influenced the overall density of spiders, web-type composition, and body size of spiders ($P < 0.004$; Table 1, Figure 1). The lowest overall spider abundance was in the secondary forests (Table 1; Figure 1A). Orb-web spiders had similar densities in the evergreen forest and the two active reforestations and lowest densities in the secondary forest (Table 1; Figure 1B) and the abundances of orb-web spiders significantly decreased with increasing coverage of shrubs (GAM-nb, $\chi^2 = 33.4$, edf = 5.3, $P < 0.001$, Figure 2A). There was no significant relationship between orb-web spiders and herb coverage (GAM-nb, $\chi^2 < 0.1$, edf = 1, $P = 0.864$). Space-web spiders had the highest densities in the evergreen forest and the lowest in the secondary forest (Table 1; Figure 1C) and there was a hump-shaped relationship between shrub coverage and their abundances (GAM-p, $\chi^2 = 33.4$, edf = 5.3, $P < 0.001$, Figure 2B). Herb coverage did not influence the distribution of space-web spiders significantly (GAM-p, $\chi^2 = 2.0$, edf = 1.0, $P = 0.156$). The abundance of sheet-web spiders was similar in all forest types (Table 1). The largest spiders were in

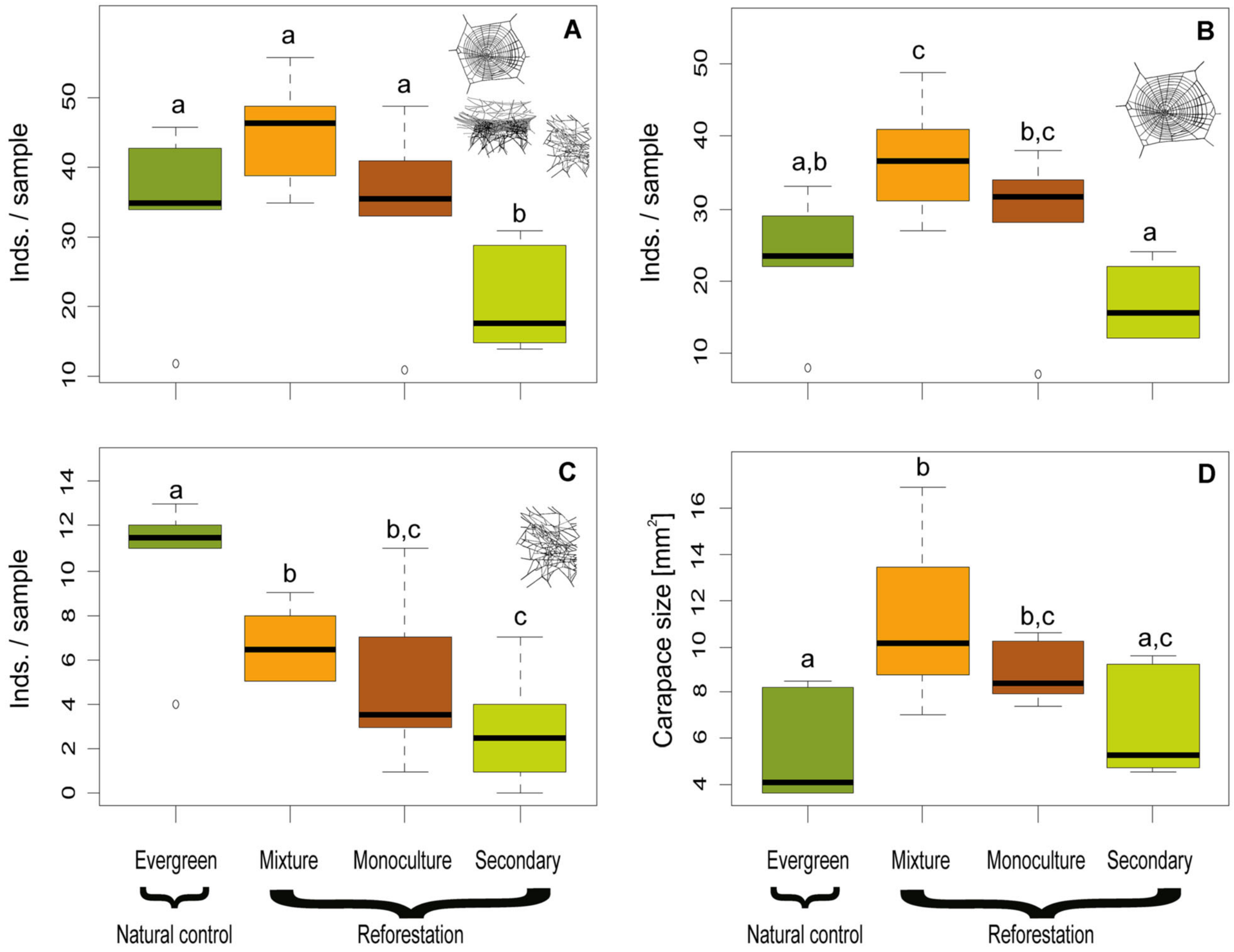
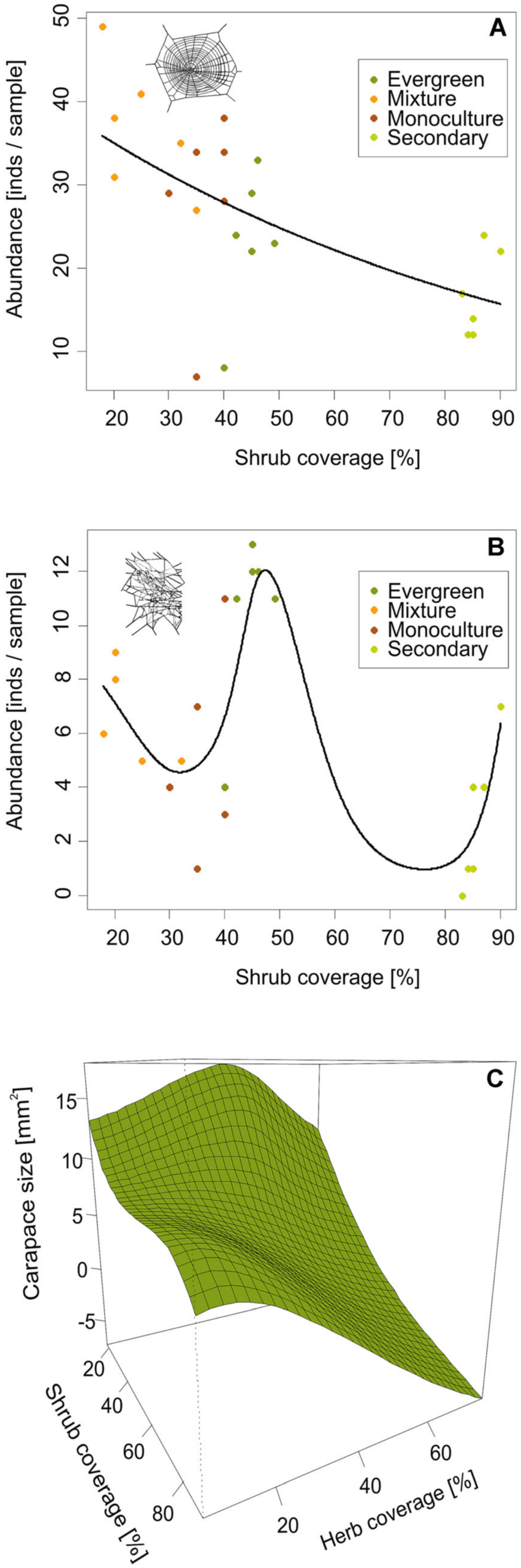


