Diversity and Trophic Ecology of Arboreal Spider (Araneae) Assemblages along a Transformation Gradient from Lowland Rainforest to Oil Palm Plantations in Jambi Province, Sumatra, Indonesia

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“I have found that it is the small everyday deed
of ordinary folks that keep the darkness at bay.
Small acts of kindness and love." ~ Gandalf
(J. R. R. Tolkien ~ The Hobbit

Contents

Chapter 1

General Introduction

Tropical rainforest conversion into rubber and oil plantations in Indonesia

Tropical rainforests are among the most important ecosystems in the world in terms of biodiversity, endemism, provisioning of ecosystem services and habitat for indigenous people (Codato et al., 2019; Arroyo-Rodríguez et al., 2022; Wunderling et al., 2022). However, since the mid-20th, century the rainforest in Southeast Asia has been logged on a large scale primarily to establish crash crops of oil palm, rubber and acacia (Wilcove & Koh, 2010; Drescher et al., 2016; Tsujino et al., 2016). Today about 87 % of the global oil palm production is produced in Indonesia and Malaysia (Austin et al., 2017). In particular, Indonesia had the most significant loss of primary rainforest in this century mainly due to conversion into oil palm and rubber plantations, the most common crops in the country (Tsujino et al., 2016; Kurniawan et al., 2018). Between 1990 and 2010, of the three million hectares of forest lost in Southeast Asia, 1.2 million occurred in Indonesia (FAO, 2010), which increased the total area of oil palm plantations by almost a factor of four from 3.5 to 12.9 million ha (USDA, 2014).

Jambi province, Sumatra, lost 1.1 million ha of rainforest between 1990 and 2010, and this included virtually all of the rainforest in lowland areas (Margono et al. 2014). In 2012 the annual rainforest loss reached a maximum in the country's history, with an estimated 0.84 million ha, the highest worldwide (Fig. 1; Margono et al., 2014). The area covered by rainforest declines across Indonesia, but Sumatra is the most affected island (Tsujino et al., 2016; Austin et al., 2017). The loss of rainforest implies high ecological costs associated with habitat degradation, which causes the loss of biodiversity above and below the ground threatening essential ecosystem functions and services (Clough et al., 2016; Potapov et al., 2020). How oil palm and rubber plantations replaced Indonesia's rainforest has been widely documented (Tsujino et al., 2016; Berkelmann et al., 2018; Kurniawan et al., 2018). Due to the strong conversion of rainforest into plantations in Sumatra, Jambi province constitutes an ideal region for investigating the ecological and socioeconomic consequences of rainforest transformation as done in the interdisciplinary research project EFForTS / CRC 990 (Drescher et al., 2016; Clough et al., 2016; Kurniawan et al., 2018) of which this thesis formed part of.

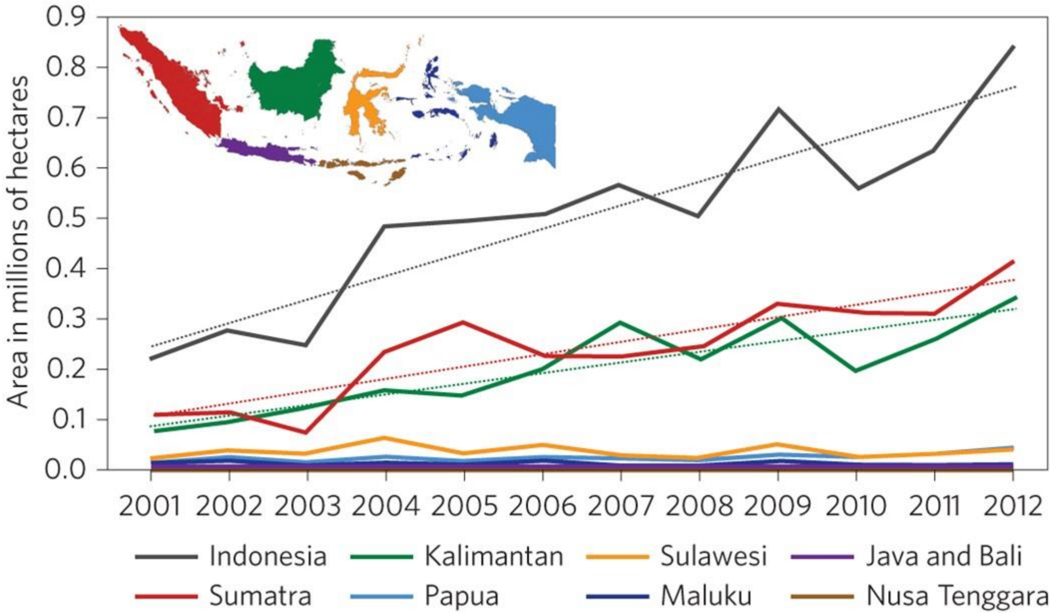

Figure 1. Annual primary forest cover loss, 2000–2012, for Indonesia as a whole and by island group (Sumatra, Kalimantan, Papua, Sulawesi, Maluku, Nusa Tenggara, and Java and Bali; from Margono et al. 2014)

Impact of tropical rainforest loss on canopy arthropods

Canopies of tropical rainforests harbor one of the most diverse arthropod fauna worldwide (Floren et al., 2014). It is estimated that canopy and understory arthropod diversity together hold approximately 5 to 12 million species, of which 20 to 25% inhabit exclusively the canopies of trees (Hamilton et al., 2013; Stork, 2018). Importantly, canopy arthropod diversity is particularly susceptible to land-use transformation and the replacement by cash crop plantations such as rubber and oil palm (Turner & Foster, 2009; Fayle et al., 2010). However, how canopy arthropod communities respond to land-use change in tropical areas remains understudied (Barrios, 2007). Recently, Floren et al. (2022) compiled data on arthropod canopy communities from 18 locations in central Europe from the last 25 years. However, how canopy arthropods respond to land-use change in Indonesia remains largely unknown.

Recent studies in the framework of EFForTS / CRC 990 investigated the response of canopy ant communities to the land-use change from rainforest to rubber and oil palm plantations (Nazarreta et al., 2020) and Kreider et al. (2021) reported associated changes in ant traits with the transformation of rainforest into plantation systems. Overall, these studies found the diversity of ants to strongly decline in plantations compared to rainforest and the trait composition to shift towards more generalist nesting and generalist feedering ant species in plantations compared to rainforest. Also in the framework of EFForTS / CRC 990, Azhar et al. (2022) studied parasitoid wasps in the canopy of trees and found a similar pattern to ants, but also provided evidence for rainfall seasonality as an important driver of the biodiversity and biomass of parasitoid wasps. Further, Junggebauer et al. (2020) studied the response of cursorial spiders (Salticidae) to the transformation of rainforest into plantation systems in the framework of EFForTS / CRC 990. Contrary to the other studies, they found the abundance of Salticidae to be little affected by land-use transformation and the richness in jungle rubber, a rubber agroforestry system, to be higher than in rainforest, with the richness in the latter exceeding that in oil palm and rubber plantations. Overall, they proposed that for understanding the mechanisms shaping spider communities community ecology, environmental factors and phylogenetic relationship need to be considered. In addition to canopy arthropods, Panjaitan et al. (2020) investigated changes in richness and abundance of butterflies with the transformation of rainforest into plantation systems in the same area and also reported a strong decline in plantations compared to rainforest.

Spiders as model arthropod predators

Spiders (Araneae) are a megadiverse group of predators colonizing all terrestrial ecosystems; currently, 50,400 species and 4200 genera are registered (World Spider Catalog, 2022). In contrast to mandibulates, their sister group, the spider body is divided into cephalothorax and opisthosoma, with the former bearing chelicerae, pedipalps and four pairs of legs, but no antennae. Spiders are unambiguously characterized by two synapomorphies, the spinnerets, which are organs to spin silk, and the male copulatory organs at the pedipalps (Agnarsson, 2004; Wheeler et al., 2017).

In terrestrial ecosystems, spiders often function as top predators, feeding on insects, other arthropods, earthworms, eggs, small vertebrates and even nectar and pollen (Nelson & Jackson, 2011; Nyffeler, 2016; Nyffeler, Olson & Symondson, 2016; Shine & Tamayo, 2016; Nyffeler & Birkhofer, 2017; Kumar et al., 2018; Babangenge et al., 2019). On a global scale, spiders are estimated to consume 400-800 million tons of prey annually (Nyffeler & Birkhofer, 2017). Although being almost uniformly predators, they adopt diverse strategies to hunt for prey. Some families build orb-webs, e.g., Araneidae and Amaurobiidae, others built more specialized webs, e.g. Deinopidae, Linyphiidae and Uloboridae, and others are free hunters, e.g.

Thomisidae, Salticidae and Lycosidae (Eberhard, 2020). This diversification sets spiders in different ecological niches and separates them from other arthropod predators such as centipedes and carabid beetles (Ashton-Butt et al., 2018; Kennedy et al., 2019; Michalko, Pekár & Entling, 2019). However, spiders also form prey of other invertebrates and vertebrates (Wise, 1993; Lawrence & Wise, 2000).

In agroecosystems, spiders contribute to pest control by feeding on a wide range of pest insects (Birkhofer et al., 2008; Suenaga & Hamamura, 2015; Lefebvre et al., 2017). The recent meta-analysis by Michalko et al. (2019) demonstrated, based on 58 studies on different crop types, that spiders suppressed agricultural pest populations in 79% of the cases. Hunting modes also influence pest control efficacy. Free hunters or ambush hunters might prey more frequently on early-stage insects, such as eggs, larvae and nymphs, while web-building spiders depend more on what they can catch in their nets and this predominantly comprises adult winged insects (Marc et al., 1999). Furthermore, it also has been documented that spiders exert indirect effects on pest insect communities besides direct feeding on prey species, e.g. by changing prey behavior (Beleznai et al., 2015; Bucher et al., 2015).

Influence of environmental variables on spiders

Many factors may influence the diversity of canopy arthropods, including environmental and structural parameters. Environmental factors, such as temperature, moisture, light, wind, precipitation, plant richness, plant abundance or the age of forests differentially affect spider diversity and abundance, with the effects depending on spatial scales (Tal et al., 2008; Ulyshen, 2011). Dassou et al. (2016) studied the effect of plant diversity on the arthropod community in plantain-based fields in Cameroon and found that spiders and other ground-dwelling predator abundance positively correlated with plant diversity. Zheng et al. (2017) studied the response of tree trunk spiders to different land-use management and found that spider assemblages were related to the amount of light, i.e. canopy cover. Petcharad et al. (2016) reported that range and average temperature are important drivers of distribution patterns, diversity and abundance of web-building spiders in secondary semi-evergreen forests in Thailand. Besides, the structure of the habitat including the structure of the canopy of trees also affects spider diversity and community composition, i.e., the height of the trees, type of foliage, plant species composition, and texture of stems of trees all have been shown to affect spider community composition (Basset et al., 2003).

For spider communities, vegetation complexity is also an important factor. Floren & Deeleman-Reinhold (2005) found that spider diversity in degraded forest patches is lower than in forests less affected by human intervention. Additionally, the richness of some orb-webbing and ambush hunting spiders, i.e., Araneidae and Thomisidae, were closely related to shrub canopy structure and ground herb cover (Jiménez-Valverde & Lobo, 2007). For spiders in the canopy of trees, canopy complexity has been identified as an important factor in structuring communities (Zheng et al., 2015). However, low canopy complexity may also beneficially affect certain spider families with specialist hunting mode, such as Liocranidae, which preferentially hunt in open areas (Deeleman-Reinhold, 2001) and benefit from high light intensity allowing them to identify prey by visual cues (Fayle et al., 2010; Ganser et al., 2017). Barton et al. (2017) found spider communities to be negatively affected by low tree density and Schuldt et al. (2011) reported that forests with tall trees and high tree species richness beneficially affect spider communities. Furthermore, Floren et al. (2011) found that spider communities vary between forests of different age, suggesting that older trees are related to more diverse spider communities. At local scale, spiders also may benefit indirectly from plant diversity as the diversity of herbivorous insects may also increase with plant diversity. A more diversified plant community may provide more resources for herbivore insects and thereby support higher diversity and abundance of insect communities (Ulyshen, 2011; Hertzog, 2017) beneficially affecting the diversity of arthropod predators (Moreira et al., 2016).

Use of stable isotopes and isotope metrics for studying food web structure

Stable isotopes are increasingly used to study feeding habitats, trophic positions, and functional aspects of vertebrates and invertebrates (Crowley, 2012; Hyodo, 2015). The $^{13}C/^{12}C$ ratio is used to identify basal food resources and the $^{15}N/^{14}N$ ratio to identify the trophic position of species (Potapov et al., 2019). In contrast to the $^{13}C/^{12}C$ ratio, the $^{15}N/^{14}N$ ratio increases in a consistent way per trophic level by an average of 3.4 ‰ (Post, 2002; Pollierer et al., 2009; Potapov, Tiunov & Scheu, 2019). To assess the structure of food webs, Layman et al. (2012) proposed the use of isotope metrics. These metrics assigned the same importance to all species in the food web in a binary perspective (i.e., presence/absence). They have been widely used in aquatic systems. Considering their limitations, however, Cucherousset & Villéger (2015) developed food web metrics incorporating functional diversity and considering asymmetries in species' dominance, which is important as in biological communities typically few species dominate and form the core of the food web.

In total, Cucherousset & Villéger (2015) proposed five metrics: (1) Isotopic divergence (IDiv), which tends to be 0 when the species with extreme values (top predators) are rare and 1 when extreme values dominate the community. (2) Isotopic dispersion (IDis), which is equal to 0 when all morphospecies have the same stable isotope value and tends to 1 when most of the points (weights) are far from the centre of gravity. (3) Isotopic evenness (IEve), which quantifies the morphospecies distribution in isotope space; it tends to be 0 when most morphospecies are packed in a small region of the stable isotope space and 1 when they are evenly distributed. (4) Isotopic uniqueness (IUni), which equals 0 when there are no other morphospecies with the same position in stable isotope space and 1 when all morphospecies are isolated in stable isotope space. (5) Isotopic richness (IRic), which represents the isotopic space of all morphospecies scaled from 0 to 1. Krause et al. (2021) used these metrics to investigate the shift in community trophic niches of oribatid mites with the transformation of rainforest into oil palm and rubber plantations. They did not find a significant difference between communities in isotopic dispersion, divergence and evenness, which might suggest that the communities are balanced and the trophic niche positions differed little. On the contrary isotopic richness varied between land-use systems being higher in rubber plantations. Using a combination of stable isotope analysis, food-web energetics along with the metrics proposed by Cucherousset & Villéger (2015), Zhou et al. (2022) studied the consequences of rainforest conversion into oil palm and rubber plantations on the structure and channeling of energy through soil animal food webs in Indonesia. They found both to be lower in the two plantations than in rainforest. Interestingly, however, there was no difference in the isotopic richness between any of the land-use systems.

Trophic niche differentiation may depend on the stability of the co-existence of species in space and time as in unstable systems, such as plantations and other human-modified habitats, trophic niches of species are likely to overlap (Giller, 1996; Chesson, 2000). On the contrary, stable environmental conditions are associated by stable community composition with pronounced niche differentiation (Giller, 1996). Korotkevich et al.(2018) tested and confirmed this prediction using belowground collembolan communities in natural and disturbed habitats. On the other hand, Klarner et al. (2017) investigated the variation in trophic niches of soil and litter centipedes in a range of ecosystems, from rainforests and jungle rubber to oil palm and rubber monoculture plantations. They found trophic niches to overlap in rainforest, jungle rubber and rubber plantations, but to differ from those in oil palm plantations. Liebke et al. (2021) also explored the response to land-use transformation in other soil predators. They reported that trophic niches of pseudoscorpions in rainforest differed from those in plantations, whereas in plantations they overlapped. However, studies on how the trophic structure of spider communities change with the transformation of rainforest into plantations is lacking.

Study area

The study was carried out as part of the collaborative research centre CRC990/EFForTS investigating ecological and socio-economic changes associated with the transformation of lowland rainforests into agricultural systems (Drescher et al., 2016). We sampled two regions each close to rainforest reserve sites in Jambi Province, Sumatra, Indonesia: the Bukit Duabelas National Park (S 01°59'41.4", E 102°45'08.5") and Harapan Rainforest landscape (S 02°09'52.9", E 103°22'04.0") (Fig. 2). Jambi Province covers an area of 50,160 km^2 (Badan Pusat Statiski, 2014) and stretches from the Barisan mountain range in the west towards the southern Malacca Strait in the east. The climate is tropical and humid, with two peak rainy seasons around March and December and a dryer period from July to August (Drescher et al., 2016).

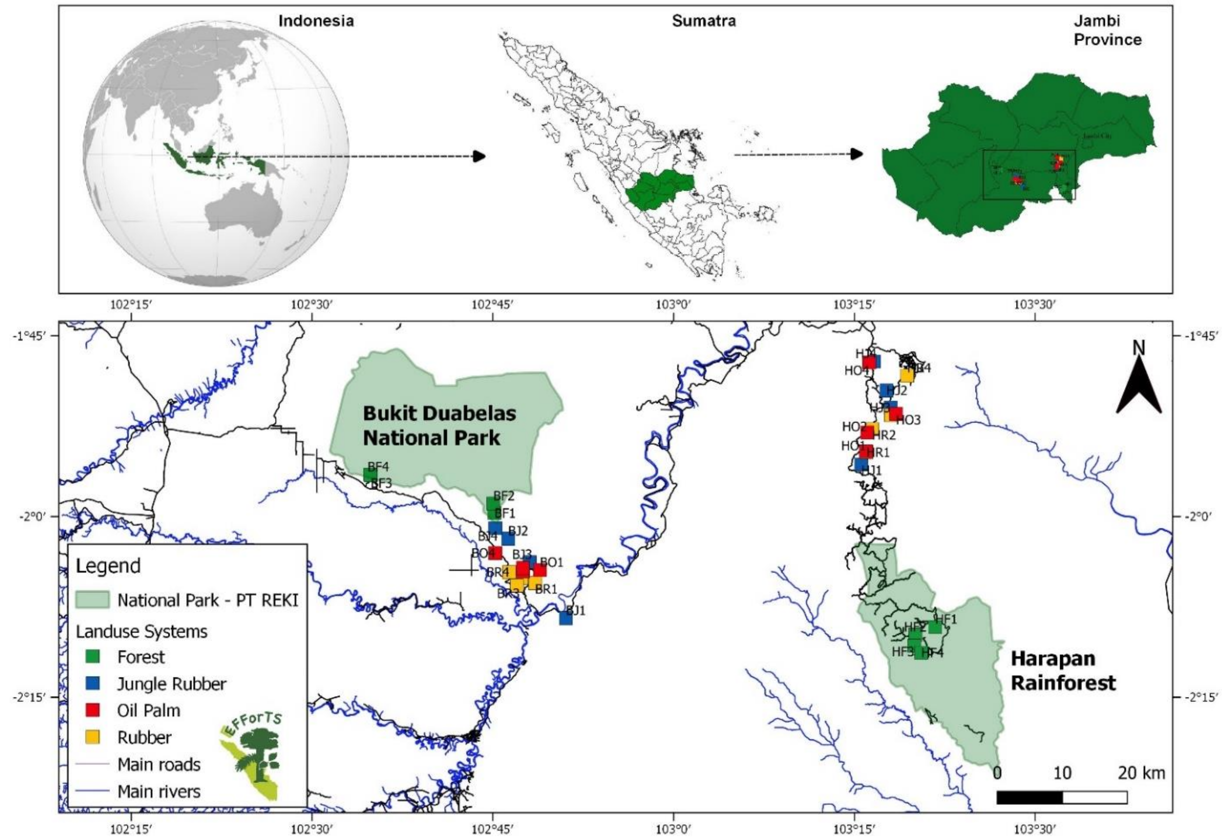

Figure 2. Location of the 32 study plots in Jambi, Sumatra, Indonesia, in two landscapes: Bukit Duabelas National Park and Harapan Rainforest. Land-use systems coded by color (green = rainforest, blue = jungle rubber, yellow = rubber, red = oil palm). From Ramos et al. (2022).

The rainforest reserve sites are surrounded by agroforestry systems of rubber and oil palm (Drescher et al., 2016), but also jungle rubber (rubber agroforest; Gouyon *et al.* 1993). We collected canopy arthropods 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. 3). Rainforest sites were primary degraded rainforests logged at least once (Margono et al., 2014). The jungle rubber system resulted from planting rubber trees (*Hevea brasiliensis*) into logged rainforest; the sites investigated were between 15 and 40 years old (Gouyon, de Foresta & Levang, 1993; Kotowska et al., 2015; Rembold et al., 2017). Jungle rubber represents a land-use system of low management intensity; no herbicide or fertilizer was applied. By contrast, rubber and oil palm (*Elaeis guineensis*) monoculture plantations represent high land-use intensity systems managed by adding fertilizers and herbicides (Drescher et al., 2016). The study was conducted based on Collection Permit No. S.710/KKH-2/2013 issued by the Ministry of Forestry (PHKA) based on recommendation

No. 2122/IPH.1/KS.02/X/2013 by the Indonesian Institute of Sciences (LIPI), and export permit SK.61/KSDAE/SET/KSA. 2/3/2019 issued by the Directorate General of Nature Resources and Ecosystem Conservation (KSDAE) based on LIPI recommendation B-1885/IPH.1/KS.02.04/ VII/2017.

Figure 3. The four land-use systems investigated, i.e. lowland rainforest (A), jungle rubber (B), and smallholder monocultures of rubber (C) and oil palm (D). Photos by Mathias Ditscherlein (A) and Jochen Drescher (B-D).

Study objectives and hypotheses

In this Ph.D. thesis, I explored the effects of land-use transformation from tropical lowland rainforest via jungle rubber to monoculture plantations oil palm and rubber on the structure and functioning of canopy spider communities. I investigated the following overall hypotheses:

1. Canopy spider abundance, biomass and richness decline from rainforest to jungle rubber to rubber and oil palm monoculture plantations, with spider community composition being similarly complex in rainforest and jungle rubber, and very different from simplified communities in rubber and oil palm monoculture plantations.
2. Canopy spider communities in both rainforest and plantations are structured by both habitat structure and climatic factors, with the former being more important in rainforest and jungle rubber, and the latter in monoculture plantations.
3. The community-level trophic niche of spiders is narrower, and the functional redundancy is higher in the more natural ecosystems of rainforest and jungle rubber than in monoculture plantations.
4. The diet of spider communities shifts towards more herbivore prey in plantation systems, whereas in rainforest the diet comprises more detritivores prey (as indicated by δ^{13} C values)

In chapter 2, I investigated the canopy spider abundance, biomass, richness and community composition across a land-use gradient from tropical lowland rainforest via jungle rubber to monocultures of rubber and oil palm. Overall, I demonstrated that canopy spider communities in oil palm and rubber plantations are less abundant, contain lower biomass, and are less diverse compared to rainforest and jungle rubber systems. I also provided evidence that community composition is similar between less intensive land-use systems, i.e. rainforest and jungle rubber, and differed from more intensive land-use systems, i.e. oil palm and rubber plantations, which also differed from one other. Investigating environmental variables that shape spider communities, I demonstrated that at family level aboveground biomass, number of trees per hectare and canopy openness were major factors determining spider community composition. I also demonstrated that at species level, the most important factors were plant richness and the number of trees per hectare. My results provided detailed information on the importance of rainforests for the conservation of canopy spider communities as only a subset of the community can tolerate the more harsh environmental conditions and disturbances in monoculture plantations. Moreover, the fact that in rainforest and jungle rubber the diversity and community composition are similar suggests that the majority of spiders might tolerate a moderate degree of disturbances. Finally, disturbed agroecosystems, such as oil palm and rubber plantations, may also contribute to the total diversity in a geographic area (γ-diversity) suggesting that landscape scale perspectives are needed for the conservation of spider diversity.

In chapter 3, I focused on changes in the trophic structure of canopy spider communities with the transformation of tropical rainforests into rubber and oil palm plantations by measuring bulk tissue $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios. Additionally, I studied in more detail the response of the families Salticidae, Clubionidae, Theridiidae, and Thomisidae, which contributed most to the abundance, biomass, and diversity of the spider communities in the studied land-use systems. Overall, we found that rainforest spider communities respond differently to land-use transformation. Generally, the range in trophic niches and use of basal resources ($\Delta^{15}N$, $\Delta^{13}C$ values) did not differ between land-use systems, but maximum $\Delta^{15}N$ values suggested that some families have narrower trophic niches in plantations. Moreover, functional diversity was similar across the four land-use systems, with the exception of isotopic divergence, which was higher in rainforest and jungle rubber than in monoculture plantations.Further, there was no difference in the trophic positions between cursorial and sheet-web building spiders, but they occupied virtually the same average position. However, maximum $\Delta^{15}N$ values in Salticidae, Clubionidae and Thomisidae were higher in plantations than rainforest and jungle rubber indicating that intra-guild predation may be more widespread in free hunting than web-building spiders but only in plantation systems. Finally, we found evidence that transformation of rainforest into monocultures plantations is associated with a shift towards more herbivore prey in canopy spiders. Overall, our study provides first insight into trophic changes in canopy spider communities associated with the transformation of tropical rainforest into plantations.

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Chapter 2

Rainforest conversion to rubber and oil palm reduces abundance, biomass and diversity of canopy spiders

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Rainforest conversion to rubber and oil palm reduces abundance, biomass and diversity of canopy spiders

Abstract

Rainforest canopies, home to one of the most complex and diverse terrestrial arthropod communities, are threatened by conversion of rainforest into agricultural 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 and monoculture plantations of rubber and 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 speciose families, Salticidae (S = 87), Theridiidae (S = 83), Araneidae (S = 48) and Thomisidae (S = 39), contained 57.8 % of all morphospecies. In lowland rainforest, average abundance, biomass and species richness of canopy spiders was at least twice as high as in rubber or oil palm plantations, with jungle rubber showing similar abundances as rainforest, and intermediate biomass and richness. The community composition was similar in rainforest and jungle rubber, but differed from rubber and oil palm, which differed from each other. Canonical Correspondence Analysis showed that canopy openness, aboveground tree biomass and tree density explained 18.2 % of the variation at family level. On a morphospecies level, vascular plant species richness and tree density significantly affected the community composition but explained only 6.8% of the variance. Abundance, biomass and diversity 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 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 in decision-making processes toward establishing cash-crop plantation management systems which foster herbivore control by spiders.

Keywords: Agriculture, Deforestation, Cash crops, Land use change, Southeast Asia, Araneae, Jambi, Biodiversity, Indonesia, EFForTS

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 palm oil (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 experienced 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, respectively, equaling the area of remaining rainforest (BPS 2018). Most remnant rainforests are located in the mountainous west of the 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 are the most conspicuous faunal 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, biomass, 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, including ants(Nazarreta *et al.* 2020, Kreider *et al.* 2021), salticids spiders (Junggebauer *et al.* 2021) and parasitoid wasps (Azhar *et al.* 2022) we hypothesized that (1) canopy spider abundance, biomass 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 which rubber trees are planted in successively degraded rainforest (Gouyon *et al.* 1993, Rembold *et al.* 2017). Canopy arthropods were sampled 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 50mL DECIS 25 (Bayer Crop Science; active ingredient deltamethrin, 25 g/L) dissolved in four liters petroleum white oil to each of the target canopies within the first hour after sunrise to avoid turbulences 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 hours after fogging, the collection traps of each target canopy were collected and stored at -20°C for future use. Arthropods of all three sampled target canopies were later determined to order. The study was conducted based on Collection Permit No. S.710/KKH-2/2013 issued by the Ministry of Forestry (PHKA) based on recommendation No. 2122/IPH.1/KS.02/X/2013 by the Indonesian Institute of Sciences (LIPI), and export permit SK.61/KSDAE/SET/KSA.2/3/2019 issued by the Directorate General of Nature Resources and Ecosystem Conservation (KSDAE) based on LIPI recommendation B-1885/IPH.1/KS.02.04/VII/2017.

Identification

From the three collected samples per plot, only the first two collected samples per plot were chosen to form the basis of this study due to the immense workload of morphological spider identification. Spiders from the first two samples 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 Araneae section of the Ecotaxonomy database (http://ecotaxonomy.org/taxa/424669). The samples forming the basis of our study are continued to be used as reference material to identify further spider collections within the EFForTS project. Upon completion of spider identification, a collection of reference material will be deposited at the Museum Zoologicum Bogoriense at the Indonesian Institute of Science, LIPI.

Biomass calculation

We measured the body length and body width of 15 randomly selected spider individuals per plot, including juveniles, to the nearest tenth of a millimeter using a ZEISS Stemi 2000 with fitted micrometer. The average spider body length and width per plot was used to calculate individual spider body mass based on taxon-specific allometric regression for tropical spiders (Sohlström *et al.* 2018), and the combined abundance of all spiders per square meter per plot was used to calculate total spider biomass per square meter per plot. All calculations, equations and raw data related to canopy spider biomass are given in the Supplements and the online data repository GRO (see data availability statement).

Environmental variables

A set of environmental variables measured in the framework of the EFForTS project (EFForTS: – Ecological and Socioeconomic functions of tropical lowland rainforest transformation systems; https://www.uni-goettingen.de/de/310995.html; Drescher *et al.* 2016) was used to explain canopy spider community composition in the four land-use systems. Measured in each plot, these variables included (1) mean canopy air temperature [°C] and (2) mean relative humidity [%], measured daily with a Thermohygrometer (Galltec Mela, Bondorf, Germany) at 2 m height between April 2013 to March 2016 (Meijide *et al.* 2018), (3) canopy openness [%], measured with a spherical densitometer four times in each plot and then used as one average value (Drescher *et al.* 2016), (4) aboveground tree biomass [Mg/ha], calculated using diameter of trees, palms and lianas with diameter at breast height ≥ 10 cm and an allometric equation

(Kotowska *et al.* 2015), (5) vascular plant species richness and (6) tree density based on 5 m × 5m sub-plots where all tress with a diameter at breast height ≥ 10 cm were measured and identified [N/ha] (Rembold *et al.* 2017) and (7) mean stand structural complexity index, based on a Focus terrestrial laser scanner (Faro Technologies Inc., Lake Mary, USA) on a tripod at 1.3 m height (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 2019). 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.

Statistical analyses

Statistical analyses were performed using R (v. 3.6.2., R Core Team 2019) and visualized using ggplot2 (Wickham 2016). Rank abundance curves were compared (vegan::radfit) and plotted (Hartke 2019; https://github.com/tamarahartke/RankAbund.). An exploratory data analysis was performed to ensure the data met underlying assumptions of the statistical tests (Zuur *et al.* 2010). The response variables abundance and biomass were analyzed using a generalized linear model (glm) with Gaussian error distribution and log link function (stats::glm). Response variables morphospecies richness and inverse Simpson Index 1/D (calculated using vegan::diversity; Oksanen *et al.* 2019) were analyzed using linear models (stats::lm). Initial models for all response variables included land use (rainforest, jungle rubber, rubber, oil palm), landscape (Bukit Duabelas, Harapan), and their interaction as fixed factors. Models were simplified in a stepwise manner discarding factors which did not significantly improve the fit of the model to find the minimal adequate model for each response variable. Model fit was checked using DHARMa (Hartig 2022) after which multiple comparisons were 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 false discovery rate adjusted (Benjamini & Hochberg 1995).

Results

In total, we collected 10,679 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 individuals could be determined to genus due to lack of relevant identification literature and a high proportion of 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 (and biomass) analysis. Overall, almost half of the specimens belonged to only four spider families (Salticidae, 2043; Oonopidae, 1878; Theridiidae, 1533; Clubionidae, 1188). 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. S5a). 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. S5b).

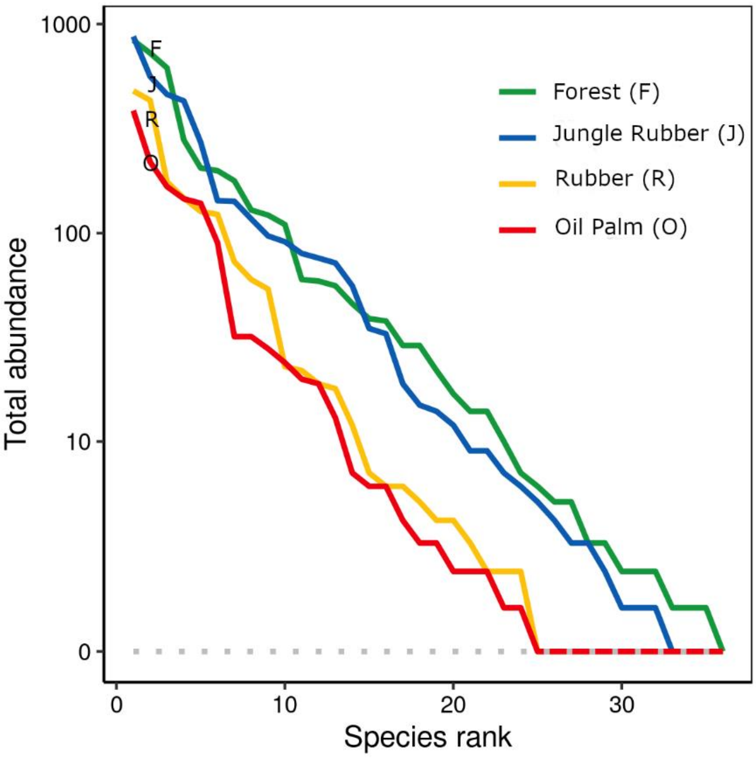

Figure 1. Rank abundance curves of 445 canopy spider morphospecies across four land-use systems in Jambi, Sumatra, Indonesia. F, lowland rainforest; J, jungle rubber; R, rubber monocultures; O, oil palm plantations.

Abundance, biomass and alpha diversity

When ranked by abundances, the number of canopy spider morphospecies 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. Similar to abundance, canopy spider biomass was significantly affected by land use (glm; $F_{3,28} = 8.2$, $P < 0.001$), in that biomass in rainforest was more than twice as high as in rubber and almost four times as high as in oil palm, and biomass in jungle rubber intermediate (Fig. 3). Landscape did not significantly affect canopy spider biomass.

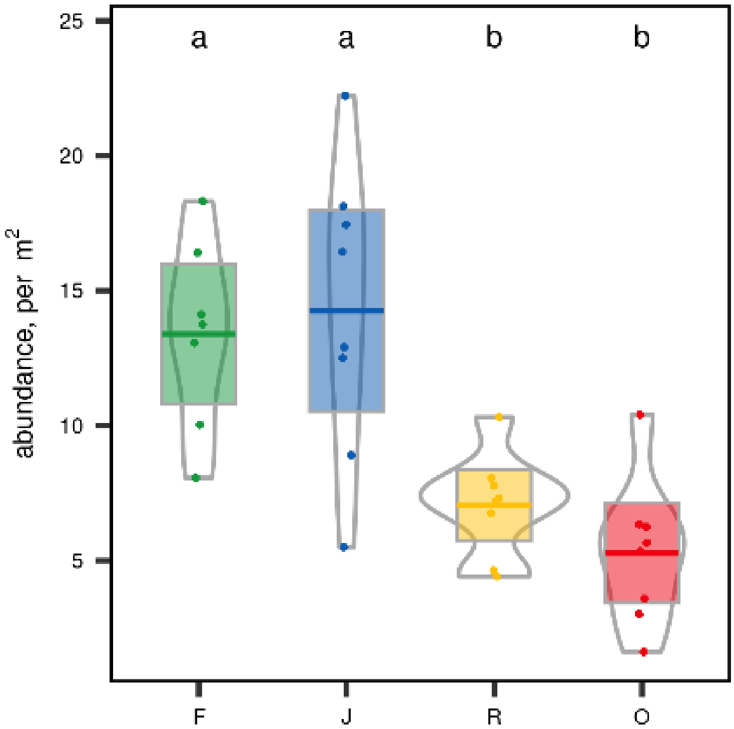

Figure 2. Pirate plots of average canopy spider abundance in four land use systems in Jambi, Sumatra, Indonesia. Different letters indicate significant differences between land-use systems as indicated by Tukey's HSD (P < 0.05; dots = data points, bars = means, boxes = 95% C. I., violins = density).

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. 4). 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. 5). This pattern was mostly driven by turnover, which contributed almost the entire overall beta diversity, while nestedness contributed only marginally (Fig. 6). Consequently, an ordination of the two beta diversity partitions showed high resemblance of overall beta diversity with turnover (Fig. S6a), but not with nestedness (Fig. S6b). Both turnover and nestedness overlapped between rainforest and jungle rubber, but were different from rubber and oil palm, which in turn overlapped.

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: $\chi^2 = 0.12$, $F = 6.80$, $P = 0.001$; CCA2: $\chi^2 = 0.05$, $F = 2.90$, $P = 0.003$; CCA3: $\chi^2 = 0.02$, $F = 1.35$, $P = 0.14$) 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. 7a,). 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_{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. 7b). The greatest number of morphospecies was associated with rainforest and jungle rubber, few with rubber plantations, and none with oil palm plantations.

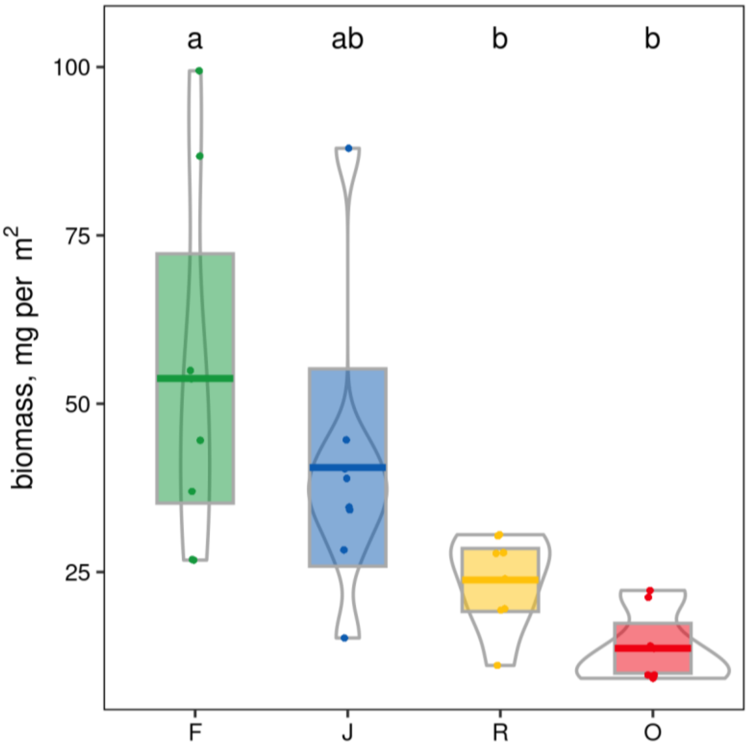

Figure 3. Pirate plots of canopy spider biomass in four land use systems in Jambi, Sumatra, Indonesia. Different letters indicate significant differences between land uses as indicated by Tukey's HSD (P < 0.05; dots = data points, bars = means, boxes = 95% C. I., violins = density).

Discussion

We investigated the effect of lowland rainforest conversion into jungle rubber, rubber and oil palm monoculture plantations on abundance, biomass, richness and community composition of canopy spiders in Sumatra, Indonesia. The study provided novel insight into the responses 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).

Abundance, biomass and alpha diversity

Abundance, biomass 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, including ants (Nazarreta et al, 2020; Kreider et al. 2021), butterflies (Panjaitan et al. 2020), salticid spiders (Junggebauer et al., 2021) and parasitoid wasps (Azhar et al. 2022). 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).

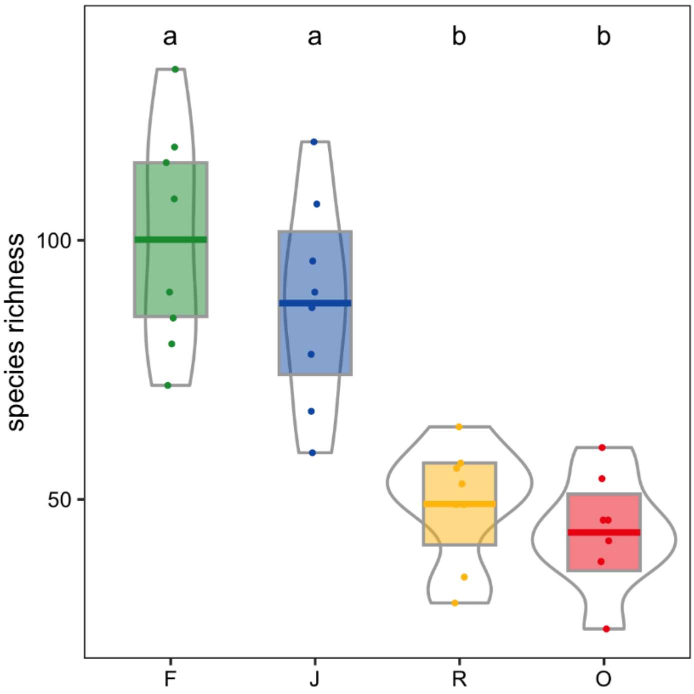

Figure 4. Pirate plots of canopy spider richness in four land-use systems in Jambi, Sumatra, Indonesia. Different letters indicate significant differences between land uses as indicated by Tukey's HSD ($P < 0.05$; dots = data points, bars = means, boxes = 95% C. I., violins = density).

Canopy spider biomass differences between land-use systems mirror the differences of abundances between the land-use systems, and suggest that the contribution of spiders to ecosystem functions and services in rainforest and jungle rubber are at least twice as high as in monocultures of rubber and oil palm(Boudreau *et al.* 1991, Barnes *et al.* 2017, Sohlström *et al.* 2018). This likely is related to the fact that total aboveground tree biomass in rainforest is more than twice that in jungle rubber, and more than four times that in rubber and oil palm (Kotowska *et al.* 2015). Canopy spider morphospecies richness in rubber and oil palm plantations was less than half that in rainforest. 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), salticid spiders (Junggebauer et al. 2021) and parasitoid wasps (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 spider species of certain families, e.g. Salticidae, Theridiidae and Oonopidae, which reach 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).

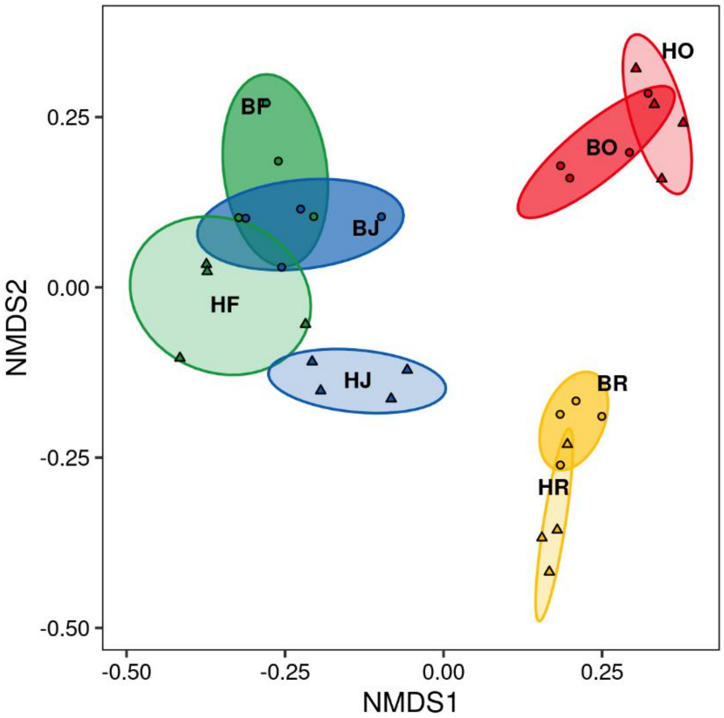

Figure 5. NMDS of canopy spider community composition (overall beta diversity) in four land-uses and two landscapes in Jambi, Sumatra, based on Sørensen dissimilarities (F = rainforest, J = jungle rubber, R = rubber, O = oil palm, B = Bukit Duabelas landscape, H = Harapan landscape).

Community composition and beta diversity

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 (Nazarreta *et al.* 2020, Kreider *et al.* 2021), butterflies (Panjaitan *et al.* 2020), pseudoscorpions (Liebke *et al.* 2021), salticid spiders (Junggebauer et al., 2021) and parasitoid wasps (Azhar *et al.* 2022). 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 methods differed between these studies, few families, including web-building Araneidae, Theridiidae and Tetragnathidae, and free hunting Corinnidae, Salticidae, Sparassidae and Thomisidae, contributed most to overall spider abundance and 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 these families are particularly sensitive to disturbance and altered abiotic and biotic conditions in plantation systems.

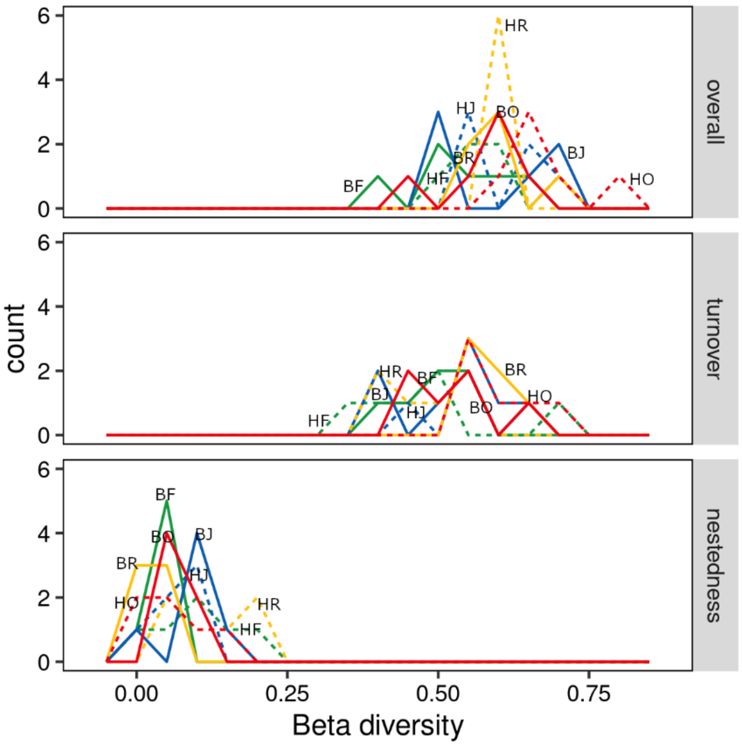

Figure 6. Overall beta diversity (top), turnover partitions (mid) and, nestedness (bottom) in four land uses (green = lowland rainforest, blue = jungle rubber, yellow = rubber and red = oil palm; B, Bukit Duabelas, H, Harapan; solid = Bukit Duabelas, dashed = Harapan in Jambi, Sumatra.

