CHANGES IN TROPHIC NICHES OF ORIBATID MITES WITH TRANSFORMATION OF TROPICAL RAINFOREST SYSTEMS – FROM RAINFOREST INTO RUBBER AND OIL PALM PLANTATIONS IN SUMATRA, INDONESIA

Dissertation

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“Soil provides the foundation of human existence, […].” from “Soil Fauna Assemblages, Global to Local Scales” from Uffe N. Nielsen

Content

Summary

During the last decades especially tropical regions suffered from degradation as well as transformation of landscapes into different land-use systems. Logged rainforest sites in Southeast Asia are often transformed into cash crop monocultures, especially oil palm and acacia plantations. Such transformation processes may threaten the functioning of ecosystems with the worldwide highest biodiversity and endemism. Effects of this transformation and degradation have mainly been studied for aboveground organisms whereas effects on the functioning and composition of soil invertebrate communities are little studied.

This thesis focuses on the effects of land-use transformation along a land-use gradient, i.e. from secondary rainforest to plantations (jungle rubber, rubber and oil palm monoculture), on microarthropod communities, using oribatid mites as model organisms. Further, I investigated the effect of management strategies within oil palm plantations on macro- and mesofauna soil animals. The field studies were conducted within the interdisciplinary project "Ecological and socioeconomic functions of tropical lowland rainforest transformation systems (Sumatra, Indonesia)" (EFForTS), established in Jambi Province, southwest Sumatra (Indonesia) in 2013.

In the first study, presented in **Chapter 2**, we investigated shifts in trophic niches of six soil-living oribatid mite species and their possible trophic plasticity with the conversion of lowland secondary rainforest into plantation systems (jungle rubber, rubber and oil palm monoculture plantations) in two regions of southwest Sumatra, Indonesia. Therefore, stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of single oribatid mite individuals were measured and, subsequently, we calculated shifts in stable isotope niches with changes in

land-use systems. On the basis of significant changes in stable isotope ratios in three of six studied oribatid mite species this study demonstrated that these species are able to shift their trophic niche in land-use transformation systems. Those shifts were either due to changes in trophic level (indicated by δ^{15}N values) or due to changes in the use of basal resources (indicated by δ^{13}C values) or both. Notably, the shifts were most pronounced between more natural systems (secondary rainforest and jungle rubber) on one side and monoculture plantation systems (rubber and oil palm plantations) on the other side; thereby indicating that the shifts were related to land-use intensity.

In the second study, presented in **Chapter 3**, we investigated shifts in community-level trophic niches of soil-living oribatid mites with the conversion of lowland secondary rainforest into plantation systems (jungle rubber, rubber and oil palm monoculture plantations) in two regions of southwest Sumatra, Indonesia. Therefore, stable isotope ratios (^{13}C/^{12}C and ^{15}N/^{14}N) of pooled oribatid mite species were measured, and subsequently, we calculated shifts in community-level trophic niche with transformation of land-use systems. This study demonstrated that the community-level trophic niche of oribatid mites is larger in rainforests than in plantation systems, suggesting that the conversion of rainforest into plantation systems is associated with reduced availability of litter resources. Results of this study further demonstrated that community-level trophic niches in rainforest and jungle rubber are separated from those in monoculture plantation systems, indicating again that the trophic niche of oribatid mite communities shifts markedly with land-use change. Additionally, ^{15}N/^{14}N ratios of oribatid mite communities indicated that the diet of microarthropods shifts towards predation and/or scavenging with changing land-use systems. This may be due to the limited amount of litter and its

low quality in rubber and oil palm plantations. Further, exceptionally low $^{13}C/^{12}C$ ratios of oribatid mite communities in rubber plantations suggest that certain oribatid mite species in these land-use systems use resources which are lacking in the other studied ecosystems. Oribatid mite communities in plantation systems present an unusual high functional richness and uniqueness compared to natural systems.

The results of the first two studies demonstrated that soil-living oribatid mite species are able to adapt to changing land-use systems and do not suffer to the same extent from these changes as many aboveground species. The third experiment, presented in **Chapter 4,** focused on investigating the effect of 'tree islands' of different size (5 x 5, 10 x 10, 20 x 20 and 40 x 40 m) and diversity level of planted native trees (0, 1, 2, 3 and 6) within oil palm plantations. Here we investigated the response of meso- and macrofauna species to the establishment of 'tree islands' three years after the experiment started. Neither the different diversity levels of native tree species nor the plot size significantly affected the abundance of soil invertebrate taxa. However, richness of soil invertebrate taxa was positively affected in 'tree islands' of diversity level 2. The result demonstrated that the diversity and abundance of plant communities little affect the structure and diversity of soil invertebrates three years after establishment suggesting soil invertebrates respond with a pronounced time lag to the experimental manipulations. Overall, by investigating the trophic ecology of oribatid mites and their response to changes in land-use systems the results of this thesis improved the understanding of how soil communities and individual species respond to the conversion of rainforest into intensively managed agricultural systems.