Figure 1. The effect of forest type on the community composition of web-building spiders: overall abundances (**A**), abundances of Orb-web spiders (**B**), abundances of Space-web spiders (**C**), and body size distribution (product of carapace width and length; **D**). The thick lines are medians, boxes are quartiles, whiskers are 1.5 times interquartile range, points are outliers. Different letters show difference at $P < 0.05$.



◀**Figure 2.** The effect of vegetation structure on the community composition of web-building spiders: the relationship between abundances of Orb-web spiders and shrub coverage (**A**), abundances of Space-web spiders and shrub coverage (**B**), and the relationship between body size distribution and shrub coverage and herb coverage (**C**). The estimated models are displayed.

the mixture reforestation (Table 1, Figure 1D) and the distribution of spider body size was interactively influenced by shrub and herb coverage (GAM, F = 5.3, edf = 4.5, $P < 0.001$; Figure 2C).

The Effect of Forest Type on Potential and Actual Prey Composition

The availability of Hemiptera, Coleoptera, Diptera, and Hymenoptera was similar across the forest types ($P = 0.161$; Table 1) but the forest type influenced the composition of spider actual prey ($P = 0.001$, Figure 3). Spiders caught similar numbers of Orthoptera and Heteroptera across the four forest types (Table 1). Spiders caught the highest number of Isoptera, Sternorrhyncha, Diptera, and other Hymenoptera in the mixture reforestation (Table 1, Figure 3A,B,F,G). Spiders caught Formicidae mostly in evergreen forest (Table 1, Figure 3H). Spiders caught the lowest number of Auchenorrhyncha, Coleoptera, other Hymenoptera, and Formicidae in the secondary forest ($P < 0.042$; Table 1, Figure 3C,D,G). Spiders did not catch any Lepidoptera in the monoculture (Figure 3E).

The Effect of Forest Type on Capture Efficacy

The prey-specific capture rate differed among the managements ($P = 0.005$, Table 1, Figure 4). Per capita captured Orthoptera, Heteroptera, Sternorrhyncha, Coleoptera, and other Hymenoptera was similar across managements (Table 1). The highest per capita captured Isoptera and Diptera were in the mixture reforestation (Table 1, Figure 4A,D). The highest number of captured Formicidae per capita was in the evergreen forest (Figure 4E). The number of captured Auchenorrhyncha per capita was lowest in the secondary forest (Figure 4B). The lowest number of captured Lepidoptera per capita was in the monoculture reforestation (Figure 4C).

The number of captured Hemiptera per capita (pooled Heteroptera, Auchenorrhyncha, and Sternorrhyncha) was not influenced by forest type (GLM-g, $F_{3,20} = 1.4$, $P = 0.272$) or the prey's