Influence of 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.

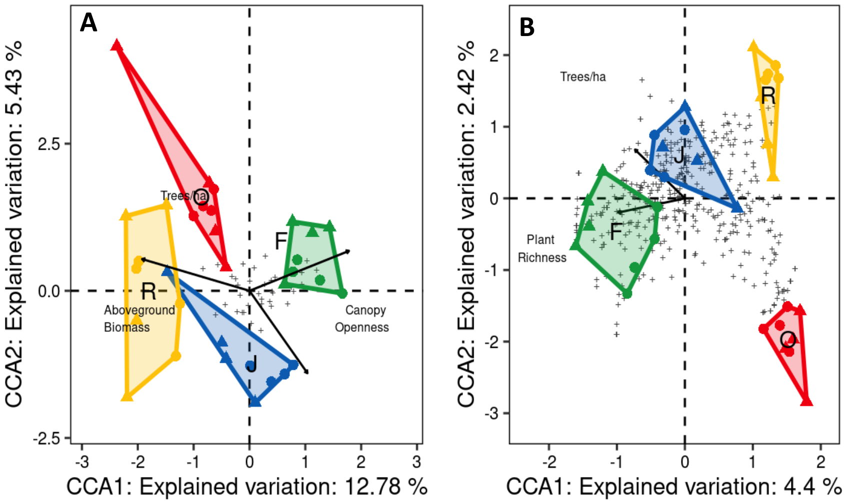

Figure 7. Canonical Correspondence Analysis (CCA) of spider community composition of four tropical land-uses. (A) Family (A), (N = 36) and morphospecies level (B), (N = 446) (F = rainforest, J = jungle rubber, R = rubber, O = oil palm). Only environmental factors significantly contributing to spider community composition are given. Plus symbols are individual families in (A), and individual morphospecies in (B).

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, contain lower biomass and are 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 and 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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Data availability statement

The data that support the findings of this study are openly available in the GRO Göttingen Research Online repository (https://data.goettingen-research-online.de/) at https://doi.org/10.25625/L17S8R (abundance by morphospecies), https://doi.org/10.25625/TOIEX0 (abundance by family), https://doi.org/10.25625/QAFDUM (body length/width, biomass) and https://doi.org/10.25625/DPPATX (environmental variables). The R script used for this study is part of the Supplemental Files.

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Appendix Chapter 2

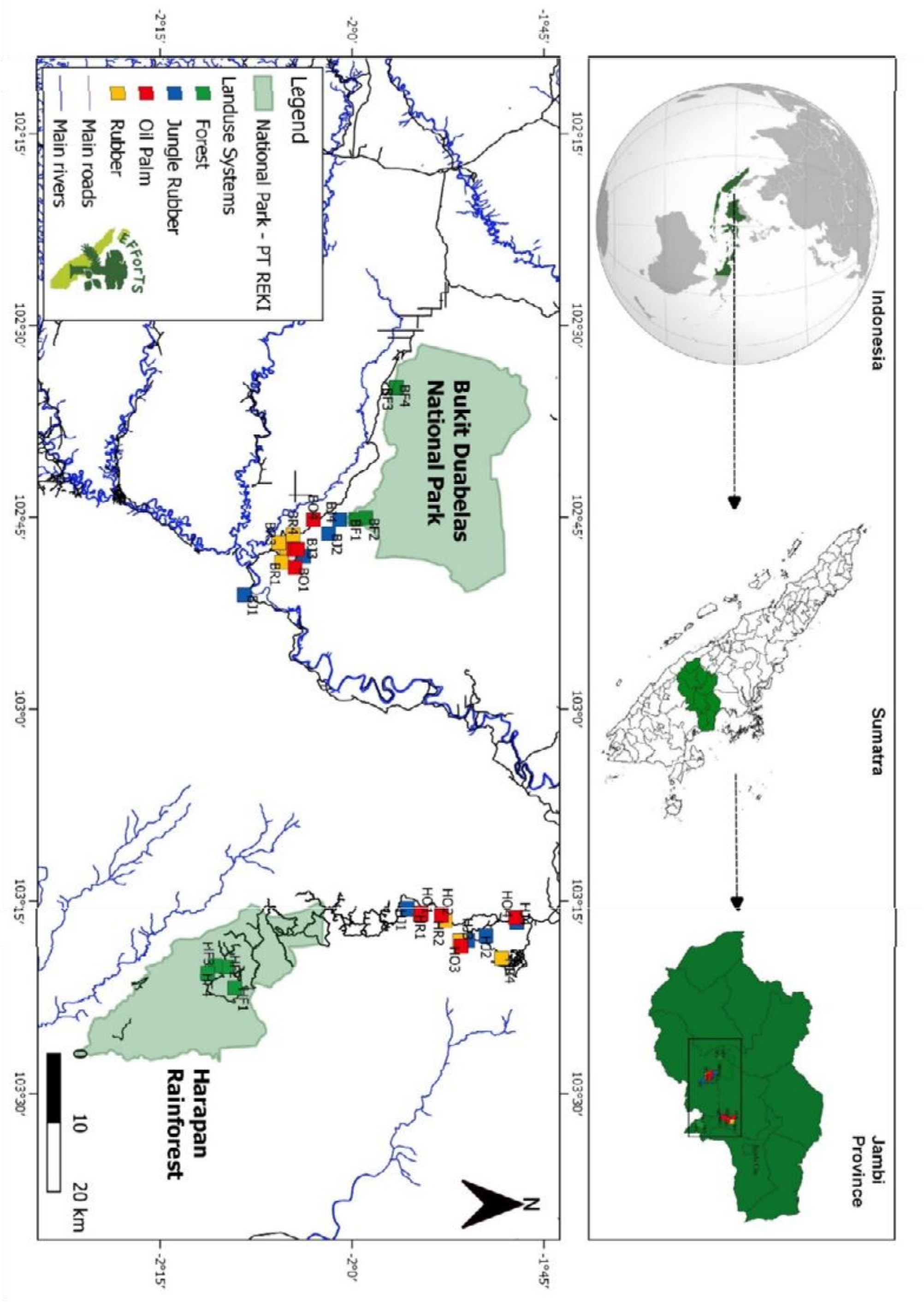


FIGURE S1. Location of the 32 study plots in Jambi Province, Sumatra, Indonesia, arranged in two landscapes near reference sites, i.e. Bukit Duabelas National Park and Harapan Rainforest. Land-use systems are coded by color (green = rainforest, blue = jungle rubber, yellow = rubber, red = oil palm).

FIGURE S2. Four land-use systems investigated. Lowland rainforest (A), jungle rubber (B), and smallholder monocultures of rubber (C) and oil palm (D). Photos by Mathias Ditscherlein (A) and Jochen Drescher (B-D)

FIGURE S3. Canopy fogging method details: (A) 16 collection traps, each 1 m * 1 m, in smallholder rubber plantation. (B) Canopy fogging in smallholder oil palm, planted 10 years previously. (C) Collecting trap, with stunned insects and spiders. (D) Plastic bottle underneath collection trap, filled with 96% EtOH and arthropods.

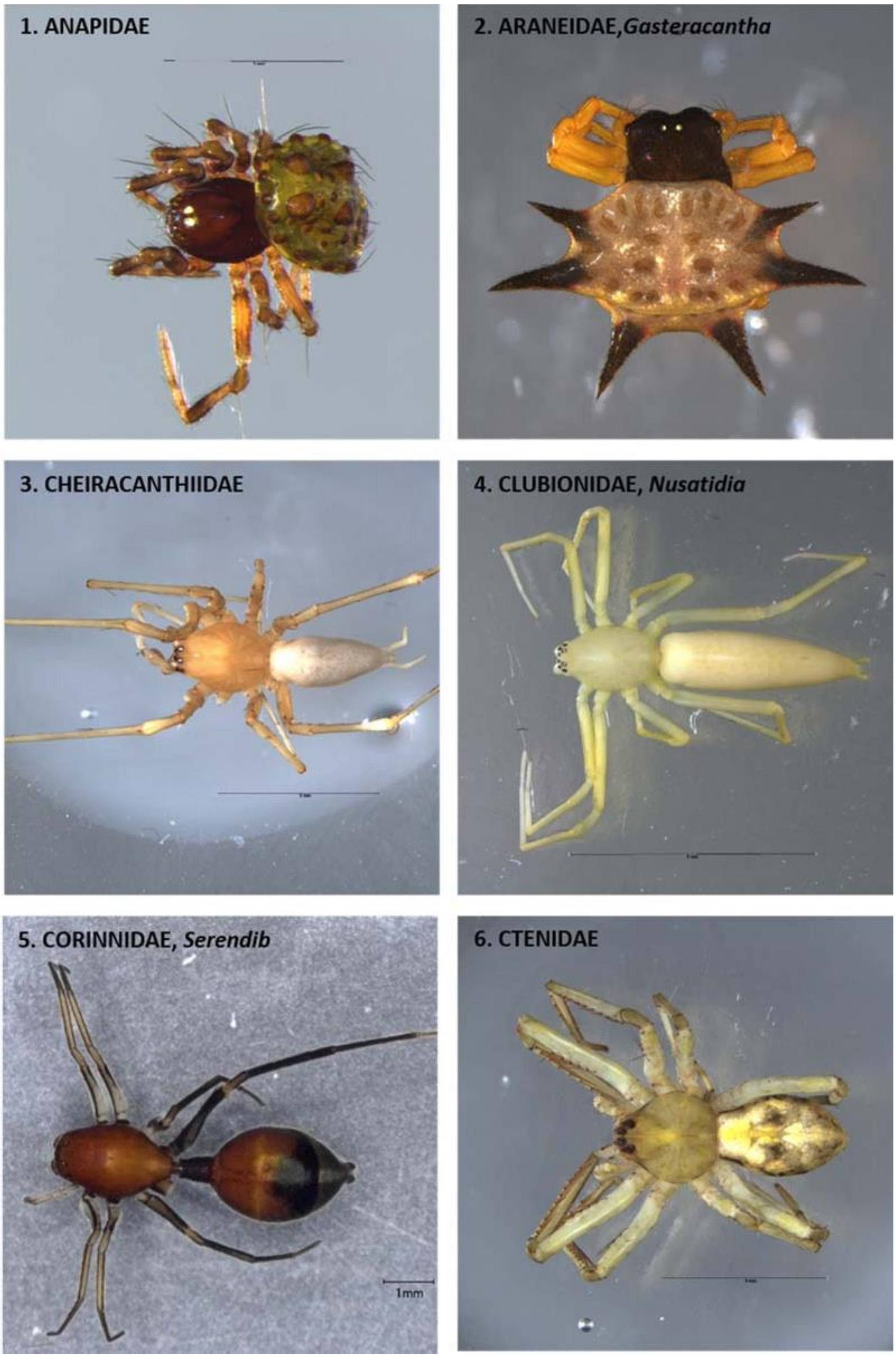


FIGURE S4: 1-6. Canopy spider families collected by canopy fogging in Jambi Province, Sumatra, Indonesia. Family names given in bold, genus names, if known, in italics.

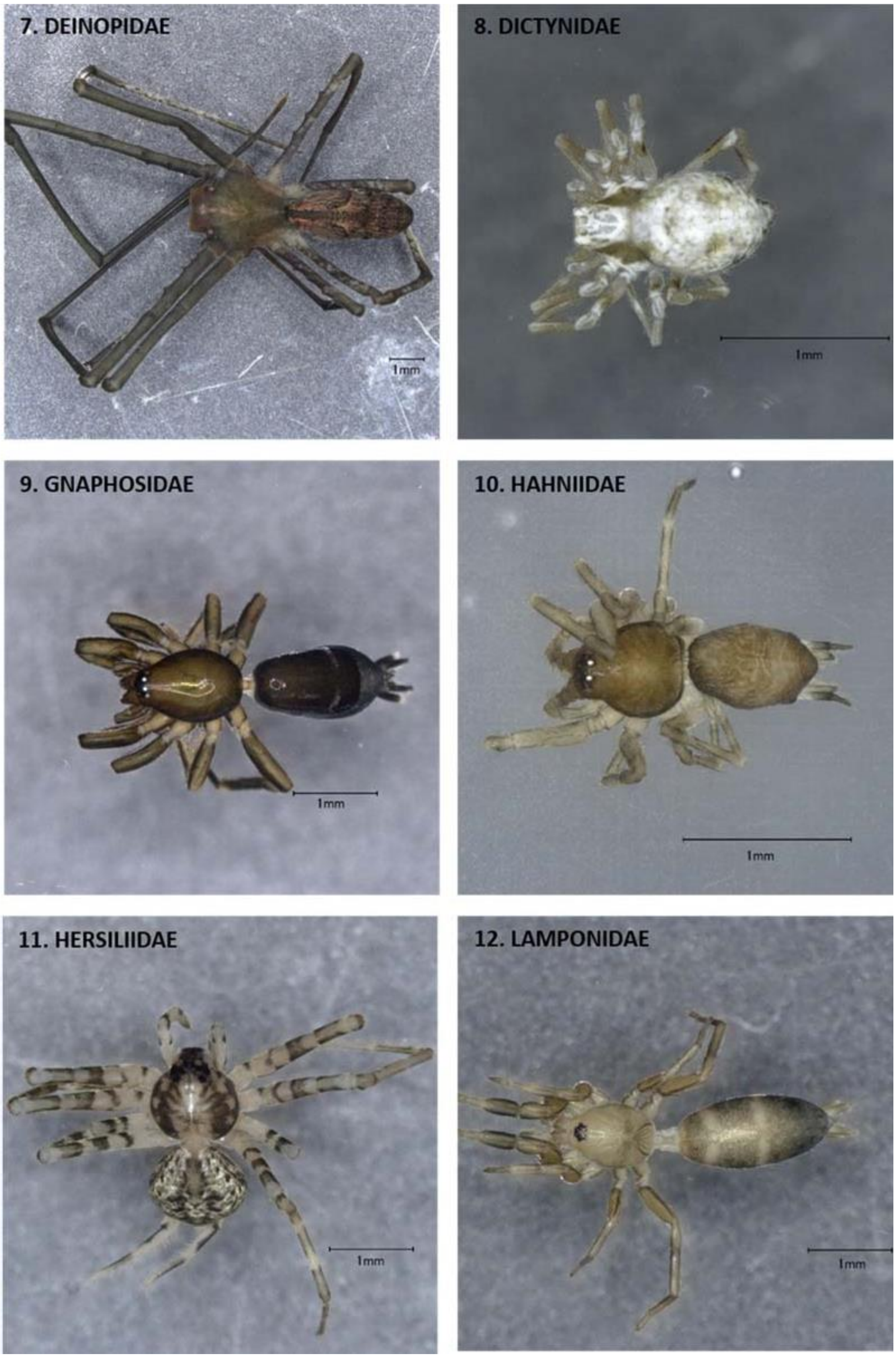


FIGURE S4: 7-12. Canopy spider families collected by canopy fogging in Jambi Province, Sumatra, Indonesia. Family names given in bold, genus names, if known, in italics.

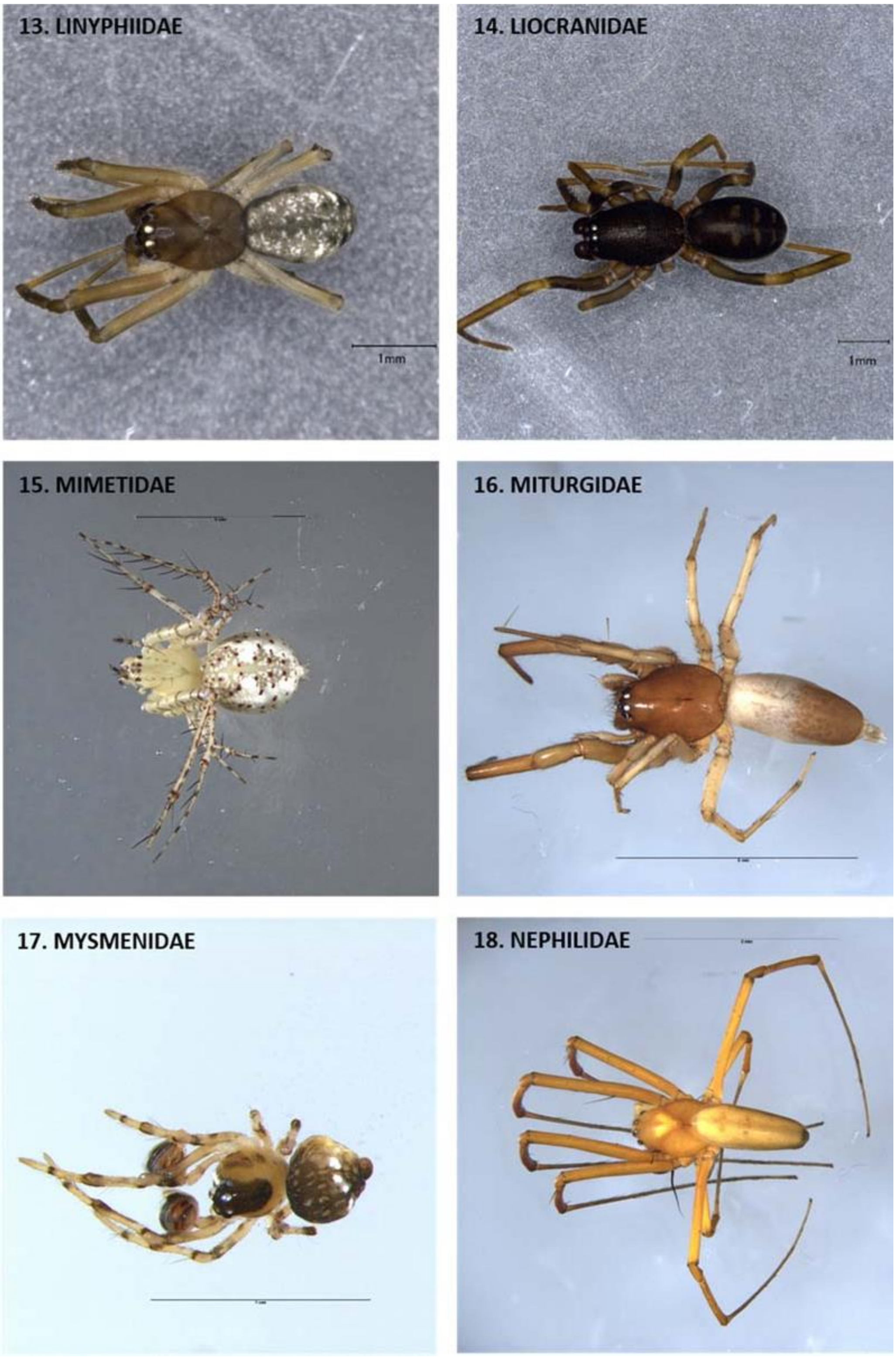
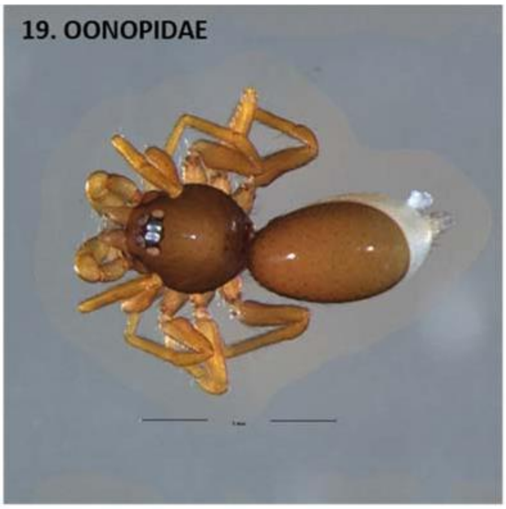
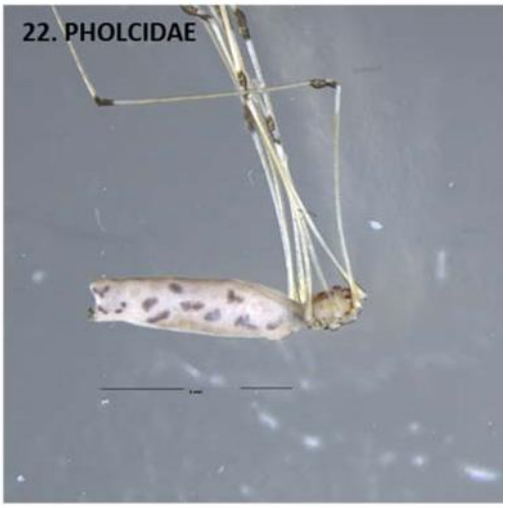


FIGURE S4: 13-18. Canopy spider families collected by canopy fogging in Jambi Province, Sumatra, Indonesia. Family names given in bold, genus names, if known, in italics.


19. OONOPIDAE


20. OXYOPIDAE


21. PHILODROMIDAE

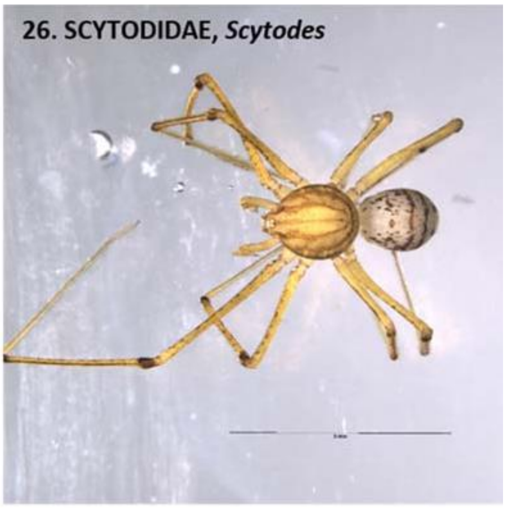

22. PHOLCIDAE


23. PISAURIDAE

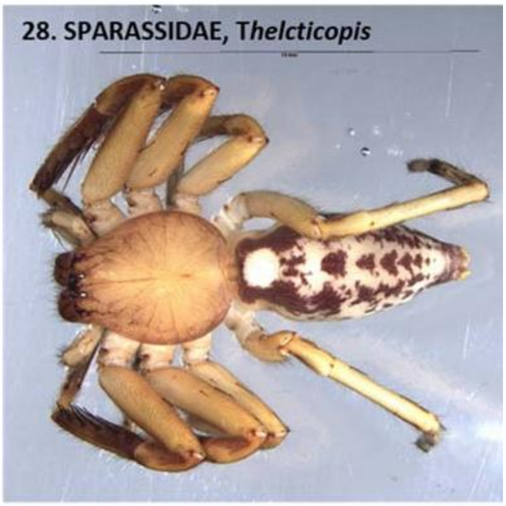

24. PSECHRIDAE

FIGURE S4: 19-24. Canopy spider families collected by canopy fogging in Jambi Province, Sumatra, Indonesia. Family names given in bold, genus names, if known, in italics.


25. SALTICIDAE


26. SCYTODIDAE, *Scytodes*


27. SELENOPIDAE


28. SPARASSIDAE, *Thelcticopis*


29. TETRABLEMIDAE

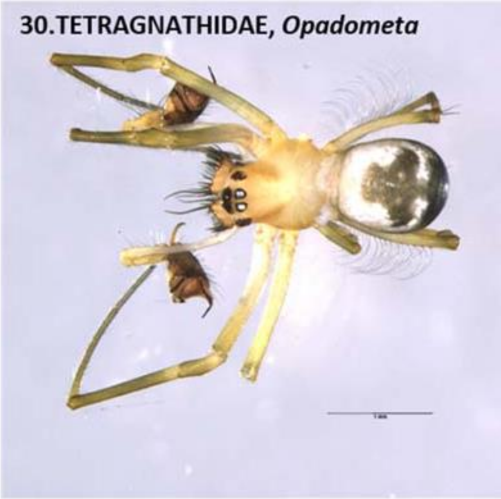
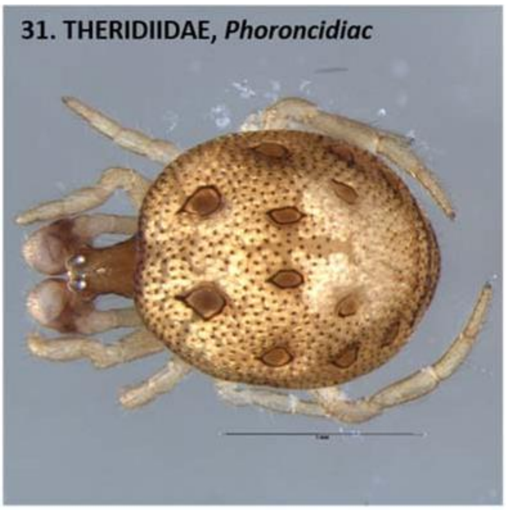
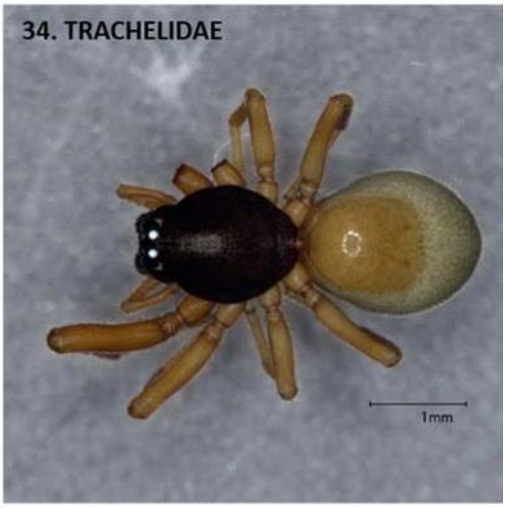

30.TETRAGNATHIDAE, *Opadometa*

FIGURE S4: 25-30. Canopy spider families collected by canopy fogging in Jambi Province, Sumatra, Indonesia. Family names given in bold, genus names, if known, in italics.


31. **THERIDIIDAE**, *Phoroncidiac*


32. **THERIDIOSOMATIDAE**


33. **THOMISIDAE**, *Oxytate*


34. **TRACHELIDAE**


35. **ULOBORIDAE**, *Uloborus*


36. **ZODARIIDAE**

FIGURE S4: 31-36. Canopy spider families collected by canopy fogging in Jambi Province, Sumatra, Indonesia. Family names given in bold, genus names, if known, in italics.

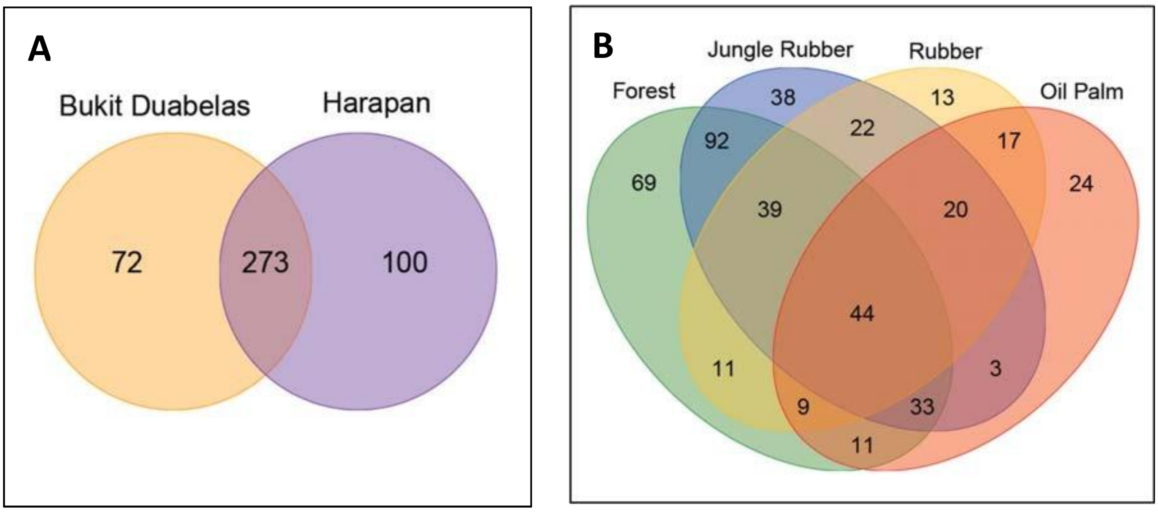


FIGURE S5. Venn diagram of overall canopy spider species overlap between (a) two landscapes (Bukit Duabelas and Harapan) and (b) among four land use systems (rainforest, jungle rubber, rubber, oil palm) in Jambi province, Sumatra, Indonesia.

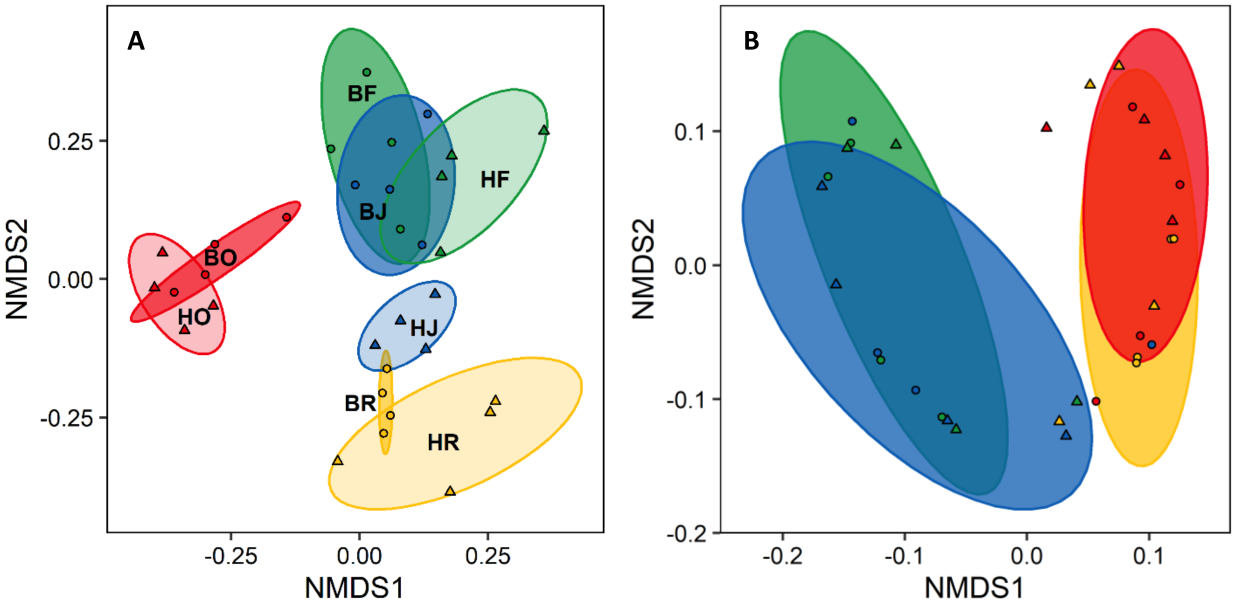


FIGURE S6. NMDS of turnover (A) and nestedness (B) of canopy spider communities in four land- use systems and two landscapes in Jambi, Sumatra, based on Sørensen dissimilarities (F = rainforest, J = jungle rubber, R = rubber, O = oil palm, B = Bukit Duabelas landscape / circles, H = Harapanlandscape / triangles). Turnover was influenced by both land use and landscape (interaction: Wilk's λ = 0.18, F3,18 = 2.5, P = 0.005; land use: Wilk's λ = 0.01, F3,18 = 16.0, P < 0.001; landscape: Wilk's λ = 0.14, F1,6 = 18.3, P < 0.001), while differences in nestedness were only driven by land use (Wilk's λ = 0.18, F3,15 = 3.2, P < 0.001).

TABLE S1. Eigenvalues of the 36 families of the overall canopy spider community.

family	CCA1	CCA2	CCA3
Anapidae	-0.93266	-0.10610	-0.43759
Araneidae	0.25724	-0.20081	-0.04978
Cheiracanthiidae	0.02836	0.24334	-0.03265
Clubionidae	0.43665	0.23970	-0.13786
Corinnidae	-0.26835	-0.11653	0.05731
Ctenidae	-0.93556	-0.31352	-0.41667
Deinopidae	-1.19780	-0.34653	-0.75539
Dictynidae	-0.07676	-0.38438	0.87916
Gnaphosidae	0.84202	-0.37112	-0.28036
Hahniidae	-0.38854	0.25690	-0.19816
Hersiliidae	-0.39782	0.01280	0.02737
Lamponidae	0.31565	-0.24417	0.71808
Linyphiidae	0.00202	-0.16293	-0.15193
Liocranidae	1.23703	-1.59540	0.70010
Mimetidae	-0.41466	0.03751	0.45101
Miturgidae	0.13382	0.36543	0.32237
Mysmenidae	-0.45189	-0.23269	0.65322
Nephilidae	0.11988	-0.45532	1.32320
Oonopidae	-0.21368	0.14561	0.02208
Oxyopidae	-0.21490	0.21521	0.12310
Philodromidae	0.61637	0.40917	-0.43098
Pholcidae	-0.75123	-0.05447	0.13186
Pisauridae	-0.02812	0.55344	0.14783
Psechridae	-0.78657	0.00454	0.48691
Salticidae	0.21565	-0.09491	0.07669
Scytodidae	-0.35584	0.18303	0.34693
Selenopidae	-1.02968	-0.50566	0.22296
Sparassidae	-0.15920	0.05524	0.08853
Tetrablemidae	-0.68486	0.22278	0.09997
Tetragnathidae	0.57204	-0.44104	0.12718
Theridiidae	-0.38896	-0.17619	-0.21874
Theridiosomatidae	-0.20280	0.67992	0.38185
Thomisidae	0.22405	0.35281	-0.01047
Trachelidae	0.16905	0.07210	-0.09073
Uloboridae	-0.27626	-0.58823	0.29443
Zodariidae	0.10403	0.37265	0.05156

TABLE S2. Eigenvalues of the 445 morphospecies of the overall canopy spider community.

Morphospecies	CCA1	CCA2	Morphospecies	CCA1	CCA2
AraCori009	-1.01037	-1.89848	AraOono003	0.06736	-0.04552
AraSpar010	-1.01037	-1.89848	AraAran041	0.99987	-0.04044
AraThom004	-1.01037	-1.89848	AraTrid092	-0.09655	-0.02948
AraTrid021	-1.01037	-1.89848	AraTrid058	1.15363	-0.02031
AraTrid044	-1.01037	-1.89848	AraTrid086	-0.98935	-0.01866
AraUlob005	-1.00014	-1.76045	AraSpar016	-0.66365	-0.01402
AraSalt067	1.14984	-1.58985	AraTrid082	-1.58156	-0.01304
AraTtra012	1.14984	-1.58985	AraTrid097	-0.53509	-0.00946
AraScyt002	1.17362	-1.57695	AraAran024	0.69042	-0.00631
AraLioc001	1.26019	-1.57024	AraSalt008	-0.09165	-0.00132
AraSalt097	1.26019	-1.57024	AraTrid060	1.09420	0.00671
AraSalt082	1.31408	-1.49405	AraCori011	-0.05565	0.00910
AraSalt065	1.30726	-1.48889	AraPhol009	-1.43137	0.01364
AraUlob001	-0.97968	-1.48437	AraTrid039	-0.10689	0.01509
AraSalt048	1.45890	-1.42220	AraLiny003	1.30199	0.01545
AraAran030	1.35779	-1.40174	AraTrid030	-0.32687	0.01572
AraTtra002	-0.89515	-1.39613	AraTrid023	-0.74682	0.01718
AraSpar004	-0.96945	-1.34634	AraAran008	0.27666	0.01961
AraAran031	1.37380	-1.31520	AraPisa001	-0.76153	0.02461
AraPisa004	1.37380	-1.31520	AraAran057	-0.08649	0.02555
AraThom046	1.37380	-1.31520	AraGnap002	1.38873	0.02616
AraGnap003	1.43071	-1.30352	AraGnap004	0.84450	0.02733
AraTtra005	1.43443	-1.30101	AraTrid029	-1.03662	0.02797
AraTtra007	1.45892	-1.30070	AraAran035	0.59691	0.03366
AraAran027	1.50775	-1.28670	AraTrid007	-0.90785	0.03431
AraUlob007	1.45916	-1.27520	AraSpar023	0.61369	0.04347
AraSalt083	1.36607	-1.24363	AraTrid045	0.69293	0.04986
AraSele001	-1.30279	-1.23646	AraAran012	-0.72432	0.05001
AraSalt006	-0.93012	-1.22662	AraTrid013	-0.21917	0.05364
AraGnap007	1.01820	-1.22538	AraAran047	0.92532	0.06314
AraSalt084	1.18543	-1.18853	AraHers002	-0.14926	0.06387
AraSalt050	1.34959	-1.17565	AraCori015	-0.69029	0.07015
AraAran049	1.55659	-1.15120	AraLiny002	-0.69029	0.07015
AraAran051	1.55659	-1.15120	AraThom010	-0.51808	0.07213
AraClub011	1.55659	-1.15120	AraSalt028	-0.81304	0.07482
AraGnap011	1.55659	-1.15120	AraThom031	-0.66704	0.07629
AraTrid072	1.55659	-1.15120	AraClub012	-0.22613	0.10687
AraAran042	-1.30363	-1.13797	AraSalt004	-0.40682	0.11080
AraTrid004	-0.48322	-1.13782	AraTrid089	-0.49670	0.11327

Morphospecies	**CCA1**	**CCA2**	**Morphospecies**	**CCA1**	**CCA2**
AraUlob012	0.87932	-1.13061	AraTrid031	-0.12495	0.11328
AraAran039	-0.67962	-1.11844	AraSalt010	0.16115	0.11362
AraDict001	-0.20063	-1.09701	AraTtra011	0.77297	0.11565
AraSalt055	0.71059	-1.09169	AraSalt001	-0.66103	0.11636
AraOxyo004	-1.15495	-1.08807	AraSalt077	-0.08037	0.13154
AraTrid005	-0.61393	-1.07336	AraCori010	0.25170	0.13626
AraTrid018	-0.94899	-1.07026	AraAran006	-0.63826	0.14046
AraSalt053	1.19282	-1.04653	AraOono007	-0.87996	0.14851
AraSalt074	1.62354	-0.97960	AraAran003	-0.65652	0.15449
AraTrid063	1.62354	-0.97960	AraTble001	-0.65811	0.15454
AraCori006	-0.77076	-0.95053	AraScyt001	-0.38007	0.15573
AraTrid080	0.82153	-0.93524	AraLiny006	-1.07042	0.16293
AraClub021	1.26120	-0.91480	AraThom011	-0.54950	0.16991
AraTrid065	0.27577	-0.90903	AraOxyo006	-0.64382	0.17548
AraSalt051	1.31472	-0.86537	AraThom041	-0.71501	0.19258
AraAran046	1.14742	-0.83872	AraClub017	0.81265	0.19343
AraUlob002	-0.32859	-0.82718	AraHahn004	-0.79027	0.19424
AraSalt002	0.56079	-0.79115	AraTrid093	-0.46769	0.19425
AraSalt022	0.14725	-0.79023	AraTrid095	-0.42999	0.19625
AraAran028	1.33769	-0.78162	AraPhol005	-0.35142	0.19705
AraAran060	0.15361	-0.77573	AraSalt061	0.17462	0.20301
AraAran062	0.15361	-0.77573	AraTrid028	0.00531	0.20407
AraThom040	1.31389	-0.76687	AraLiny004	-0.95066	0.21178
AraSalt080	0.93833	-0.76658	AraSalt023	-0.00513	0.21268
AraAran005	0.87792	-0.74627	AraTrid054	-0.60558	0.21672
AraTtra009	0.67494	-0.73478	AraSalt095	0.97751	0.23869
AraTrid001	-0.47859	-0.73304	AraAran053	1.05750	0.23881
AraSalt009	-0.89047	-0.71133	AraAran010	-0.35343	0.23937
AraLiny001	-0.23110	-0.71021	AraSalt071	-0.86320	0.24812
AraSalt049	1.28086	-0.70921	AraTrid079	-0.92994	0.25069
AraLiny008	-0.64435	-0.69203	AraLiny005	-0.90176	0.25439
AraTrid053	-1.22724	-0.68286	AraClub016	-0.03411	0.26094
AraAran001	-1.20202	-0.64738	AraTsom001	-0.35533	0.26114
AraUlob003	-0.48228	-0.64234	AraSalt068	0.65525	0.26223
AraTrid083	-1.19591	-0.63710	AraAran014	-0.22889	0.26955
AraMysm001	-0.35716	-0.63194	AraCori016	-0.22889	0.26955
AraSpar007	-0.95080	-0.62636	AraTrid098	-0.22889	0.26955
AraTrid047	1.37698	-0.62015	AraGnap006	-0.02522	0.27621
AraPsec002	-0.31095	-0.60305	AraTrid014	-0.11059	0.28118
AraTrid099	-1.34092	-0.58844	AraSalt018	-0.32711	0.28712
AraTrid012	-0.58040	-0.58781	AraTrid052	-0.10414	0.29641
AraTrid026	0.46216	-0.58074	AraCori018	-0.31069	0.29729

Morphospecies	CCA1	CCA2	Morphospecies	CCA1	CCA2
AraDein001	-1.59521	-0.57444	AraThom008	-0.43347	0.30495
AraLiny011	-1.59521	-0.57444	AraTrid043	0.09755	0.30535
AraUlob009	-1.59521	-0.57444	AraTrid050	1.03899	0.31162
AraAran043	0.58865	-0.57161	AraAran040	-0.41020	0.31837
AraLamp001	0.58865	-0.57161	AraOxyo009	-0.08072	0.32719
AraSalt064	0.58865	-0.57161	AraSalt089	-0.08561	0.33572
AraThom033	0.58865	-0.57161	AraTrid062	-0.49541	0.33638
AraThom034	0.58865	-0.57161	AraCten003	-0.04005	0.34068
AraTrid066	0.58865	-0.57161	AraOxyo007	-0.04005	0.34068
AraOono005	0.60873	-0.56781	AraThom028	-0.04005	0.34068
AraSalt086	1.31807	-0.53597	AraClub014	0.66865	0.34294
AraPhol011	-1.22049	-0.52531	AraClub007	-0.05298	0.34882
AraPhol002	-0.67621	-0.52524	AraSalt011	0.35574	0.34923
AraOono002	-0.40335	-0.51603	AraAran058	-1.56623	0.35137
AraAran029	1.40056	-0.51603	AraGnap005	-1.56623	0.35137
AraOxyo012	0.93967	-0.51113	AraPsec001	-1.56623	0.35137
AraSalt003	-0.87385	-0.50675	AraThom036	-1.56623	0.35137
AraSalt058	0.66687	-0.48726	AraTrid096	-1.56623	0.35137
AraSpar008	-1.12342	-0.48310	AraOxyo010	-0.38646	0.35805
AraTtra014	0.76679	-0.47890	AraTrid025	-0.50183	0.36332
AraUlob008	-1.59605	-0.47594	AraSalt026	0.04598	0.36506
AraSalt017	-0.11074	-0.47209	AraAran020	0.38861	0.36674
AraTrid069	-0.82467	-0.46572	AraZoda001	0.02723	0.37090
AraSalt056	0.71177	-0.46251	AraTrid076	-0.31422	0.37122
AraThom009	1.22162	-0.45665	AraGnap009	-0.35874	0.37801
AraTrid008	0.19054	-0.45301	AraSalt066	0.87309	0.37844
AraTrid020	0.50080	-0.45100	AraSalt024	0.66595	0.38056
AraAran015	1.25419	-0.45024	AraChei003	-0.27589	0.38142
AraTrid067	-1.59632	-0.44311	AraSalt087	-1.00341	0.38184
AraTrid061	-1.37003	-0.41499	AraSpar005	-0.30843	0.39268
AraThom006	-0.25466	-0.41424	AraOxyo015	-0.53843	0.40621
AraSalt007	-0.58894	-0.40036	AraThom035	0.23145	0.41576
AraSpar003	0.12432	-0.39554	AraThom002	0.27746	0.42246
AraTrid002	-0.71795	-0.39040	AraTrac001	-0.05028	0.42283
AraClub002	-0.70020	-0.38724	AraOxyo002	-0.02675	0.42681
AraTtra001	0.96667	-0.38553	AraSalt060	0.02582	0.43380
AraClub009	0.74737	-0.38270	AraOxyo011	-0.94808	0.43488
AraSalt054	-0.08247	-0.37875	AraMysm002	1.00109	0.43641
AraSalt032	0.51159	-0.37863	AraThom007	-0.32097	0.46222
AraAran055	-1.59688	-0.37745	AraClub008	0.37857	0.47296
AraCori026	-1.59688	-0.37745	AraAran002	0.29205	0.48055
AraSalt075	-1.59688	-0.37745	AraSalt025	-0.35581	0.48609

Morphospecies	**CCA1**	**CCA2**	**Morphospecies**	**CCA1**	**CCA2**
AraThom032	-1.59688	-0.37745	AraSalt092	-0.90170	0.48822
AraThom044	-1.59688	-0.37745	AraClub006	-0.20841	0.49208
AraUlob004	-1.02400	-0.36575	AraThom019	1.00497	0.49581
AraLiny012	-1.44793	-0.36038	AraTrid015	0.36033	0.49636
AraPhol010	-1.44793	-0.36038	AraSalt088	0.38553	0.49732
AraOono008	0.57220	-0.35981	AraSalt085	-0.56764	0.50060
AraNeph001	0.69733	-0.35502	AraUlob006	1.26890	0.50434
AraPhol003	-0.91007	-0.35423	AraClub018	-0.27833	0.51442
AraSpar019	-1.00469	-0.35410	AraClub020	-0.27833	0.51442
AraCori004	-0.83355	-0.34204	AraOxyo016	-0.27833	0.51442
AraThom001	-0.78802	-0.33557	AraAran056	0.05143	0.51664
AraTtra015	-0.80713	-0.33511	AraClub010	0.21631	0.51775
AraHers001	-0.69002	-0.33376	AraSalt079	0.21631	0.51775
AraSalt073	0.92021	-0.32670	AraSalt081	0.21631	0.51775
AraAran021	1.28086	-0.32208	AraTrid074	0.21631	0.51775
AraNeph003	1.08772	-0.31502	AraThom037	0.02174	0.52930
AraSpar009	0.15492	-0.31047	AraMitu001	0.42535	0.56428
AraClub025	1.17055	-0.30853	AraThom021	0.21180	0.56838
AraLiny010	1.17055	-0.30853	AraPhol007	-0.20024	0.57585
AraSalt070	1.17055	-0.30853	AraSalt069	0.05774	0.57621
AraTrid075	1.17055	-0.30853	AraTrid070	0.25436	0.58088
AraMime001	-0.53930	-0.30314	AraThom005	-0.39329	0.59107
AraAran048	-1.37387	-0.30260	AraSalt043	0.19420	0.59803
AraAran044	-0.51978	-0.30258	AraPhil002	0.00951	0.59844
AraAran025	0.82404	-0.30120	AraPisa003	-0.28273	0.59913
AraCori017	-0.14448	-0.29790	AraOxyo014	-0.55448	0.60314
AraTtra003	-1.06418	-0.29757	AraThom043	-0.27384	0.60540
AraSalt062	1.13255	-0.29649	AraSalt040	0.70141	0.61020
AraTrid038	-0.45390	-0.29338	AraChei004	0.27339	0.61244
AraOxyo005	-0.45308	-0.28697	AraSalt090	0.27339	0.61244
AraMime002	-0.29733	-0.28467	AraTrid078	0.27339	0.61244
AraAran045	-0.32421	-0.28052	AraClub004	0.90946	0.61506
AraSpar002	-0.41543	-0.27139	AraSalt047	0.48306	0.62084
AraCori012	0.43936	-0.27006	AraThom038	-0.57522	0.63599
AraTrid048	0.73997	-0.26888	AraTrid084	0.43468	0.64391
AraHahn001	-0.27787	-0.26367	AraOxyo013	-0.20241	0.66256
AraTrid024	-0.15548	-0.25758	AraTrid087	-0.08666	0.66590
AraOxyo001	-0.46862	-0.25403	AraAnap002	-0.89143	0.67323
AraOxyo008	-1.37428	-0.25335	AraAran061	-0.81837	0.69404
AraAnap001	0.11758	-0.25135	AraLiny009	-0.20753	0.69845
AraCori014	0.11758	-0.25135	AraGnap001	1.14813	0.72088
AraTrid034	0.11758	-0.25135	AraTrid035	0.27094	0.72340

Morphospecies	**CCA1**	**CCA2**	**Morphospecies**	**CCA1**	**CCA2**
AraClub024	0.41134	-0.24378	AraSpar018	0.06165	0.72461
AraAran004	-1.23141	-0.24284	AraSalt072	0.53656	0.73059
AraClub003	0.47772	-0.23946	AraClub023	0.66543	0.74651
AraTrid056	-1.59075	-0.23169	AraTrid027	-0.25772	0.75016
AraChei002	0.81205	-0.23130	AraSpar021	0.70593	0.75035
AraCori027	-0.93249	-0.22418	AraThom027	-0.15693	0.76020
AraLiny007	0.87326	-0.22109	AraTtra013	-0.69266	0.76335
AraPhil001	0.00943	-0.21889	AraSalt046	0.88981	0.77494
AraTrid091	-1.24039	-0.21829	AraSalt021	-0.20464	0.77848
AraTrid077	-1.30008	-0.21199	AraCori021	-0.10733	0.78038
AraTrid090	-1.21505	-0.19285	AraThom015	0.96200	0.78570
AraSalt078	0.33415	-0.19173	AraAran063	0.08034	0.78858
AraThom029	0.53279	-0.19010	AraThom025	0.04287	0.80165
AraSalt005	-0.66131	-0.18959	AraSalt052	0.39936	0.80627
AraSalt091	-0.09137	-0.18513	AraSalt063	0.63854	0.80939
AraAran038	-1.00037	-0.18379	AraTtra006	1.13521	0.81629
AraTrid068	0.96246	-0.17953	AraThom026	-0.29429	0.81648
AraTrid011	-0.03216	-0.17539	AraClub001	0.73353	0.81946
AraTrid033	-0.96138	-0.17402	AraSalt037	-0.05242	0.82431
AraOono006	-0.72860	-0.16995	AraSpar022	0.46089	0.84116
AraClub022	-0.15044	-0.16932	AraAran023	0.57138	0.84388
AraSalt027	0.38231	-0.16465	AraPhol006	0.16516	0.84597
AraSpar001	-0.10333	-0.15578	AraSpar013	0.27665	0.84788
AraTrac003	0.27856	-0.15229	AraSalt076	0.61564	0.89871
AraUlob010	0.17988	-0.15103	AraClub013	-0.20866	0.92418
AraTrid010	-0.73240	-0.14381	AraClub019	0.43051	0.92646
AraSalt019	-0.32800	-0.14380	AraSpar011	0.67994	0.93109
AraThom016	0.95249	-0.14059	AraAran054	0.27582	0.94637
AraCori025	-1.58666	-0.13451	AraCori024	-0.25588	0.96934
AraTrid006	-1.19209	-0.13042	AraHahn003	-0.25588	0.96934
AraTrid064	0.72886	-0.12932	AraSpar014	-0.25588	0.96934
AraClub015	-1.15169	-0.12926	AraSpar015	-0.25588	0.96934
AraCten002	-1.15169	-0.12926	AraThom045	-0.25588	0.96934
AraSalt093	-1.15169	-0.12926	AraClub005	0.89875	0.97472
AraSalt094	-1.15169	-0.12926	AraThom018	0.23747	1.02098
AraTrid094	-1.15169	-0.12926	AraSalt029	0.56867	1.02365
AraUlob013	-1.15169	-0.12926	AraSalt014	0.95225	1.02428
AraPhol004	-0.51818	-0.12275	AraSpar017	0.79522	1.03396
AraCten001	-0.49186	-0.12006	AraGnap010	0.64562	1.04227
AraThom030	0.71415	-0.10496	AraPhil003	0.62699	1.05010
AraTrid055	0.90830	-0.10100	AraThom042	1.26425	1.05152
AraPisa002	0.17944	-0.09944	AraTrid081	1.26425	1.05152

Morphospecies	**CCA1**	**CCA2**	**Morphospecies**	**CCA1**	**CCA2**
AraCori003	-0.34454	-0.09939	AraTrid085	0.25377	1.06341
AraPhol001	-0.40252	-0.09420	AraSalt059	-0.06210	1.07892
AraSpar020	0.21087	-0.08193	AraAran037	-0.65171	1.10569
AraPhol008	-0.82935	-0.07982	AraSalt099	-0.65171	1.10569
AraTrid051	1.22333	-0.07932	AraSalt045	0.94534	1.14935
AraSalt039	-0.55747	-0.07817	AraSpar012	0.73008	1.16017
AraSalt030	0.00209	-0.07771	AraAran016	0.59136	1.17623
AraThom012	0.01545	-0.07573	AraTrid049	1.12588	1.23362
AraCori005	-0.48406	-0.06507	AraSalt015	1.22305	1.25558
AraTrid059	-1.12239	-0.06132	AraSalt042	1.32022	1.27754
AraTrid003	-0.40855	-0.05672	AraSalt044	1.32022	1.27754
AraTtra004	-0.58350	-0.04992	AraThom039	-0.20130	1.35951
AraOono001	-0.45112	-0.04823	AraAran034	-0.50884	1.42543
AraSalt034	-0.36171	-0.04762	AraThom017	1.10662	1.64355
AraChei001	-0.44021	-0.04669	AraSalt098	-0.63531	1.65348
AraTrac002	0.05720	-0.04600			

Chapter 3

Variation in community-level trophic niches of canopy spiders with conversion of rainforest into rubber and oil palm plantations as indicated by stable isotope analysis

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Variation in community-level trophic niches of canopy spiders with conversion of rainforest into rubber and oil palm plantations as indicated by stable isotope analysis

Abstract

Rainforest transformation into rubber and oil palm plantations causes losses in biodiversity and shifts in trophic functionality across arthropod taxa. However, the effects of such a land-use transformation on spider communities and their functional diversity, trophic position and use of basal resources it is little understood. To address this, we investigated variations in the trophic structure of canopy spider communities with the transformation of tropical rainforest into jungle rubber (agroforest system), and rubber and oil palm monoculture plantations by measuring bulk tissue $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios. In addition to the total community, we investigated in more detail the cursorial families Salticidae, Clubionidae and Thomisidae, and the sheet-web building Theridiidae. Overall, we found that rainforest spider communities respond differently to land-use transformation. Generally, the range in trophic niches and use of basal resources ($\Delta^{15}N$, $\Delta^{13}C$ values) did not differ between land-use systems, but maximum $\Delta^{15}N$ values suggested that some families have narrower trophic niches in plantations. Moreover, functional diversity was similar across the four land-use systems, with the exception of isotopic divergence, which was higher in rainforest and jungle rubber than in monoculture plantations. This suggests that in more natural systems species with extreme niches reach higher dominance. Further, there was no difference in the trophic positions between cursorial and sheet-web building spiders, but they occupied virtually the same average position. However, maximum $\Delta^{15}N$ values in Salticidae, Clubionidae and Thomisidae were higher in plantations than rainforest and jungle rubber indicating that intra-guild predation may be more widespread in free hunting than web-building spiders but only in plantation systems. Finally, we found evidence that transformation of rainforest into monocultures plantations is associated with a shift towards more herbivore prey in canopy spiders. Overall, our study provides first insight into trophic changes in canopy spider communities associated with the transformation of tropical rainforest into plantations.

Keywords: Deforestation, rainforest, stable isotopes, trophic niches, isotopic metrics, Spiders, Indonesia.

Introduction

Tropical rainforests are one of the most biologically diverse ecosystems worldwide. They are assumed to hold more than half of the animal and plant species described, with an exceptionally high level of endemism (Myers et al., 2000; Zhao et al., 2022). Further, they provide essential ecosystem services, including the provisioning of timber, buffering adverse climatic conditions and carbon storage (Hansen et al., 2015; Böhnert et al., 2016; Codato et al., 2019). However, tropical rainforests are under increasing pressure due to increasing global demands for food, biofuel, extraction of minerals and conversion into plantations, particularly for the production of soybeans and palm oil (Sodhi et al., 2004; Laurance et al., 2014; Meijide et al., 2018; Codato et al., 2019). Deforestation is a critical problem in Indonesia, which in 2012 had the highest deforestation rate worldwide (Margono et al. 2014), with Sumatra being the most affected island (Miettinen et al., 2011). Much of the loss of rainforest is due to the conversion of rainforest into cash crop agricultural systems, in particular rubber and oil palm plantations (BPS, 2019). This conversion has been shown to detrimentally affect abundance, richness, biomass, and functional and taxonomic diversity of a range of plant and animal taxa (Fitzherbert et al., 2008; Wilcove & Koh, 2010; Rembold et al., 2017; Paoletti et al., 2018; Potapov et al., 2020; Ramos et al., 2022). In terms of diversity and biomass, arthropods are among the most severely affected taxa (Hamilton et al., 2010; Bar-On, Phillips & Milo, 2018), and this may result the loss of ecosystem functions and stability (Cardinale et al., 2006; Potapov et al., 2019).

The trophic niche concept is fundamental to species coexistence (Hutchinson, 1959) by providing the basis on how species may impact each other thereby modifying their contribution to the functioning of ecosystems (Korotkevich et al., 2018). Niches of species also critically define their response to disturbances and the conversion of forest into arable land. Species with broader trophic niches are assumed to be more resistant to disturbances and land-use change. On the other hand, species with narrow trophic niches may be more severely affected and, if disturbances prevail, eventually may go extinct (Bommarco et al., 2010; Gan et al. 2014). These changes are likely to alter interactions of species resulting in changes in the functioning of animal communities. One approach for studying community-level functionality is using community level metrics of trophic niches. Previous studies demonstrated that metrics, such as functional richness, functional evenness and functional divergence, are related to ecosystem functioning (Krause et al., 2021; Zhou et al., 2022). Functional richness represents the total isotopic space occupied by all the species within a particular community, functional divergence quantifies to what extent rare or abundant species occupy extreme trophic positions, and isotopic evenness provides information on how uniform species are distributed across the community niche space (Bremner, Rogers & Frid, 2003; Cucherousset & Villéger, 2015).

Spiders are important top predators, feeding mainly on insects, other invertebrates and small vertebrates (Nelson & Jackson, 2011; Shine & Tamayo, 2016; Nyffeler & Vetter, 2018). Nyffeler & Birkhofer (2017) estimated that globally spiders consume 400 - 800 million tons of prey annually. However, how land-use change affects the trophic structure of spider communities is poorly studied. Earlier studies focused on how the conversion of rainforest into plantation systems changes the trophic structure and use of basal resources of other predators groups, such as Chilopoda (Klarner et al., 2017) and Pseudoscoropionida (Liebke et al., 2021) as well as forest floor invertebrates (Hyodo et al., 2010; Potapov et al., 2020). As major predators in virtually any terrestrial ecosystem, spiders have different hunting strategies, including web-building, free hunting and ambush hunting (Cardoso et al., 2011), which contribute to their prominent role as predators in terrestrial ecosystems. Both in natural and agroecosystems, spiders contribute significantly to pest control (Birkhofer et al., 2008; Lefebvre et al., 2017). Michalko et al. (2019) demonstrated in a meta-analysis of 58 studies that spiders suppressed 79% of agricultural pest species. Cursorial or ambush huntering spiders may prey more on early developmental stages of pest species, such as eggs, larvae or nymphs, contrary to web-building spiders that depend predominantly on adult winged insects (Marc et al., 1999). In addition to preying on lower trophic level taxa such as herbivores, spiders also engage in cannibalism, intra-guild predation or supplement their diet with plant food and this is more pronounced in free hunting than in web-building species (Nyffeler et al, 2016; Hyodo et al., 2018; Michalko et al., 2021). These diverse feeding strategies make spiders an ideal model taxon to investigate their response to land-use change and the consequences for community functioning.

Natural variations in stable isotopes ($^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios) are widely used to characterize trophic niches of arthropods because they reflect the trophic level, basal resources and general trophic structure of communities (Potapov et al., 2019). The $^{15}N/^{14}N$ ratio reflects the tropic position of species as it increases in a rather uniform way per trophic level, while the $^{13}C/^{12}C$ ratio changes little with trophic levels, thereby reflecting the basal resource the species relies on (Potapov et al., 2019). Using the $^{13}C/^{12}C$ ratio of soil predators, it has been shown that their prey spectrum shifts from detritivore prey towards more herbivore prey with the conversion of rainforest into plantation systems (Klarner et al., 2017; Liebke et al., 2021). However, until today only few studies used stable isotopes for studying how land-use transformation affects trophic niches of animal consumers (Korotkevich et al., 2018; Krause et al., 2019; Potapov et al., 2020).

Here we focus on variations in the trophic structure of canopy spider communities with the transformation of tropical rainforest into “jungle rubber” (rubber agroforest) and into rubber and oil palm monoculture plantations by measuring bulk tissue $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios. In addition to the total community, we investigated in more detail four spider families, i.e. Salticidae, Clubionidae, Theridiidae and Thomisidae, which contribute most to the abundance, biomass and diversity of the spider communities in the studied land-use systems (Ramos et al., 2022). We hypothesized that (1) the community-level trophic niche of canopy spiders is narrower in more natural ecosystems such as rainforest and jungle rubber, than in disturbed systems such as rubber and oil palm plantations, and (2) functional diversity is higher in rainforest compared to rubber and oil plantations, and this is reflected by high isotopic richness, redundancy, evenness and divergence. Further, we hypothesized that (3) cursorial spiders, i.e. Clubionidae and Salticidae, occupy higher trophic positions compared to web building spiders, i.e. Theridiidae. Finally, we hypothesized that (4) predators rely more on herbivore prey in more intensively managed systems, such rubber and oil palm plantations, than in ore natural systems, such as rainforest and jungle rubber, due to higher abundance of herbivore pest species.

Materials & Methods

Sampling sites and collecting

The sampling was carried out in two landscapes of Jambi Province, Sumatra: Bukit Duabelas (S 01°59'41.4", E 102°45'08.5") and Harapan Rainforest (S 02°09'52.9", E 103°22'04.0"). In both landscapes large remnants of degraded secondary rainforest are present surrounded by agroforestry systems of jungle rubber, and monoculture plantations of rubber (*Hevea brasiliensis*) and oil palm (*Elais guinensis*) (Drescher et al., 2016). Jungle rubber represents a rubber agroforest system in which rubber plants are planted into degraded rainforest (Gouyon, de Foresta & Levang, 1993; Rembold et al., 2017).

Canopy spiders were sampled from three target canopies in eight research plots of 50 m × 50 m per land-use system, i.e. lowland rainforest, jungle rubber, rubber and oil palm; four replicate plots were located in each the Bukit Duabelas and Harapan landscape. In each plot three target canopies (subplots) were sampled by fogging. Using a Swingtec SN50 fogger, we applied 50 mL DECIS 25 (Bayer Crop Science; active ingredient deltamethrin, 25 g/L) dissolved in four liters petroleum white oil to each of the target canopies early in the morning to avoid turbulences during the day. Under each target canopy 16 1 m × 1 m collection traps were suspended from ropes attached to height-adjustable tent poles; each trap was fitted with a plastic bottle containing 100 mL of 96% EtOH. After sampling, the collected animals were stored at -20°C. More details on the study design and sampling are given in Drescher et al., (2016) and Ramos et al. (2022).

Morphospecies determination

First, spiders were separated from the samples and identified at family level based on general morphological features. Then, based on particular features we assigned all spiders to morphospecies. In some cases, the genus or species could be identified after closer inspection in particular of genital characters. The determination was based on monographs and checklists (Deeleman-Reinhold, 2001; Jocqué & Dippenaar-Schoeman, 2007; Murphy & Roberts, 2015; Ramos, 2020), the world spider catalog (https://wsc.nmbe.ch/) and the arachnological collections at the Zoological Museum in Hamburg. More details on the identification is given in Ramos et al., (2022) and in the pictorial database Ecotaxonomy (Potapov, Sandmann & Scheu, 2019; http://ecotaxonomy.org/taxa/424669)

Stable isotope analysis

The selection of morphospecies for stable isotope analysis was based on abundance. In each subplot, the families representing 80% of the total individuals were identified (Table S1). Of these families we analyzed all morphospecies present in the subplot. We assumed that 80% of the total individuals represent the local “functional” community (Krause et al., 2020). Across the four land-use systems sixteen spider families contributed 80% of the total individuals at plot level. In addition to the functional community, we analyzed the four most abundant families, i.e. Salticidae (most abundant family), Theridiidae (second most abundant family), Clubionidae (third most abundant family) and Thomisidae (fourth most abundant family)

(Ramos et al. 2022). For presenting the results we ordered these families according to their hunting mode starting with the cursorial Salticidae and Clubionidae, the sheet web building Theridiidae and finally the ambush hunting Thomisidae.

For stable isotope analysis spider morphospecies were grouped into small, i.e. 100 – 1000 µg, and large individuals, i.e. 1000 – 1300 µg. Depending on body size we pooled between one (e.g., in Sparassidae and Araneidae) to six individuals (e.g., in Oonopidae and Theridiosomatidae). In total, we measured 1073 individuals of 299 morphospecies of the total of 445 morphospecies recorded (Ramos et al. 2022). Before stable isotope analysis, samples were dried at 40°C for 24 h. Samples were analysed with a coupled system of an elemental analyser (NA 1500, Carlo Erba, Milan, Italy) and a mass spectrometer (MAT 251, Finnigan, Bremen, Germany). Stable isotope abundance (δX) was calculated using the delta notation with δX (‰) = $(R_{sample} - R_{standard})/R_{standard}$ x1000, where X represent the ratio of $^{15}N/^{14}N$ and $^{13}C/^{12}C$, respectively. Vienna PD Belemnite and ^{15}N atmospheric nitrogen were used as standard for ^{13}C and ^{15}N, respectively; Acetanilide was used for internal calibration.

For calibration $\delta^{13}C$ and $\delta^{15}N$ values of leaves from each subplot were used. Five leaves were collected from the centre of each core plot at head height. In rainforest, leaves from five different tree species were chosen. In jungle rubber, we collected leaves from two jungle rubber trees and from three different adjacent tree species. In rubber plantations, leaves were taken from the nearest individuals to the core plot centre. In oil palm plantations we collected 40 cm^2 of leaf material from five different palms close to the center of the core plot. Calibrated stable isotopes values of canopy spiders were obtained as the difference between plot-specific leave $\delta^{13}C$ and $\delta^{15}N$ values and plot-specific canopy spider $\delta^{13}C$ and $\delta^{15}N$ values, noted as $\Delta^{13}C$ and $\Delta^{15}N$, respectively. Calibrated $\Delta^{13}C$ and $\Delta^{15}N$ were used for statistical analysis.

Statistical analysis

Data analyses were done in R V. 4.2.0 (RStudio Team, 2022) with the R studio interface. The trophic structure of spider communities was evaluated based on "isotopic metrics"(Layman et al., 2007; Cucherousset & Villéger, 2015), which placed the morphospecies in a two dimensional space of $\delta^{13}C$ and $\delta^{15}N$ values. To ensure equal contribution of $\Delta^{13}C$ and $\Delta^{15}N$ values in the multidimensional metrics, the values were scaled between 0 to 1 (Cucherousset & Villéger, 2015). Prior to calculating multidimensional metrics we weighted all morphospecies in each coreplot according to their contribution to spider community biomass. Doing that we aimed at ensuring that the metrics reflect the functional relevance of the morphospecies (Cucherousset & Villéger, 2015). Spider biomass (BM) was calculated based on allometric regressions provided by Sohlström et al. (2018) as BM = 10^(-0.410 + 1.486*log10(length) +1.492*log10(width)), where length and width correspond to the measured the length and width of individual spiders (Table S4). Overall, we calculated thirteen isotopic metrics for each coreplot in the full community and, based on the presence of the individual families, in 31, 28, 21 and 17 plots in Salticidae, Theridiidae, Clubionidae and Thomisidae.

We calculated single dimensional metrics including minimum, maximum, range and biomass-weighted mean of $\Delta^{13}C$ and $\Delta^{15}N$ values. Minimum and maximum $\Delta^{13}C$ and $\Delta^{15}N$ values represent the extreme values of the morphospecies in each particular community. The range of $\Delta^{13}C$ and $\Delta^{15}N$ values was calculated as difference between maximum and minimum $\Delta^{13}C$ and $\Delta^{15}N$ values. Further, we calculated five multidimensional isotopic metrics weighted by biomass, i.e. diverge, dispersion, evenness, uniqueness and richness (Cucherousset & Villéger, 2015). Isotopic divergence (IDiv) represents the distance between all morphospecies and the centre of the convex hull area. IDiv tends to 0 when the spiders with extreme values (primary decomposer or top predators) are rare in the community and tends to 1 when extreme values dominate the community. Isotopic dispersion (IDis) combines the IDiv and the hull area, which provide a value of “scaled multidimensional variance”. IDis is equal to 0 when all morphospecies have the same stable isotope value and tends to 1 when most of the points (weights) are far from the centre of gravity. Isotopic evenness (IEve) quantifies the morphospecies distribution in the isotope space. IEve tends to 0 when most of the morphospecies are packed in a small region of the stable isotope space and tends to 1 when morphospecies are evenly distributed. Isotopic uniqueness (IUni) quantifies the closeness of stable isotope values of the morphospecies within the community. IUni equals 0 when there is no other morphospecies with same position in the stable isotope space and equals 1 when all morphospecies are isolated in stable isotope space. Isotopic richness (IRic) represents the isotopic space of all morphospecies scaled from 0 to 1. More comprehensive explanations on the multidimensional metrics are given in Mason et al. (2005), Villéger et al. (2008) and Cucherousset & Villéger (2015).

One-dimensional and multi-dimensional data were analyzed using the ANOVA function with land-use system and landscape as factors, however, we here focus on variations in isotopic metrics with land-use system rather than landscape, i.e. changes with the conversion of rainforest into jungle rubber, rubber and oil palm plantations. To explore differences among land-use systems means were compared using the post hoc HSD.test function. Graphics were generated with the ggplot2 package (Wickham, 2016). Each point in the graphics represent community values.

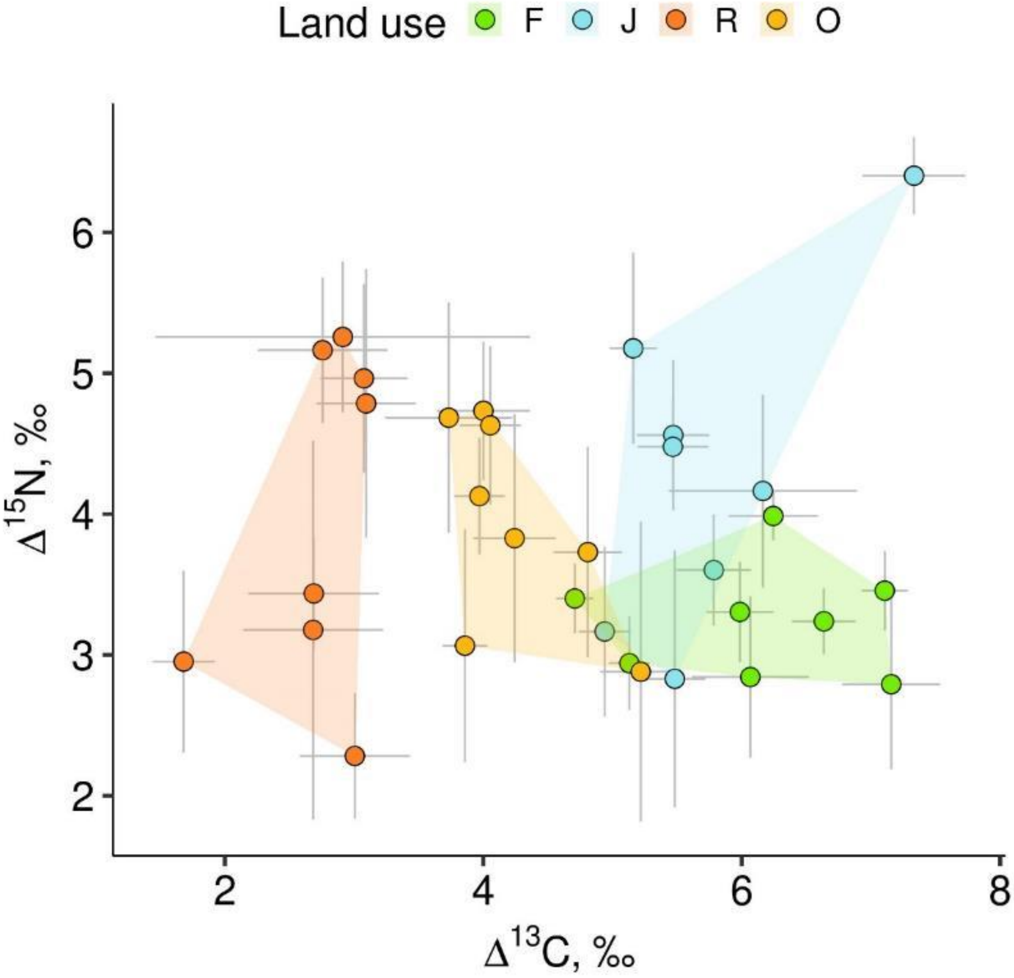

Figure 1. Weighted means of $\Delta^{13}C$ and $\Delta^{15}N$ values of the canopy spider communities in rainforest (green), jungle rubber (blue), rubber (red) and oil palm plantations (yellow) (eight replicates each). Each point represents a weighted mean (isotopic position) for one community. 32 communities were analysed.

RESULTS

Community level - One-dimensional metrics

The isotope position expressed as biomass weighted means of Δ^{13}C and Δ^{15}N values of (functional) canopy spider communities clearly separated rubber plantations on one side from rainforest and jungle rubber on the other, with spider communities of oil palm plantations positioned in between with little overlap with rainforest and jungle rubber (Fig. 1). This separation was mainly based on Δ^{13}C values, i.e. resource use, rather than Δ^{15}N values, i.e. trophic position. The biomass weighted Δ^{13}C and Δ^{15}N values of spider communities varied significantly between land-use systems, but not between landscapes (Fig. 2A, 3A, Table 1). Average Δ^{13}C values in rainforest and jungle rubber were similar and exceeded those in rubber by 3.04 and 2.77 ‰, and those in oil palm plantations by 1.70 and 1.47 ‰, respectively (Fig. 2A, Table S2).

On the contrary, average Δ^{15}N values were low in rainforest (3.28 ‰) and compared to rainforest 1.02 – 1.31 ‰ higher in jungle rubber, rubber and oil palm plantations (Fig. 3A, Table S2). Maximum biomass weighted Δ^{13}C and Δ^{15}N values varied significantly between land-use systems (Table 1). Δ^{13}C values were similarly high in rainforest and jungle rubber and on average exceeded those in rubber and oil palm plantations by 2.45 and 1.75 ‰, respectively (Fig. 2B, Table S2). By contrast, Δ^{15}N values were lowest in rainforest (4.44 ‰) and compared to rainforest 1.28 – 1.73 ‰ higher in jungle rubber, rubber and oil palm plantations (Fig. 3B, Table S2). Also, minimum Δ^{13}C but not minimum Δ^{15}N values varied significantly between land-use systems (Table 1). Minimum Δ^{13}C values were similarly high in rainforest and jungle rubber (4.8 ‰) and exceeded those in rubber and oil palm plantations by an average of 3.4 and 1.4 ‰, respectively (Fig. 2C, Table S2). Contrasting the previous metrics, the range of Δ^{13}C and Δ^{15}N values did not vary significantly between land-use systems (Fig. 2D, 3D, Table 1, S2). Across land use system the range of Δ^{13}C and Δ^{15}N values averaged 2.15 and 3.63 ‰, respectively

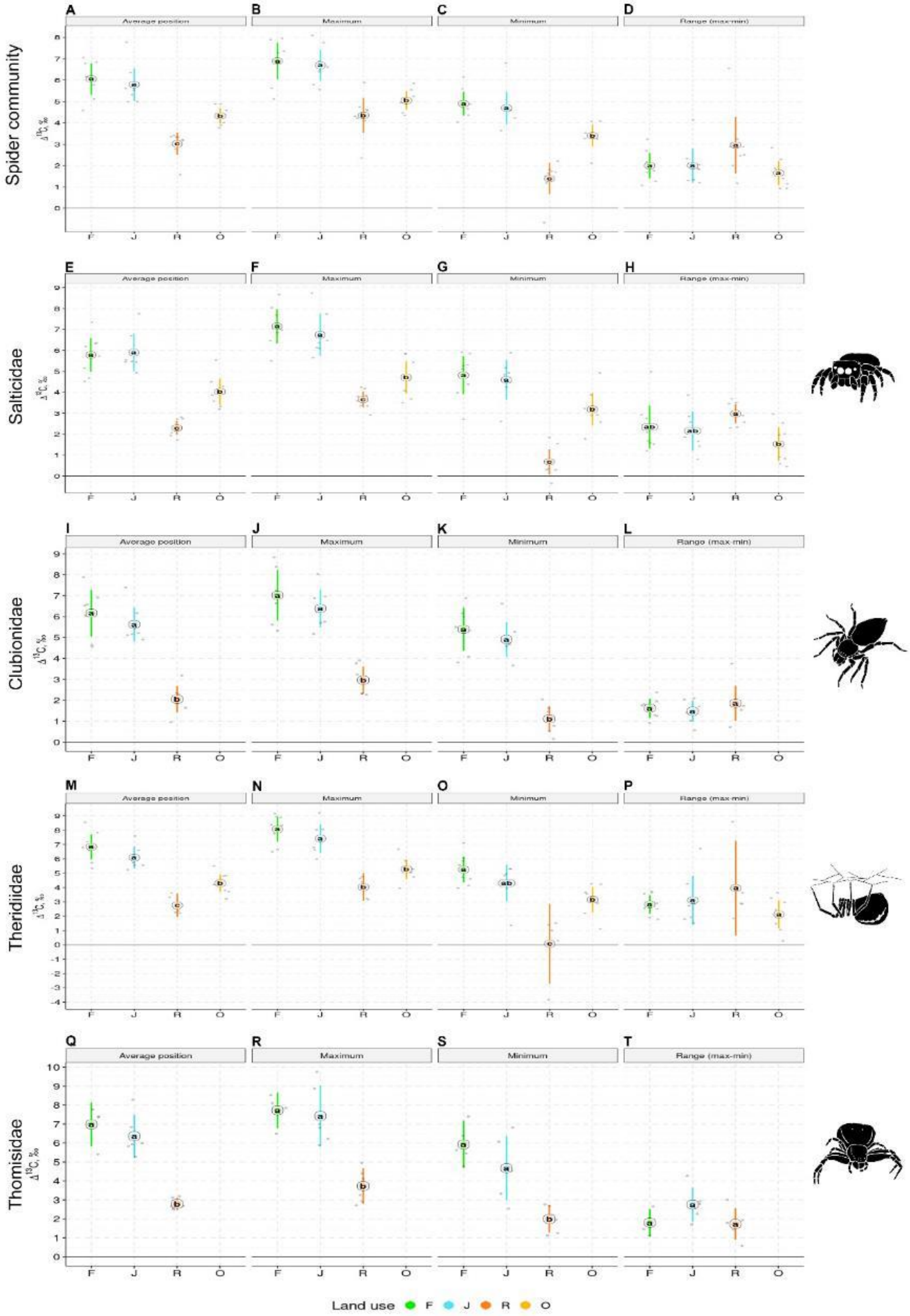

Figure 2. One-dimensional metrics for $\Delta^{13}C$ of canopy spider communities and families Salticidae, Clubionidae, Theridiidae and Thomisidae, in rainforest, jungle rubber, rubber and oil palm plantations. Average position (A,E,I,M,Q), maximum (B,F,J,N,R), minimum (C,G, K,O,S), and range between minimum and maximum (D,H,L,P,T); means (circles) and confidence intervals. Each point represents one community.

Community level - Multidimensional metrics

Isotopic richness, dispersion, evenness and uniqueness did not vary significantly between land-use systems; only isotopic divergence differed significantly (Fig. 4A-E, Tables 2, S3). Isotopic divergence was highest in jungle rubber and lowest in oil palm plantations with rainforest and rubber plantations being intermediate. None of the multidimensional metrics differed significantly between landscapes (Table 2). For multidimensional metrics at plot level see supplementary figure S1-5.

Family level - One-dimensional metrics

The stable isotope position expressed as means of Δ^{13}C and Δ^{15}N values of the four spider families followed a similar pattern than that of the total (functional) spider community. In each of the spider families rainforest and jungle rubber were clearly separated from rubber plantations. The cursorial Salticidae and sheet web building Theridiidae in oil palm plantations occupied an intermediate position; Clubionidae and Thomisidae were not recorded in oil palm plantations (Fig. 5 A-D). As in the total spider community, the separation of the four families was mainly based on Δ^{13}C rather than Δ^{15}N values. The biomass weighted Δ^{13}C values of the four families varied significantly between land-use systems, and between landscapes in Salticidae (Table 1). Biomass weighted Δ^{15}N did not vary significantly in any of the families, neither between land-use systems nor between landscapes and averaged 4.04 ‰ (Fig. 3E, I, M, Q, Tables 1, S2).

In Salticidae and Theridiidae, which were present in all four land-use systems, Δ^{13}C values in rainforest and jungle rubber exceeded those in rubber and oil palm plantations by on average 3.55 and 1.81‰, and 3.71 and 2.16 ‰, respectively (Fig. 2E, M, Table S2). In Clubionidae and Thomisidae, which were not present in oil palm plantations, Δ^{13}C values in rainforest and jungle rubber exceeded those in rubber by on average 3.85 and 3.86‰, respectively (Fig. 2I, Q). Maximum biomass weighted Δ^{13}C values of the four spider families varied significantly between land-use systems and also between landscapes with the exception of Clubionidae (Table 1, Fig. 2F, J, N, R). In each of the four families maximum Δ^{13}C values in rainforest and jungle rubber were similarly high and exceeded those in rubber and oil palm plantations; in Salticidae and Theridiidae by on average 3.29 and 2.24 ‰ and 3.71 and 2.47 ‰, respectively (Fig. 2F, N, Table S2). In Clubionidae and Thomisidae, which were no present in oil palm

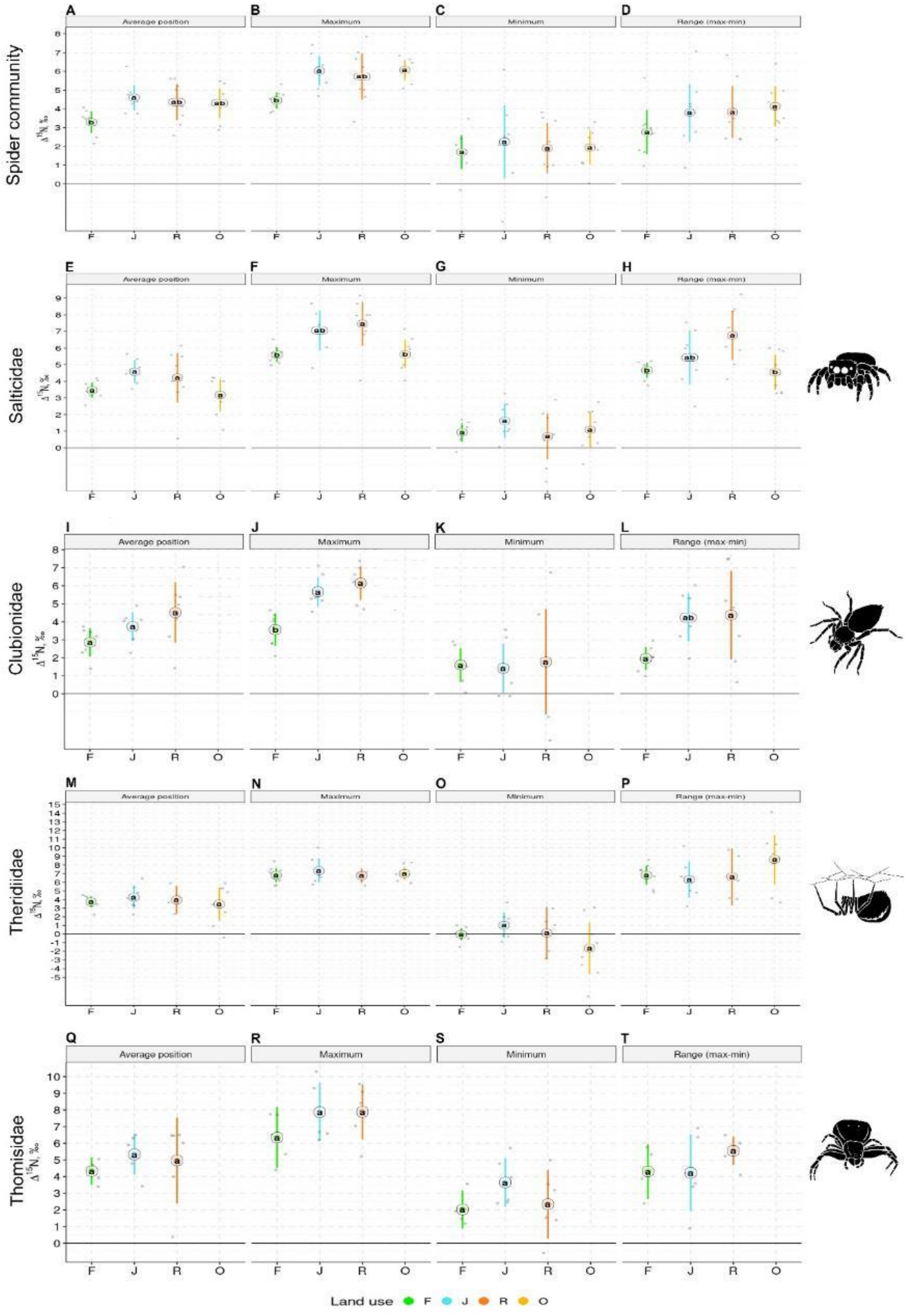

Figure 3. One-dimensional metrics for $\Delta^{15}N$ of canopy spider communities and families Salticidae, Clubionidae, Theridiidae and Thomisidae, in rainforest, jungle rubber, rubber and oil palm plantations. Average position (A,E,I,M,Q), maximum (B,F,J,N,R), minimum (C,G, K,O,S), and range between minimum and maximum (D,H,L,P,T); means (circles) and confidence intervals. Each point represents one community.

Plantations, $\Delta^{13}C$ values in rainforest and jungle rubber exceeded those in rubber on an average by 3.74 and 3.85 ‰, respectively (Fig. 2J, R). Maximum biomass weighted $\Delta^{15}N$ values only varied significantly in Salticidae and Clubionidae (Table 1, Fig. 3F, J). In Salticidae they were similarly low in rainforest and oil palm plantations (average 5.61 ‰) and 1.45 ‰ and 1.84 ‰ higher in jungle rubber and rubber plantations, respectively (Fig 3F, Table S2). In Clubionidae $\Delta^{15}N$ values were also low in rainforest (3.56 ‰.) and 2.1 and 2.58 ‰ higher in jungle rubber and rubber plantations, respectively (Fig. 3J, Table S2). In Theridiidae and Thomisidae maximum $\Delta^{15}N$ values across land-use systems averaged 6.98 and 7.36 ‰, respectively (Fig. 3N, R, and Table S2). Minimum biomass weighted $\Delta^{13}C$ values of the four spider families also varied significantly between land-use systems, but not between landscapes (Table 1). Generally, they followed a similar pattern than maximum $\Delta^{13}C$ values. In Salticidae and Theridiidae, $\Delta^{13}C$ values in rainforest and jungle rubber exceeded those in rubber and oil palm plantations on average by 4.02 and 1.52 ‰, and 4.71 and 1.63 ‰, respectively (Fig. 2G, O, Table S2). In Clubionidae and Thomisidae, which were not recorded in oil palm plantations, $\Delta^{13}C$ values in rainforest and jungle rubber exceeded those in rubber on average by 4.04 and 3.3 ‰ (Fig. 2K, S, Table S2). Minimum biomass weighted $\Delta^{15}N$ values neither varied significantly between land-use systems nor between landscapes (Table 1). Across land-use systems they averaged 1.08, 1.60, -0.13 and 2.67 ‰ for Salticidae, Clubionidae, Theridiidae and Thomisidae, respectively (Fig. 3 G, K, O, S, Table S2).

The biomass weighted range of $\Delta^{13}C$ values only varied significantly between land-use systems in Salticidae, and between landscapes in Salticidae, Theridiidae and Thomisidae (Table 1). In Salticidae values in rainforest and jungle rubber were similar (average 2.25 ‰) and exceeded those in oil palm plantations by 0.72‰, but were 0.73 ‰ lower than those in rubber plantations (Fig. 2H, Table S2). In Clubionidae, Theridiidae and Thomisidae the values averaged 1.65, 3.01 and 2.09 ‰ across the four land-use systems, respectively (Fig. 2L, P, T, Table S2). The biomass weighted range of $\Delta^{15}N$ values varied significantly between land-use systems in Salticidae and Clubionidae, and between landscapes in Thomisidae (Table 1). In Salticidae values were highest in rubber plantations (6.77 ‰) and exceeded those in jungle rubber, rainforest and oil palm plantations by 1.33, 2.10 and 2.22 ‰, respectively (Fig. 3H, Table S2).In Clubionidae, values in rainforest (1.96 ‰) were 2.28 and 2.41 ‰ lower than those in jungle rubber and rubber plantations, respectively (Fig. 3L, Table S2). In Theridiidae and Thomisidae the range of $\Delta^{15}N$ values across land-use systems averaged 7.11 and 4.69 ‰, respectively (Fig. 3P, T, and Table S2).