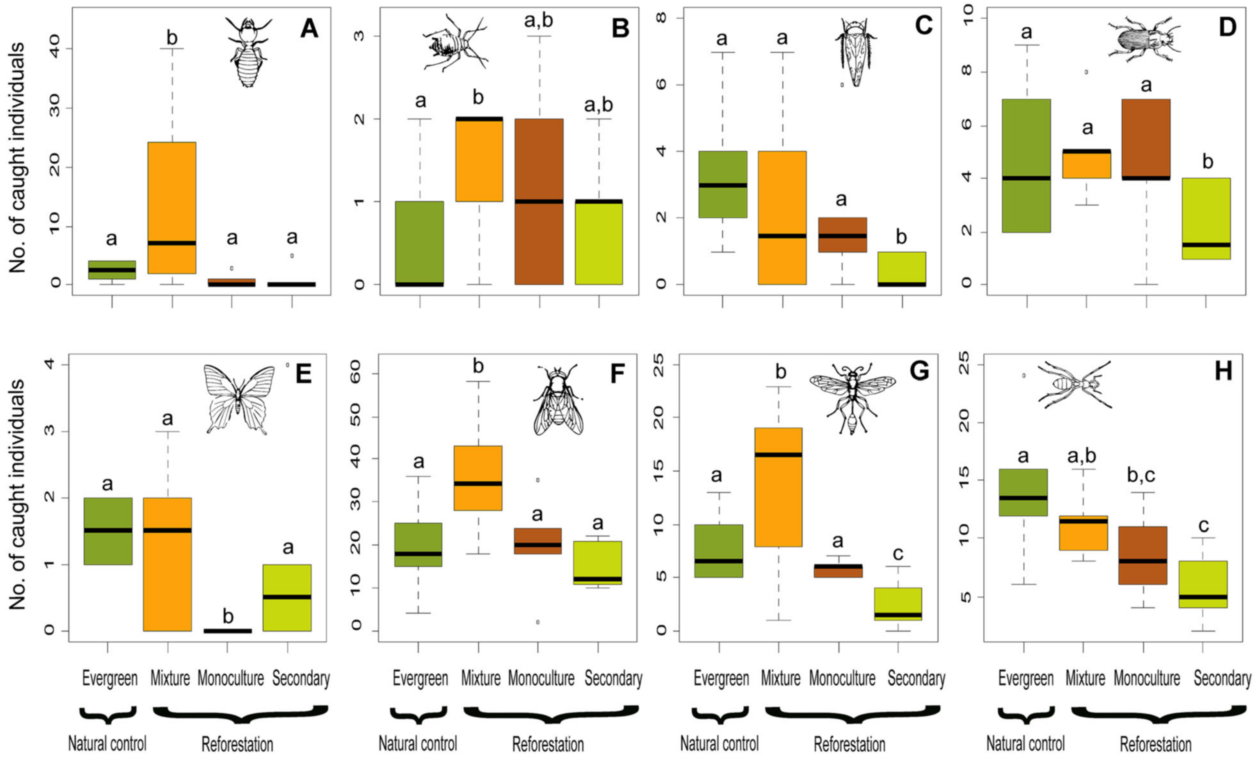


Figure 3. The effect of forest type on the number of caught Isoptera (**A**), Sternorrhyncha (**B**), Auchenorrhyncha (**C**), Coleoptera (**D**), Lepidoptera (**E**), Diptera (**F**), other Hymenoptera (**G**), and Formicidae (**H**). The thick lines are medians, boxes are quartiles, whiskers are 1.5 times interquartile range, points are outliers. Different letters show difference at $P < 0.05$.

availability (GLM-g, $F_{1,19} = 0.2$, $P = 0.668$). In the case of Coleoptera, the forest type interacted with the availability of Coleoptera to determine the per capita capture rate (LM, $F_{3,16} = 3.3$, $P = 0.048$; Figure 5A). Only in the monoculture reforestation the per capita captured Coleoptera decreased with their availability (contrasts, $P = 0.025$). There was no trend in other forest types (contrasts, $P > 0.165$). The forest type (LM, $F_{3,19} = 4.7$, $P = 0.013$; Figure 5B) additively influenced how the per capita caught Diptera increased with their availability (LM, $F_{1,19} = 11.0$, $P = 0.004$; Figure 5B). The forest additively influenced (GLM-g, $F_{3,19} = 3.3$, $P = 0.042$; Figure 5C) how the per capita captured Hymenoptera decreased with their availability (GLM-g, $F_{1,19} = 9.7$, $P = 0.006$; Figure 5C).

The Relationship Between Trait and Actual Prey Composition

The trait composition of web spiders influenced the actual prey composition but it was driven only by the web-type composition ($P < 0.001$; Table 2). The body size distribution did not affect the actual prey composition ($P = 0.309$; Table 2). When the effect of forest type was filtered out, the trait composition still influenced the actual prey composition ($P = 0.001$; Table 2). The forest type influenced the actual prey composition if the trait composition of spider community was not filtered out as well when the trait composition was filtered out ($P < 0.045$, Table 2).

Discussion

We investigated how various reforestation types, namely naturally regenerating secondary dry evergreen forest, monoculture of *Eucalyptus camaldulensis*, and a mixture of *Acacia mangium* and *E. camaldulensis*, affect the interactions between web-building spiders and their prey in comparison to natural dry evergreen forest. The actual prey composition did not mirror the prey availability. The actual prey composition of the web-building spiders differed among all forest types because forest type influenced interactively the density of spiders and their prey-specific capture efficacy. Through the differences in vegetation structure the forest type also influenced distributions of web-types and body sizes of spiders. However, the prey