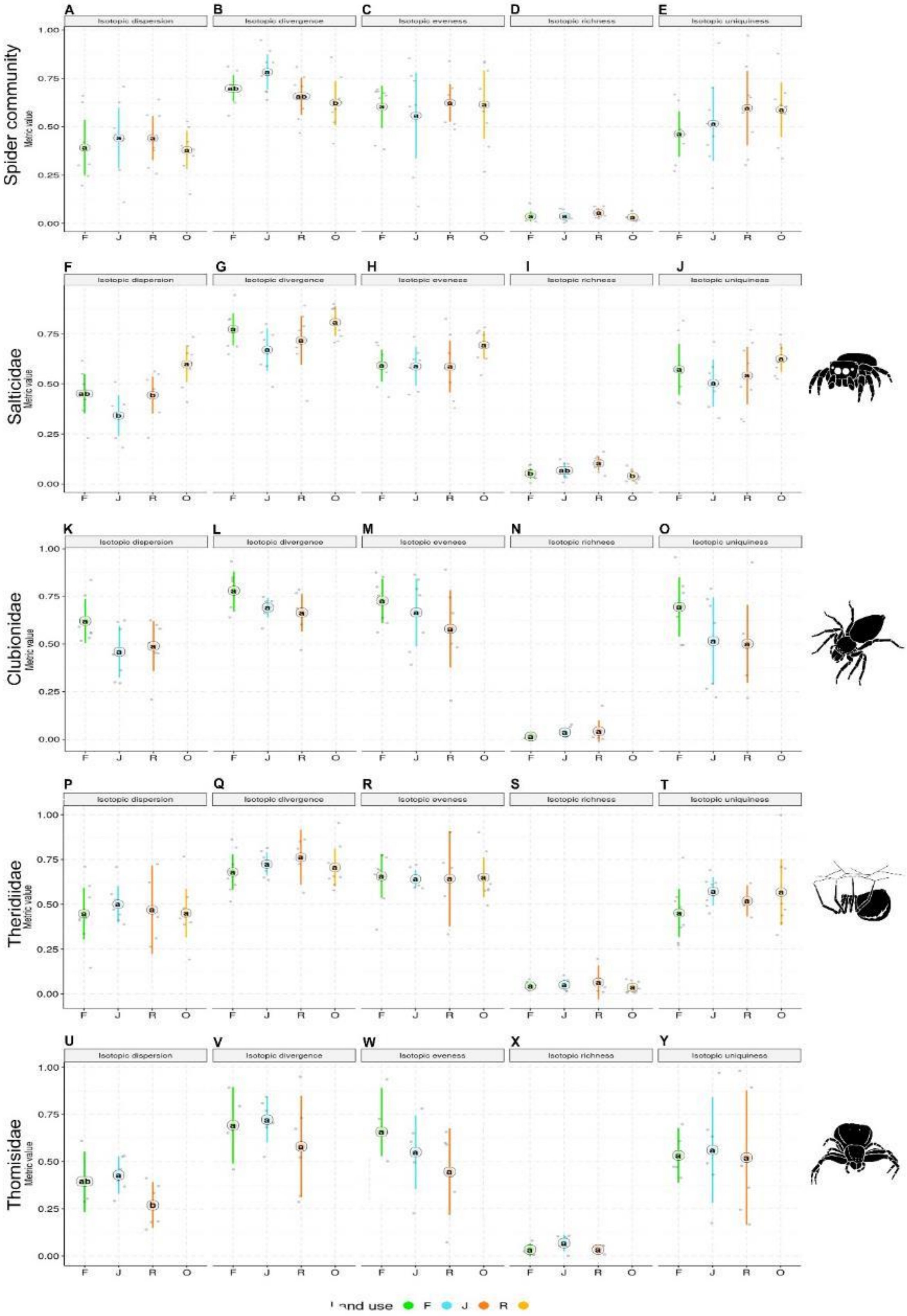

Figure 4. Multidimensional isotopic metrics of canopy spider communities of four land-use systems, rainforest, jungle rubber, rubber and oil palm plantations. Isotopic dispersion (A,F,K,P,U), isotopic divergence (B,G,L,Q,V), isotopic evenness (C,H,M,R,W), Isotopic richness (D,I,N,S,X) and isotopic uniqueness (E,J,O,T,Y); means (circles) and confidence intervals. Each point represents one community.

Family level - Multidimensional metrics

Overall, most of the multidimensional metrics of the four spider families neither varied significantly between land-use systems nor between landscapes (Table 2, Fig. 4F - Y). Only isotopic dispersion varied significantly between land-use systems in Salticidae and Thomisidae (Fig. 4 F, U), and isotopic richness in Salticidae (Fig. 4I). Isotopic dispersion was highest in oil palm plantations, lowest in jungle rubber and rubber plantations and intermediate in rainforest (Figs 4F, S2, Table S3). In Thomisidae values in rainforest and jungle rubber were similar and exceeded those in rubber plantations (Fig. 4U). Isotopic richness values were generally low, but in Salticidae values in rubber plantations exceeded those in the other three land-use systems (Fig. 4I, Tables 2, S3). For details on multidimensional metrics at plot level see supplementary figure 4.

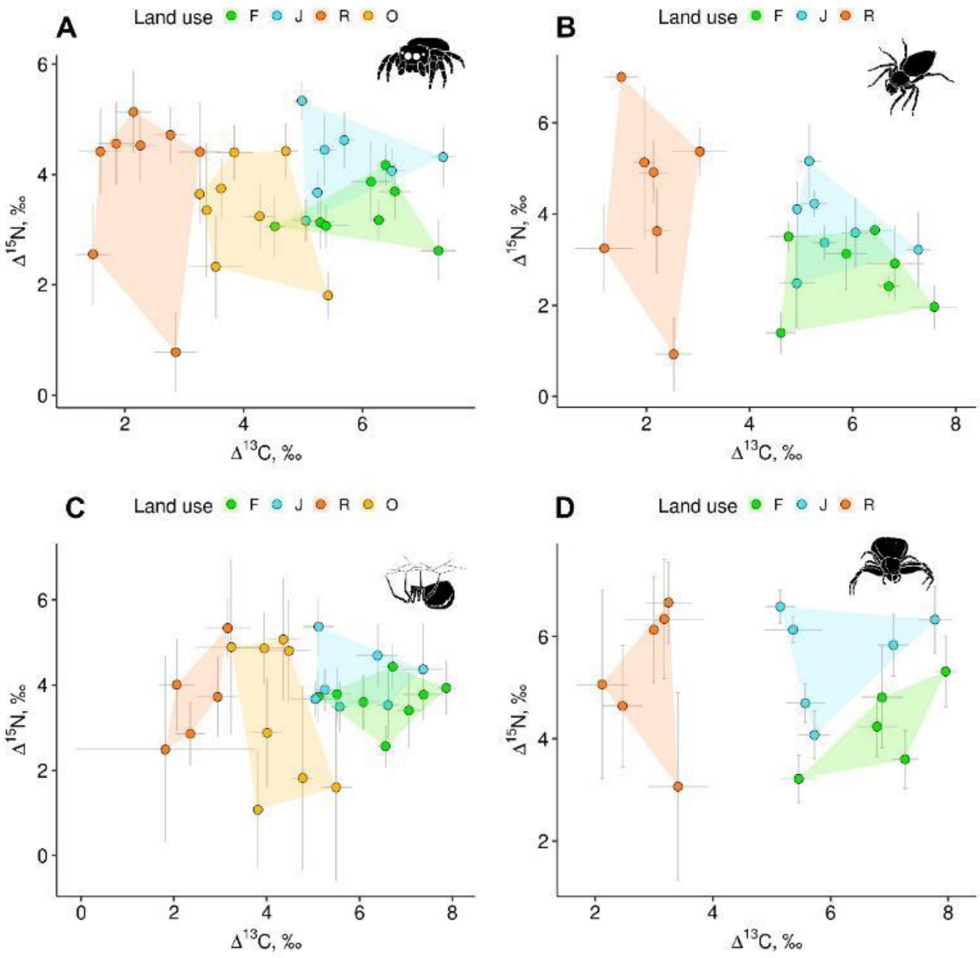

Figure 5. Weighted means of Δ^{13}C and Δ^{15}N values of the canopy spider communities in rainforest (green), jungle rubber (blue), rubber (red) and oil palm plantations (yellow) (eight replicates each). Each point represents a weighted mean (isotopic position) for one community. 32 communities were analysed.

Discussion

We investigated the effects of the transformation of rainforest into plantation systems on the trophic structure of canopy spiders as model taxon of canopy predator arthropods. Our results provided new insights into how spider communities in the tropics respond to land-use changes (Hyodo et al., 2010; Klarner et al., 2017; Potapov et al., 2020). Our approach was based on the morphospecies accounting for 80% of total spiders individuals in each land-use system, thus likely representing in large the response of the ('functional') spider community to land-use changes. The results partially support our hypotheses indicating that (1) canopy spider communities differ most between more natural systems and monoculture plantations, (2) functional diversity generally differs little between land-use systems, except for isotopic divergence. However, in contrast to our hypothesis (3) $^{15}N/^{14}N$ ratios indicated that cursorial spiders did not uniformly occupy a higher trophic position than web-building species. Supporting hypothesis (4) $^{13}C/^{12}C$ ratios indicated that total canopy spider communities as well as individual spider families in plantations rely more on herbivore prey than those in more natural ecosystems such as rainforest and jungle rubber.

Community level trophic niches across land-use systems

Generally, the range (maximum - minimum) in trophic positions ($\Delta^{15}N$ values) and the use of basal resources ($\Delta^{13}C$ values) of spider communities did not differ significantly between land-use systems. However, the range in trophic positions in rainforest (2.76 ‰) in fact was narrower than in the other three land-use systems (averaging 3.92 ‰). Further, in Clubionidae the range in trophic positions was particularly low in rainforest (1.96 ‰) and differed from those in jungle rubber and rubber by >2‰. Also, in Salticidae the range in trophic positions in rainforest was lower than in jungle rubber and rubber, but in oil palm it was similarly low than in rainforest. By contrast, the range in trophic positions differed little between land-use system in Theridiidae and Thomisidae indicating that they feed on a similar prey spectrum irrespective of land use. Overall, although the results do not uniformly support our hypothesis 1, they in fact suggest that at least in certain families of spiders the range in trophic niches is narrower in rainforest than in plantation systems.

Table 1. ANOVA table of F- and p-values on the effect of land-use system (rainforest, jungle rubber, rubber plantation, oil pal plantation) and landscape (Bukit Duabelas, Harapan) on one dimensional metrics for total spiders, Salticidae, Clubionidae, Theridiidae and Thomisidae. Significant effects are given in bold.

			Total community			Salticidae			Clubionidae			Theridiidae			Thomisidae		
System	Metric	variable	df	F	p	df	F	p	df	F	P	df	F	p	df	F	p
Land-use	Average	$\Delta^{13}C$	3	**30.14**	**<0.01**	3	**45.15**	**<0.01**	2	**40.73**	**<0.01**	3	**30.59**	**<0.01**	2	**52.36**	**<0.01**
Landscape	Average	$\Delta^{13}C$	1	1.83	0.19	1	**8.82**	**<0.05**	1	1.82	0.19	1	1.85	0.19	1	4.11	0.06
Land-use	Average	$\Delta^{15}N$	3	**3.22**	**<0.05**	3	2.37	0.09	2	3.11	0.07	3	0.32	0.81	2	0.47	0.63
Landscape	Average	$\Delta^{15}N$	1	0.75	0.39	1	1.00	0.33	1	1.44	0.25	1	0.49	0.49	1	0.02	0.88
Land-use	Maximum	$\Delta^{13}C$	3	**16.61**	**<0.01**	3	**42.12**	**<0.01**	2	**33.53**	**<0.01**	3	**32.36**	**<0.01**	2	**31.48**	**<0.01**
Landscape	Maximum	$\Delta^{13}C$	1	1.36	0.25	1	**15.60**	**<0.01**	1	1.90	0.19	1	**7.52**	**<0.05**	1	**6.89**	**<0.05**
Land-use	Maximum	$\Delta^{15}N$	3	**4.96**	**<0.05**	3	**5.23**	**<0.05**	2	**13.73**	**<0.01**	3	0.41	0.74	2	1.63	0.23
Landscape	Maximum	$\Delta^{15}N$	1	0.52	0.48	1	0.05	0.83	1	0.18	0.67	1	1.08	0.31	1	0.62	0.44
Land-use	Minimum	$\Delta^{13}C$	3	**33.66**	**<0.01**	3	**31.69**	**<0.01**	2	**45.86**	**<0.01**	3	**14.55**	**<0.01**	2	**16.04**	**<0.01**
Landscape	Minimum	$\Delta^{13}C$	1	0.49	0.49	1	0.91	0.35	1	0.64	0.43	1	0.39	0.54	1	0.74	0.41
Land-use	Minimum	$\Delta^{15}N$	3	0.15	0.93	3	0.78	0.52	2	0.06	0.95	3	1.75	0.19	2	2.02	0.17
Landscape	Minimum	$\Delta^{15}N$	1	0.04	0.84	1	1.79	0.19	1	3.26	0.09	1	1.80	0.19	1	2.42	0.14
Land-use	Range	$\Delta^{13}C$	3	2.44	0.09	3	**3.43**	**<0.05**	2	0.56	0.58	3	1.59	0.22	2	4.18	0.06
Landscape	Range	$\Delta^{13}C$	1	2.33	0.14	1	**4.47**	**<0.05**	1	0.88	0.36	1	**4.49**	**0.05**	1	**4.79**	**0.05**
Land-use	Range	$\Delta^{15}N$	3	1.14	0.35	3	**4.29**	**<0.05**	2	**4.63**	**<0.05**	3	1.40	0.27	2	1.88	0.19
Landscape	Range	$\Delta^{15}N$	1	0.05	0.82	1	1.83	0.19	1	3.55	0.08	1	2.99	0.10	1	**7.27**	**<0.05**

Variations in the range of trophic niches between habitats have been reported before. Dehart et al. (2017) found the trophic niches of cursorial spiders in forests and old fields to be wider than in web-building spiders. Moreover, Sanders et al. (2015) found free hunting Salticidae, but also web-building Araneidae and Theridiidae, to have wider trophic niches than Agelenidae along forest edges. Differences in trophic ranges of spider families between land-use systems likely reflect differences in community composition as trophic niches of species within families may also differ due to different hunting modes or by colonizing specific microhabitats, where only a limited spectrum of prey is available (McNabb et al., 2001; Cardoso et al., 2011; Pitilin et al., 2020). In particular the latter may explain the narrow trophic range of Clubionidae and Salticidae in rainforest. On the contrary, the similar trophic range in Theridiidae and Thomisidae across land-use systems indicate that they feed on a similar prey spectrum across the different land-use systems studied.

Interestingly, the lower range in trophic positions in Clubionidae and Salticidae (as well as spiders in total) in rainforest was uniformly due to lower maximum Δ^{15}N values, whereas minimum Δ^{15}N values generally did not differ significantly among land-use systems. The lower maxima also were reflected in a uniformly lower average trophic position of the spider community in rainforest than in the other three land-use systems. These results indicate that in natural ecosystems such as rainforest at least certain spider families rely less on intra-guild predation than in more disturbed systems. Feeding consistently on low trophic level prey in rainforest may reflect that food webs in more natural habitats tend to be more bottom-heavy as also has been shown for the canopy food web at our study sites (M. Pollierer & J. Drescher, unpubl. data). High incidence of intra-guild predation in disturbed ecosystems such as agricultural fields also has been observed by Hambäck et al. (2021). By contrast, using stable isotope analysis, Sanders et al. (2015) demonstrated that spiders along forest edges predominantly dwell on prey of medium to low trophic positions such as springtails, cockroaches and flies. Low trophic positions of decomposers and herbivores in rainforest at our study sites (Zhou et al. 2022) may also have contributed to the low maximum Δ^{15}N values in Clubionidae and Salticidae.

In respect to Δ^{13}C values the spider community and the four spider families showed a very similar pattern across the land-use systems studied indicating consistency in in the use of basal resources. As in the spider community in total, the range in Δ^{13}C values did not differ with land-use in each of the spider families except for Salticidae, which had a slightly lower range

Table 2. ANOVA table of F- and p-values on the effect of land-use system (rainforest, jungle rubber, rubber plantation, oil pal plantation) and landscape (Bukit Duabelas, Harapan) on multidimensional metrics for total spiders, Salticidae, Clubionidae, Theridiidae and Thomisidae. Significant effects are given in bold.

		Total community			Salticidae			Clubionidae			Theridiidae			Thomisidae		
System	Metric	df	F	*p*	df	F	*p*	df	F	*p*	df	F	*p*	df	F	*p*
Land-use	Isotopic richness	3	1.20	0.33	3	**4.78**	**<0.05**	2	1.11	0.35	3	0.67	0.58	2	2.98	0.09
Landscape	Isotopic richness	1	1.14	0.29	1	4.26	0.06	1	3.69	0.07	1	8.18	0.06	1	4.52	0.06
Land-use	Isotopic divergence	3	**3.06**	**0.05**	3	2.32	0.10	2	2.93	0.08	3	0.58	0.64	2	0.87	0.44
Landscape	Isotopic divergence	1	1.83	0.19	1	2.59	0.12	1	1.33	0.26	1	0.00	1.00	1	0.00	0.95
Land-use	Isotopic dispersion	3	0.37	0.78	3	**6.73**	**<0.01**	2	2.62	0.10	3	0.16	0.93	2	**4.27**	**<0.05**
Landscape	Isotopic dispersion	1	1.71	0.20	1	0.58	0.45	1	0.22	0.64	1	0.09	0.77	1	5.38	0.06
Land-use	Isotopic evenness	3	0.18	0.91	3	1.67	0.20	2	1.14	0.34	3	0.02	1.00	2	2.02	0.17
Landscape	Isotopic evenness	1	0.32	0.58	1	0.73	0.40	1	0.93	0.35	1	0.15	0.70	1	5.27	0.06
Land-use	Isotopic uniqueness	3	0.84	0.48	3	1.05	0.39	2	1.79	0.20	3	0.97	0.42	2	0.04	0.96
Landscape	Isotopic uniqueness	1	1.30	0.27	1	0.62	0.44	1	1.34	0.26	1	0.09	0.76	1	1.80	0.20

in oil palm plantations than in the other three land-use systems. Interestingly, average position as well as maxima and minima $\Delta^{13}C$ values showed a remarkably similar pattern across the land-use systems being higher in the more natural systems of rainforest and jungle rubber than in rubber and oil palm plantations. With average $\Delta^{13}C$ values of ca. 6 ‰, spiders in rainforest and jungle rubber were remarkably enriched in ^{13}C. By contrast, in oil palm, but in particular in rubber the enrichment was much less pronounced. This pattern of strong enrichment in ^{13}C in the more natural and less enrichment in plantation systems was true for virtually all taxa of the canopy food web (M. Pollierer & J. Drescher, unpubl. data; see below).

One limitation when working on spider communities of the tropics is that the trophic niche of most of the species is poorly studied. Knowing that the trophic position of spiders may not only vary among ecosystems and habitats, as well as spider body size and age (Pekár et al., 2012; Sanders et al., 2015) differences in trophic niches at the level of family certainly at least in part are due to changes in community composition between land-use systems. Ramos et al. (2022) confirmed that the community spider composition varied significantly between rainforest and monoculture plantations in Indonesia. They reported that 14 families which were present in rainforest were absent in monoculture plantations including Anapidae, Ctenidae and Deinopidae.

Community functional diversity across land-use systems

Overall, the multidimensional metrics of spiders differed little between the four land-use systems studied. At community level, only isotopic divergence differed between land-use systems and at family level it was mainly isotopic dispersion. This suggests that, from a functional perspective, spider communities in total as well as spider families are similar across the four land-use systems, with little shifts in community trophic niches due to land-use intensification, arguing against our second hypothesis. This may generally reflect that spiders are generalist predators, with the capability to adapt to new environmental conditions and prey availability (Wise, 1993; Nelson & Jackson, 2011; Leroy et al., 2013). The differences in isotopic divergence at community level, with somewhat higher values in the more natural systems of rainforest and jungle rubber than the intensively used systems of rubber and oil palm plantations, indicates that in the more natural systems species with extreme niches / stable isotopes reach higher dominance, which may be due to spiders with specialist hunting strategies being more abundant supporting our hypothesis 2. Overall, however, isotopic divergence scored minimum values of 0.62 indicating that the trophic spectrum of spider communities is balanced (Cucherousset & Villéger, 2015). In addition to isotopic divergence at community level, isotopic dispersion varied significantly among land-use systems in Salticidae and Thomisidae, being higher in oil palm plantations than in the three other land-use systems in Salticidae, but higher in rainforest and jungle rubber than in rubber plantations in Thomisidae. These findings suggest that trophic positions of Salticidae are least coherent in oil palm plantations, whereas in Thomisidae they were least coherent in rainforest and jungle rubber (Cucherousset & Villéger, 2015). Potentially, their contrasting response to land-use changes reflects niche partitioning as observed before in cursorial spiders (Balfour et al., 2003; Michalko et al., 2021). Supporting this conclusion, Saqib et al. (2021) found that, although Salticidae and Thomisidae may share a similar prey spectrum in agricultural systems, the relative importance of individual prey taxa may differ between these two families.

Studying ground-dwelling spiders at our study sites Potapov et al. (2020) found density, richness, predation and functional diversity to be reduced by 57 – 98% in plantations compared to rainforest. In contrast to our study, which was exclusively based on variations in trophic ecology as indicated by stable isotope values, Potapov et al. (2020) included a wider range of functional traits, such as hunting strategy, body coloration, habitat, desiccation resistance and body mass. Moreover, focussing on Salticidae Junggebauer et al. (2021) found richness and phylogenetic diversity to decline with the transformation of rainforest to monoculture plantations of rubber and oil palm. By contrast, Benítez-Malvido et al. (2020) found functional diversity to be increased in forest fragments compared to continuous forest although species diversity declined. Further, Joseph et al. (2018) found that even when anthropogenic intervention does not affect species diversity, it may still be associated by a loss in functionality. Overall, our results therefore at least in part contradict previous studies. The different results might be due to different definitions of functional communities of spiders and potentially reflect that the focus on trophic ecology may be too narrow to draw general conclusions on how land-use changes affect the functioning of spider communities.

Trophic positions in free-hunting and web building spiders

On average, the trophic position of the two free-hunting families Salticidae and Clubionidae were very similar with average $\Delta^{15}N$ values of 3.86 and 3.70 ‰, respectively, but Theridiidae also occupied virtually the same trophic position with average $\Delta^{15}N$ values of 3.86 ‰, arguing against our hypothesis 3. Contrasting the average trophic position, maximum $\Delta^{15}N$ values in Salticidae and Clubionidae (as well as in total spider community, see above) varied with land use and generally reached higher values in plantations than in rainforest (with the exception of Salticidae in oil palm plantations). A similar pattern existed in the ambush hunting family Thomisidae, although this was not significant, but not in the web-building family Theridiidae. Conform to our hypothesis 3 this may have been due to intra-guild predation being more widespread in free hunting than web-building spiders, but only in plantation systems as suggested earlier (Hodge, 1999; Petráková et al., 2016). However, the average enrichment in ^{15}N in spiders in total as well as in each of the four spider families (compared to leaves) was unexpectedly low and typically ranged between 3 - 5 ‰.

Considering that spiders live as predators of herbivores we expected them to be enriched by at least 6.8 ‰ assuming an enrichment of 3.4 ‰ per trophic level (Post 2002, Potapov et al. 2019). Assuming somewhat lower trophic level enrichment as reported by Vanderklift & Ponsard (2003) one still would have expected spiders to be enriched by at least 5.7 ‰. Notably, even maximum Δ^{15}N values were rather low averaging 5.9 ‰ in plantations and 5.6 ‰ for spiders in total, arguing against intra-guild predation playing a major role in tropical canopy spider communities. However, maximum Δ^{15}N values in Salticidae and Thomisidae in jungle rubber and rubber plantations ranged between 7 and 8 ‰ indicating that in these spiders intra-guild predation in rubber plantations is more important. Mezőfi et al. (2020) investigated Clubionidae, Salticidae and Thomisidae in agroecosystems and also found indications for high levels of intra-guild predation, although the spiders of each of these families generally preferentially fed on herbivore prey. Petráková et al. (2016) investigated the width of trophic niches and prey preferences of the cursorial spider families Anyphaenidae and Philodromidae and also found evidence for intra-guild predation although being generally of little importance. Notably, minimum Δ^{15}N values also were very low in particular in Theridiidae, with average values across land use systems of ca. 0 ‰, as well as in Salticidae with average values of ca. 1 ‰. This suggests that across land-use systems certain species in these families feed on prey of very low Δ^{15}N values, i.e. considerably below the Δ^{15}N values of plants. These prey taxa likely include in particular Collembola and / or Psocoptera, which presumably predominantly feed on algae and lichens and therefore are characterized by Δ^{15}N values considerably below 0 ‰ across the studied land-use systems (M. Pollierer and J. Drescher, unpubl. data). Similar to our results in the canopy of rainforest trees, Zhou et al. (2022) also found trophic positions in spiders as well as other predators including Chilopoda to change little with the transformation of rainforests into plantations Similarly, Liebke et al. (2021) found the trophic position in Pseudoscorpionida to be similar across land-use systems at our study sites.

Changes in spider prey due to land-use change

We assumed that $\Delta^{13}C$ values, i.e. the shift in $\delta^{13}C$ values between leaves and spiders reflect their relative dependence on herbivore vs detritivore prey. It has been documented widely that the detritivore food web is generally enriched in ^{13}C and the increase in $\delta^{13}C$ values in consumers compared to litter as basal resource has been termed “detrital shift” (Potapov et al. (2019). By contrast, in herbivores $\delta^{13}C$ values typically are little enriched and this also applies to predators feeding on herbivores (Post, 2002; Potapov et al., 2019). Surprisingly, ^{13}C values of spiders in total as well as in virtually all spider families in each of the land-use systems, with the exception of rubber, were strongly enriched. Notably, in spiders in total as well as in each of the four spider families this enrichment was much more pronounced in rainforest and jungle rubber, as more natural land-use systems, than in monoculture plantations of rubber and oil palm. Conform to our hypothesis 4 this difference in enrichment indicates that the transformation of rainforest into monocultures plantations is associated with a shift towards herbivore prey in spiders. Lower enrichment in ^{13}C in spiders in monoculture plantations than in rainforest and jungle rubber resembles that in spiders and other predators in the soil animal food web in the studied land-use systems (Klarner et al., 2017; Liebke et al., 2021; Zhou et al., 2022).

However, interpreting the lower enrichment in ^{13}C values in the canopy food web is less straightforward than in the soil animal food web. Soil animals are generally enriched in ^{13}C (see above) and lower enrichment therefore can be reliably interpreted as shift towards herbivore prey. Surprisingly, spiders in the canopy of rainforest and jungle rubber showed a similar enrichment in ^{13}C as spiders in the soil animal food web (on average by ca. 6 ‰; see above). This strong enrichment contrasts the assumption that species in the herbivore food web are little enriched in ^{13}C compared to plants. Interestingly, not only spiders but also other predators as well as herbivores in the canopy of rainforest and jungle rubber at our study sites are strongly enriched in ^{13}C (M. Pollierer and J. Drescher, unpubl. data). Two processes might have contributed to this strong enrichment. (1) We calibrated spider $\delta^{13}C$ values to $\delta^{13}C$ values of leaves, which we picked at a high of about 2 m and it has been demonstrated that $\delta^{13}C$ values of leaves in the lower canopy of trees might be less enriched than in those higher in the canopy ("canopy effect"; van der Merwe & Medina, 1991). However, this difference is unlikely to explain the strong enrichment of spiders (and other canopy arthropods) compared to leaves. (2) A second factor that might have contributed to the strong enrichment in $\delta^{13}C$ is the selective use of certain compounds of canopy leaves by herbivores. In particular lignin and waxes are depleted in ^{13}C (Pollierer et al., 2009; Bufacchi et al., 2020) and selective feeding on other plant leaf compounds, such as liquid substances and cellulose, may result in herbivores being enriched in ^{13}C compared to average leave δ^{13}C values. This may be particularly relevant in tropical rainforests as leaves of tropical trees typically are richer in lignin and waxes than leaves of deciduous trees allowing them to stay active for years and resist attack by pathogens and herbivores. Importantly, if it is true that similar to the food web in soil also canopy spider communities shift towards more herbivore prey in plantations this may contribute to pronounced control of herbivore prey in plantations despite spider density, biomass and diversity is strongly reduced compared to rainforest (Ramos et al. 2021).

Conclusions

Overall, the results indicate that the transformation of rainforest into plantation systems not only affects canopy spider density and community composition, but also their trophic structure and thereby their functioning in the canopy food web. As hypothesized, certain spider families have narrower trophic niches in rainforest than in monoculture plantations of rubber and oil palm, although the trophic range of total spider communities was similar across land-use systems. Shifts in trophic ranges with land-use change were mainly due to lower maximum trophic positions in rainforest compared to plantations indicating that intra-guild predation is particularly low in rainforest spider communities. Very low δ^{13}C values in particular in Theridiidae and Salticidae indicated that their prey spectrum includes species feeding on other resources than leaves of trees, presumably predominantly Collembola and Psocoptera feeding on algae and / or lichens. Strong increase in ^{13}C values in particular in the more natural ecosystems of rainforest and jungle rubber supports this conclusion. Lower shift in ^{13}C values in monoculture plantations, in particular in rubber, may indicate a shift towards more herbivore prey in plantations (compared to more detritivore prey such as Collembola and Psocoptera in rainforest and jungle rubber). Overall, similar trophic ranges and multidimensional trophic metrics of canopy spiders across the studied land-use systems including spider families of different hunting occupy reflect the consistent functioning of canopy spider communities as generalist predators. However, the results also highlight that the four studied spider families do not respond uniformly to the transformation of rainforest into plantations, but at least in part their shift in trophic positions and use of basal resources differs suggesting that at least in part they complement each other in regulating prey populations.

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Appendix Chapter 3

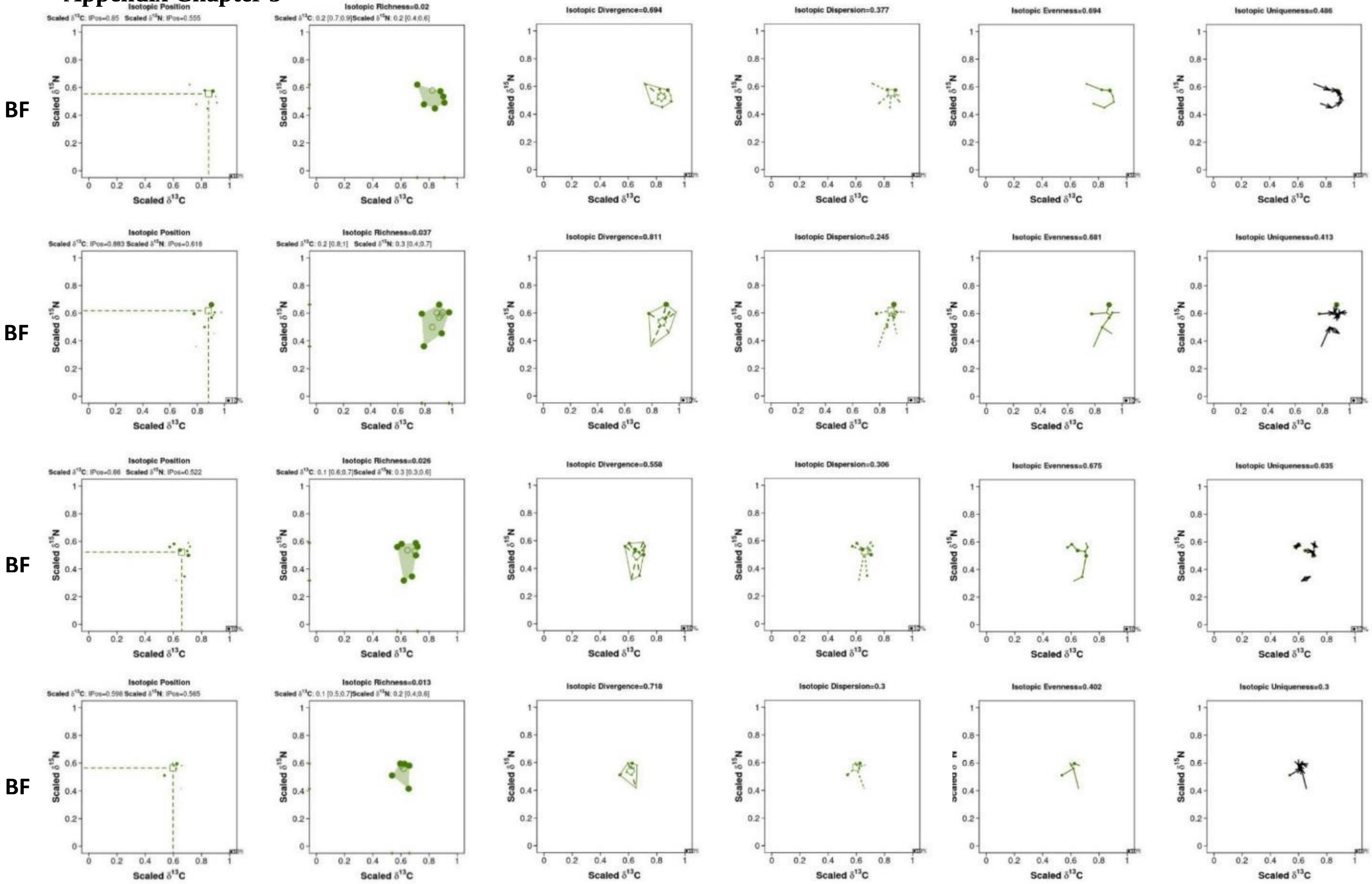


Figure S1. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider canopy communities in the four replicates of rainforest in Bukit Duabelas National Park landscape (BF 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods.

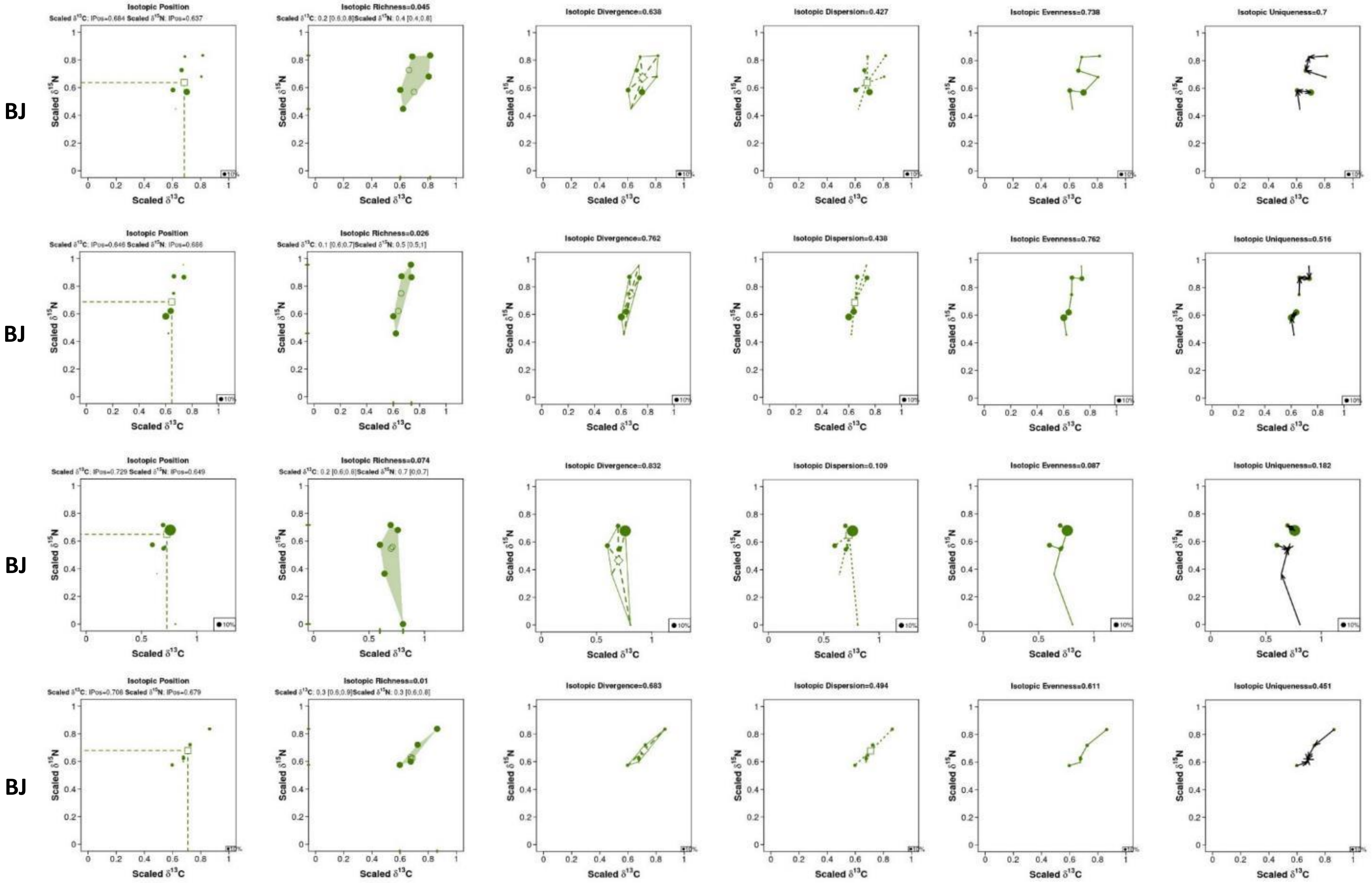
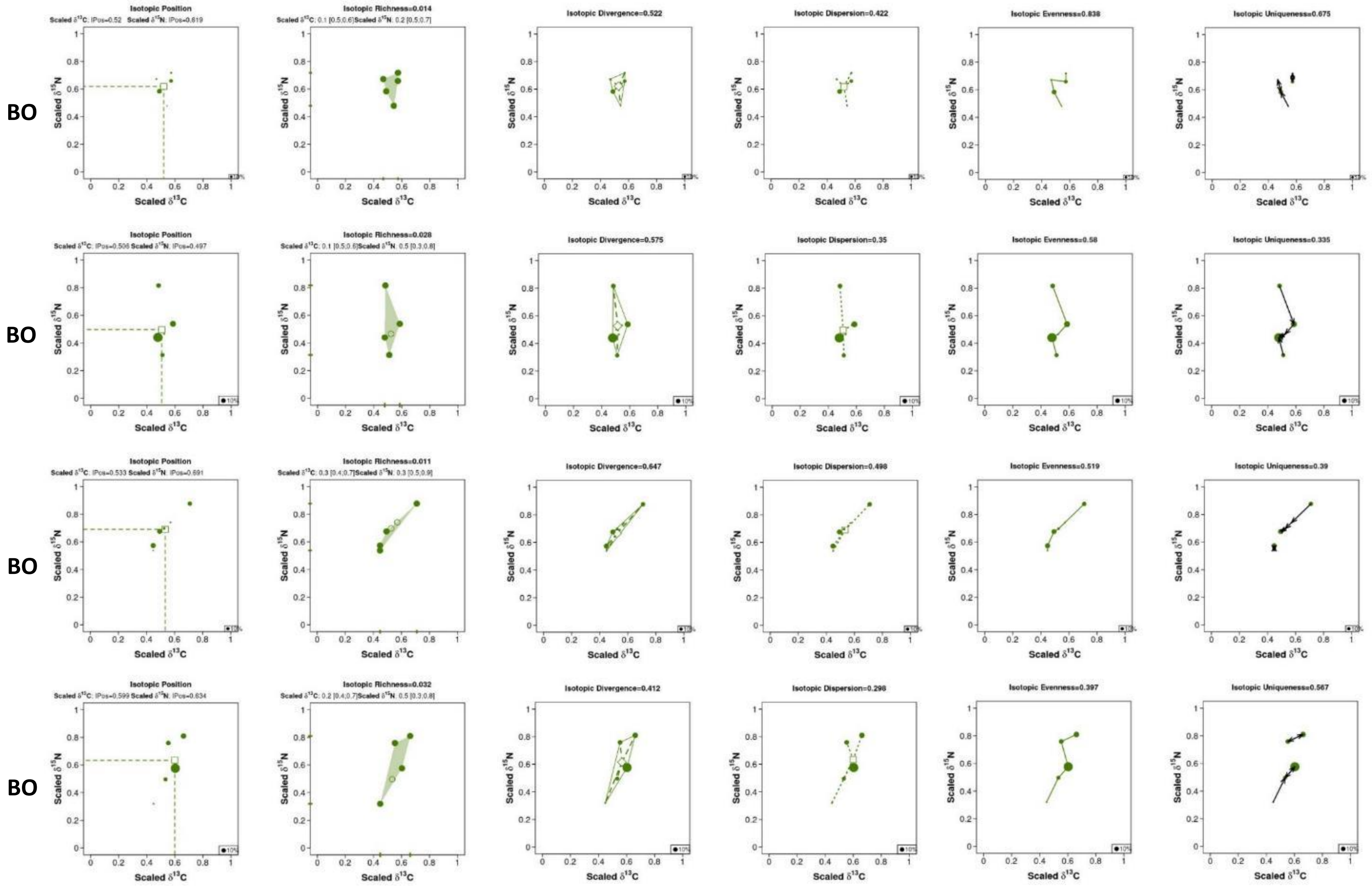


Figure S1. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider canopy communities in the four replicates of jungle rubber in Bukit Duabelas National Park landscape (BFJ3 - 6). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods.