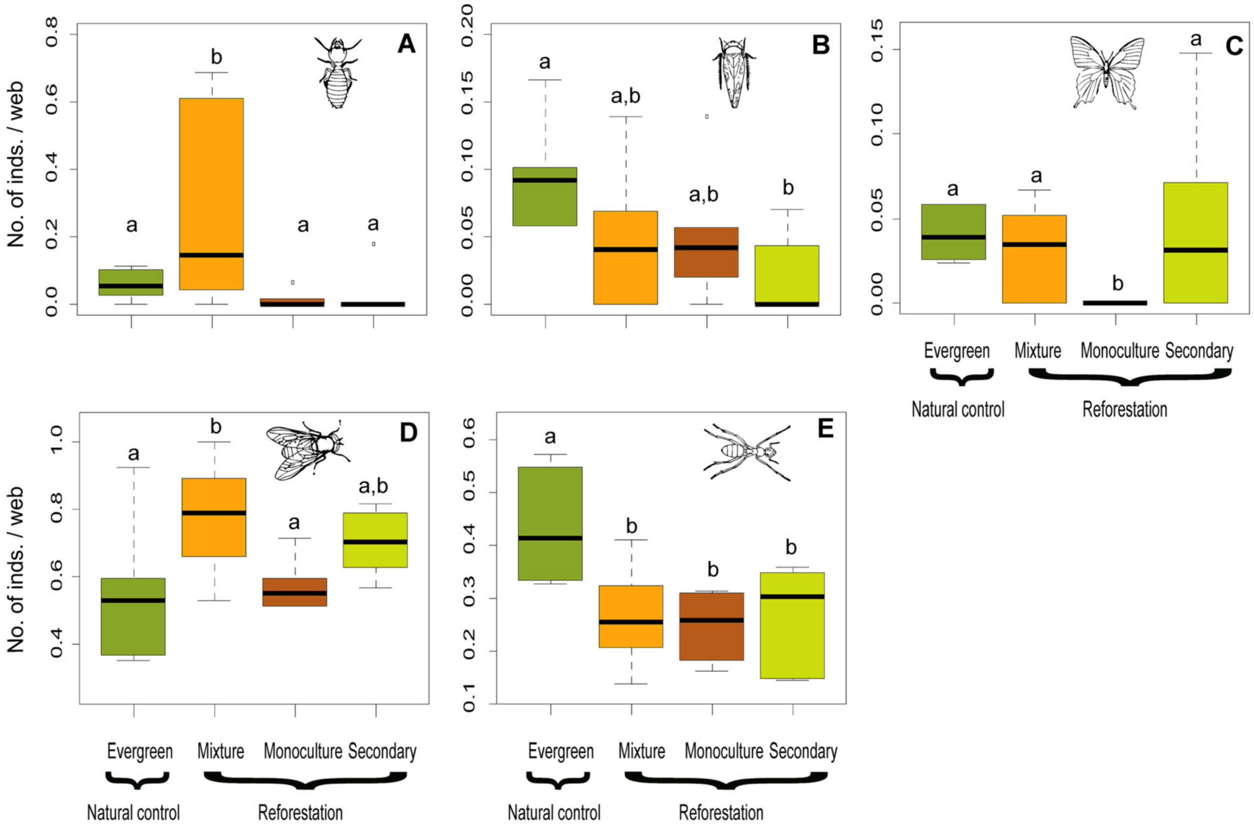


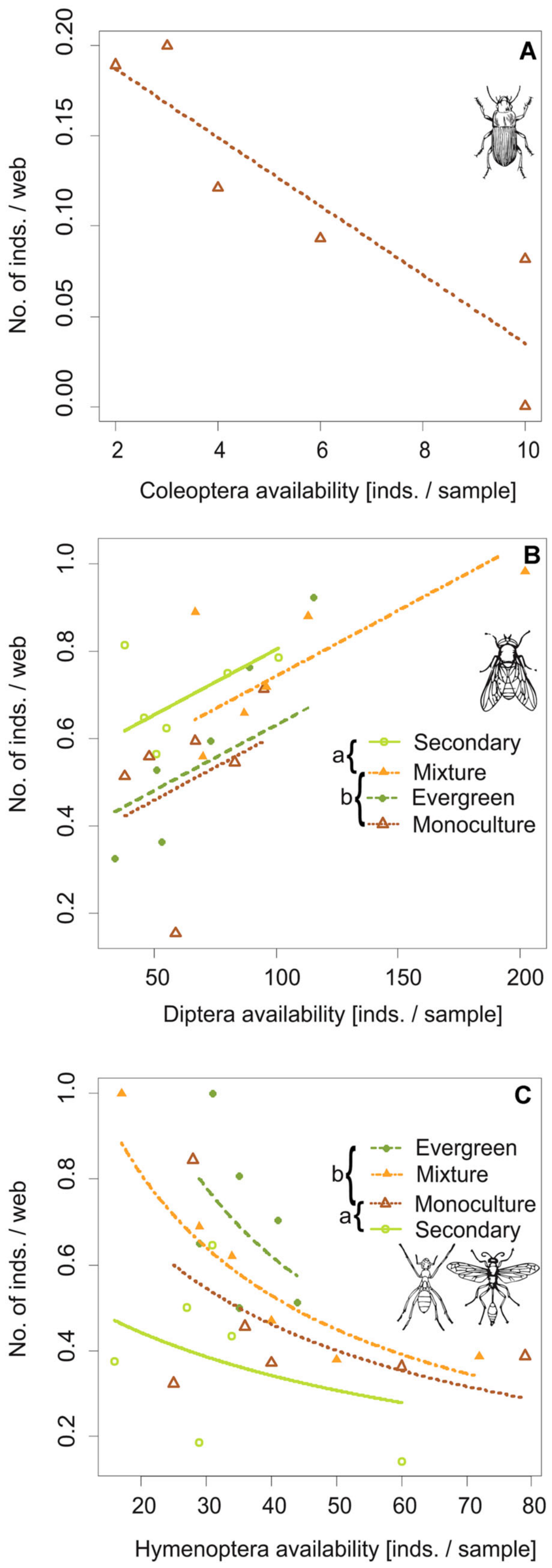
Figure 4. The effect of forest type on the per capita captured Isoptera (**A**), Auchenorrhyncha (**B**), Lepidoptera (**C**), Diptera (**D**), and Formicidae (**E**). The thick lines are medians, boxes are quartiles, whiskers are 1.5 times interquartile range, points are outliers. Different letters show difference at $P < 0.05$.

composition was only related to the web type but not to the spider mean body size. In addition, the forest type influenced the prey composition also through some additional effects that might be various biotic and abiotic factors. Our study is therefore in concordance with the few previous studies on soil food-webs that show that various reforestations or forest types affect food-web characteristics (Barnes and others 2014; Derhé and others 2016; Klarner and others 2017; Potapov and others 2019).

Effect of Forest Type on Interaction Between Spider Community and Their Prey

The forest type influenced the prey composition of the web-building spiders but it did not simply mirror the differences among forest types in prey availabilities. The availability of Hemiptera, Coleoptera, Diptera, and Hymenoptera was similar among the forest types while their representation (overall and per capita) in spider webs differed substantially among the forest types. Therefore, the forest type affected the community-wide prey selection of web-building spiders, similarly as crop management practices affect prey selection in web-building spiders (Diehl and others 2013; Birkhofer and others 2016) and other generalist predators (Roubinet and others 2017; Staudaucher and others 2018).

The forest type influenced both components that determine the consumptive effect of predators on their prey, that is, predator density and prey-specific capture efficacy (Solomon 1949). The prey-specific capture efficacy and spider densities then interacted in a complex way to determine the differences in prey composition among forest types. For example, despite the densities of web-building spiders being lowest in the secondary forest the overall number of caught dipterans was similar to the dry evergreen forest because the capture efficacy of spiders was much higher in the secondary forest. However, spiders caught the most dipterans in the mixture reforestation because both the densities and the capture efficacy were high in this habitat. Such a complex pattern arose because the forest type influenced the composition of web types



◀**Figure 5.** The effect of forest type that represents a natural control (dry evergreen forest) and three reforestations (mixture, monoculture, and secondary) on per capita captured Coleoptera in monoculture reforestation (**A**), Diptera in four forest types (**B**), and Hymenoptera in four forest types (**C**). The estimated relationships are displayed. Different letters show difference at $P < 0.05$.

which differ in their capture efficacy for some prey types but for other prey types their capture efficacy is similar (Michalko and Pekár 2016).

The community-wide capture rate along prey densities changed in a prey specific way. The forest type influenced the pattern as discussed above. The capture rate of Diptera increased with prey density while capture rate for Hymenoptera and Coleoptera decreased. In fact, the capture rate of Diptera and Hymenoptera showed almost the opposite pattern. The availability of Diptera and Hymenoptera positively correlated with each other (results not shown) and Diptera are more preferable prey for web-building spiders than Hymenoptera (Michalko and Pekár 2016). Web-building spiders might alter their web-properties to maximize the interception of the preferable Diptera, which might consequently decrease the web-efficiency to intercept and retain Hymenoptera (Sandoval 1994; Tso and others 2007). Hymenoptera might also be, theoretically, able to better spot and avoid the webs when it contained more Diptera. The contrasting patterns (positive, negative, none) in the relationship between prey availability and capture rate show that predation by the community of web-building spiders was far from density-dependent. However, it remains unclear to what degree is the density-independent prey selection caused by active prey selection (for example, alteration of web properties) and passive prey selection (for example, difference in phenology of a species among forest types or in apparent competition among prey).

The Connection Between Trait Composition of Spider Community, Forest Type, and Prey Composition

The forest type influenced the prey composition caught by a spider community mostly by altering the composition of spider web-types which differ in their efficacy to capture particular prey types but also often in the microhabitat distribution (Michalko and Pekár 2016; Ludwig and others 2018). The differences in the composition of spider web-

Table 2. The Results of Permutational (Beta Generalized) Linear Models Investigating the Composed and Sole (Residual) Effects of Trait Composition of Web-building Spider Community and Forest Type (Dry Evergreen Forest, Secondary Forest, Monoculture of *Eucalyptus camaldulensis*, and Mixture of *Acacia mangium* and *E. camaldulensis*) on Prey Composition of Web-building Spiders

Context	Trait	Method	*P* value	r^2
Trait composition	Overall	permGLM-beta	0.001	0.33
	Web type	permGLM-beta	0.001	0.34
	Body size	permGLM-beta	0.309	0.06
Trait composition without forest type	Overall	permLM	0.001	0.28
Forest type	–	permGLM-beta	0.001	0.21
Forest type without trait composition	–	permLM	0.044	0.11

permLM—permutational linear models; permGLM-beta permutational generalized linear models with beta-distribution and logit link function. The P values are based on 999 permutations. r^2—Pearson correlation coefficient.

types were caused by differences in the structure of shrub layers among the forest types. The results agree with Rypstra (1983) who experimentally showed that the Orb-web and Space-web spiders respond more intensively to changes in habitat complexity than the Sheet-web spiders. Number of attachment points and vegetation spacing are both important for web-building spiders as they need to not only anchor but also expand their webs (Vasconcellos-Neto and others 2017). Orb-web spiders, for example, need relatively large open vegetation architecture to build their webs (Vasconcellos-Neto and others 2017), which explains why their abundances decreased in dense shrub layers in our study.