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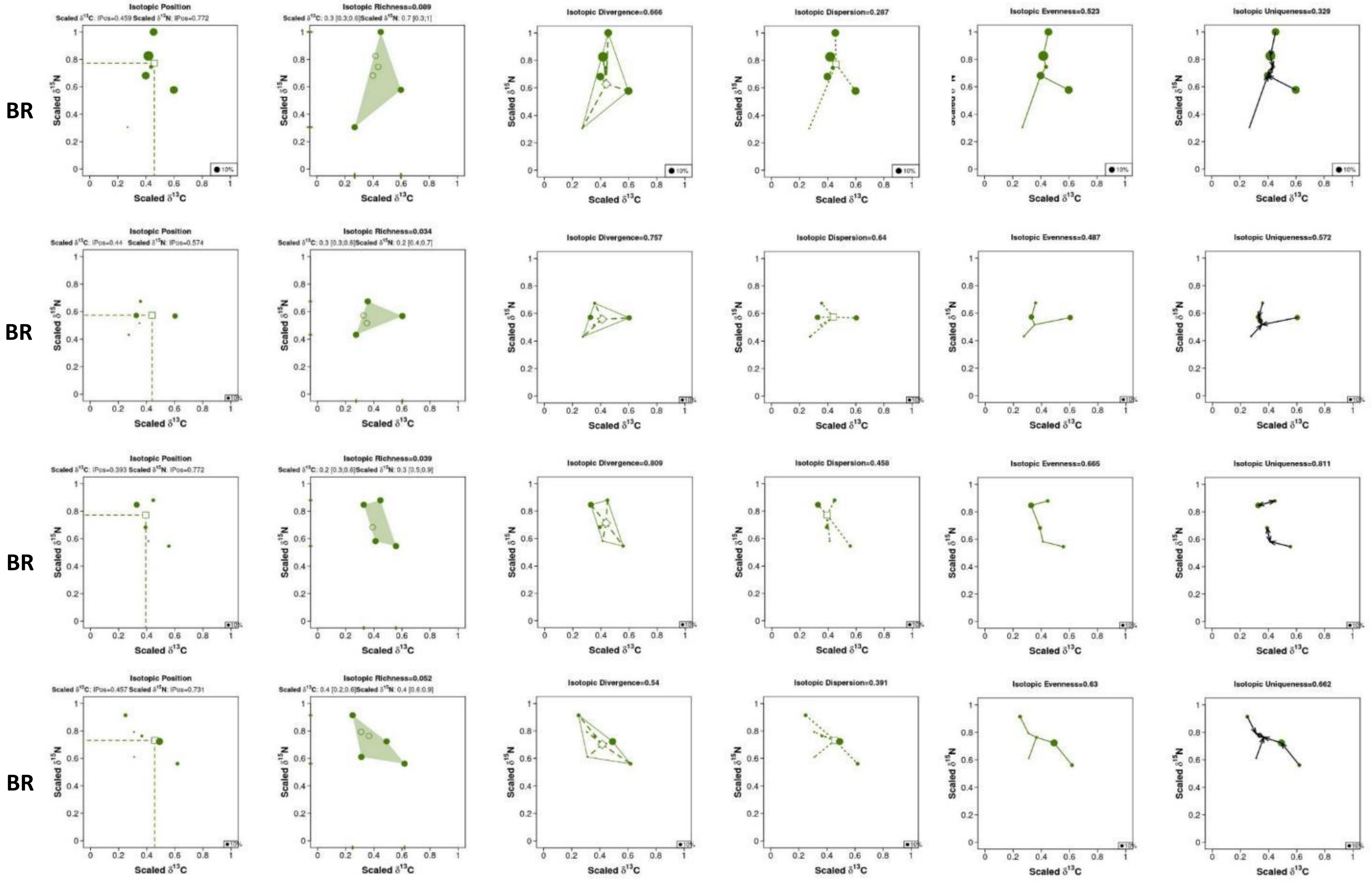

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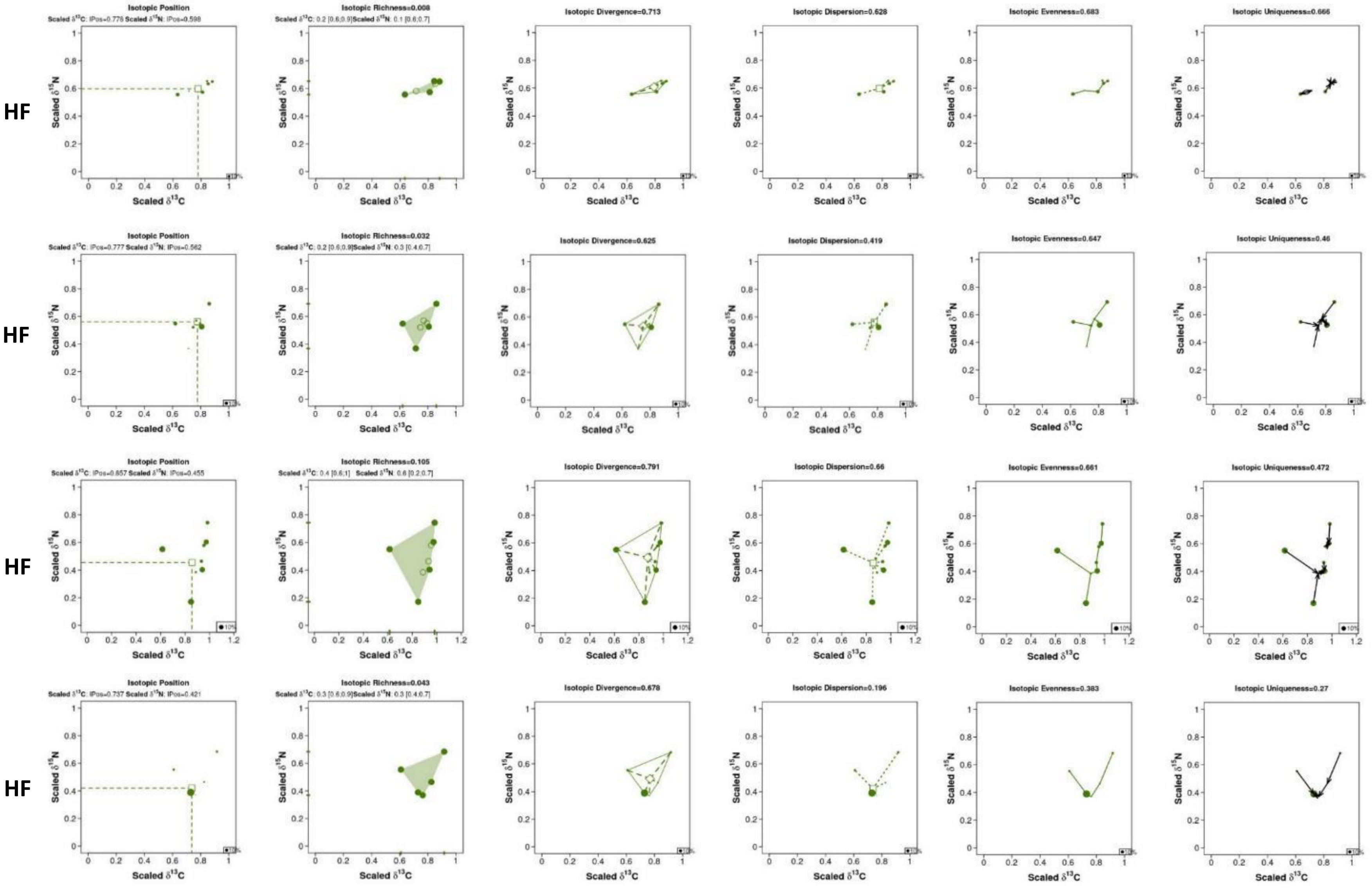
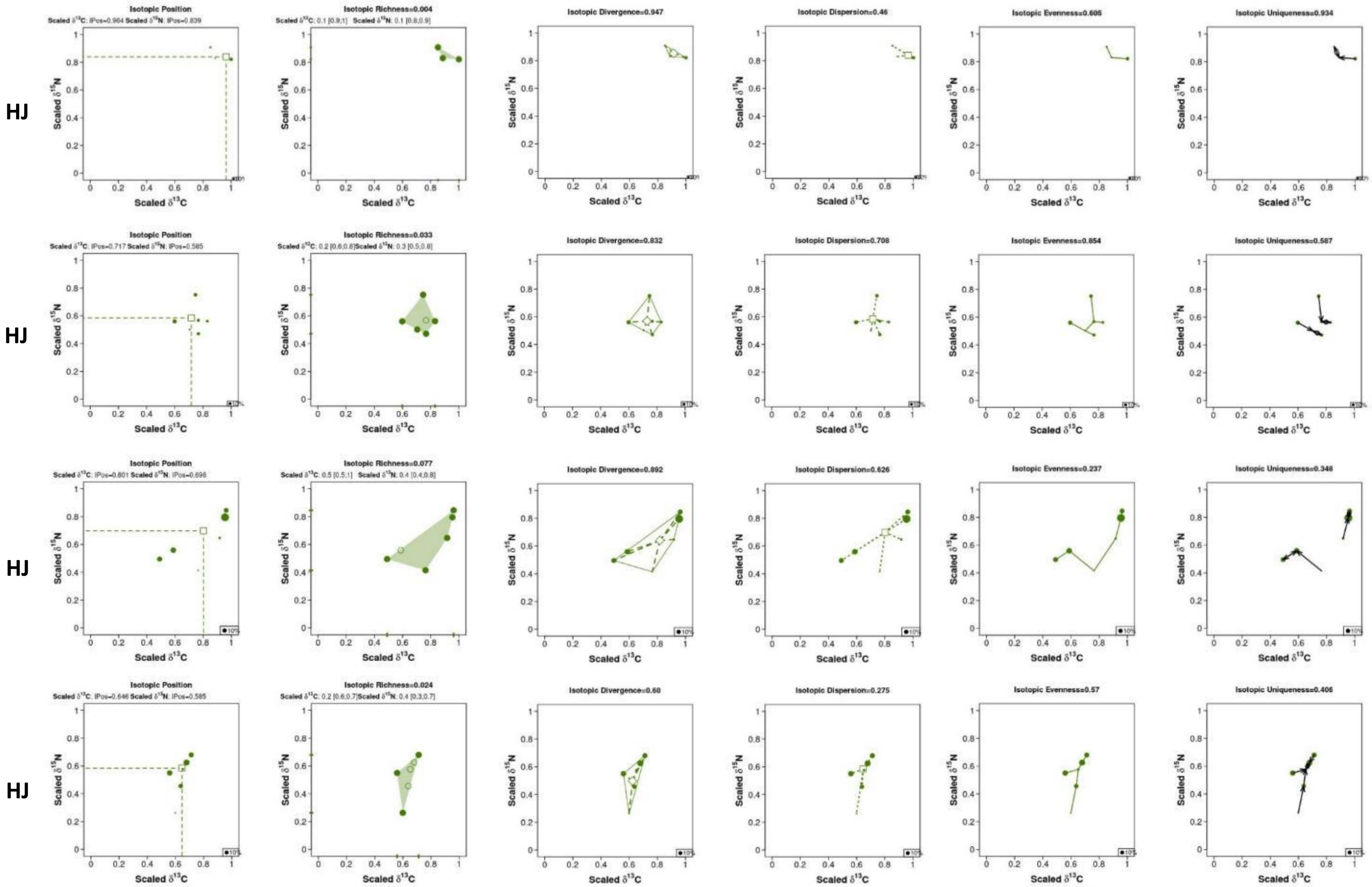


Figure S1. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider canopy communities in the four replicates of rainforest in Hutan Harapan landscape (HF1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods



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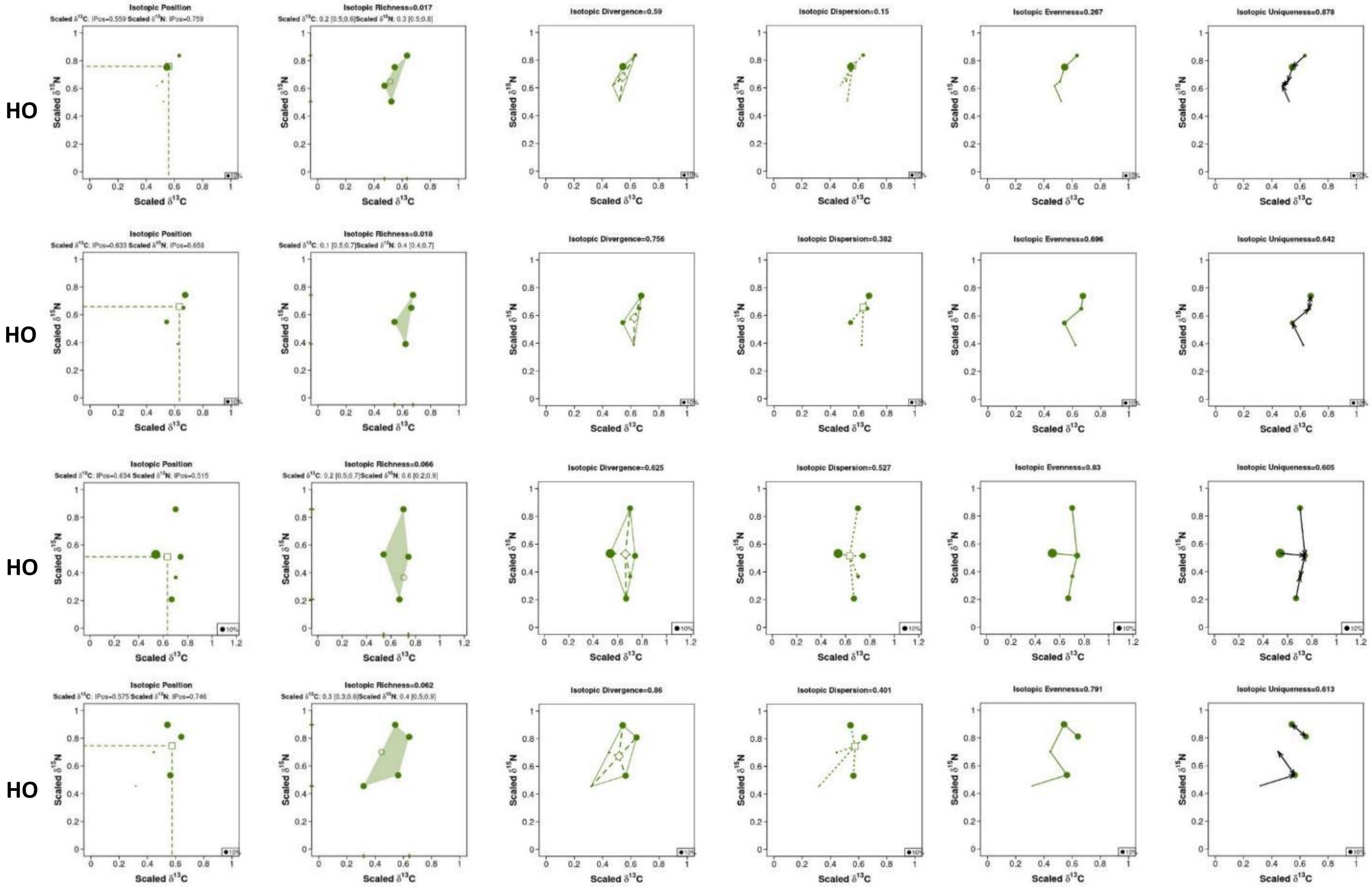

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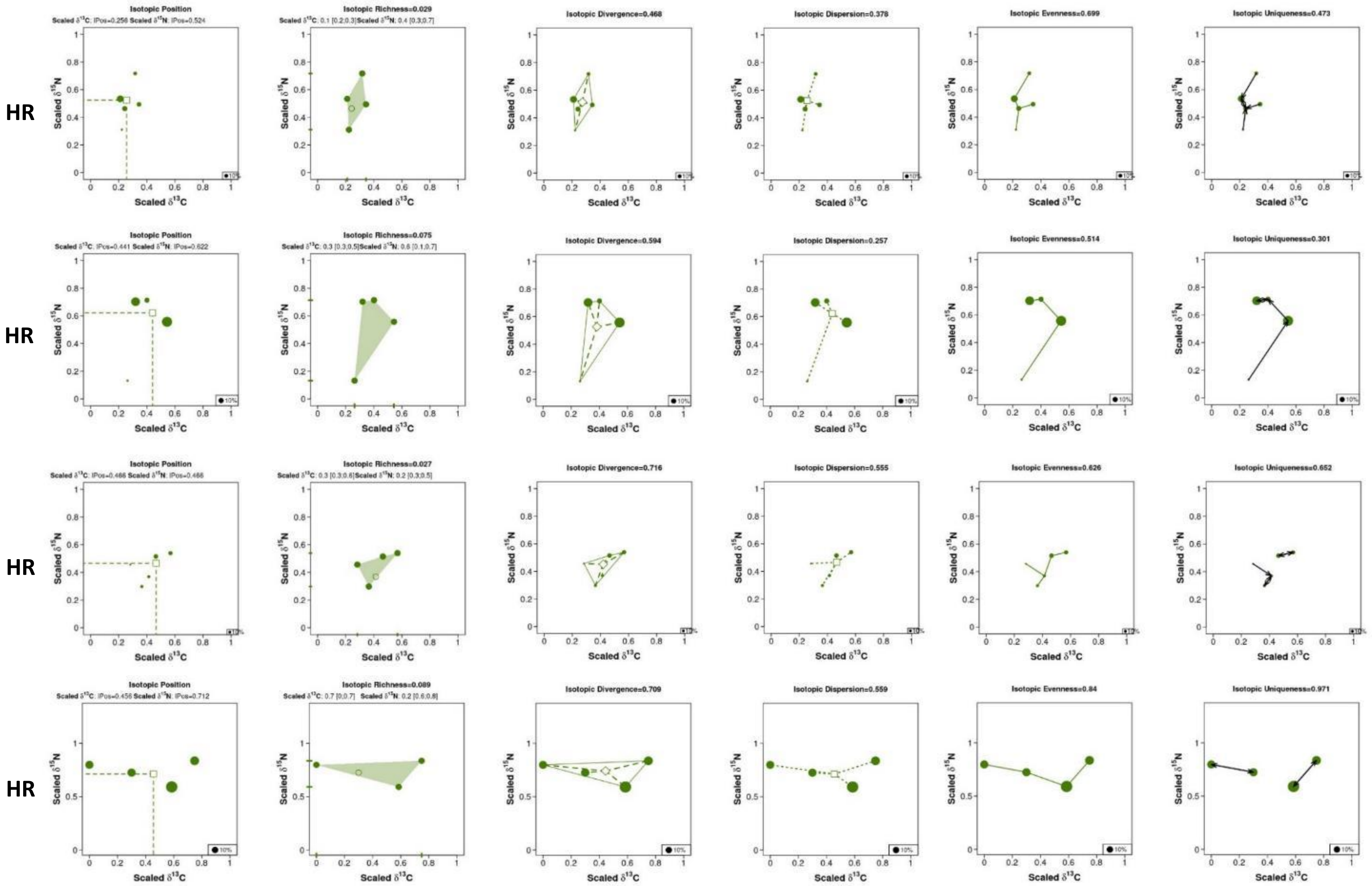

Figure S1. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider canopy communities in the four replicates of rubber in Hutan Harapan landscape (HR). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods.

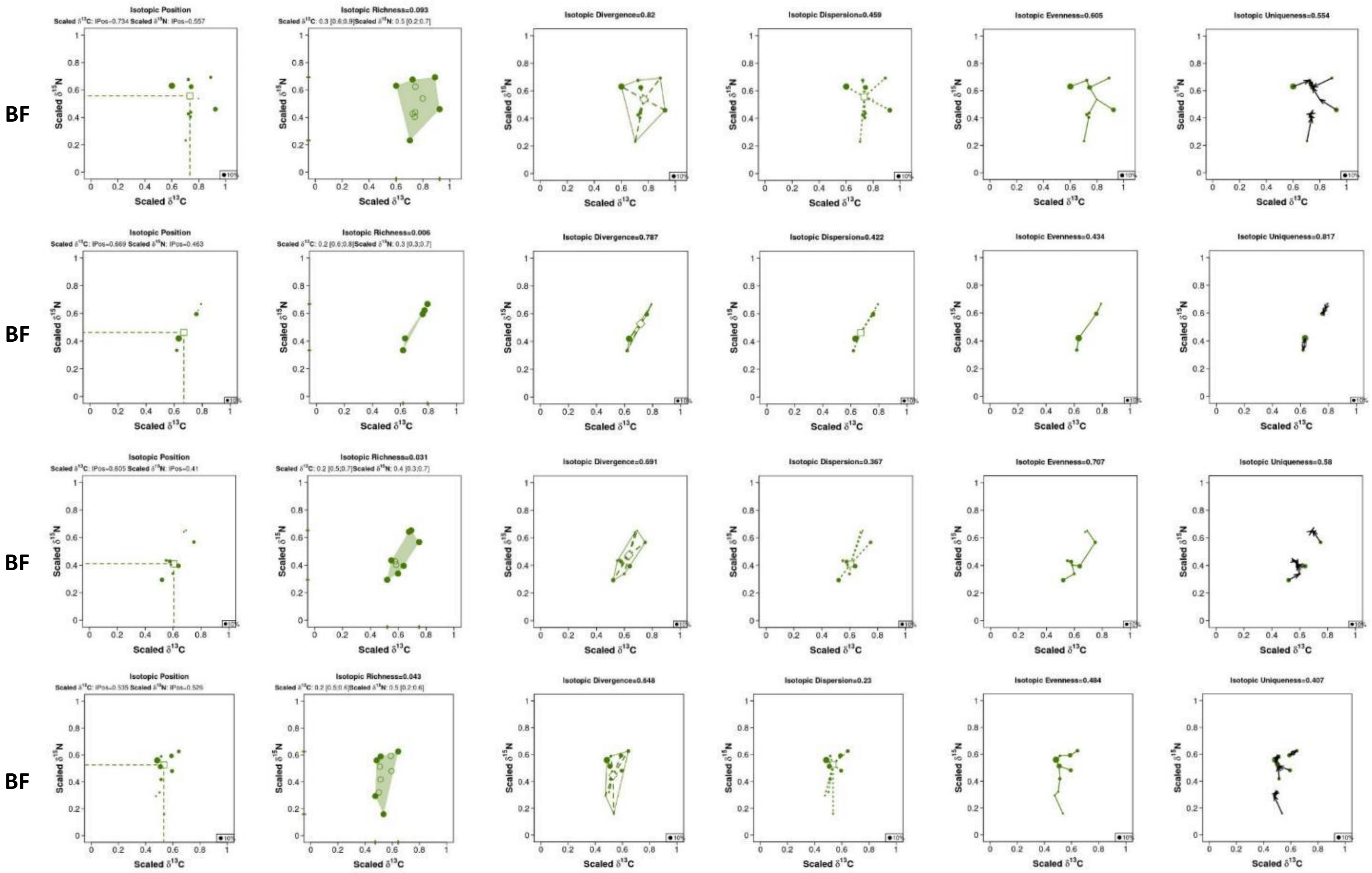

Figure S2. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Salticidae in the four replicates of rainforest in Bukit Duabelas National Park landscape (BF 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

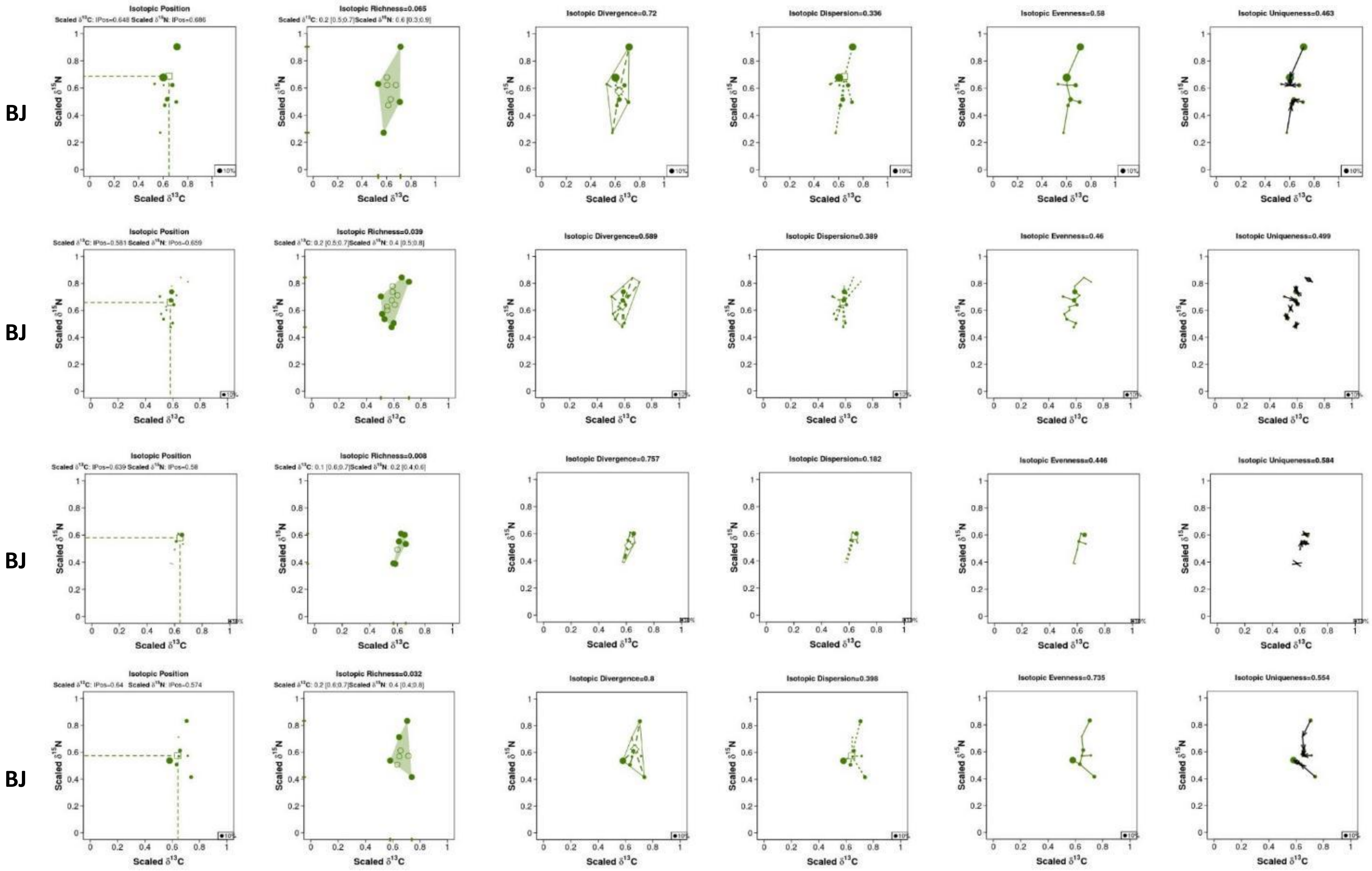

Figure S2. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Salticidae in the four replicates of rainforest in Bukit Duabelas National Park landscape (BJ 3 - 6). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

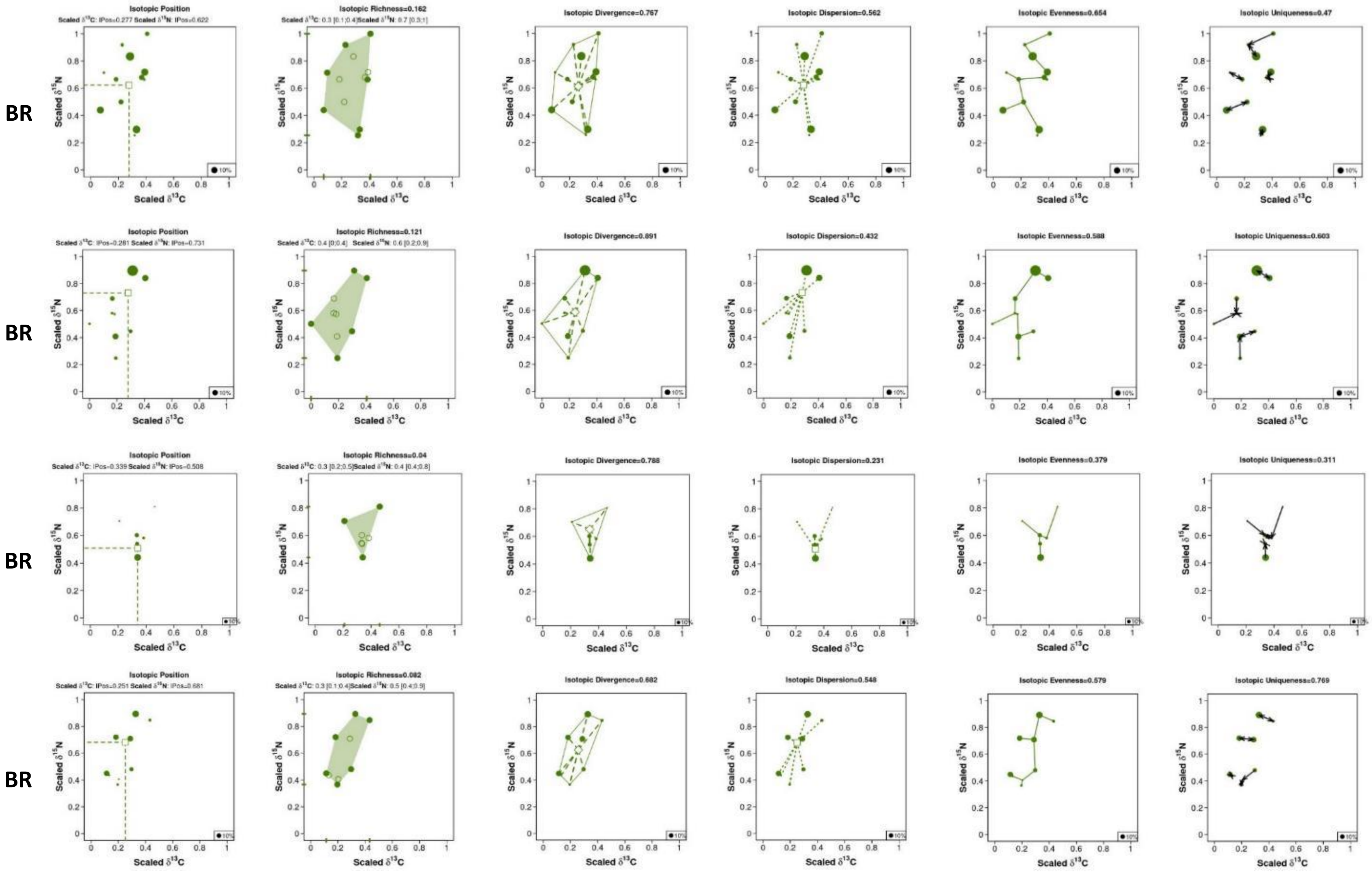

Figure S2. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Salticidae in the four replicates of rainforest in Bukit Duabelas National Park landscape (BR 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

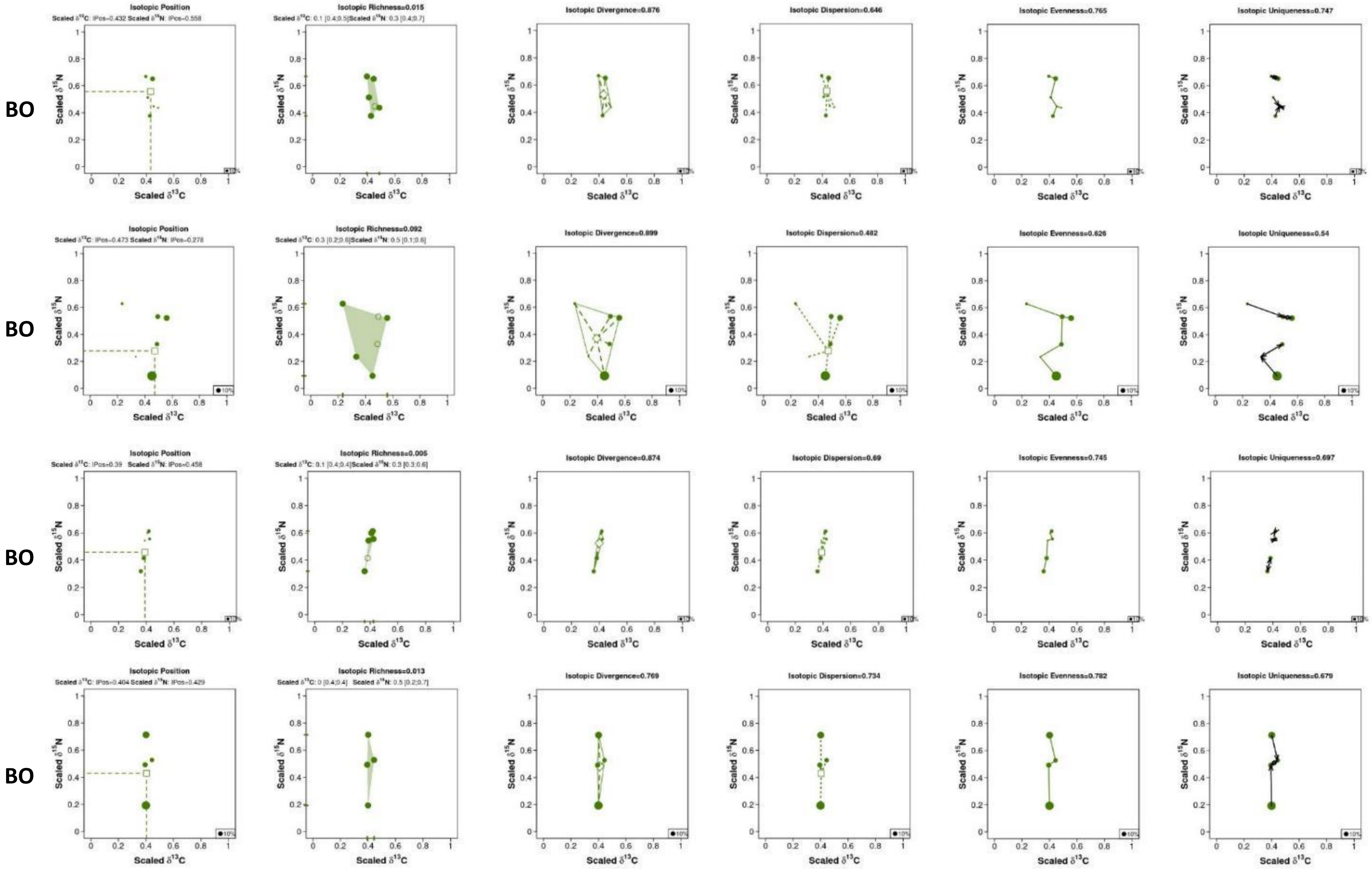

Figure S2. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Salticidae in the four replicates of rainforest in Bukit Duabelas National Park landscape (BO 2 - 5). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

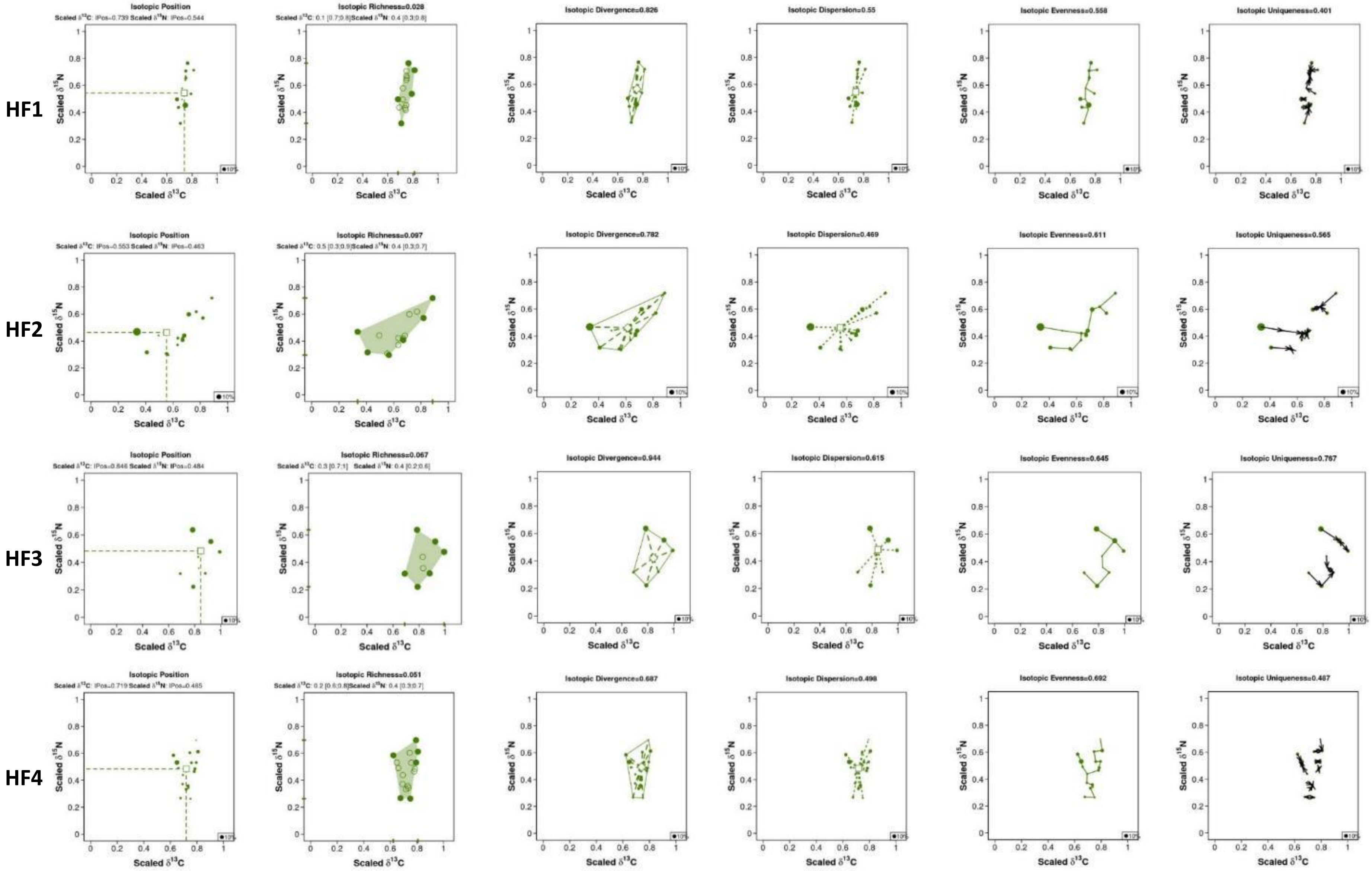

Figure S2. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Salticidae in the four replicates of rainforest in Harapan landscape (HF 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

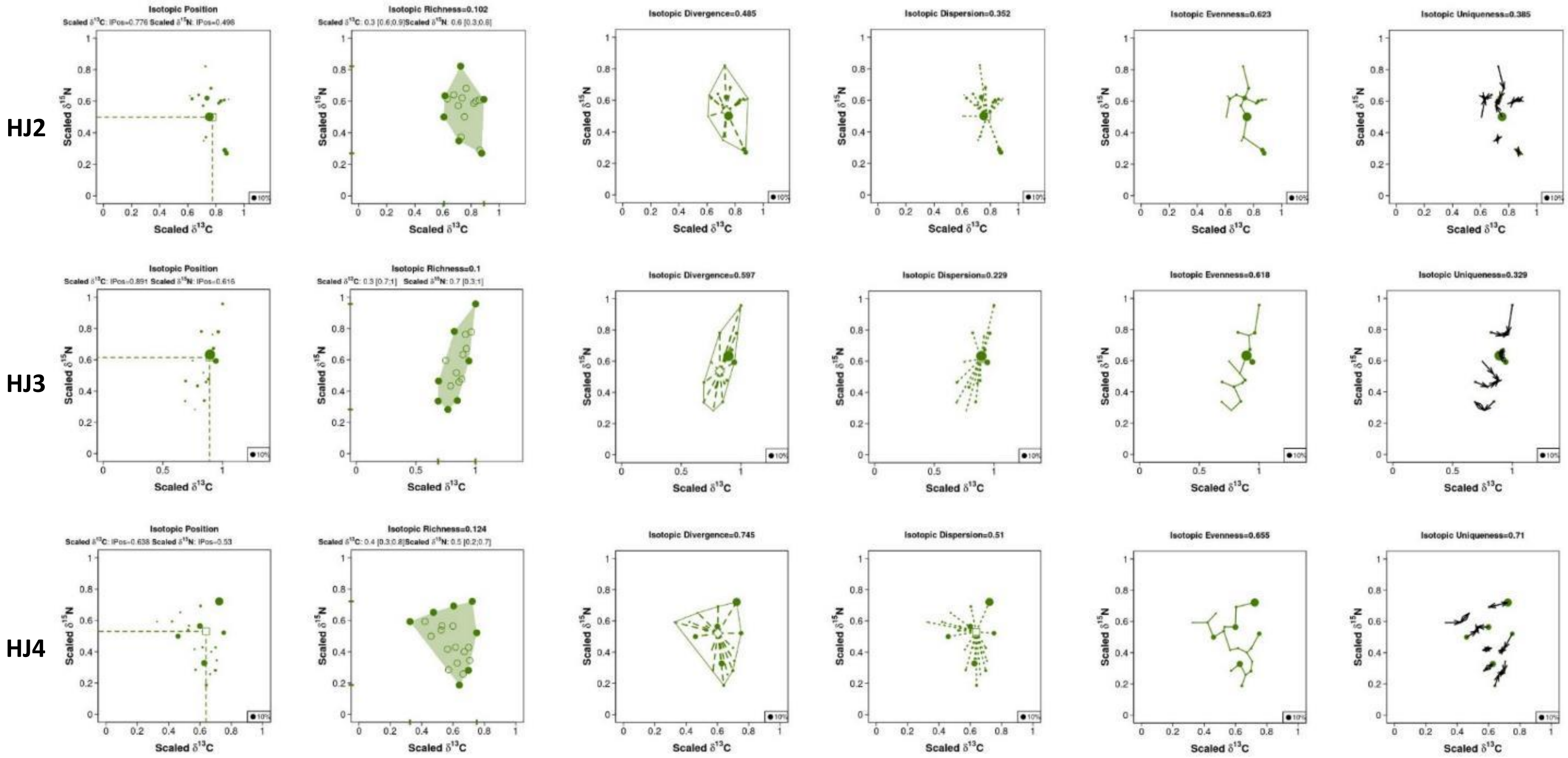

Figure S2. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Salticidae in the four replicates of jungle rubber in Harapan landscape (HJ 2 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

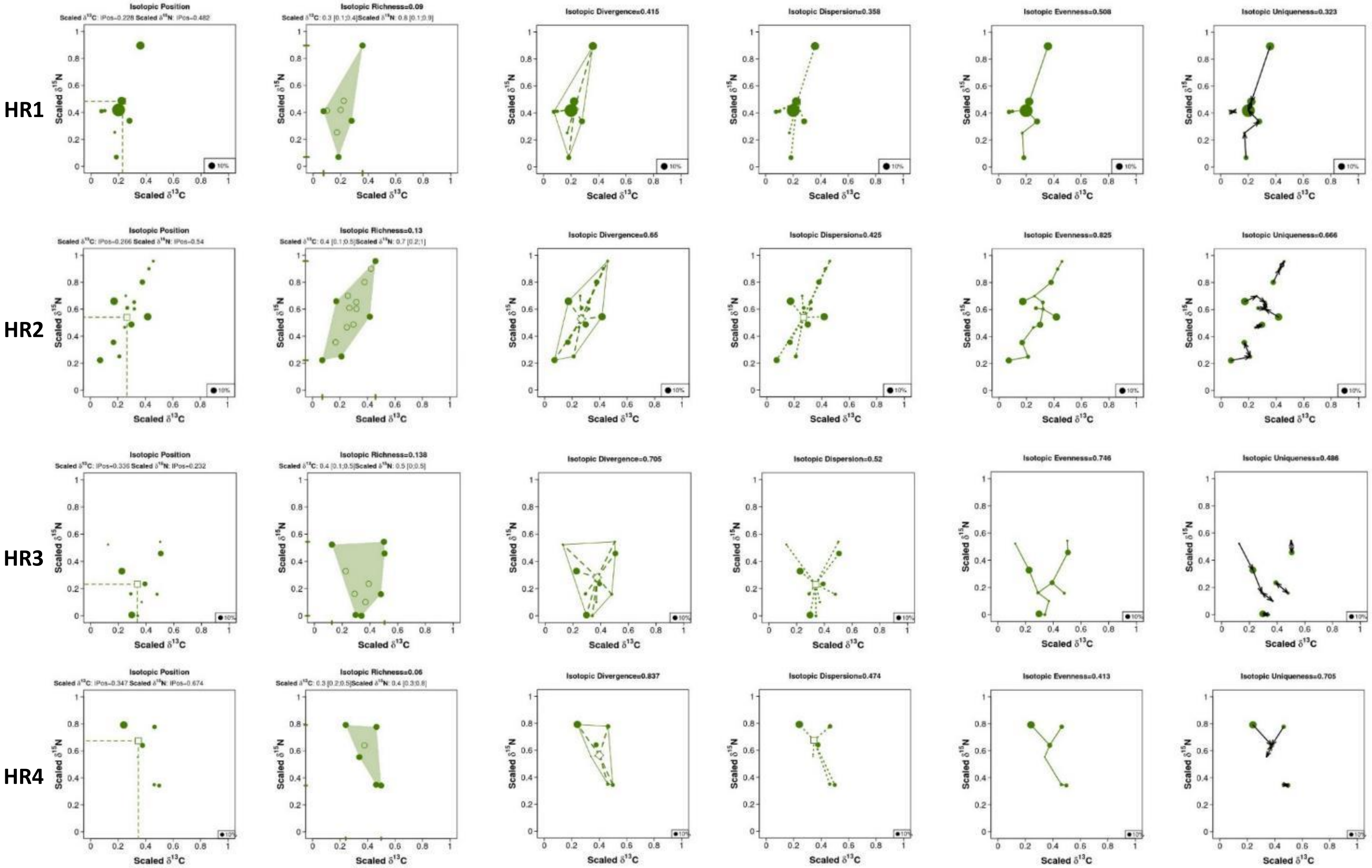

Figure S2. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Salticidae in the four replicates of rubber in Harapan landscape (HR 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

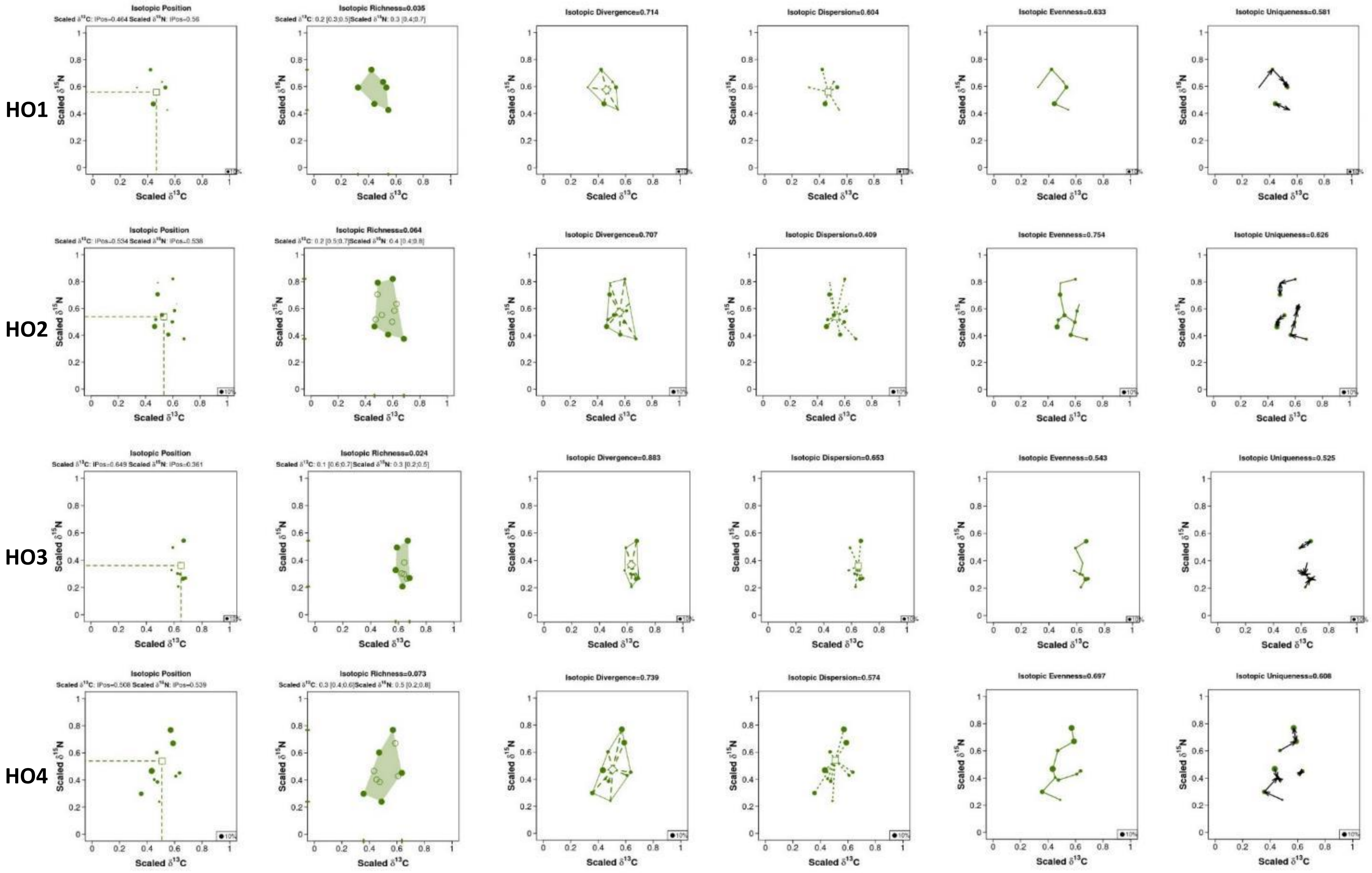

Figure S2. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Salticidae in the four replicates of oil palm in Harapan landscape (HO 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

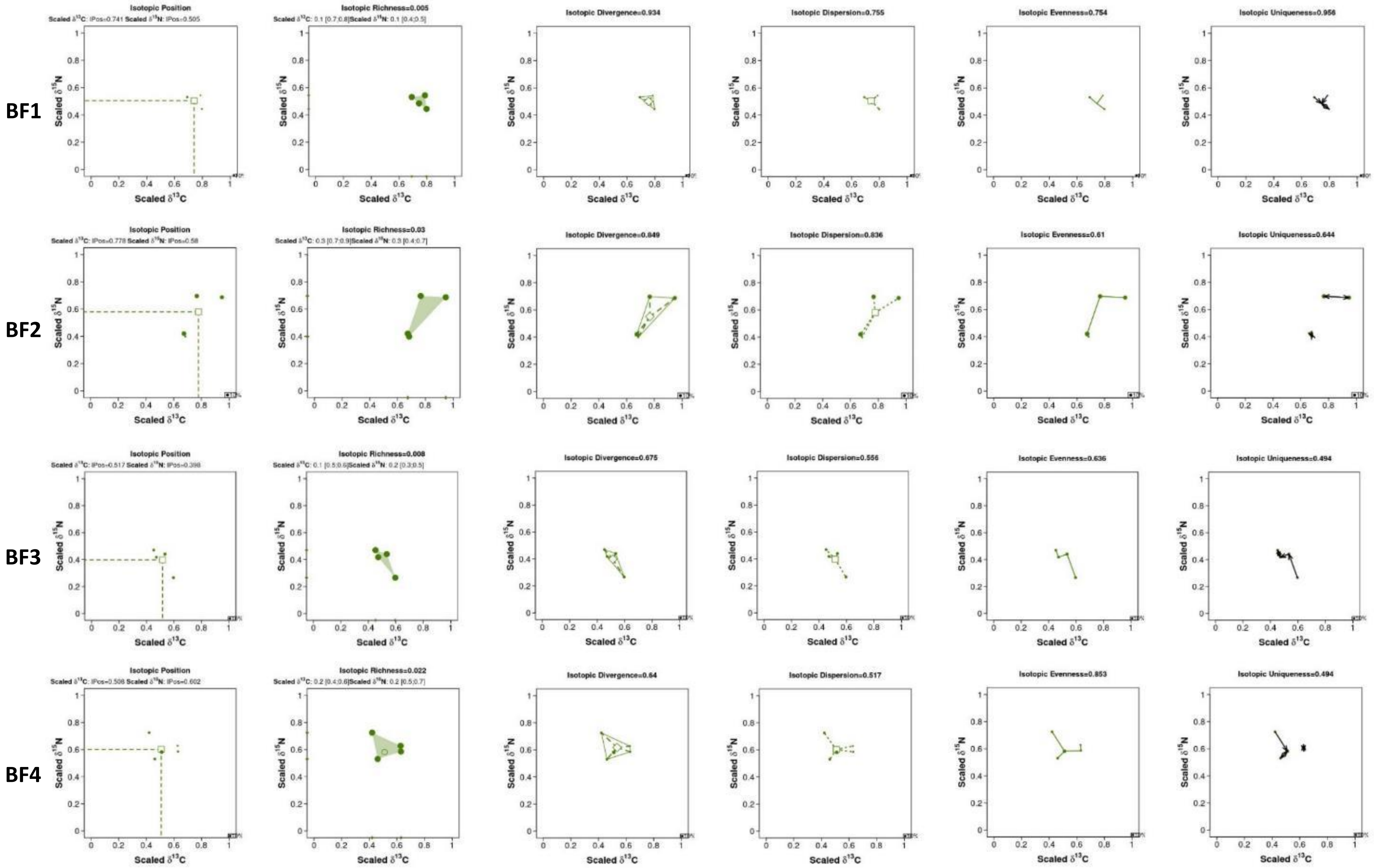

Figure S3. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Clubionidae in the four replicates of rainforest in Bukit Duabelas National Park landscape (BF 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

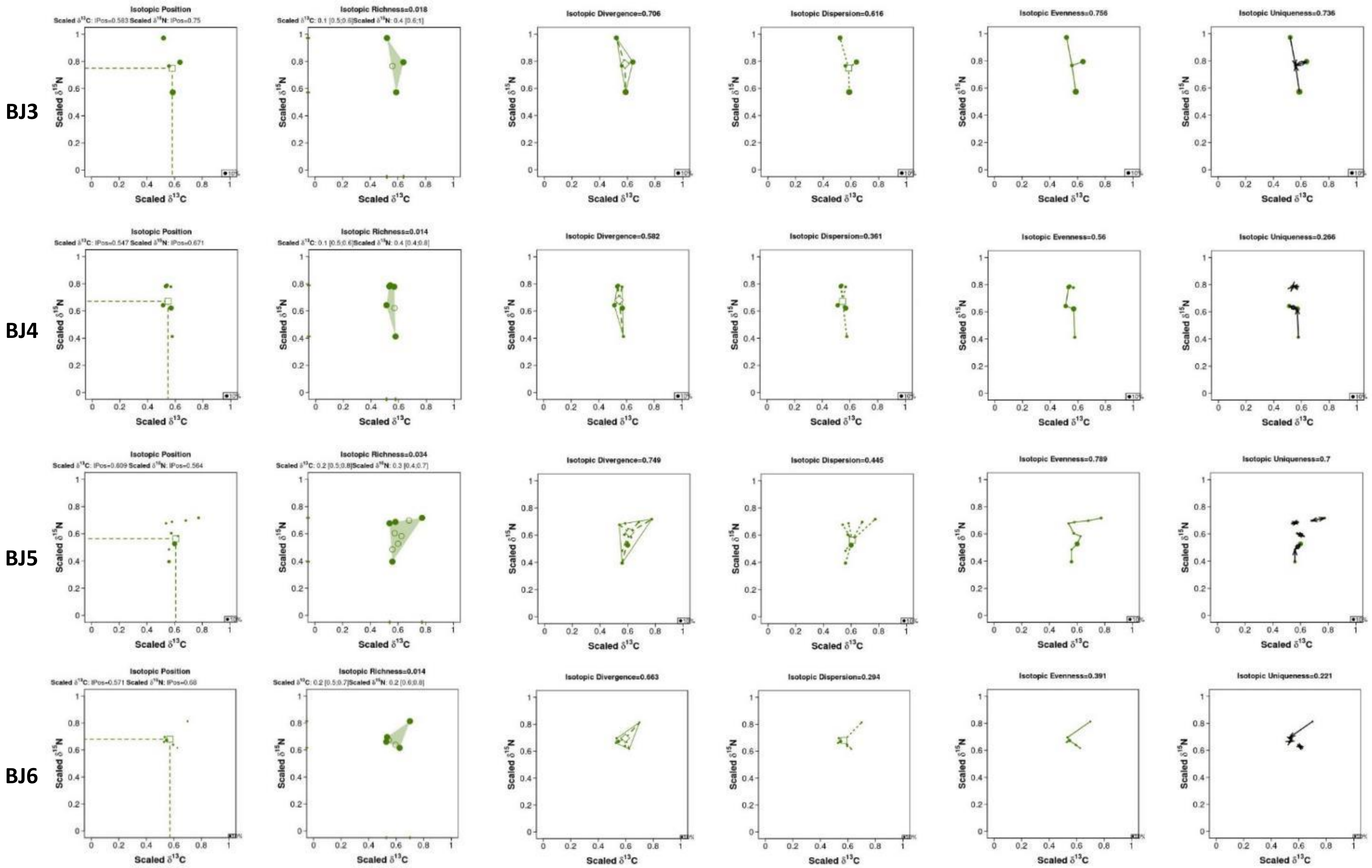

Figure S3. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Clubionidae in the four replicates of jungle rubber in Bukit Duabelas National Park landscape (BJ 3 - 6). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

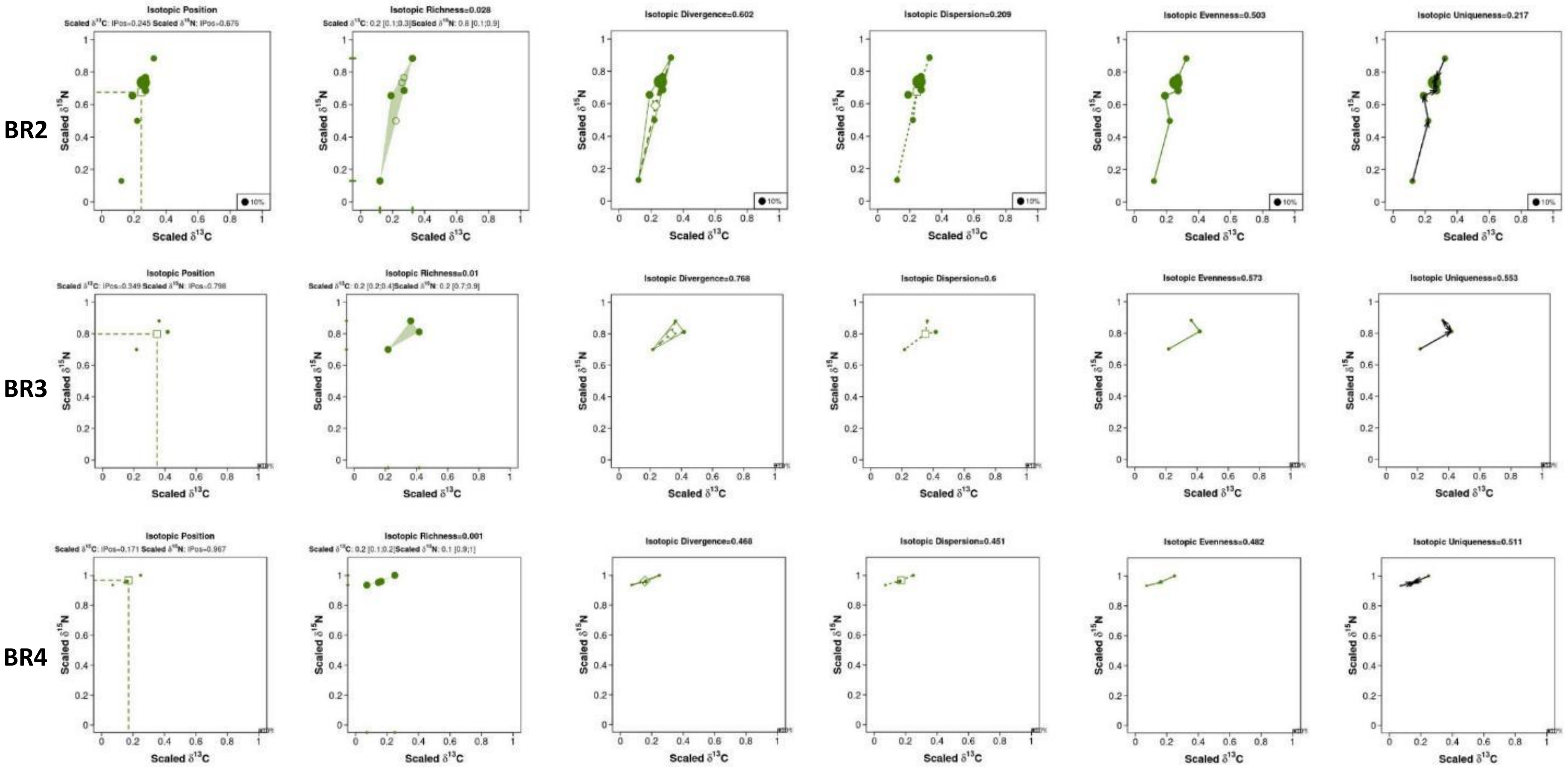

Figure S3. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, Isotopic evenness, isotopic uniqueness) of spider family Clubionidae in the three replicates of rubber plantations in Bukit Duabelas National Park landscape (BR 2, 3, 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

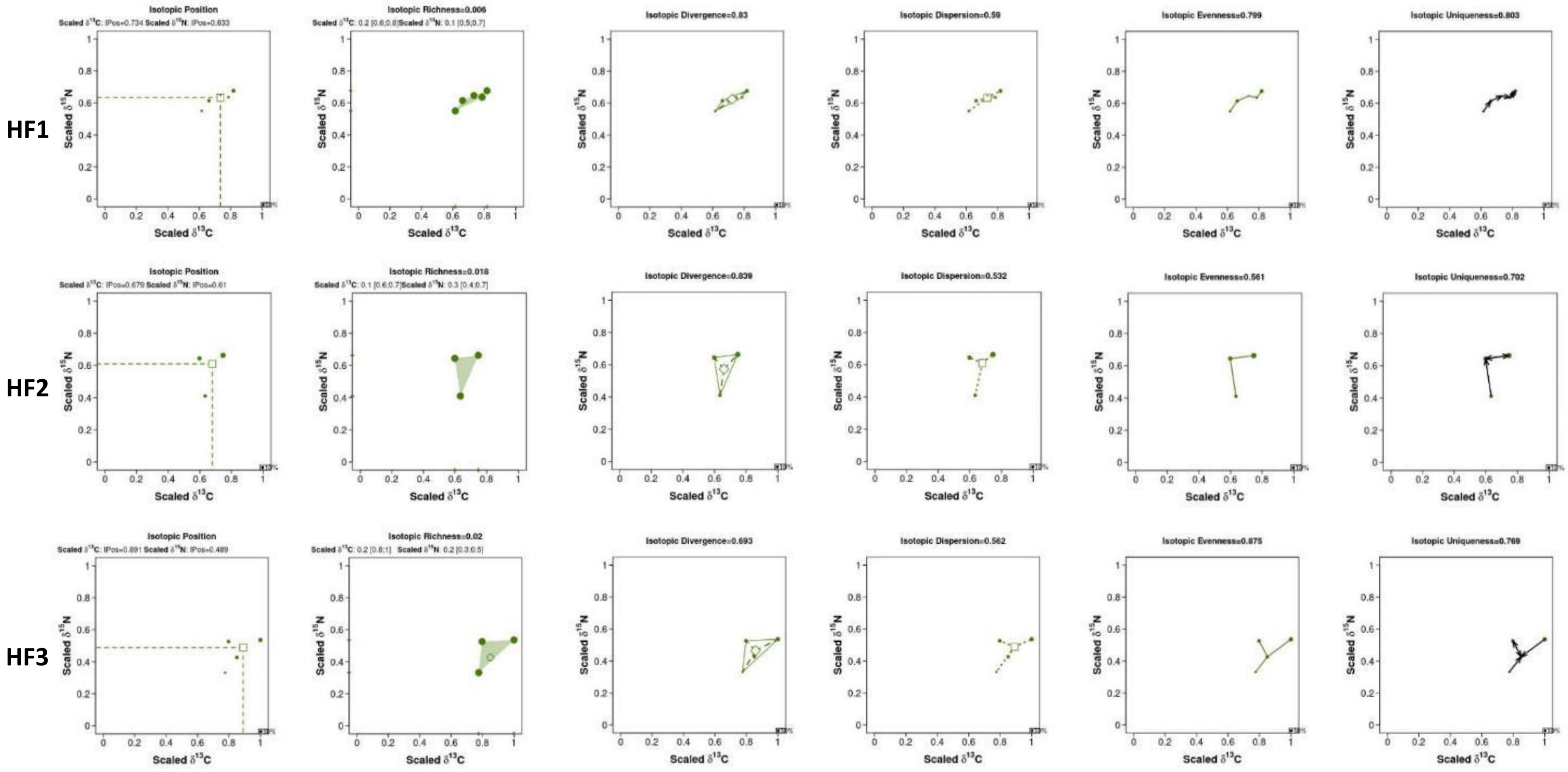

Figure S3. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Clubionidae in the three replicates of rainforest in Harapan landscape (HF 1 - 3). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

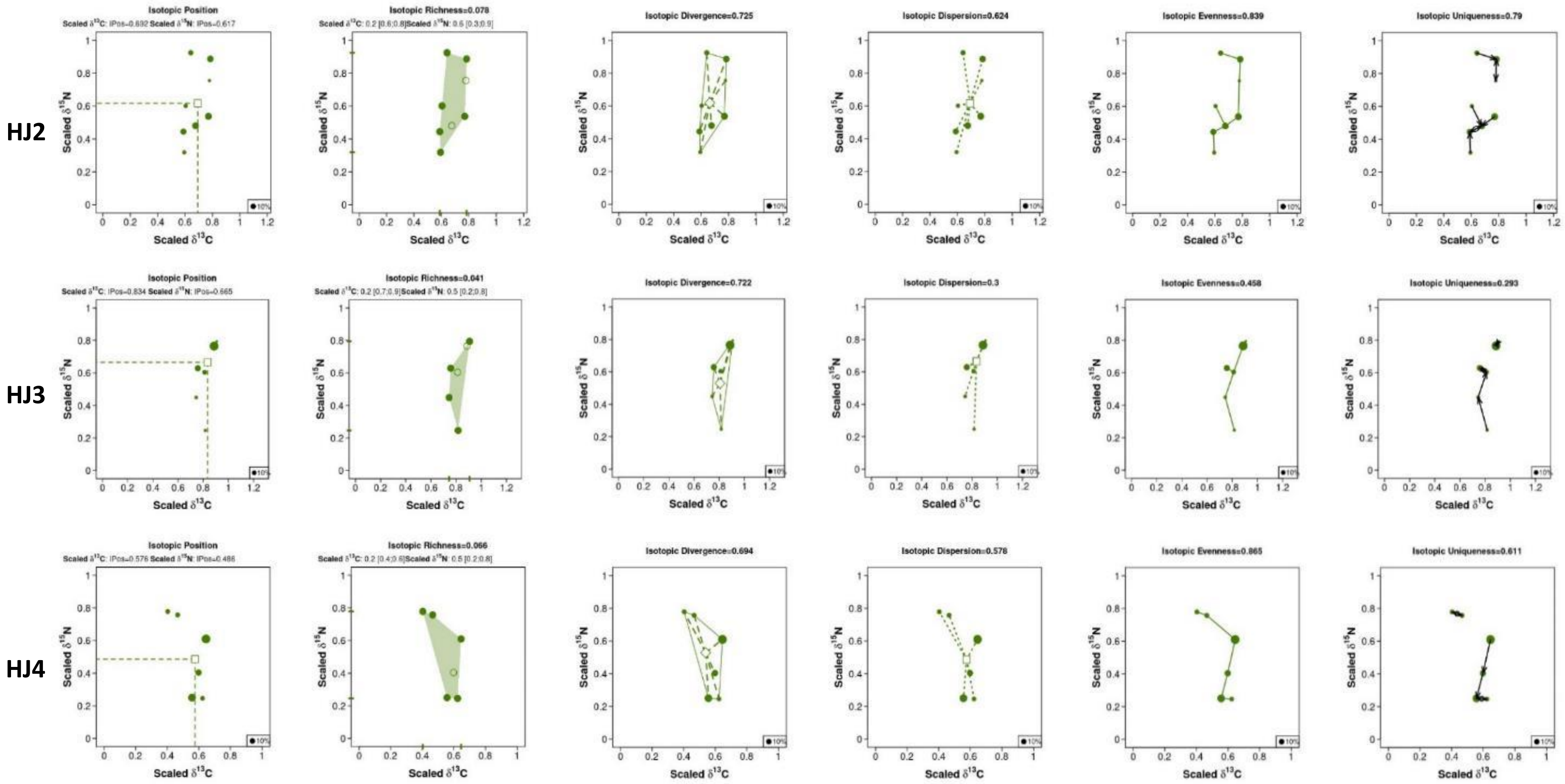

Figure S3. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Clubionidae in the three replicates of jungle rubber in Harapan landscape (HJ 2 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

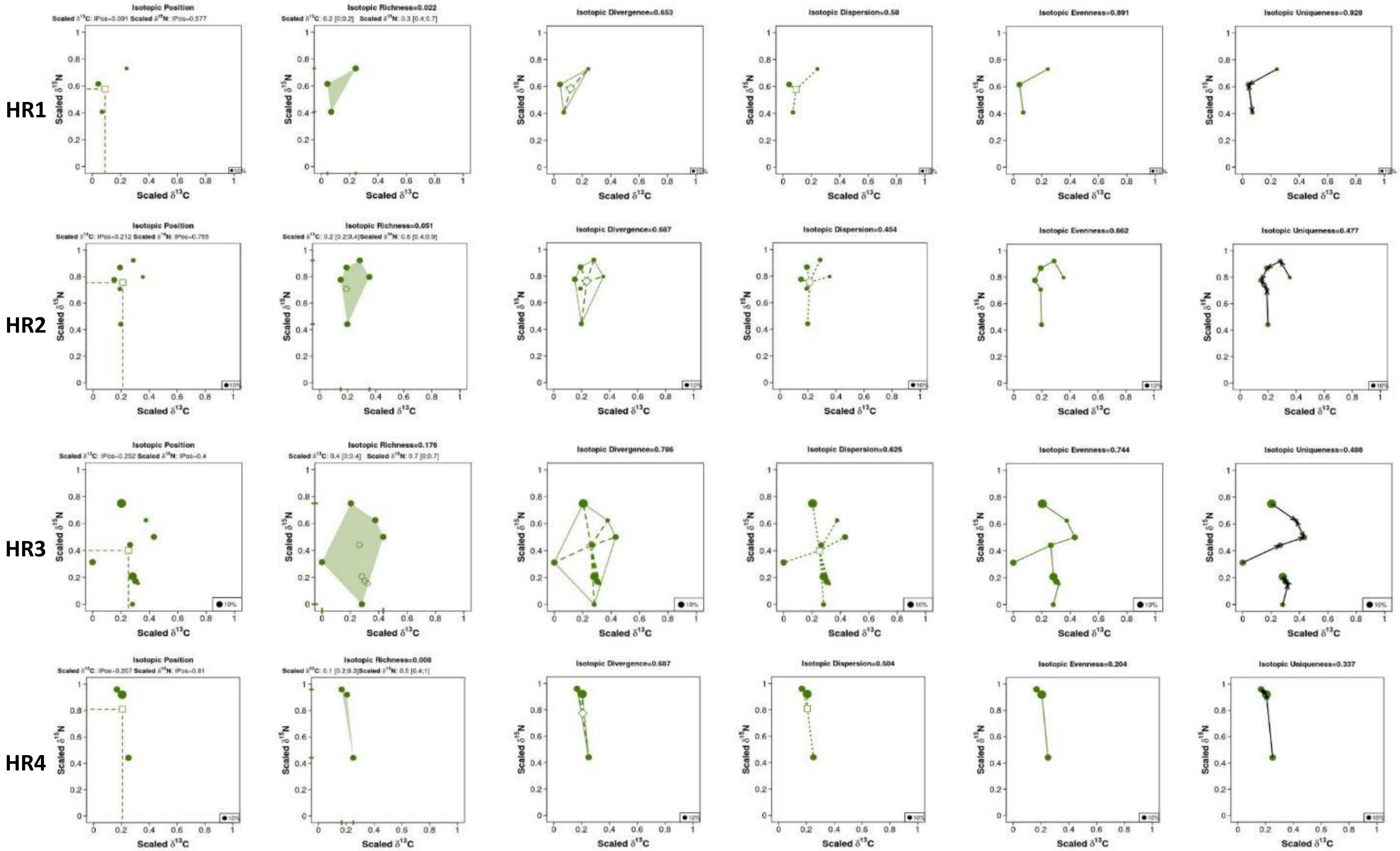

Figure S3. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Clubionidae in the four replicates of rubber plantations in Harapan landscape (HR 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

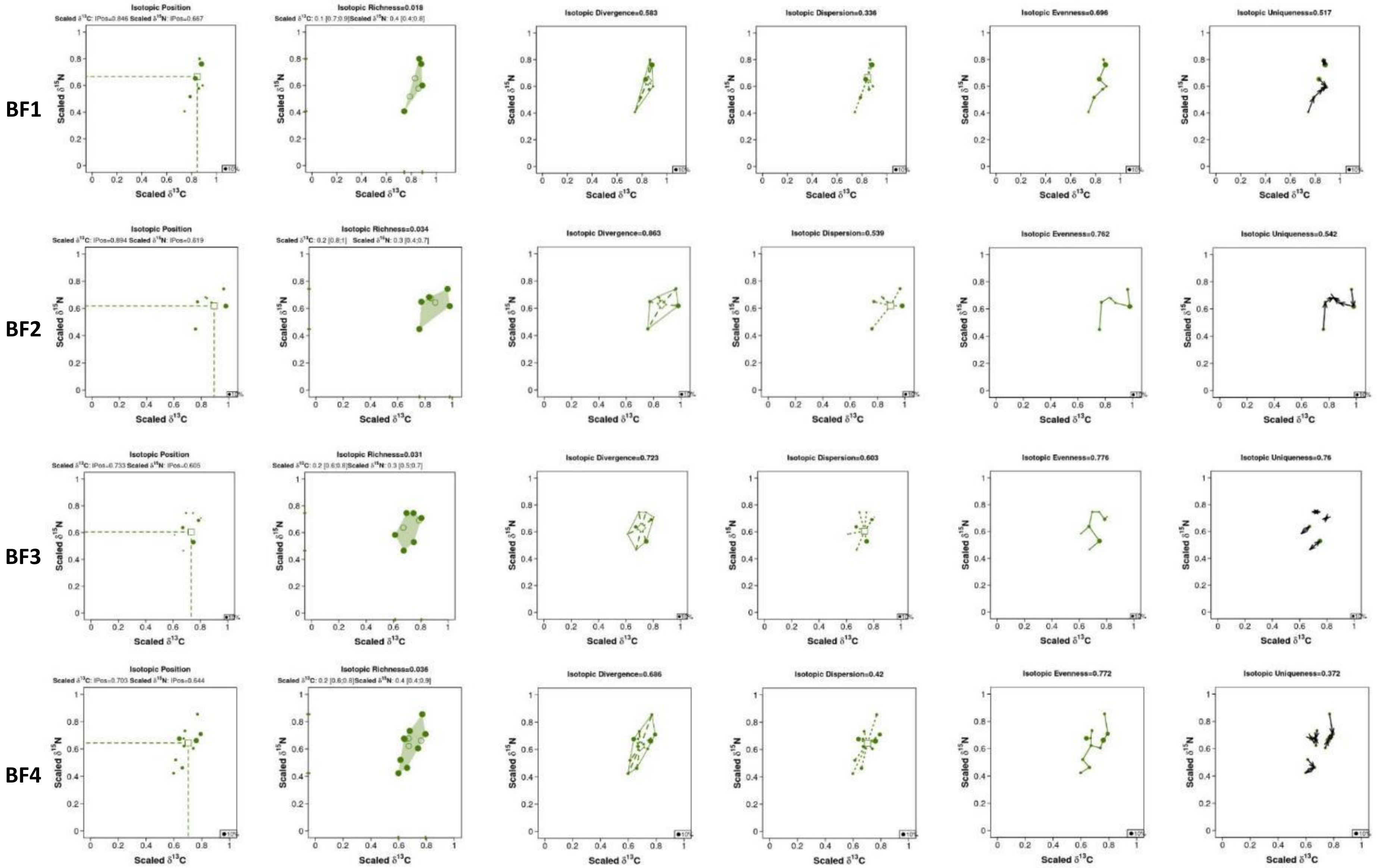

Figure S4. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Theridiidae in the four replicates of rainforest in Bukit Duabelas National Park landscape (BF 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

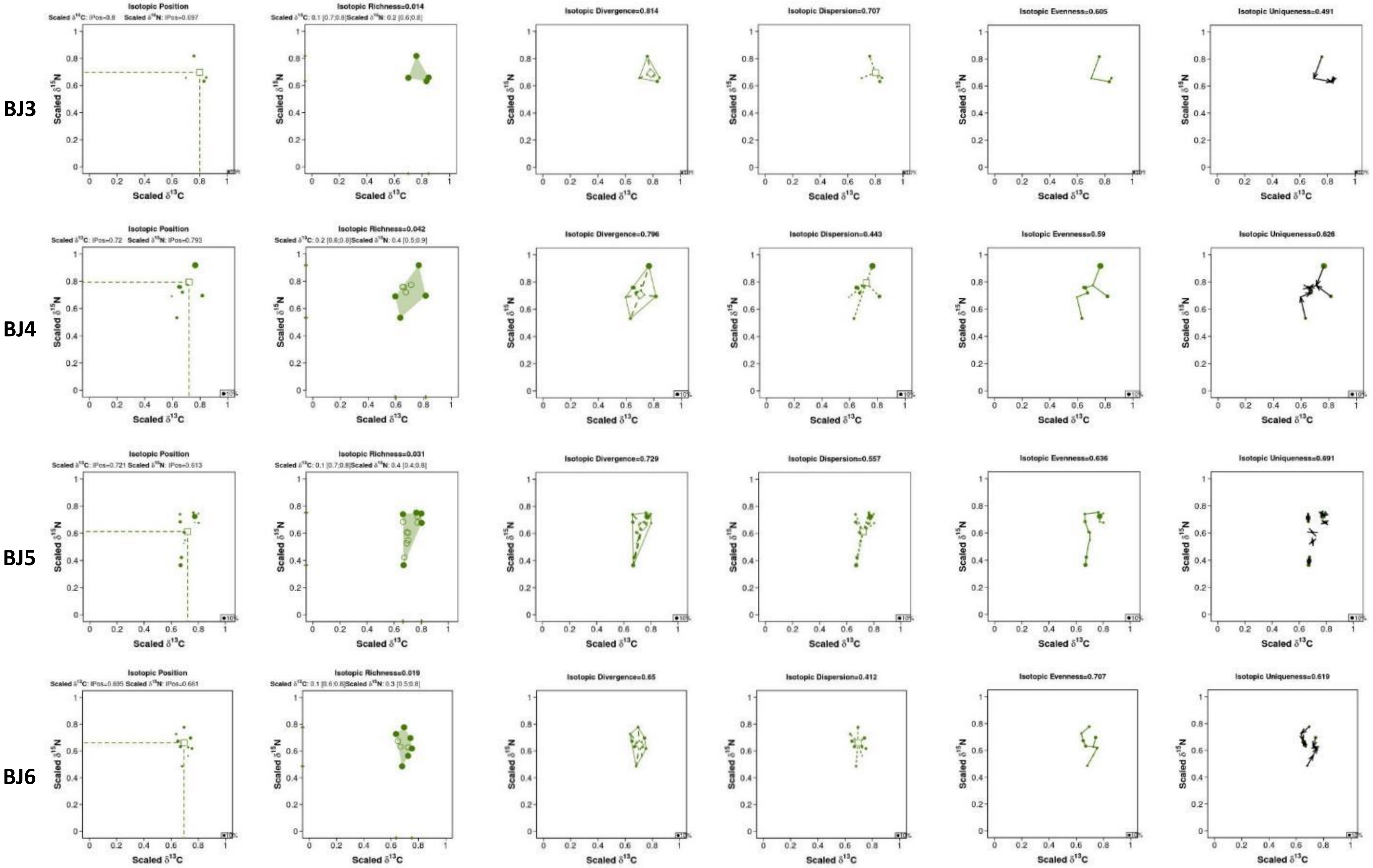

Figure S4. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Theridiidae in the four replicates of jungle rubber in Bukit Duabelas National Park landscape (BJ 3 - 6). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

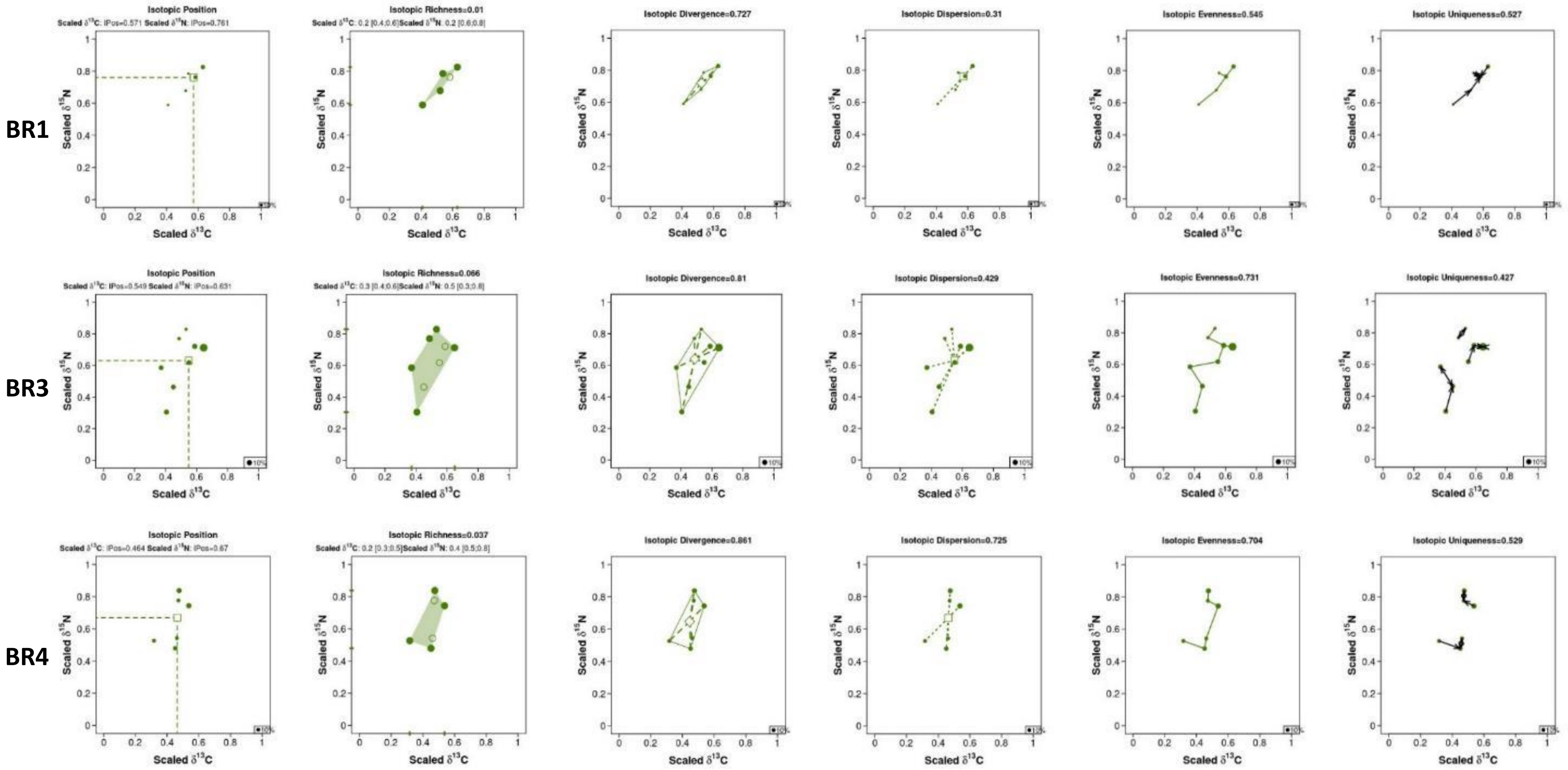

Figure S4. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, Isotopic evenness, isotopic uniqueness) of spider family Theridiidae in the four replicates of rubber plantations in Bukit Duabelas National Park landscape (BR 1, 3, 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

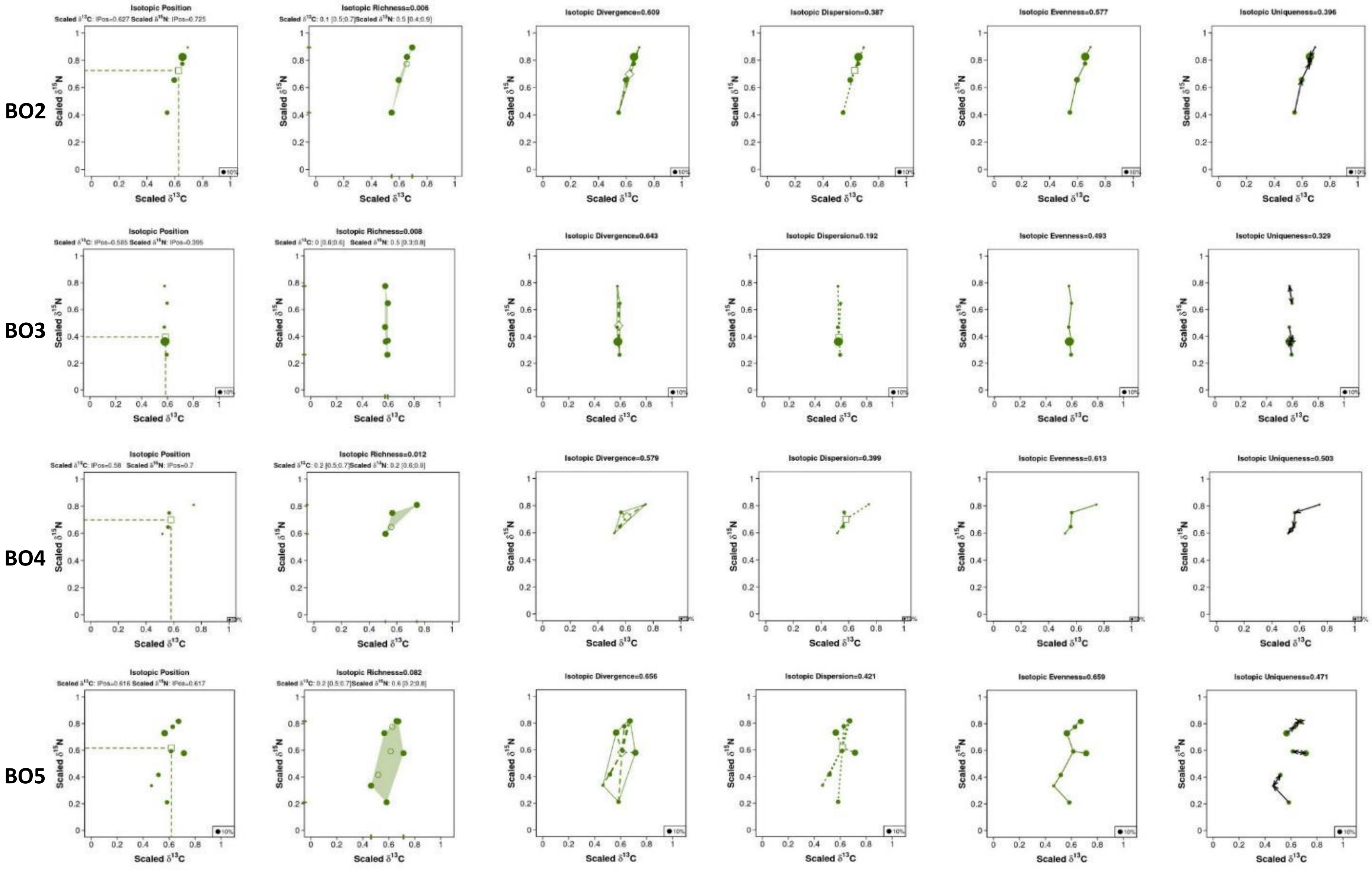

Figure S4. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Theridiidae in the four replicates of oil palm plantations in Bukit Duabelas National Park landscape (BO 2 - 5). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

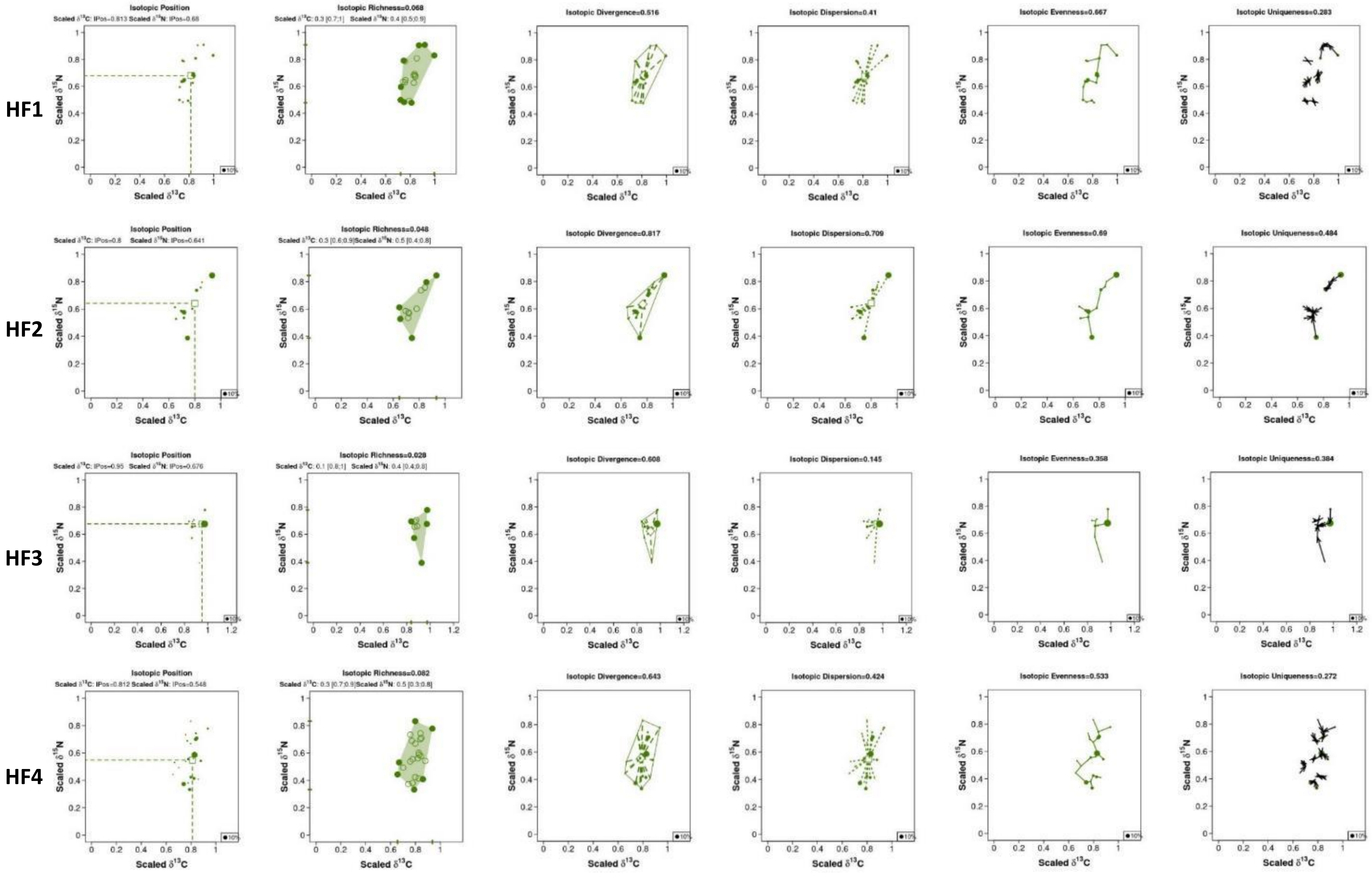

Figure S4. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Theridiidae in the four replicates of rainforest in Harapan landscape (HF 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

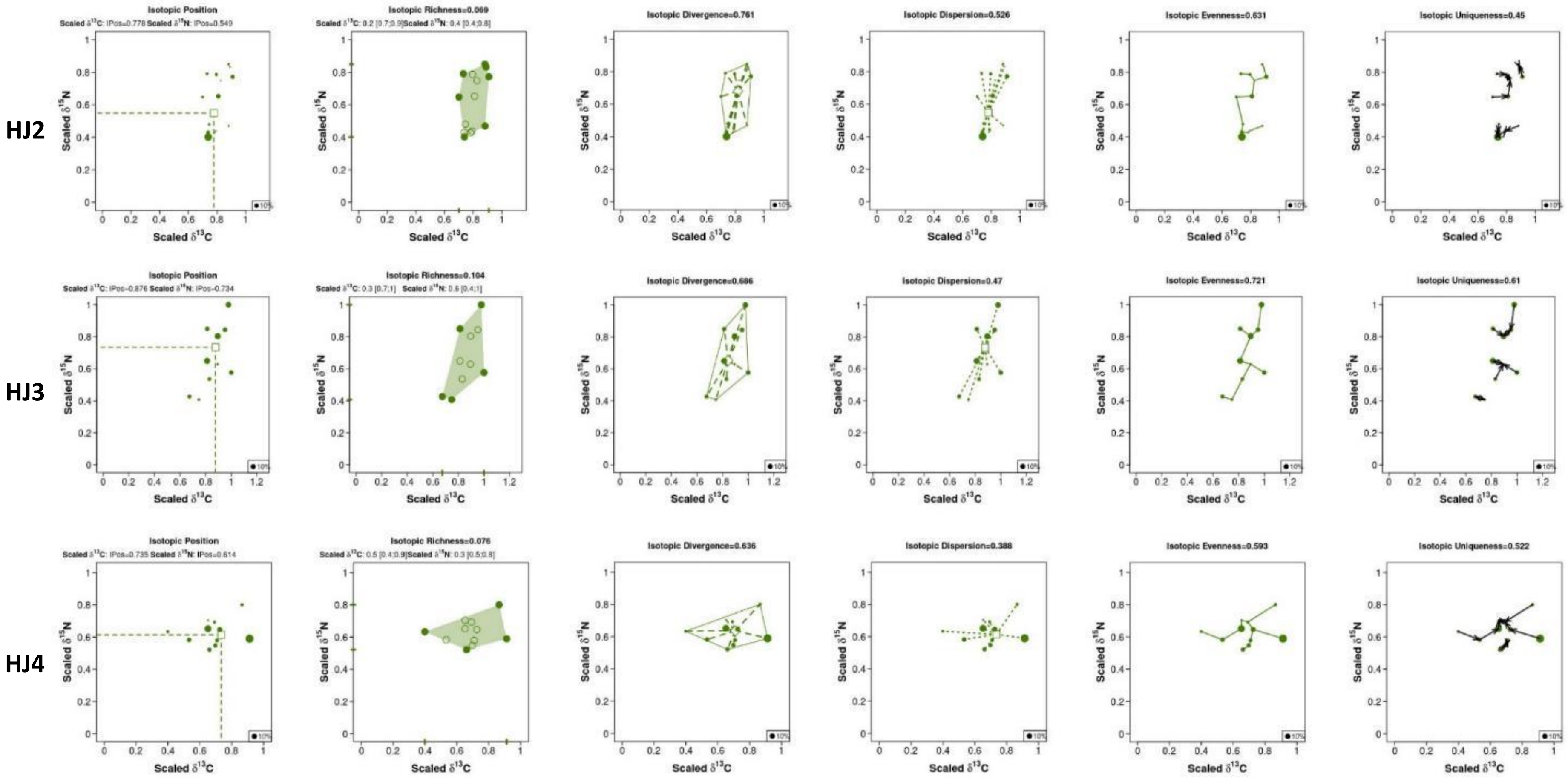

Figure S4. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Theridiidae in the four replicates of jungle rubber in Harapan landscape (HJ 2 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

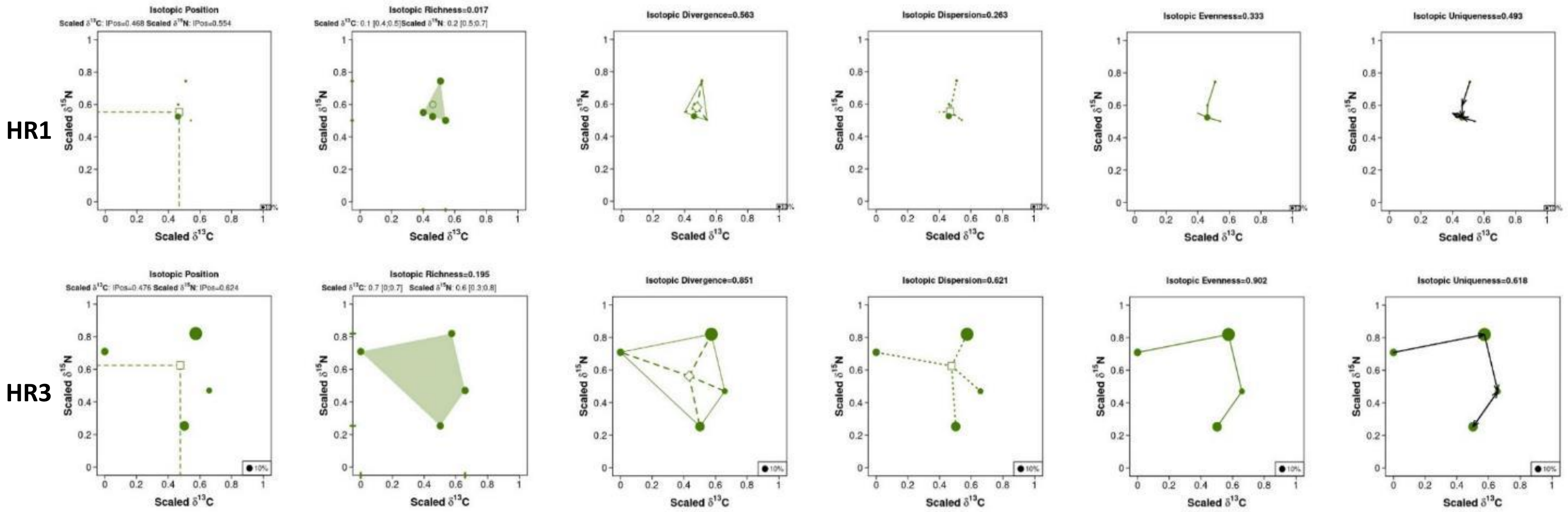

Figure S4. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Theridiidae in the four replicates of rubber plantations in Harapan landscape (HR 1, 3). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

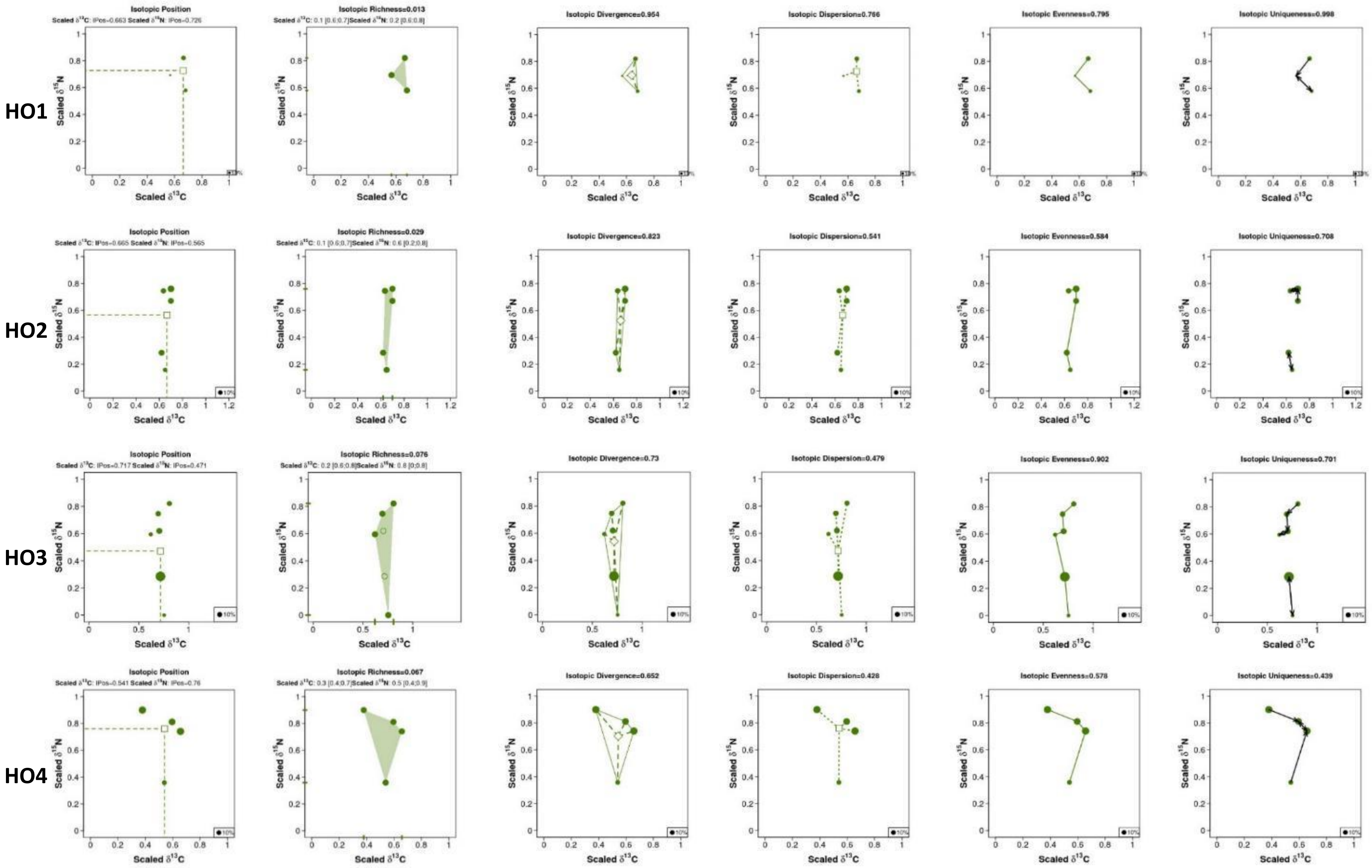

Figure S4. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Theridiidae in the four replicates of oil palm plantations in Harapan landscape (HO 1 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods.