Surprisingly, the spider mean body size did not affect the prey composition although it generally determines the trophic niche of web-building spiders (Nentwig and Wissel 1986; Sanders and others 2015; Turney and Buddle 2019). One possible explanation is that the prey body size was strongly variable within the distinguished prey categories. The spider body size differences might then determine the trophic niche partitioning at a finer scale, that is, partitioning within the prey types. The results therefore do not mean that body size did not affect the food-web dynamics. Instead, they indicate that spider body size was of lower importance than the hunting strategy. This points out that the food-web models need to incorporate hunting strategies of generalist predators, such as web-building spiders, to improve their predictive abilities, especially in highly complex ecosystems like tropical forests (Jonsson and others 2018).

Besides the composition of spider web-type, the forest type influenced the prey composition by some other additional factors. These factors might be various direct (for example, interference among spiders) and indirect (for example, apparent competition and interference among prey) biotic interactions, environmental conditions (for example, temperature, humidity, and vegetation height and complexity) that might affect the prey selection at inter- and intra-specific levels (Schmitz 2017; Michalko and others 2019).

Implication for Reforestation Management

As the prey composition of web-building spiders differed between the natural forest and all reforestations, no reforestation was able to restore the natural predator–prey interactions between the web-building spiders and their prey in understory vegetation. However, this might be because the 20–30-year-old reforestations are not mature in comparison to the natural forest and the diversity and ecological dynamics changes with succession (Grimbacher and others 2007; Magura and others 2015; Derhé and others 2016).

The monocultures were the most similar to the dry evergreen forest in the observed topology of predator–prey interactions as they differed in the lowest number of observed characteristics while the secondary naturally regenerating forest differed the most from the evergreen forest. This contrasts with our expectations based on the diversity patterns that show better restoration success of naturally regenerating forests than the active reforestations in tropical forests (Grimbacher and others 2007; Crouzilles and others 2017). Our results are also in contrasts with Barnes and others (2014) who showed that the soil food-webs are mostly altered in monocultures where the energy fluxes are very low. The discrepancy may be because the studied forest stands could easily act as a meta-ecosystem (Loreau and others 2003) as they did not cover large areas and all of them formed a mosaic of habitats with each other and other ecosystems in the studied area. The highly mobile flying insects, the main prey of web-building spiders, do not have a problem moving among such patches. Therefore, the allochthonous subsidy of prey might theoretically prevent the negative impact on above-ground food-webs as, for example, in the large monocultures of oil-palms (Loreau and others 2003; Barnes and others 2014). Moreover, *Eucalyptus* is a fast-growing woody plant (Gabrielle and others 2013). The faster growth of *Eucalyptus* than *Accacia* and other trees in secondary forests might provide more similar structural conditions to the evergreen forest. Therefore, the structural similarity due to faster growth than other trees and the allochthonous subsidy might near the monoculture to the evergreen forest but the pattern may switch with age.

Limitation of the Study

It can be argued that the evergreen and secondary forests formed mostly one block and the active reforestations formed the second block of forests in the studied landscape. However, the results do not correspond with the pattern that is expected from a pseudoreplication, that is, the treatments within a block would be more similar than the treatments between blocks. Moreover, it would be nearly impossible to find enough sample sites and their distribution for the three reforestation managements and natural control that would enable to reliably filter out several confounding effects (Crouzeilles and others 2017) and that would be still reasonably labour-manageable.

The forest types differed in area size but the area size alone cannot explain the observed differences in predator–prey interactions. The studied forest stands formed a large compact forest complex without any disjointed forest patches (see FigureS1). Therefore, if the habitat structure was not the main driver, we would not observe any changes in the predator–prey interactions. However, we admit that the habitat structure, relatively small area size of reforestations, and surrounding landscape composition interactively influenced the spider-prey interactions by means of meta-ecosystem dynamics (see chap. 4.3. *Implication for reforestation management* for discussion).

CONCLUSIONS

We show that studying interactions between the community of web-building spiders and prey collected from spider webs is an effective tool to evaluate the success of a restoration management. As we used predator guilds and relatively broad taxonomic resolution of prey this approach is especially useful in mega-diverse ecosystems where many species have not been described yet.

Each forest type hosted unique interactions between web-building spiders and their prey. Thus no studied reforestation has restored yet the natural predator–prey interactions between the web-building spiders and their prey in the understories. The forest type altered the predator–prey interactions by influencing spider density and prey-specific capture efficacy of spider community, which consequently interacted in a complex way. As it seems that the 20–30 years reforestations in the tropics cannot fully restore ecosystem function in particular predator–prey interactions, the conservation management in the tropics should aim to establish the protected areas in pristine areas instead of relying on reforestations.

The prey composition of the web-building spiders was related to the web-type but not to the spider mean body size. This indicates that the food-web models need to incorporate hunting strategies of generalist predators to improve their predictive power.

ACKNOWLEDGEMENT

We would like to thank Nirun Pojprasat, Chaipat Wimolsuthikul, and Prapinya Siripaiboon for their help in the field. We are grateful to Nicole H. Cernohorsky for English editing. We would like to thank also to the editor Donald DeAngelis and the two anonymous reviewers for their valuable comments that helped to improve our manuscript. This research was financially supported by the Specific University Research Fund of the FFWT Mendel University in Brno (Reg. Numbers: LDF_PSV_2017004 and LDF_TP_2020006).

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

REFERENCES

Araújo MS, Bolnick DI, Layman CA. 2011. The ecological causes of individual specialisation. Ecol Lett 14:948–958.