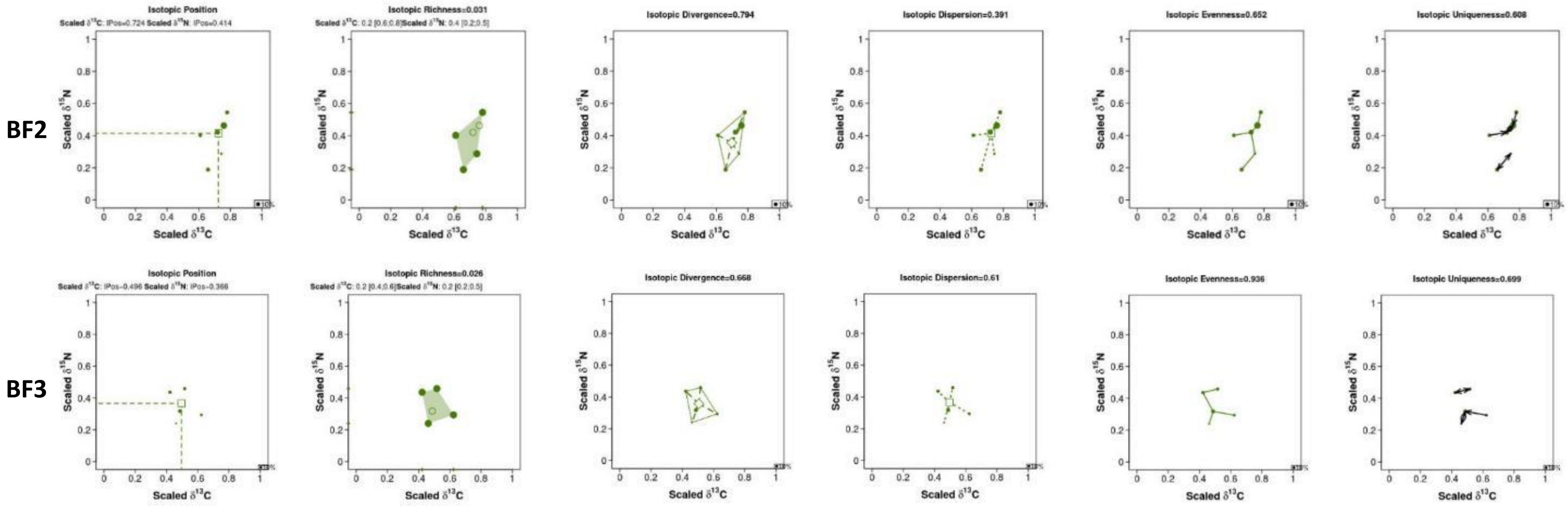

Figure S5. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Thomisidae in the two replicates of rainforest in Bukit Duabelas National Park landscape (BF 2 - 3). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

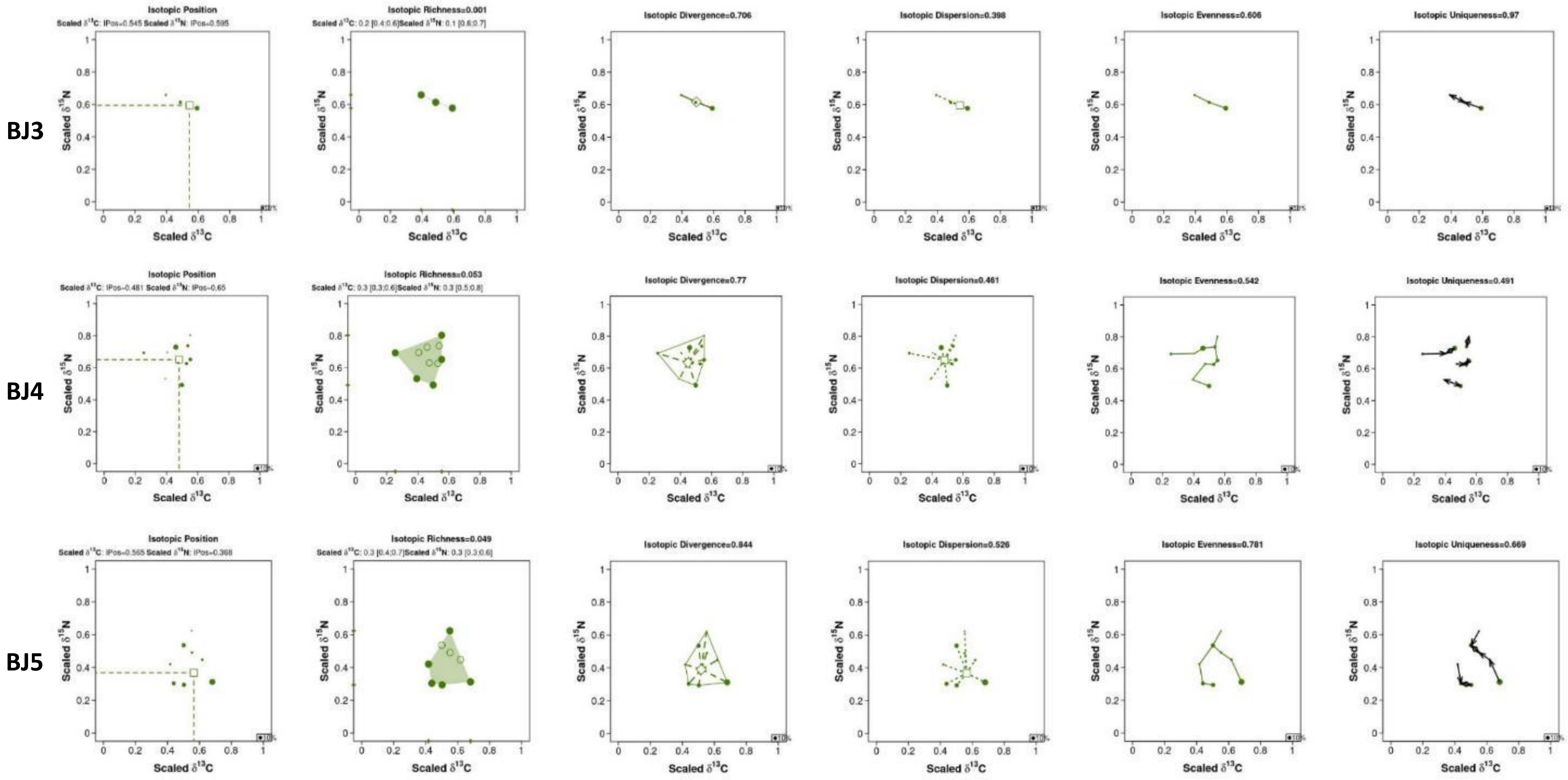

Figure S5. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Thomisidae in the three replicates of jungle rubber in Bukit Duabelas National Park landscape (BJ 3 - 5). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

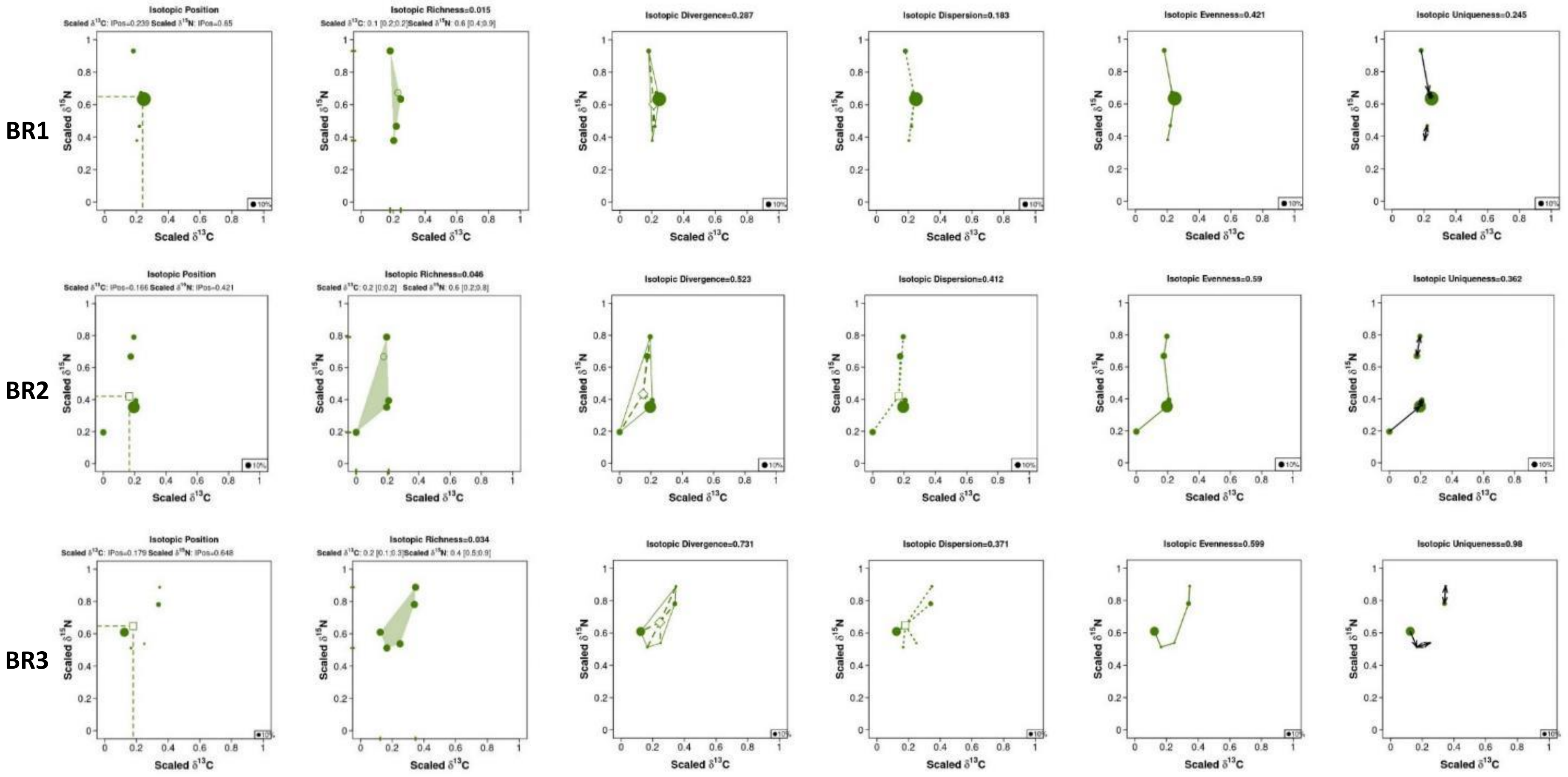

Figure S5. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Thomisidae in the three replicates of rubber plantations in Bukit Duabelas National Park landscape (BR 1 - 3). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

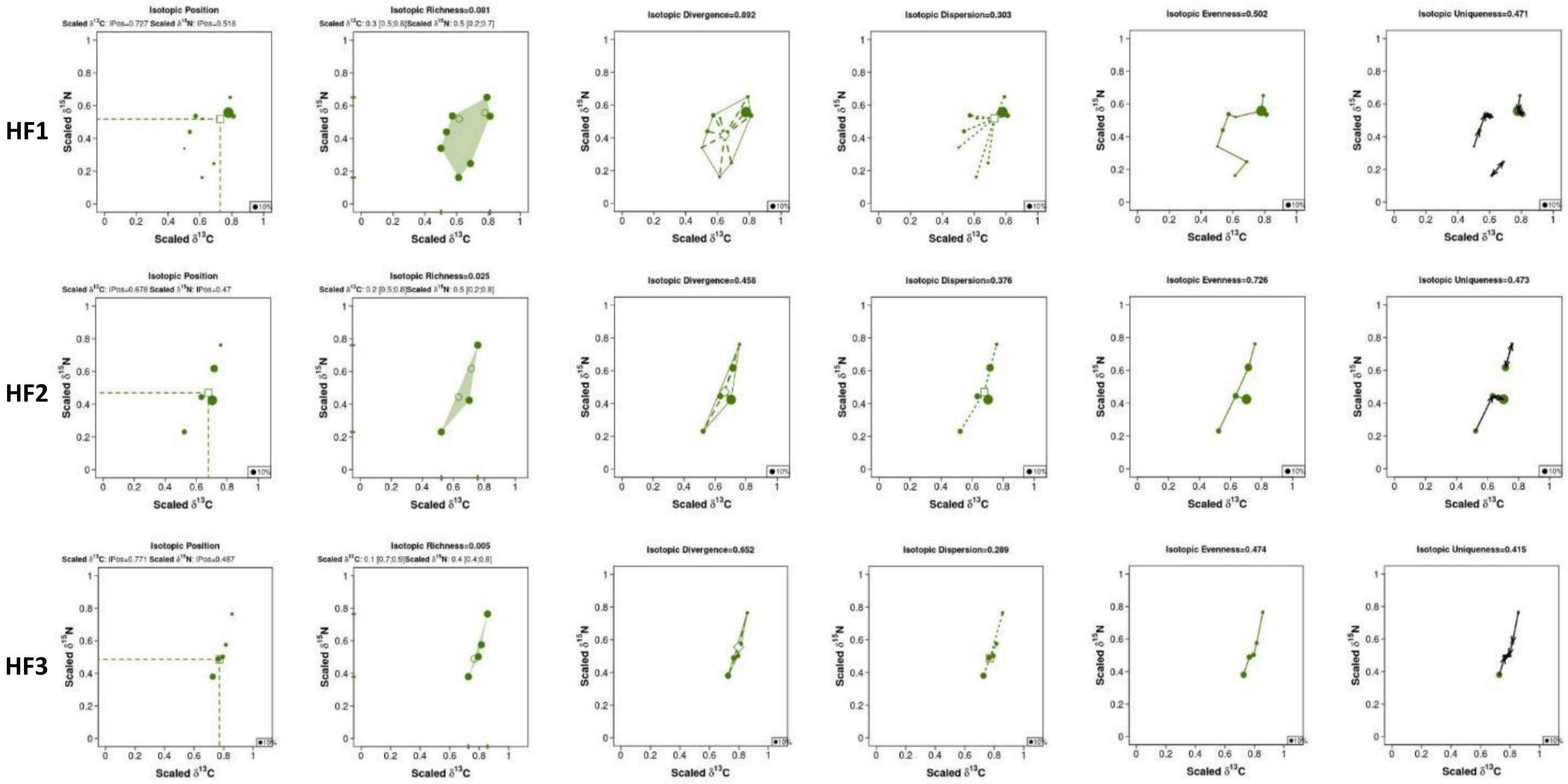

Figure S5. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Thomisidae in the three replicates of rainforest in Harapan landscape (HF 1 - 3). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

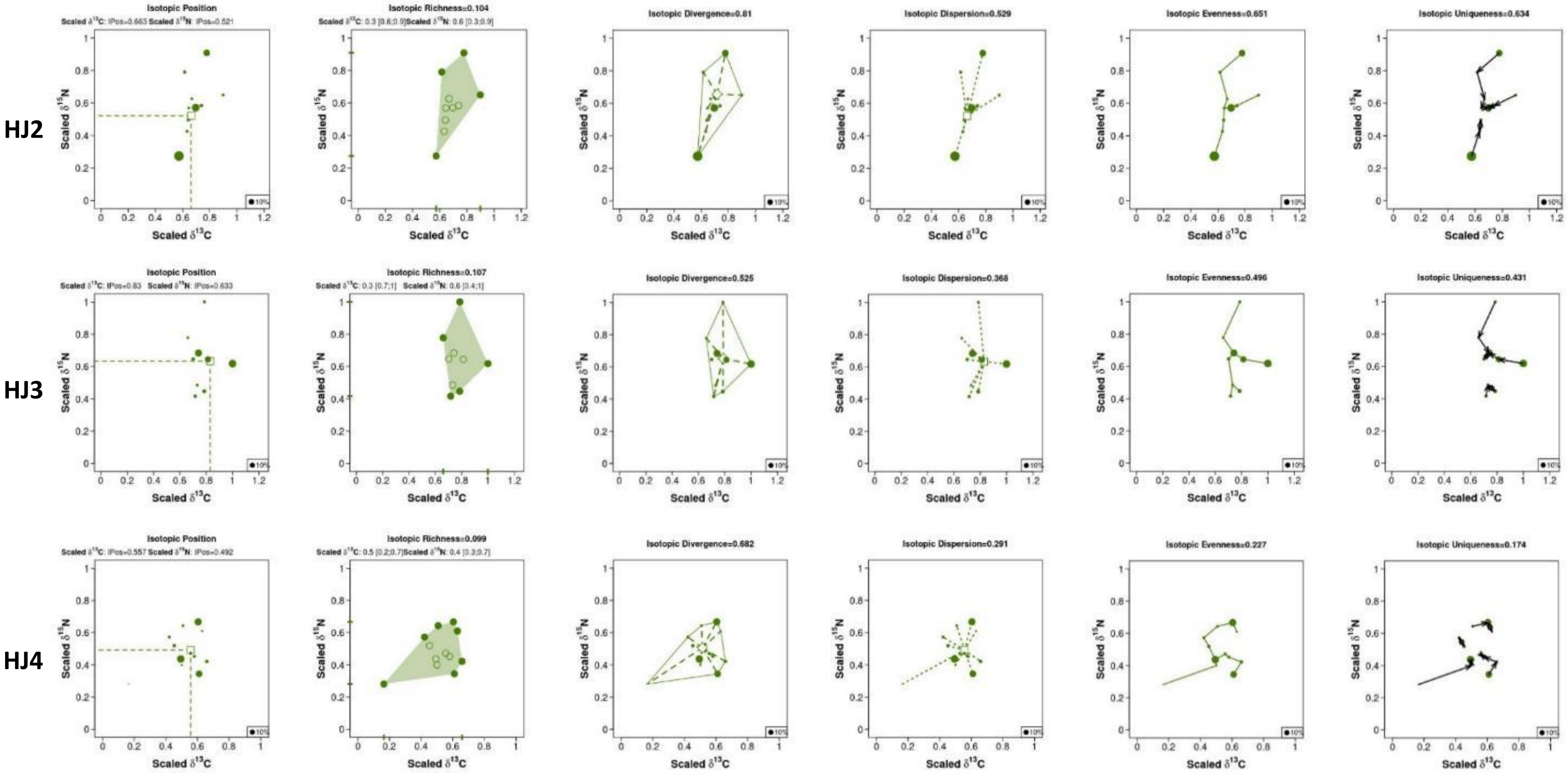

Figure S5. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Thomisidae in the three replicates of jungle rubber in Harapan landscape (HJ 2 - 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods

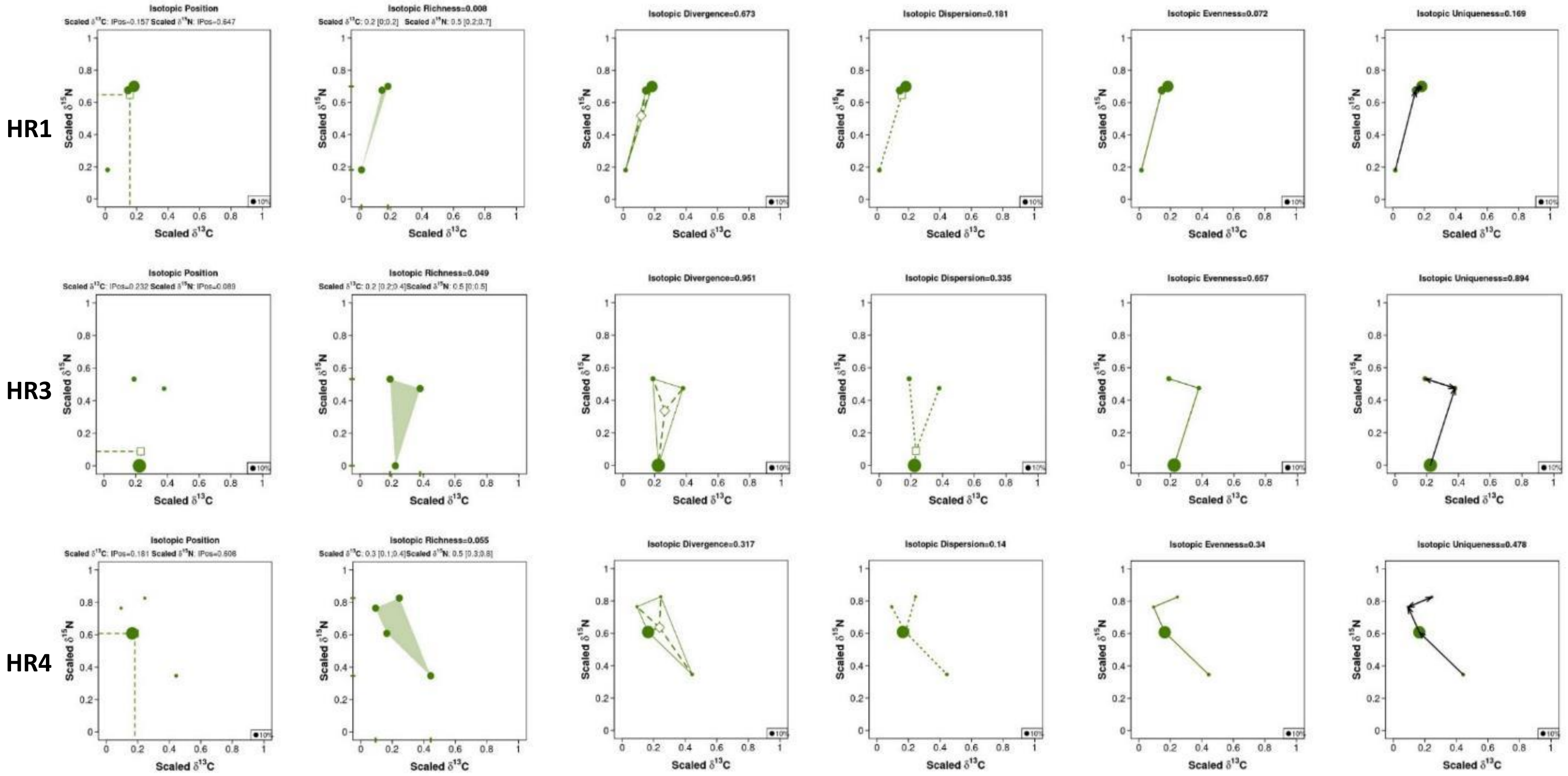

Figure S5. Stable isotope metrics (Isotopic position, isotopic richness, isotopic diverge, isotopic dispersion, isotopic evenness, isotopic uniqueness) of spider family Thomisidae in the three replicates of rubber plantations in Harapan landscape (HR 1, 3, 4). The axes (scaled δ13 C and scaled δ15 N) are scale from 0 to 1. See methods.

Table S1. Absolute and calibrated stable isotope mean values of the full canopy spider morphospecies in four land-use systems [rainforest (F), jungle rubber (J), rubber monoculture (R), oil palm monoculture (O)] in two landscapes [Bukit Duabelas(B) and Harapan (H)]. Absolute δ13C and δ15N values, Leaves-calibrated δ13C and δ15N, Biomass species % - percentage biomass of species per plot.

Year	Season	LS	LU	Core Plot	Sub Plot	Orden	Family	15N Absolute	13C Absolute	13C Calibrated	15N Calibrated	biomass
2013	Dry	BD	F	BF1	BF1.1	Aranae	Araneidae	2.98	-26.75	7.30	2.83	4.08
2013	Dry	BD	F	BF1	BF1.1	Aranae	Clubionidae	2.57	-27.34	6.70	2.42	4.97
2013	Dry	BD	F	BF1	BF1.1	Aranae	Oonopidae	2.86	-28.02	6.02	2.71	3.94
2013	Dry	BD	F	BF1	BF1.1	Aranae	Pholcidae	3.42	-26.82	7.23	3.27	2.00
2013	Dry	BD	F	BF1	BF1.1	Aranae	Salticidae	3.85	-27.50	6.55	3.69	14.55
2013	Dry	BD	F	BF1	BF1.1	Aranae	Sparassidae	3.80	-27.00	7.05	3.65	29.21
2013	Dry	BD	F	BF1	BF1.1	Aranae	Theridiidae	3.61	-26.81	5.61	4.11	3.27
2013	Dry	BD	F	BF2	BF2.1	Aranae	Clubionidae	3.16	-27.75	6.82	2.91	5.71
2013	Dry	BD	F	BF2	BF2.1	Aranae	Corinnidae	4.19	-27.46	7.11	3.94	1.11
2013	Dry	BD	F	BF2	BF2.1	Aranae	Oonopidae	1.80	-28.29	6.28	1.55	0.52
2013	Dry	BD	F	BF2	BF2.1	Aranae	Sparassidae	4.77	-27.31	7.26	4.52	35.87
2013	Dry	BD	F	BF2	BF2.1	Aranae	Tetragnathidae	4.21	-27.09	7.48	3.96	4.52
2013	Dry	BD	F	BF2	BF2.1	Aranae	Theridiidae	4.03	-27.19	7.38	3.78	1.76
2013	Dry	BD	F	BF2	BF2.1	Aranae	Thomisidae	3.85	-27.31	7.27	3.60	7.86
2013	Dry	BD	F	BF2	BF2.1	Aranae	Uloboridae	4.22	-26.67	7.90	3.97	0.98
2013	Dry	BD	F	BF2	BF2.2	Aranae	Mysmenidae	2.72	-27.14	7.43	2.47	0.04
2013	Dry	BD	F	BF2	BF2.2	Aranae	Salticidae	4.12	-28.43	6.14	3.87	10.64
2013	Dry	BD	F	BF3	BF3.1	Aranae	Clubionidae	3.01	-27.13	4.37	3.51	6.40
2013	Dry	BD	F	BF3	BF3.1	Aranae	Corinnidae	3.71	-28.04	5.00	3.28	15.08
2013	Dry	BD	F	BF3	BF3.1	Aranae	Oonopidae	1.54	-28.27	4.77	1.11	0.60
2013	Dry	BD	F	BF3	BF3.1	Aranae	Pholcidae	3.96	-27.42	5.63	3.53	3.07
2013	Dry	BD	F	BF3	BF3.1	Aranae	Scytodidae	1.83	-27.76	5.28	1.40	4.41
2013	Dry	BD	F	BF3	BF3.1	Aranae	Sparassidae	3.34	-27.51	5.53	2.91	14.12
2013	Dry	BD	F	BF3	BF3.1	Aranae	Theridiidae	4.22	-27.52	5.52	3.79	1.98
2013	Dry	BD	F	BF3	BF3.1	Aranae	Thomisidae	3.65	-27.58	5.46	3.22	5.13
2013	Dry	BD	F	BF3	BF3.2	Aranae	Salticidae	3.28	-26.88	4.63	3.72	8.12

2013	Dry	BD	F	BF4	BF4.1	Aranae	Clubionidae	3.58	-27.39	4.76	3.51	8.47
2013	Dry	BD	F	BF4	BF4.1	Aranae	Corinnidae	3.10	-28.11	4.04	3.03	19.66
2013	Dry	BD	F	BF4	BF4.1	Aranae	Oonopidae	2.15	-27.08	5.07	2.08	0.64
2013	Dry	BD	F	BF4	BF4.1	Aranae	Pholcidae	3.94	-27.60	4.55	3.87	4.01
2013	Dry	BD	F	BF4	BF4.1	Aranae	Sparassidae	3.93	-27.34	4.81	3.86	30.72
2013	Dry	BD	F	BF4	BF4.1	Aranae	Theridiidae	3.80	-27.04	5.11	3.73	2.22
2013	Dry	BD	F	BF4	BF4.2	Aranae	Salticidae	3.26	-26.85	4.62	3.73	8.07
2013	Dry	BD	J	BJ3	BJ3.1	Aranae	Corinnidae	0.78	-27.03	5.48	3.60	14.12
2013	Dry	BD	J	BJ3	BJ3.1	Aranae	Oonopidae	-0.42	-27.72	4.79	2.39	0.16
2013	Dry	BD	J	BJ3	BJ3.1	Aranae	Pholcidae	3.39	-26.04	6.48	6.20	2.17
2013	Dry	BD	J	BJ3	BJ3.1	Aranae	Theridiidae	1.88	-26.12	6.39	4.70	1.51
2013	Dry	BD	J	BJ3	BJ3.1	Aranae	Thomisidae	3.32	-27.15	5.36	6.13	1.88
2013	Dry	BD	J	BJ3	BJ3.2	Aranae	Clubionidae	2.34	-27.35	5.16	5.16	6.05
2013	Dry	BD	J	BJ3	BJ3.2	Aranae	Salticidae	3.24	-26.82	4.62	3.74	7.51
2013	Dry	BD	J	BJ4	BJ4.1	Aranae	Araneidae	4.38	-26.61	5.80	6.52	3.49
2013	Dry	BD	J	BJ4	BJ4.1	Aranae	Clubionidae	1.96	-27.48	4.93	4.11	6.15
2013	Dry	BD	J	BJ4	BJ4.1	Aranae	Theridiidae	3.23	-27.29	5.12	5.37	1.15
2013	Dry	BD	J	BJ4	BJ4.1	Aranae	Theridiosomatidae	5.27	-26.64	5.77	7.41	0.11
2013	Dry	BD	J	BJ4	BJ4.1	Aranae	Thomisidae	4.44	-27.26	5.14	6.59	2.92
2013	Dry	BD	J	BJ4	BJ4.2	Aranae	Oonopidae	1.88	-27.46	4.77	2.50	0.34
2013	Dry	BD	J	BJ4	BJ4.2	Aranae	Salticidae	3.30	-26.82	4.60	3.73	7.52
2013	Dry	BD	J	BJ5	BJ5.1	Aranae	Clubionidae	3.38	-27.19	5.46	3.37	5.73
2013	Dry	BD	J	BJ5	BJ5.1	Aranae	Oonopidae	1.59	-27.71	4.94	1.58	0.13
2013	Dry	BD	J	BJ5	BJ5.1	Aranae	Sparassidae	4.70	-26.65	5.99	4.69	45.26
2013	Dry	BD	J	BJ5	BJ5.1	Aranae	Theridiidae	3.49	-27.07	5.57	3.49	2.77
2013	Dry	BD	J	BJ5	BJ5.1	Aranae	Theridiosomatidae	-2.01	-26.24	6.40	-2.02	0.54
2013	Dry	BD	J	BJ5	BJ5.1	Aranae	Thomisidae	4.52	-26.50	5.43	5.05	6.17
2013	Dry	BD	J	BJ5	BJ5.2	Aranae	Salticidae	3.31	-26.79	4.58	3.64	7.73
2013	Dry	BD	J	BJ6	BJ6.1	Aranae	Clubionidae	2.55	-27.85	5.26	4.23	5.52
2013	Dry	BD	J	BJ6	BJ6.1	Aranae	Scytodidae	2.42	-27.85	5.26	4.10	5.98
2013	Dry	BD	J	BJ6	BJ6.1	Aranae	Sparassidae	3.42	-27.43	5.68	5.10	8.56

2013	Dry	BD	J	BJ6	BJ6.1	Aranae	Theridiidae	2.21	-27.85	5.25	3.89	0.84
2013	Dry	BD	J	BJ6	BJ6.2	Aranae	Araneidae	4.55	-26.22	6.89	6.23	7.22
2013	Dry	BD	J	BJ6	BJ6.2	Aranae	Oonopidae	2.46	-27.75	5.36	4.14	0.66
2013	Dry	BD	J	BJ6	BJ6.2	Aranae	Salticidae	3.30	-26.78	4.57	3.65	7.52
2013	Dry	BD	O	BO2	BO2.1	Aranae	Araneidae	4.17	-25.49	4.35	4.49	4.22
2013	Dry	BD	O	BO2	BO2.1	Aranae	Oonopidae	2.39	-25.74	4.09	2.71	0.19
2013	Dry	BD	O	BO2	BO2.1	Aranae	Tetragnathidae	4.30	-26.40	3.43	4.62	0.68
2013	Dry	BD	O	BO2	BO2.2	Aranae	Salticidae	3.43	-26.22	3.62	3.75	7.94
2013	Dry	BD	O	BO2	BO2.2	Aranae	Theridiidae	4.75	-25.48	4.36	5.07	1.02
2013	Dry	BD	O	BO3	BO3.1	Aranae	Araneidae	3.85	-25.70	4.47	3.30	4.62
2013	Dry	BD	O	BO3	BO3.1	Aranae	Oonopidae	3.14	-26.25	3.92	2.58	0.24
2013	Dry	BD	O	BO3	BO3.1	Aranae	Tetragnathidae	6.59	-26.60	3.57	6.04	2.68
2013	Dry	BD	O	BO3	BO3.1	Aranae	Theridiidae	1.63	-26.35	3.81	1.08	2.02
2013	Dry	BD	O	BO3	BO3.2	Aranae	Salticidae	2.88	-26.64	3.53	2.33	11.82
2013	Dry	BD	O	BO4	BO4.1	Aranae	Araneidae	6.58	-24.72	5.55	6.64	3.25
2013	Dry	BD	O	BO4	BO4.1	Aranae	Oonopidae	3.23	-27.01	3.26	3.29	0.20
2013	Dry	BD	O	BO4	BO4.1	Aranae	Sparassidae	4.60	-26.61	3.66	4.65	4.32
2013	Dry	BD	O	BO4	BO4.1	Aranae	Tetragnathidae	5.24	-25.93	4.34	5.30	0.32
2013	Dry	BD	O	BO4	BO4.1	Aranae	Theridiidae	4.81	-26.32	3.95	4.87	1.02
2013	Dry	BD	O	BO4	BO4.2	Aranae	Salticidae	3.59	-27.01	3.26	3.64	4.54
2013	Dry	BD	O	BO5	BO5.1	Aranae	Araneidae	6.93	-24.69	5.13	5.98	2.50
2013	Dry	BD	O	BO5	BO5.1	Aranae	Oonopidae	2.09	-26.56	3.26	1.14	0.15
2013	Dry	BD	O	BO5	BO5.1	Aranae	Tetragnathidae	6.43	-25.64	4.18	5.47	1.73
2013	Dry	BD	O	BO5	BO5.1	Aranae	Theridiidae	3.84	-25.81	4.01	2.88	1.22
2013	Dry	BD	O	BO5	BO5.2	Aranae	Salticidae	3.34	-26.78	4.62	3.67	7.56
2013	Dry	BD	R	BR1	BR1.1	Aranae	Araneidae	6.72	-25.31	3.31	7.85	7.12
2013	Dry	BD	R	BR1	BR1.1	Aranae	Clubionidae	3.57	-25.80	2.83	4.71	7.20
2013	Dry	BD	R	BR1	BR1.1	Aranae	Theridiidae	4.20	-25.46	3.16	5.34	1.67
2013	Dry	BD	R	BR1	BR1.1	Aranae	Thomisidae	4.99	-25.63	2.99	6.13	12.16
2013	Dry	BD	R	BR1	BR1.2	Aranae	Oonopidae	-0.15	-26.93	1.69	0.99	0.20
2013	Dry	BD	R	BR1	BR1.2	Aranae	Salticidae	3.32	-26.78	4.57	3.68	7.60

2013	Dry	BD	R	BR2	BR2.1	Aranae	Araneidae	1.39	-26.61	1.74	2.24	0.89
2013	Dry	BD	R	BR2	BR2.1	Aranae	Tetragnathidae	2.22	-25.94	2.41	3.08	0.43
2013	Dry	BD	R	BR2	BR2.1	Aranae	Thomisidae	3.78	-25.88	2.47	4.64	2.04
2013	Dry	BD	R	BR2	BR2.2	Aranae	Clubionidae	2.77	-26.14	2.21	3.63	7.96
2013	Dry	BD	R	BR2	BR2.2	Aranae	Salticidae	3.25	-26.80	4.62	3.59	7.64
2013	Dry	BD	R	BR3	BR3.1	Aranae	Clubionidae	3.18	-27.10	4.22	3.37	6.37
2013	Dry	BD	R	BR3	BR3.1	Aranae	Sparassidae	5.04	-27.50	2.21	6.34	22.59
2013	Dry	BD	R	BR3	BR3.1	Aranae	Theridiidae	2.42	-26.77	2.94	3.73	1.45
2013	Dry	BD	R	BR3	BR3.1	Aranae	Thomisidae	5.36	-26.47	3.24	6.66	7.61
2013	Dry	BD	R	BR3	BR3.2	Aranae	Salticidae	3.41	-26.95	2.76	4.72	8.90
2013	Dry	BD	R	BR4	BR4.1	Aranae	Araneidae	4.11	-26.47	2.54	5.52	4.12
2013	Dry	BD	R	BR4	BR4.1	Aranae	Clubionidae	5.59	-27.49	1.51	7.00	7.79
2013	Dry	BD	R	BR4	BR4.1	Aranae	Sparassidae	4.86	-27.52	3.63	5.12	31.89
2013	Dry	BD	R	BR4	BR4.1	Aranae	Tetragnathidae	4.39	-26.96	2.05	5.81	1.19
2013	Dry	BD	R	BR4	BR4.1	Aranae	Theridiidae	2.59	-26.94	2.06	4.01	0.90
2013	Dry	BD	R	BR4	BR4.2	Aranae	Salticidae	3.23	-26.82	4.75	3.52	7.57
2013	Dry	HR	F	HF1	HF1.1	Aranae	Araneidae	2.75	-27.25	7.05	4.40	3.90
2013	Dry	HR	F	HF1	HF1.1	Aranae	Clubionidae	1.99	-27.86	6.43	3.65	7.12
2013	Dry	HR	F	HF1	HF1.1	Aranae	Oonopidae	2.07	-28.70	5.59	3.72	0.51
2013	Dry	HR	F	HF1	HF1.1	Aranae	Salticidae	3.20	-26.83	4.89	3.47	7.62
2013	Dry	HR	F	HF1	HF1.1	Aranae	Theridiidae	2.78	-27.58	6.71	4.44	1.83
2013	Dry	HR	F	HF1	HF1.1	Aranae	Thomisidae	2.59	-27.51	6.79	4.24	5.56
2013	Dry	HR	F	HF2	HF2.1	Aranae	Araneidae	2.48	-27.13	6.41	3.17	21.12
2013	Dry	HR	F	HF2	HF2.1	Aranae	Clubionidae	2.43	-27.66	5.88	3.13	3.88
2013	Dry	HR	F	HF2	HF2.1	Aranae	Salticidae	3.21	-26.79	4.77	3.39	7.73
2013	Dry	HR	F	HF2	HF2.1	Aranae	Theridiidae	2.91	-27.45	6.08	3.60	1.86
2013	Dry	HR	F	HF2	HF2.1	Aranae	Thomisidae	4.12	-26.66	6.87	4.81	8.45
2013	Dry	HR	F	HF2	HF2.2	Aranae	Oonopidae	0.92	-27.95	5.59	1.62	0.39
2013	Dry	HR	F	HF2	HF2.2	Aranae	Pholcidae	2.72	-27.25	6.29	3.42	1.51
2013	Dry	HR	F	HF3	HF3.1	Aranae	Araneidae	2.30	-27.96	7.52	2.56	2.12
2013	Dry	HR	F	HF3	HF3.1	Aranae	Clubionidae	1.70	-27.89	7.58	1.96	6.69