Arvidsson F, Addison P, Addison M, Haddad CR, Birkhofer K. 2020. Weed species, not mulching, affect web-building spiders and their prey in organic fruit orchards in South Africa. Ecosphere 11(3):e03059.

Barnes AD, Jochum M, Mumme S, Haneda NF, Farajallah A, Widarto TH, Brose U. 2014. Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. Nat Commun 5:5351.

Baudrot V, Perasso A, Fritsch C, Giraudoux P, Raoul F. 2016. The adaptation of generalist predators' diet in a multi-prey context: insights from new functional responses. Ecology 97:1832–1841.

Birkhofer K, Arvidsson F, Ehlers D, Mader VL, Bengtsson J, Smith HG. 2016. Organic farming affects the biological control of hemipteran pests and yields in spring barley independent of landscape complexity. Lands Ecol 31:567–579.

Brook BW, Sodhi NS, Bradshaw CJ. 2008. Synergies among extinction drivers under global change. Trends Ecol Evol 23:453–460.

Cardoso P, Pekár S, Jocqué R, Coddington JA. 2011. Global patterns of guild composition and functional diversity of spiders. PloS One 6:e21710.

Chazdon RL. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458–1460.

Chazdon RL. 2013. Making tropical succession and landscape reforestation successful. J Sustai For 32:649–658.

Crouzeilles R, Ferreira MS, Chazdon RL, Lindenmayer DB, Sansevero JB, Monteiro L, Iribarrem A, Latawiec AE, Strassburg BB. 2017. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. Sci Adv 31:e1701345.

Deeleman-Reinhold CL. 2001. Forest spiders of South East Asia: with a revision of the sac and ground spiders. Leiden: Brill Academic pub.

Denno RF, Finke DL, Langellotto GA. 2005. Direct and indirect effects of vegetation structure and habitat complexity on predator-prey and predator-predator interactions. In: Barbosa P, Castellanos I, Eds. Ecology of predator-prey interactions, . Oxford: Oxford University Press. pp 211–239.

Derhé MA, Murphy H, Monteith G, Menéndez R. 2016. Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. J Appl Ecol 53:1714–1724.

Diehl E, Mader VL, Wolters V, Birkhofer K. 2013. Management intensity and vegetation complexity affect web-building spiders and their prey. Oecologia 173:579–589.

Edwards DP, Woodcock P, Newton RJ, Edwards FA, Andrews DJ, Docherty TD, Mitchell SI, Ota T, Benedick S, Bottrell SH, Hamer KC. 2013. Trophic flexibility and the persistence of understory birds in intensively logged rainforest. Conserv Biol 27:1079–1086.

Elek Z, Kovács B, Aszalós R, Boros G, Samu F, Tinya F, Ódor P. 2018. Taxon-specific responses to different forestry treatments in a temperate forest. Sci Rep 81:16990.

Evans DM, Zipper CE, Burger JA, Strahm BD, Villamagna AM. 2013. Reforestation practice for enhancement of ecosystem services on a compacted surface mine: path toward ecosystem recovery. Ecol Eng 51:16–23.

Gabrielle B, Maupu P, Vial E. 2013. Life cycle assessment of eucalyptus short rotation coppices for bioenergy production in southern France. Global Change Biol 51:30–42.

Gotelli NJ, Ellison AM. 2004. Primer of ecological statistics. Oxford: Oxford University Press.

Grimbacher PS, Catterall CP, Kanowski J, Proctor HC. 2007. Responses of ground-active beetle assemblages to different styles of reforestation on cleared rainforest land. Biodivers Conserv 16:2167–2184.

Hall JS, Ashton MS, Garen EJ, Jose S. 2011. The ecology and ecosystem services of native trees: Implications for reforestation and land restoration in Mesoamerica. For Ecol Manag 261:1553–1557.

Hu N, Li H, Tang Z, Li Z, Tian J, Lou Y, Li J, Li G, Hu X. 2016. Community diversity structure and carbon footprint of nematode food web following reforestation on degraded Karst soil. Sci Rep 6:28138.

Jäger P, Praxaysombath B. 2011. Spiders from Laos with forty-two new records and first results from the provinces Bolikhamsay and Champasak Arachnida: Araneae. Acta Arachnol 60:9–31.

Jonsson T, Kaartinen R, Jonsson M, Bommarco R. 2018. Predictive power of food web models based on body size decreases with trophic complexity. Ecol Lett 21:702–712.

Klarner B, Winkelmann H, Krashevska V, Maraun M, Widyastuti R, Scheu S. 2017. Trophic niches diversity and community composition of invertebrate top predators Chilopoda as affected by conversion of tropical lowland rainforest in Sumatra Indonesia. PloS ONE 12:e0180915.

Kruse PD, Toft S, Sunderland KD. 2008. Temperature and prey capture: opposite relationships in two predator taxa. Ecol Entomol 33:305–312.

Leidinger J, Seibold S, Weisser WW, Lange M, Schall P, Türke M, Gossner MM. 2019. Effects of forest management on herbivorous insects in temperate Europe. For Ecol Manag 437:232–245.

Loreau M, Mouquet N, Holt RD. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. Ecol Lett 6:673–679.

Ludwig L, Barbour MA, Guevara J, Avilés L, González AL. 2018. Caught in the web: Spider web architecture affects prey specialization and spider–prey stoichiometric relationships. Ecol Evol 8:6449–6462.

Magura T, Bogyó D, Mizser S, Nagy DD, Tóthmérész B. 2015. Recovery of ground-dwelling assemblages during reforestation with native oak depends on the mobility and feeding habits of the species. For Ecol Manag 33:117–126.