2013	Dry	HR	F	HF3	HF3.1	Aranae	Linyphiidae	1.52	-28.36	7.12	1.78	0.83
2013	Dry	HR	F	HF3	HF3.1	Aranae	Pholcidae	3.44	-27.77	7.70	3.69	2.05
2013	Dry	HR	F	HF3	HF3.1	Aranae	Salticidae	3.27	-26.72	4.73	3.42	8.04
2013	Dry	HR	F	HF3	HF3.1	Aranae	Theridiidae	3.67	-27.61	7.87	3.93	6.02
2013	Dry	HR	F	HF3	HF3.1	Aranae	Thomisidae	5.06	-27.52	7.96	5.32	2.71
2013	Dry	HR	F	HF3	HF3.2	Aranae	Cheiracanthiidae	-0.59	-28.70	6.78	-0.33	8.13
2013	Dry	HR	F	HF4	HF4.1	Aranae	Araneidae	4.62	-26.86	7.36	4.74	8.91
2013	Dry	HR	F	HF4	HF4.1	Aranae	Oonopidae	1.51	-28.20	6.02	1.63	0.36
2013	Dry	HR	F	HF4	HF4.1	Aranae	Salticidae	3.31	-26.69	4.66	3.45	8.28
2013	Dry	HR	F	HF4	HF4.1	Aranae	Sparassidae	1.71	-28.49	5.73	1.83	113.48
2013	Dry	HR	F	HF4	HF4.1	Aranae	Theridiidae	2.45	-27.66	6.56	2.57	3.11
2013	Dry	HR	J	HJ1	HJ1.1	Aranae	Salticidae	5.25	-25.91	7.10	6.17	4.35
2013	Dry	HR	J	HJ1	HJ1.1	Aranae	Tetragnathidae	5.17	-24.91	8.10	6.09	46.26
2013	Dry	HR	J	HJ1	HJ1.1	Aranae	Thomisidae	6.02	-26.21	6.80	6.94	12.05
2013	Dry	HR	J	HJ2	HJ2.1	Aranae	Cheiracanthiidae	1.07	-27.15	6.06	2.64	4.88
2013	Dry	HR	J	HJ2	HJ2.1	Aranae	Clubionidae	2.02	-27.15	6.06	3.59	4.19
2013	Dry	HR	J	HJ2	HJ2.1	Aranae	Oonopidae	1.36	-27.69	5.51	2.93	1.03
2013	Dry	HR	J	HJ2	HJ2.1	Aranae	Salticidae	3.35	-26.57	4.58	3.52	8.40
2013	Dry	HR	J	HJ2	HJ2.1	Aranae	Theridiidae	1.96	-26.59	6.62	3.53	3.21
2013	Dry	HR	J	HJ2	HJ2.1	Aranae	Thomisidae	5.00	-26.16	5.88	5.41	5.98
2013	Dry	HR	J	HJ3	HJ3.1	Aranae	Oonopidae	0.57	-27.14	6.02	2.07	0.25
2013	Dry	HR	J	HJ3	HJ3.1	Aranae	Salticidae	3.44	-26.51	4.48	3.50	7.99
2013	Dry	HR	J	HJ3	HJ3.1	Aranae	Theridiidae	2.87	-25.80	7.37	4.37	1.16
2013	Dry	HR	J	HJ3	HJ3.1	Aranae	Thomisidae	4.83	-25.40	7.77	6.33	5.90
2013	Dry	HR	J	HJ3	HJ3.2	Aranae	Clubionidae	3.28	-26.78	3.63	2.87	6.28
2013	Dry	HR	J	HJ3	HJ3.2	Aranae	Tetragnathidae	4.34	-25.47	7.70	5.84	16.92
2013	Dry	HR	J	HJ4	HJ4.1	Aranae	Clubionidae	3.02	-27.33	4.92	2.48	5.05
2013	Dry	HR	J	HJ4	HJ4.1	Aranae	Oonopidae	1.12	-27.66	4.58	0.58	0.32
2013	Dry	HR	J	HJ4	HJ4.1	Aranae	Salticidae	3.50	-26.60	4.23	3.41	7.98
2013	Dry	HR	J	HJ4	HJ4.1	Aranae	Sparassidae	4.69	-26.97	5.28	4.15	9.80
2013	Dry	HR	J	HJ4	HJ4.1	Aranae	Theridiidae	4.21	-27.20	5.05	3.67	1.41

2013	Dry	HR	J	HJ4	HJ4.1	Aranae	Thomisidae	5.23	-26.68	5.57	4.69	6.75
2013	Dry	HR	O	HO1	HO1.1	Aranae	Araneidae	5.46	-25.81	4.13	5.42	123.58
2013	Dry	HR	O	HO1	HO1.1	Aranae	Clubionidae	4.14	-26.44	3.49	4.10	1.70
2013	Dry	HR	O	HO1	HO1.1	Aranae	Salticidae	4.44	-26.10	3.84	4.40	5.99
2013	Dry	HR	O	HO1	HO1.1	Aranae	Theridiidae	3.87	-26.04	3.92	2.98	2.12
2013	Dry	HR	O	HO1	HO1.2	Aranae	Scytodidae	6.28	-25.04	4.89	6.24	27.28
2013	Dry	HR	O	HO2	HO2.1	Aranae	Araneidae	5.33	-24.92	5.24	5.31	14.50
2013	Dry	HR	O	HO2	HO2.1	Aranae	Salticidae	3.40	-26.55	4.09	3.39	7.91
2013	Dry	HR	O	HO2	HO2.1	Aranae	Tetragnathidae	4.42	-25.02	5.13	4.40	4.81
2013	Dry	HR	O	HO2	HO2.1	Aranae	Theridiidae	1.83	-25.38	4.78	1.82	1.12
2013	Dry	HR	O	HO3	HO3.1	Aranae	Araneidae	4.41	-25.11	5.84	3.07	3.31
2013	Dry	HR	O	HO3	HO3.1	Aranae	Clubionidae	1.38	-25.76	5.20	0.04	3.63
2013	Dry	HR	O	HO3	HO3.1	Aranae	Salticidae	3.29	-26.64	4.06	3.24	8.36
2013	Dry	HR	O	HO3	HO3.1	Aranae	Tetragnathidae	7.79	-25.47	5.49	6.45	3.35
2013	Dry	HR	O	HO3	HO3.2	Aranae	Theridiidae	2.94	-25.46	5.50	1.60	1.19
2013	Dry	HR	O	HO4	HO4.1	Aranae	Araneidae	6.54	-25.25	4.95	5.97	7.83
2013	Dry	HR	O	HO4	HO4.1	Aranae	Oonopidae	3.03	-28.08	2.12	2.47	0.20
2013	Dry	HR	O	HO4	HO4.1	Aranae	Salticidae	3.80	-25.93	4.27	3.24	8.18
2013	Dry	HR	O	HO4	HO4.1	Aranae	Tetragnathidae	7.40	-26.11	4.09	6.84	8.83
2013	Dry	HR	O	HO4	HO4.1	Aranae	Theridiidae	5.46	-26.96	3.24	4.89	0.66
2013	Dry	HR	R	HR1	HR1.1	Aranae	Clubionidae	4.36	-26.86	1.18	3.25	14.63
2013	Dry	HR	R	HR1	HR1.1	Aranae	Linyphiidae	2.16	-26.75	1.29	1.04	1.01
2013	Dry	HR	R	HR1	HR1.1	Aranae	Salticidae	3.67	-26.58	1.46	2.55	7.53
2013	Dry	HR	R	HR1	HR1.1	Aranae	Theridiidae	3.97	-25.69	2.35	2.86	6.30
2013	Dry	HR	R	HR1	HR1.1	Aranae	Thomisidae	6.17	-25.92	2.12	5.06	3.79
2013	Dry	HR	R	HR2	HR2.1	Aranae	Clubionidae	4.88	-26.26	2.14	4.92	6.31
2013	Dry	HR	R	HR2	HR2.1	Aranae	Linyphiidae	-0.75	-26.76	1.64	-0.72	0.26
2013	Dry	HR	R	HR2	HR2.1	Aranae	Salticidae	3.25	-26.80	4.10	3.48	8.57
2013	Dry	HR	R	HR2	HR2.1	Aranae	Tetragnathidae	4.99	-25.55	2.85	5.03	1.92
2013	Dry	HR	R	HR3	HR3.1	Aranae	Araneidae	3.83	-26.41	2.96	1.63	4.13
2013	Dry	HR	R	HR3	HR3.1	Aranae	Clubionidae	3.13	-26.85	2.53	0.93	4.45

2013	Dry	HR	R	HR3	HR3.1	Aranae	Salticidae	3.07	-26.95	4.32	3.31	8.75
2013	Dry	HR	R	HR3	HR3.2	Aranae	Theridiidae	4.70	-27.56	1.81	2.49	1.21
2013	Dry	HR	R	HR3	HR3.2	Aranae	Thomisidae	5.27	-25.97	3.41	3.07	10.56
2013	Dry	HR	R	HR4	HR4.1	Aranae	Salticidae	3.19	-27.07	4.47	3.81	8.84
2013	Dry	HR	R	HR4	HR4.1	Aranae	Thomisidae	4.96	-26.35	5.89	6.23	5.21
2013	Dry	HR	R	HR4	HR4.2	Aranae	Clubionidae	4.04	-28.07	1.96	5.13	4.47

Table S2. One-dimensional metrics of the total spider canopy communities, and selected families [average position, maximum, minimum and range (max-min)]; Variable analyzed (Δ13C and Δ15N), Land-use system – land use system ordered by value, Value – stable isotope value, Letter – indicator of significant difference within respective variable. Δ13C and Δ15N values were scaled between 0 and 1 based on maximum and minimum across communities to ensure equal contribution. No scaled values are also presented.

TOTAL COMMUNITY					
Metric	**variable**	**Land-use system**	**Value (0-1)**	**value(no scaled)**	**letter**
Average position	$\Delta^{13}C$	Rainforest	0.77	6.06	a
Average position	$\Delta^{13}C$	Jungle rubber	0.74	5.79	a
Average position	$\Delta^{13}C$	Oil palm	0.57	4.33	b
Average position	$\Delta^{13}C$	Rubber	0.42	3.02	c
Average position	$\Delta^{15}N$	Jungle rubber	0.67	4.59	a
Average position	$\Delta^{15}N$	Rubber	0.65	4.36	ab
Average position	$\Delta^{15}N$	Oil palm	0.64	4.30	ab
Average position	$\Delta^{15}N$	Rainforest	0.54	3.28	b
Maximum	$\Delta^{13}C$	Rainforest	0.86	6.90	a
Maximum	$\Delta^{13}C$	Jungle rubber	0.84	6.70	a
Maximum	$\Delta^{13}C$	Oil palm	0.65	5.05	b
Maximum	$\Delta^{13}C$	Rubber	0.57	4.35	b
Maximum	$\Delta^{15}N$	Oil palm	0.82	6.07	a
Maximum	$\Delta^{15}N$	Jungle rubber	0.82	6.03	a
Maximum	$\Delta^{15}N$	Rubber	0.78	5.72	ab
Maximum	$\Delta^{15}N$	Rainforest	0.66	4.45	b
Minimum	$\Delta^{13}C$	Rainforest	0.64	4.90	a
Minimum	$\Delta^{13}C$	Jungle rubber	0.61	4.70	a
Minimum	$\Delta^{13}C$	Oil palm	0.46	3.41	b
Minimum	$\Delta^{13}C$	Rubber	0.23	1.39	c
Minimum	$\Delta^{15}N$	Jungle rubber	0.43	2.24	a
Minimum	$\Delta^{15}N$	Oil palm	0.40	1.94	a
Minimum	$\Delta^{15}N$	Rubber	0.40	1.90	a
Minimum	$\Delta^{15}N$	Rainforest	0.38	1.69	a
Range (max-min)	$\Delta^{13}C$	Rubber	0.34	2.96	a
Range (max-min)	$\Delta^{13}C$	Jungle rubber	0.23	2.00	a
Range (max-min)	$\Delta^{13}C$	Rainforest	0.23	2.00	a
Range (max-min)	$\Delta^{13}C$	Oil palm	0.19	1.65	a
Range (max-min)	$\Delta^{15}N$	Oil palm	0.42	4.13	a
Range (max-min)	$\Delta^{15}N$	Rubber	0.39	3.82	a
Range (max-min)	$\Delta^{15}N$	Jungle rubber	0.38	3.80	a
Range (max-min)	$\Delta^{15}N$	Rainforest	0.28	2.76	a

SALTICIDAE					
Metric	**variable**	**Land-use system**	**value (0-1)**	**value(no scaled)**	**letter**
Average position	$\Delta^{13}C$	Jungle rubber	0.69	5.90	a
Average position	$\Delta^{13}C$	Rainforest	0.68	5.79	a
Average position	$\Delta^{13}C$	Oil palm	0.48	4.03	b
Average position	$\Delta^{13}C$	Rubber	0.29	2.30	c
Average position	$\Delta^{15}N$	Jungle rubber	0.59	4.59	a
Average position	$\Delta^{15}N$	Rubber	0.56	4.22	a
Average position	$\Delta^{15}N$	Rainforest	0.49	3.46	a
Average position	$\Delta^{15}N$	Oil palm	0.47	3.17	a
Maximum	$\Delta^{13}C$	Rainforest	0.83	7.15	a
Maximum	$\Delta^{13}C$	Jungle rubber	0.78	6.74	a
Maximum	$\Delta^{13}C$	Oil palm	0.56	4.71	b
Maximum	$\Delta^{13}C$	Rubber	0.44	3.66	c
Maximum	$\Delta^{15}N$	Rubber	0.85	7.46	a
Maximum	$\Delta^{15}N$	Jungle rubber	0.81	7.06	ab
Maximum	$\Delta^{15}N$	Oil palm	0.69	5.63	b
Maximum	$\Delta^{15}N$	Rainforest	0.68	5.60	b
Minimum	$\Delta^{13}C$	Rainforest	0.57	4.81	a
Minimum	$\Delta^{13}C$	Jungle rubber	0.54	4.59	a
Minimum	$\Delta^{13}C$	Oil palm	0.39	3.18	b
Minimum	$\Delta^{13}C$	Rubber	0.11	0.68	c
Minimum	$\Delta^{15}N$	Jungle rubber	0.33	1.63	a
Minimum	$\Delta^{15}N$	Oil palm	0.28	1.09	a
Minimum	$\Delta^{15}N$	Rainforest	0.26	0.93	a
Minimum	$\Delta^{15}N$	Rubber	0.24	0.69	a
Range (max-min)	$\Delta^{13}C$	Rubber	0.33	2.98	a
Range (max-min)	$\Delta^{13}C$	Rainforest	0.26	2.34	ab
Range (max-min)	$\Delta^{13}C$	Jungle rubber	0.24	2.15	ab
Range (max-min)	$\Delta^{13}C$	Oil palm	0.17	1.53	b
Range (max-min)	$\Delta^{15}N$	Rubber	0.61	6.77	a
Range (max-min)	$\Delta^{15}N$	Jungle rubber	0.49	5.44	ab
Range (max-min)	$\Delta^{15}N$	Rainforest	0.42	4.66	b
Range (max-min)	$\Delta^{15}N$	Oil palm	0.41	4.55	b

CLUBIONIDAE					
Metric	**variable**	**Land-use system**	**value(0-1)**	**value(no scaled)**	**letter**
Average position	$\Delta^{13}C$	Rainforest	0.69	6.17	a
Average position	$\Delta^{13}C$	Jungle rubber	0.63	5.63	a
Average position	$\Delta^{13}C$	Rubber	0.22	2.05	b
Average position	$\Delta^{15}N$	Rubber	0.71	4.52	a
Average position	$\Delta^{15}N$	Jungle rubber	0.63	3.74	a
Average position	$\Delta^{15}N$	Rainforest	0.55	2.86	a
Maximum	$\Delta^{13}C$	Rainforest	0.79	7.02	a
Maximum	$\Delta^{13}C$	Jungle rubber	0.72	6.39	a
Maximum	$\Delta^{13}C$	Rubber	0.32	2.97	b
Maximum	$\Delta^{15}N$	Rubber	0.88	6.15	a
Maximum	$\Delta^{15}N$	Jungle rubber	0.83	5.66	a
Maximum	$\Delta^{15}N$	Rainforest	0.62	3.56	b
Minimum	$\Delta^{13}C$	Rainforest	0.60	5.40	a
Minimum	$\Delta^{13}C$	Jungle rubber	0.55	4.91	a
Minimum	$\Delta^{13}C$	Rubber	0.11	1.11	b
Minimum	$\Delta^{15}N$	Rubber	0.44	1.77	a
Minimum	$\Delta^{15}N$	Rainforest	0.42	1.60	a
Minimum	$\Delta^{15}N$	Jungle rubber	0.40	1.42	a
Range (max-min)	$\Delta^{13}C$	Rubber	0.21	1.86	a
Range (max-min)	$\Delta^{13}C$	Rainforest	0.19	1.62	a
Range (max-min)	$\Delta^{13}C$	Jungle rubber	0.17	1.48	a
Range (max-min)	$\Delta^{15}N$	Rubber	0.44	4.37	a
Range (max-min)	$\Delta^{15}N$	Jungle rubber	0.43	4.24	ab
Range (max-min)	$\Delta^{15}N$	Rainforest	0.20	1.96	b

THERIDIIDAE

Metric	variable	Land-use system	value(0-1)	value (no scaled)	letter
Average position	$\Delta^{13}C$	Rainforest	0.82	6.85	a
Average position	$\Delta^{13}C$	Jungle rubber	0.76	6.09	a
Average position	$\Delta^{13}C$	Oil palm	0.62	4.30	b
Average position	$\Delta^{13}C$	Rubber	0.51	2.75	c
Average position	$\Delta^{15}N$	Jungle rubber	0.67	4.26	a
Average position	$\Delta^{15}N$	Rubber	0.65	3.95	a
Average position	$\Delta^{15}N$	Rainforest	0.64	3.73	a
Average position	$\Delta^{15}N$	Oil palm	0.62	3.47	a
Maximum	$\Delta^{13}C$	Rainforest	0.91	8.07	a
Maximum	$\Delta^{13}C$	Jungle rubber	0.86	7.42	a
Maximum	$\Delta^{13}C$	Oil palm	0.70	5.27	b
Maximum	$\Delta^{13}C$	Rubber	0.60	4.03	b
Maximum	$\Delta^{15}N$	Jungle rubber	0.84	7.34	a
Maximum	$\Delta^{15}N$	Oil palm	0.82	7.00	a
Maximum	$\Delta^{15}N$	Rainforest	0.81	6.81	a
Maximum	$\Delta^{15}N$	Rubber	0.81	6.76	a
Minimum	$\Delta^{13}C$	Rainforest	0.70	5.25	a
Minimum	$\Delta^{13}C$	Jungle rubber	0.62	4.30	ab
Minimum	$\Delta^{13}C$	Oil palm	0.54	3.15	b
Minimum	$\Delta^{13}C$	Rubber	0.30	0.07	c
Minimum	$\Delta^{15}N$	Jungle rubber	0.48	1.03	a
Minimum	$\Delta^{15}N$	Rubber	0.43	0.13	a
Minimum	$\Delta^{15}N$	Rainforest	0.42	-0.03	a
Minimum	$\Delta^{15}N$	Oil palm	0.32	-1.64	a
Range (max-min)	$\Delta^{13}C$	Rubber	0.30	3.96	a
Range (max-min)	$\Delta^{13}C$	Jungle rubber	0.24	3.11	a
Range (max-min)	$\Delta^{13}C$	Rainforest	0.22	2.82	a
Range (max-min)	$\Delta^{13}C$	Oil palm	0.16	2.13	a
Range (max-min)	$\Delta^{15}N$	Oil palm	0.50	8.65	a
Range (max-min)	$\Delta^{15}N$	Rainforest	0.40	6.84	a
Range (max-min)	$\Delta^{15}N$	Rubber	0.39	6.64	a
Range (max-min)	$\Delta^{15}N$	Jungle rubber	0.37	6.32	a

THOMISIDAE					
Metric	**variable**	**Land-use system**	**value(0-1)**	**value(no scaled)**	**letter**
Average position	$\Delta^{13}C$	Rainforest	0.68	6.99	a
Average position	$\Delta^{13}C$	Jungle rubber	0.61	6.36	a
Average position	$\Delta^{13}C$	Rubber	0.19	2.79	b
Average position	$\Delta^{15}N$	Jungle rubber	0.54	5.33	a
Average position	$\Delta^{15}N$	Rubber	0.51	4.97	a
Average position	$\Delta^{15}N$	Rainforest	0.45	4.33	a
Maximum	$\Delta^{13}C$	Rainforest	0.77	7.73	a
Maximum	$\Delta^{13}C$	Jungle rubber	0.73	7.43	a
Maximum	$\Delta^{13}C$	Rubber	0.30	3.73	b
Maximum	$\Delta^{15}N$	Rubber	0.78	7.88	a
Maximum	$\Delta^{15}N$	Jungle rubber	0.78	7.87	a
Maximum	$\Delta^{15}N$	Rainforest	0.64	6.34	a
Minimum	$\Delta^{13}C$	Rainforest	0.56	5.93	a
Minimum	$\Delta^{13}C$	Jungle rubber	0.41	4.67	a
Minimum	$\Delta^{13}C$	Rubber	0.10	2.00	b
Minimum	$\Delta^{15}N$	Jungle rubber	0.39	3.65	a
Minimum	$\Delta^{15}N$	Rubber	0.27	2.34	a
Minimum	$\Delta^{15}N$	Rainforest	0.24	2.03	a
Range (max-min)	$\Delta^{13}C$	Jungle rubber	0.32	2.75	a
Range (max-min)	$\Delta^{13}C$	Rainforest	0.21	1.80	a
Range (max-min)	$\Delta^{13}C$	Rubber	0.20	1.73	a
Range (max-min)	$\Delta^{15}N$	Rubber	0.51	5.54	a
Range (max-min)	$\Delta^{15}N$	Rainforest	0.40	4.31	a
Range (max-min)	$\Delta^{15}N$	Jungle rubber	0.39	4.22	a

Table S3. Multi-dimensional metrics of the full canopy spider communities, and selected families [isotopic dispersion ('IDis'), isotopic divergence ('IDiv'), isotopic evenness ('IEve'), isotopic richness ('IRic'), isotopic uniqueness ('IUni')]; Land-use system –ordered by value, Letter – indicator of significant difference within respective metrics. Δ13C and Δ15N values were scaled between 0 and 1 based on maximum and minimum across communities to ensure equal contribution.

TOTAL COMMUNITY				**SALTICIDAE**			
Multidimensional Metrics	**Land-use system**	**Value**	**Letter**	**Multidimensional Metrics**	**Land-use system**	**Value**	**Letter**
IRic	Rubber	0.05	a	IRic	Rubber	0.10	a
IRic	Jungle rubber	0.04	a	IRic	Jungle rubber	0.07	ab
IRic	Rainforest	0.04	a	IRic	Rainforest	0.05	b
IRic	Oil palm	0.03	a	IRic	Oil palm	0.04	b
IDiv	Jungle rubber	0.78	a	IDiv	Oil palm	0.81	a
IDiv	Rainforest	0.70	ab	IDiv	Rainforest	0.77	a
IDiv	Rubber	0.66	ab	IDiv	Rubber	0.72	a
IDiv	Oil palm	0.62	b	IDiv	Jungle rubber	0.67	a
IDis	Jungle rubber	0.44	a	IDis	Oil palm	0.60	a
IDis	Rubber	0.44	a	IDis	Rainforest	0.45	ab
IDis	Rainforest	0.39	a	IDis	Rubber	0.44	b
IDis	Oil palm	0.38	a	IDis	Jungle rubber	0.34	b
IEve	Rubber	0.62	a	IEve	Oil palm	0.69	a
IEve	Oil palm	0.61	a	IEve	Rainforest	0.59	a
IEve	Rainforest	0.60	a	IEve	Jungle rubber	0.59	a
IEve	Jungle rubber	0.56	a	IEve	Rubber	0.59	a
IUni	Rubber	0.60	a	IUni	Oil palm	0.63	a
IUni	Oil palm	0.59	a	IUni	Rainforest	0.57	a
IUni	Jungle rubber	0.52	a	IUni	Rubber	0.54	a
IUni	Rainforest	0.46	a	IUni	Jungle rubber	0.50	a

CLUBIONIDAE				THERIDIIDAE			
Multidimensional Metrics	**Land-use system**	**Value**	**Letter**	**Multidimensional Metrics**	**Land-use system**	**Value**	**Letter**
IRic	Rubber	0.04	a	IRic	Rubber	0.06	a
IRic	Jungle rubber	0.04	a	IRic	Jungle rubber	0.05	a
IRic	Rainforest	0.02	a	IRic	Rainforest	0.04	a
IRic	Oil palm	N/A	N/A	IRic	Oil palm	0.04	a
IDiv	Rainforest	0.78	a	IDiv	Rubber	0.76	a
IDiv	Jungle rubber	0.69	a	IDiv	Jungle rubber	0.72	a
IDiv	Rubber	0.66	a	IDiv	Oil palm	0.71	a
IDiv	Oil palm	N/A	N/A	IDiv	Rainforest	0.68	a
IDis	Rainforest	0.62	a	IDis	Jungle rubber	0.50	a
IDis	Rubber	0.49	a	IDis	Rubber	0.47	a
IDis	Jungle rubber	0.46	a	IDis	Oil palm	0.45	a
IDis	Oil palm	N/A	N/A	IDis	Rainforest	0.45	a
IEve	Rainforest	0.73	a	IEve	Rainforest	0.66	a
IEve	Jungle rubber	0.67	a	IEve	Oil palm	0.65	a
IEve	Rubber	0.58	a	IEve	Rubber	0.64	a
IEve	Oil palm	N/A	N/A	IEve	Jungle rubber	0.64	a
IUni	Rainforest	0.69	a	IUni	Jungle rubber	0.57	a
IUni	Jungle rubber	0.52	a	IUni	Oil palm	0.57	a
IUni	Rubber	0.50	a	IUni	Rubber	0.52	a
IUni	Oil palm	N/A	N/A	IUni	Rainforest	0.45	a

THOMISIDAE			
Multidimensional Metrics	**Land-use system**	**Value**	**Letter**
IRic	Jungle rubber	0.07	a
IRic	Rubber	0.03	a
IRic	Rainforest	0.03	a
IDiv	Jungle rubber	0.72	a
IDiv	Rainforest	0.69	a
IDiv	Rubber	0.58	a
IDis	Jungle rubber	0.43	a
IDis	Rainforest	0.39	ab
IDis	Rubber	0.27	b
IEve	Rainforest	0.66	a
IEve	Jungle rubber	0.55	a
IEve	Rubber	0.45	a
IUni	Jungle rubber	0.56	a
IUni	Rainforest	0.53	a
IUni	Rubber	0.52	a

Chapter 4

General Discussion

General discussion

Tropical rainforests in Asia are one of the most diverse and important terrestrial ecosystems worldwide and provide important ecosystem services (Böhnert et al., 2016; Milheiras & Mace, 2019). It is, however, under increasing pressure due to high rates of deforestation to extract timber and minerals, or the establishment of extensive monoculture plantations (Renó et al., 2011; Vijay et al., 2016). Particularly Sumatra in Indonesia has experienced high deforestation rates due the conversion of rainforest into oil palm and rubber plantations (Miettinen, Shi & Liew, 2011; Margono et al., 2014). How the transformation of rainforest into agricultural systems affects diversity and trophic niches, particularly in arthropod communities, have been documented in recent studies (Hamilton et al., 2013; Barnes et al., 2014, 2017; Nyffeler et al., 2017; Potapov et al., 2020b; Zhou et al., 2022). The canopy arthropod fauna is among the most affected (Turner & Foster, 2009; Fayle et al., 2010). Spiders (Araneae) are an important component of terrestrial food webs since they are top predators and also are food for other arthropods and vertebrates. Therefore, changes in their abundance, richness and functional diversity of spiders might affect the general functioning of the ecosystem (Wise et al., 1999; Potapov et al., 2020b).

This thesis is one of the first studies investigating the effects of land-use transformation from rainforest to rubber and oil palm monoculture plantations on spider communities in the canopy of trees from an ecological and trophic perspective. Using morphological identification and stable isotope analysis, I demonstrated that the conversion of rainforest into plantations changes the taxonomic composition and the trophic niches and utilization of basal resources of canopy spider communities. In general, the effects of the conversion of rainforest was most pronounced in rubber and oil palm monoculture plantations than in jungle rubber as low intensity agroforestry system. The following discussion is structured following the main hypotheses presented in the general introduction. Overall the results suggest that the conversion of rainforests into agricultural systems changes spider diversity in terms of biomass, abundance and richness (Hypothesis 1). Additionally, rainforest spider communities were more affected by structural factors, while spider communities in plantations were more affected by climatic factors (Hypothesis 2). Moreover, trophic niches and functional redundancy were not uniformly affected by land-use changes (Hypothesis 3) and spider communities shifted their diet from rainforest to monoculture plantations by increasingly feeding on herbivores (Hypothesis 4).

Canopy spider diversity and composition across land-use systems

Following my expectations, the abundance, biomass and richness declined from more natural systems such as rainforest and jungle rubber to monoculture plantation systems of oil palm and rubber, and the community composition was similar between rainforest and jungle rubber on one hand and differed from the spider communities in monocultures of oil palm and rubber. My results, along with earlier studies on arthropod communities in the same area such as ants (Nazarreta et al., 2020; Kreider et al., 2021), butterflies (Panjaitan et al., 2020), parasitoid wasps (Kasmiatun et al. 2022) and salticid spiders (Junggebauer et al., 2021) reflect the strong decline in diversity with the conversion of rainforest into plantation systems. Such loss of arthropod biodiversity due to land-use transformation has been observed not only in Asia but in many studies worldwide (Hallmann et al., 2017; Janzen & Hallwachs, 2019; Sánchez-Bayo & Wyckhuys, 2019). Similar to diversit, also the abundance of arthropods declined with the conversion of rainforest into plantation systems and this also was true for spiders in the present study. Differences in the extent of the decline in diversity and abundance of spiders among studies are likely to be due to different methods applied, but also regional differences in spider densities. Overall, the abundance decline pattern I report provides evidence of the potential risk of local extinction of spider species (Ceballos, Ehrlich & Dirzo, 2017; Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019), which might ultimately compromise ecosystem functioning (Soliveres et al., 2016; Dislich et al., 2017).

Interestingly, the decrease in spider biomass with the conversion of rainforest into plantations followed the same pattern as in abundance. This might suggest that the contribution of spiders to ecosystem functions in oil palm and rubber plantations is twice lower as in rainforest and jungle rubber (Boudreau, Dickie & Kerr, 1991; Dislich et al., 2017). Similarly, previous studies have documented an alarming rate of arthropod biomass decline in other biomes. Hallmann et al. (2017) measured the total insect biomass over 27 years in nature protection areas in Germany and concluded a drastic decline in insects by 76% to 82%. Further, Seibold et al. (2019) analyzed an extensive dataset covering 10 years from 2008 to 2017 of over 1 million arthropods in grasslands and forests in Germany and concluded that the biomass declined by 78 % over the years. The richness of canopy spiders in the monoculture plantations studied was less than half that in the rainforest, showing a similar decline in abundance and biomass. Our findings also are in line with previous studies comparing preserved and degraded systems in tropical and temperate ecosystems (Otto & Floren, 2007; Zheng, Li & Yang, 2015). Overall, the data provide support that the conversion of rainforests into monocultures results in a strong biodiversity decline, which is conform to earier studies (Sala et al., 2000; Steffan-Dewenter et al., 2007; Sodhi et al., 2010; Mumme et al., 2015; Grass, 2020; Potapov et al., 2020a; Liebke et al., 2021).

Shifts in arthropod community composition due to land-use transformation in tropical or temperate ecosystems have been investigated in ground spiders, jumping spiders, ants, butterflies and pseudoscorpions (Nazarreta et al., 2020; Panjaitan et al., 2020; Junggebauer et al., 2021; Kreider et al., 2021; Liebke et al., 2021; Azhar et al., 2022). My results along with these studies found that generalist arthropod species tolerate a certain degree of disturbance as long as major habitat requirements are met. In particular in web-building spiders essential habitat requirements include structural elements to attach their webs. A number of studies found common spider families such as Araneidae, Theridiidae, Tetragnathidae, Corinnidae, Salticidae and Thomisidae to dominate in both rainforest as well as plantation systems (61-94% respectively; Floren & Linsenmair, 2001; Chen & Tso, 2004; Floren & Deeleman-Reinhold, 2005; Zheng et al., 2017; Potapov et al., 2020a). Similar to these studies, these spider families also contributed most to the total abundance and richness of spiders in rainforest and plantation systems in the present study (57% and 59% respectively).

Effect of environmental variables in the spider canopy communities

In accordance with my expectations, four of the seven environmental variables studied affected the canopy spider community structure, both at family and morphospecies level. At family level, aboveground biomass, trees per hectare and canopy openness contributed to the shift in community composition, with the former two variables associated with rainforest and jungle rubber, and the latter with oil palm monoculture plantations. Interestingly, the communities at the morphospecies level were also influenced by habitat structure variables such as plant richness and trees per hectare, which were associated with rainforest.

Our findings are supported by previous studies. Floren & Deeleman-Reinhold (2005) found that arboreal spider diversity in southeast Asia was reduced in disturbed areas with more open canopies compared to primary lowland rainforest. Further, Jiménez-Valverde & Lobo (2007) found that vegetation complexity in temperate ecosystems was an important predictor for species richness in orb-web (Araneidae) and ambush hunting spiders (Thomisidae).

Aboveground biomass which increases with plant richness, vegetation cover, and height and age of trees (Vogel et al., 2019), also was found previously as an important factor structuring spider communities. Barton et al. (2017) found that low tree density negatively affected spider communities, while Schuldt et al. (2011) demonstrated that high tree species richness may benefit spider diversity in forests in China. Furthermore, Floren et al. (2011) showed that spider richness was positively correlated with older trees. Plant richness, which influenced significantly spider communities at morphospecies level in our study, was previously shown to be an important factor for arthropod predators such as spiders and ants in tropical and temperate forest ecosystems (Drescher et al., 2016; Junggebauer et al., 2021; Matevski & Schuldt, 2021). Samu et al. (2014) found that 26% of the variation in spider community assembly in temperate forests was explained by tree species richness, and that certain species were associated with individual tree species. Moreover, vegetation complexity was also reported to be related to spider diversity in tropical forests (Zheng, Li & Yang, 2015). Finally, spider canopy communities in monoculture plantations were related to canopy openness. This might be in part due to lower canopy complexity of rubber and oil palm plantations compared to rainforest (Drescher et al., 2016; Zemp et al., 2019).

More natural land-use systems are associated with narrower trophic niches and higher functional redundancy

The results of this study do not uniformly support my hypothesis concerning changes in spider trophic positions with land-use changes. Generally, the range in $\Delta^{15}N$ values of spider communities did not differ among the studied land-use systems, and this was also true for the use of basal resources ($\Delta^{13}C$ values). However, although not significant, the range in trophic positions in rainforest (2.76 ‰) was narrower than in the other three land-use systems (averaging 3.92 ‰). Particularly, the range in trophic positions in Clubionidae was low in the rainforest compared to jungle rubber and rubber. In Salticidae, the trophic range was similar between rainforest and oil palm, but lower than jungle rubber and rubber. By contrast, the range in trophic positions differed little between land-use systems in Theridiidae and Thomisidae suggesting they might feed on a similar prey spectrum irrespective of land-use system. Further, my results suggest that in certain families the trophic range is narrower in rainforest compared to plantations. Trophic shifts between habitats and hunting modes in spiders have been observed previously. Dehart et al. (2017) and Sanders et al. (2015) found that cursorial spiders (Salticidae) occupy wider trophic niches than orb-web spiders in forests and that cursorial spiders have wider trophic niches compared to cursorial spiders in disturbed ecosystems such as forest edges. This may reflect different community composition associated with differences in hunting modes, but also shifts in the spectrum of prey (Cardoso et al., 2011; Pitilin et al., 2020). Prey availability might explain the narrow trophic range we found for Salticidae and Clubionidae in rainforest. Further, similar trophic ranges in Thomisidae and Theridiidae might indicate that they feed on asimilar prey spectrum in the four land-use systems studied. Interestingly, the narrower trophic ranges in Clubionidae and Salticidae, as well as the total spider community in rainforest were uniformly due to lower maximum $\Delta^{15}N$ values. These results suggest that intraguild predation is more widespread in disturbed areas than in rainforest. Feeding consistently on low trophic level prey in rainforest may reflect that food webs in more natural habitats tend to be more bottom-heavy as also has been shown for the canopy food web at our study sites (M. Pollierer & J. Drescher, unpubl. data). A high incidence of intra-guild predation in disturbed ecosystems such as agricultural fields also has been observed by Hambäck et al. (2021). Moreover, Sanders et al. (2015) demonstrated that spiders along forest edges predominantly dwell on prey of medium to low trophic positions such as springtails, cockroaches and flies. Low trophic positions of decomposers and herbivores in rainforest at our study sites (Zhou et al. 2022) may also have contributed to the low maximum $\Delta^{15}N$ values in Clubionidae and Salticidae.

The total spider community and the four spider families showed similar $\Delta^{13}C$ values, suggesting consistency in the use of basal resources. Generally, the range in $\Delta^{13}C$ values did not differ with land-use, except for a lower range in Salticidae in oil palm plantations. With average $\Delta^{13}C$ values of ca. 6 ‰ spiders in rainforest and jungle rubber were remarkably enriched in ^{13}C. By contrast, in oil palm plantations, but in particular in rubber, the enrichment was much less pronounced. This pattern of strong enrichment in ^{13}C in the more natural and less enrichment in plantation systems was true for virtually all taxa of the canopy food web (M. Pollierer & J. Drescher, unpubl. data; see below). Trophic positions in spider communities are likely affected by body size and age of individuals, but this is little studied in tropical ecoystems (Pekár et al., 2012; Sanders et al., 2015). However, differences in trophic niches at least in part are due to changes in community composition between land-use systems. Ramos et al. (2022) confirmed that spider community composition varies significantly between rainforest and monoculture plantations at our study sites. They found 14 families to exclusively colonize rainforest including Anapidae, Ctenidae, and Deinopidae.

As indicated by the multidimensional metrics used, the total spider community as well as the four spider families studied, were similar from a functional perspective across the four land-use systems studied, with little shifts in community trophic niches due to land-use intensification. At the community level, only isotopic divergence differed between land-use systems and at the family level, it was mainly isotopic dispersion arguing against a high functional redundancy in rainforest. This reflects that spiders are mainly generalist predators (Wise, 1993; Nelson & Jackson, 2011; Leroy et al., 2013). However, the higher isotopic divergence values in rainforest at community level indicate that species with more extreme stable isotope values, i.e. specialist hunters, might be more abundant in more natural ecosystems. Overall, however, isotopic divergence scored a minimum value of 0.62 indicating that the trophic spectrum of spider communities is balanced (Cucherousset & Villéger, 2015). Moreover, isotopic dispersion was highest in Salticidae in oil plantations and in Thomisidae in rainforest. These findings suggest that the trophic positions of Salticidae are least coherent in oil palm plantations, whereas in Thomisidae they were least coherent in rainforest (and jungle rubber) (Cucherousset & Villéger, 2015). Potentially, their contrasting response to land-use changes reflects niche partitioning as observed before in cursorial spiders (Balfour et al., 2003; Michalko et al., 2021). Supporting this conclusion, Saqib et al. (2021) found that, although Salticidae and Thomisidae may share a similar prey spectrum in agricultural systems, the relative importance of individual prey taxa may differ between these two families.

Potapov et al. (2020) found density, richness, predation and functional diversity in ground-dwelling spiders to be reduced by 57 – 98% in plantations compared to rainforest. In contrast to our study, which was exclusively based on variations in trophic ecology as indicated by stable isotope values, Potapov et al. (2020) included a wider range of functional traits, such as hunting strategy, body coloration, habitat, desiccation resistance and body mass. Further, Junggebauer et al. (2021) found Salticidae richness and phylogenetic diversity to decline with the transformation of rainforest to monoculture plantations of rubber and oil palm. By contrast, Benítez-Malvido et al. (2020) found functional diversity to be increased in forest fragments compared to continuous forests although species diversity declined. Finally, our results at least in part contradict previous studies. The different results might be due to different definitions of functional communities of spiders and potentially reflect that the focus on trophic ecology may be too narrow to draw general conclusions on how land-use changes affect the functioning of spider communities.

Spider communities shift their diet from detritivores to herbivore prey due to land-use transformation

Following my expectations, Δ^{13}C enrichment in the total spider community and the four spider families studied was much more pronounced in rainforest and jungle rubber than in monoculture plantations of rubber and oil palm. This indicates that the transformation of rainforest into monoculture plantations is associated with a shift towards herbivore prey in spiders. My findings resemble those in spiders and other predators in the soil animal food web in the studied land-use systems (Klarner et al., 2017; Liebke et al., 2021; Zhou et al., 2022). However, interpreting the lower enrichment in ^{13}C values in the canopy food web is less straightforward than in the soil animal food web. Soil animals are generally enriched in ^{13}C and lower enrichment, therefore, can be reliably interpreted as a shift towards herbivore prey. Surprisingly, spiders in the canopy of rainforest and jungle rubber showed a similar enrichment in ^{13}C as spiders in the soil animal food web (on average by ca. 6 ‰).

Interestingly, not only spiders but also other predators as well as herbivores in the canopy of rainforest and jungle rubber at our study sites are strongly enriched in ^{13}C (M. Pollierer and J. Drescher, unpubl. data). Two processes might have contributed to this strong enrichment. (1) We calibrated spider δ^{13}C values to δ^{13}C values of leaves, which we picked at a hight of about 2 m and it has been demonstrated that δ^{13}C values of leaves in the lower canopy of trees might be less enriched than in those higher in the canopy ("canopy effect"; van der Merwe & Medina, 1991). However, this difference is unlikely to explain the strong enrichment of spiders (and other canopy arthropods) compared to leaves. (2) A second factor that might have contributed to the strong enrichment in δ^{13}C is the selective use of certain compounds of canopy leaves by herbivores. In particular lignin and waxes are depleted in ^{13}C (Pollierer et al., 2009; Bufacchi et al., 2020), and selective feeding on other plant leaf compounds, such as liquid substances and cellulose, may result in herbivores being enriched in ^{13}C compared to average leave δ^{13}C values. The latter process seems to be more relevant in tropical rainforests as the leaves typically are richer in lignin and waxes allowing them to stay active for years and resist attack by pathogens and herbivores. Importantly, if it is true that, similar to the food web in soil, also canopy spider communities shift towards more herbivore prey in plantations this may contribute to pronounced control of herbivore prey in plantations despite spider density, biomass and diversity is strongly reduced compared to rainforest (Ramos et al. 2021).

Overall conclusions

My thesis provided novel insight into the effects of rainforest conversion into oil palm and rubber monoculture plantations on the diversity and trophic ecology in canopy spider communities. First, I demonstrated that canopy spider communities in oil palm and rubber plantations are less abundant, have lower biomass and are less diverse compared to the more natural ecosystems rainforest and jungle rubber. Further, I showed that spider community composition is similar in rainforest and jungle rubber, and differed strongly from that in oil palm and rubber plantations. Moreover, I demonstrated the importance of aboveground plant biomass, number of trees per hectare and canopy openness and plant richness as major environmental factors determining spider community composition. These findings highlight the importance of rainforest for the conservation of canopy spider communities as only a subset of the community can tolerate environmental disturbances in monoculture plantations. However, my findings also highlight that a large fraction of spiders of more natural ecosystems tolerates moderate environmental disturbances indicating that agroforest systems may contribute substantially to the conservation of tropical canopy spider communities.

Furthermore, I demonstrated that rainforest transformation also affect the community trophic structure of spiders and thereby their functioning in the canopy food web. The results showed that certain spider families have narrower trophic niches in rainforest than in plantations, although the trophic range in total spider communities was similar across land-use systems. Further, the results indicated that intra-guild predation is particularly low in rainforest spider communities compared to more disturbed plantation systems. Moreover, I provided evidence that the prey spectrum of the sheet-web building Theridiidae and the cursorial Salticidae includes species feeding on other resources than leaves of trees, presumably predominantly Collembola and Psocoptera feeding on algae and / or lichens. Further, lower shift in ^{13}C values in monoculture plantations may indicate a shift towards more herbivore prey in disturbed plantation systems compared to more detritivore prey such as Collembola and Psocoptera in rainforest and jungle rubber. Overall, I demonstrated that the similar trophic ranges and multidimensional trophic metrics of canopy spiders across the studied land-use systems reflect the consistent functioning of canopy spider communities as generalist predators. Finally, my results highlight that the four studied spider families do not respond uniformly to the transformation of rainforest into plantations, but at least in part their shift in trophic positions and use of basal resources differ suggesting that in part they might complement each other in regulating prey populations.

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List of publications

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Thesis declarations

Declaration of the author’s own contribution to manuscripts with multiple authors

Chapter 2 comprises a manuscript that has been published in a peer-reviewed journal;
Chapter 3 comprises a manuscript that is currently in preparation for peer-reviewed journals.

In all chapters, I am the first author; I have analyzed the data, writing the manuscripts, developed the main ideas, and created tables, figures, and appendices. All co-authors contributed to the interpretation and finalizing of the manuscripts.

Plagiarism declaration

I, Daniel Eugenio Ramos Gutierrez, declare that I have written this doctoral dissertation independently. All persons contributing to the manuscripts have been named. All sentences or passages quoted from other people’s work have been specifically acknowledged by clear cross-referencing.

I have not submitted this dissertation in any form for another degree at any university or institution. I confirm that the content of the digital version is identical to the written version.

Daniel Eugenio Ramos Gutierrez
Göttingen, December 2022