Menz MH, Dixon KW, Hobbs RJ. 2013. Hurdles and opportunities for landscape-scale restoration. Science 339:526–527.

Michalko R, Pekár S. 2016. Different hunting strategies of generalist predators result in functional differences. Oecologia 181:1187–1197.

Michalko R, Pekár S, Entling MH. 2019. An updated perspective on spiders as generalist predators in biological control. Oecologia 189:21–36.

Murphy F, Murphy J. 2000. An introduction to the Spiders of South East Asia: With Notes on All the Genera. Malaysia: Malaysian Nature Society.

Nentwig W, Wissel C. 1986. A comparison of prey lengths among spiders. Oecologia 68:595–600.

Perkins MJ, Inger R, Bearhop S, Sanders D. 2018. Multichannel feeding by spider functional groups is driven by feeding strategies and resource availability. Oikos 127:23–33.

Petcharad B, Miyashita T, Gale GA, Sotthibandhu S, Bumrungsri S. 2016. Spatial patterns and environmental determinants of community composition of web-building spiders in understory across edges between rubber plantations and forests. J Arachnol 44:182–194.

Potapov AM, Klarner B, Sandmann D, Widyastuti R, Scheu S. 2019. Linking size spectrum energy flux and trophic multifunctionality in soil food webs of tropical land-use systems. J Anim Ecol 88:1845–1859.

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing Vienna Austria Online. http://www.R-project.org.

Rosa IM, Smith MJ, Wearn OR, Purves D, Ewers RM. 2016. The environmental legacy of modern tropical deforestation. Curr Biol 26:2161–2166.

Roubinet E, Birkhofer K, Malsher G, Staudacher K, Ekbom B, Traugott M, Jonsson M. 2017. Diet of generalist predators reflects effects of cropping period and farming system on extra-and intraguild prey. Ecol Appl 27:1167–1177.

Rypstra AL. 1983. The importance of food and space in limiting web-spider densities; a test using field enclosures. Oecologia 59:312–316.

Sanders D, Vogel E, Knop E. 2015. Individual and species-specific traits explain niche size and functional role in spiders as generalist predators. J Anim Ecol 84:134–142.

Sandoval CP. 1994. Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. Funct Ecol 8:701–707.

Scheu S, Albers D, Alphei J, Buryn R, Klages U, Migge S, Platner C, Salamon JA. 2003. The soil fauna community in pure and mixed stands of beech and spruce of different age: trophic structure and structuring forces. Oikos 101:225–238.

Schmitz O. 2017. Predator and prey functional traits: understanding the adaptive machinery driving predator–prey interactions. F1000Research 6:1767.

Segan DB, Murray KA, Watson JE. 2016. A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions. Global Ecol Conserv 5:12–21.

Solomon ME. 1949. The natural control of animal populations. J Anim Ecol 18:1–35.

Staudacher K, Rubbmark OR, Birkhofer K, Malsher G, Sint D, Jonsson M, Traugott M. 2018. Habitat heterogeneity induces rapid changes in the feeding behaviour of generalist arthropod predators. Funct Ecol 32:809–819.

Thompson RM, Brose U, Dunne JA, Hall RO Jr, Hladyz S, Kitching RL, Martinez ND, Rantala H, Romanuk TN, Stouffer DB, Tylianakis JM. 2012. Food webs: reconciling the structure and function of biodiversity. Trends Ecol Evol 27:689–697.

Tilman D, Fargione J, Wolff B, D'antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D. 2001. Forecasting agriculturally driven global environmental change. Science 292:281–284.

Trisurat Y. 2010. Land use and forested landscape changes at Sakaerat Environmental Research Station in Nakhorn Ratchasima province Thailand. Ekológia 29:99–109.

Tso IM, Chiang SY, Blackledge TA. 2007. Does the giant wood spider *Nephila pilipes* respond to prey variation by altering web or silk properties? Ethology 113:324–333.

Vander Zanden MJ, Olden JD, Gratton C, Tunney TD. 2016. Food web theory and ecological restoration. In: Palmer MA, Zelder JB, Falk DA, Eds. Foundations of restoration ecology, . Washington, DC: Island Press. pp 301–329.

Vasconcellos-Neto J, Messas YF, da Silva Souza H, Villanueva-Bonila GA, Romero GQ. 2017. Spider–plant interactions: an ecological approach. In Behaviour and ecology of spiders (pp. 165–214). Springer, Cham.

Wallis DR, Shaw PW. 2008. Evaluation of coloured sticky traps for monitoring beneficial insects in apple orchards. N. Z. Plant Prot 61:328–332.

Wang YI, Naumann U, Wright ST, Warton DI. 2012. mvabund–an R package for model-based analysis of multivariate abundance data. Methods Ecol Evol 3:471–474.

Warton DI, Wright ST, Wang Y. 2012. Distance-based multivariate analyses confound location and dispersion effects. Methods Ecol Evol 3:89–101.

Wood SN. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R Stat Soc B 73:3–36.

World Spider Catalog 2019. World Spider Catalog. Version 20.0. Natural History Museum Bern online at http://wsc.nmbe.ch accessed on {16th June 2019}.

Zhang D, Stanturf J. 2008. Forest plantations. In: Ecology Ecosystem, Ed. Jorgensen SE, . Elsevier BV: Amsterdam Netherlands. pp 264–270.

Zuur AF, Hilbe JM, Ieno EN. 2015. A beginner's guide to GLM and GLMM with R. Newburgh UK: A frequentist and Bayesian perspective for ecologists. Highland Statistics Ltd.