Chapter I

General Introduction

Land-use change and different land-use systems

The worldwide rapidly growing human population is leading to a rising need for food, fuel and fiber, and therefore transformation as well as degradation of landscapes is increasing (Dirzo and Raven, 2003; Foley et al., 2005; Gibbs et al., 2010; Newbold et al., 2015). It is estimated, that the worldwide population size will increase to 9.7 billion by 2050 (UN, 2015) leading to an increase in the demand for food by 70 % (Godfray et al., 2010). These demands lead to high pressure on ecosystems worldwide, leading to a higher conversion of natural ecosystems into plantations, with more pressure on the production and yield of those agricultural systems (Godfray et al., 2010; Lambin and Meyfroidt, 2011; Tscharntke et al., 2012). Human activity strongly impacts natural ecosystems, directly e.g., via building infrastructure and houses, as well as indirectly e.g., via climate change and nutrient deposition (DeFries et al., 2004; Foley et al., 2005, 2011). About 40 % of the terrestrial surface has been transformed into agricultural systems, with an increasing proportion being degraded resulting in habitat loss and desertification e.g., due to erosion, due to construction of infrastructure and additionally due to human behavior (Bridges and Oldeman, 1999; Reynolds et al., 2007; Foley et al., 2011; Pavao-Zuckerman and Sookhdeo, 2017; Francini et al., 2018). This is mainly caused by high levels of fertilizer application and atmospheric deposition. Additionally, external input of nitrogen and phosphorus has been increasing since the 19th centuries (Peñuelas et al., 2012).

In the last decades, especially tropical regions suffered from degradation and transformation into land-use systems, such as oil palm or rubber plantations (Sodhi et al., 2010; Wilcove et al., 2013; Meijide et al., 2018). In South East Asia these transformations are threatening ecosystems with the highest biodiversity and endemism worldwide

(Jones, 2013). Since the mid-20th century rainforests in Southeast Asia have been logged, often followed by the transformation of logged sites into cash crop monocultures, such as rubber, oil palm and acacia plantations (Koh and Wilcove, 2008; Wilcove and Koh, 2010; Drescher et al., 2016). The process of expanding as well as intensification of agricultural landscapes poses the greatest threat to biodiversity (Tilman et al., 2001; Donald, 2004; Green et al., 2005). In my thesis, a gradient of different land-use systems was studied. Rainforest sites were represented by 'primary degraded forest', classified after Margono (2014). Jungle rubber land-use systems were rubber agroforests systems (*Hevea brasiliensis*) that resemble secondary rainforest, where naturally occurring species of different trees were included (Beukema et al., 2007). Rubber monoculture plantations exclusively include rubber trees (*Hevea brasiliensis*), and oil palm monoculture plantations exclusively include oil palm trees (*Elaeis guineensis*) (Drescher et al., 2016).

One of the agricultural land-use systems that is rapidly increasing are vegetable oils (Clay, 2013), with oil palm as one of the most quickly expanding crops (Carter et al., 2007; Fitzherbert et al., 2008). Additionally, biofuel markets and rising food demand in the European Union as well as in Indonesia, India and China result in increasing global oil palm production, currently by about 9 % each year (European Comission, 2006; Clay, 2013), with Malaysia and Indonesia as the main producers of palm oil (Koh and Wilcove, 2007). Palm oil belongs to one of the versatile oils, which has not only many different functions and therefore is widely used but it is also one of the most efficient crops worldwide (Zimmer, 2010; Ashraf et al., 2018). Moreover, it is the crop which produces the highest yield per land area (Zimmer, 2010; Ashraf et al., 2018).

Transformation of rainforest into agricultural systems strongly increased in Indonesia. Commercial oil palm cultivation in Indonesia started in 1911, with Sumatra as starting point (Abdullah and Nobukazu, 2007; Corley et al., 2008). After the 1980s oil palm plantations were also established in other parts of Indonesia (Abdullah and Nobukazu, 2007; Corley et al., 2008). Oil palm as well as rubber plantations often were established on rainforest sites which were already logged or degraded by fire (Curran et al., 2004; Dennis et al., 2005; Fitzherbert et al., 2008; Drescher et al., 2016). Nevertheless, conversion of rainforest into oil palm plantations may account for 16 % of recent deforestation in Indonesia (Fitzherbert et al., 2008), whereas the conversion of rainforest into rubber plantations and therefore the production of natural rubber has increased more than 50 % since 2000 (Ahrends et al., 2015).

In 2012, 0.84 million hectares rainforest were converted into agricultural systems in Indonesia, the highest rate worldwide (Margono et al., 2014; Drescher et al., 2016). One of the highest losses of primary forest occurred in Sumatra (Indonesia), with 0.40 million hectares per year between 2009 and 2011 (Laumonier et al., 2010; Miettinen et al., 2011; Margono et al., 2014). Oil palm plantations are known to hold less than half as many vertebrate species as primary rainforest (Danielsen et al., 2009). However, the effects of conversion of rainforest into plantation systems have been rarely studied for belowground arthropods (Newbold et al., 2015).

Soil communities

Agricultural production essentially depends on soil, and soils therefore are important for human welfare, e.g. food, fiber and fuel production (Nielsen, 2019). In fact, one of the key factors for the survival of humankind relies on soils and soil processes which are based on the activity of soil biota. However, until today understanding of the structure of soil communities and the functioning of soil systems still is limited.

Up to 90 % of the primary production of plants enters the soil system as leaf/wood detritus and rhizodeposits (McNaughton et al., 1989; Bardgett, 2005). Therefore, decomposition, together with primary production, is the most important process for terrestrial ecosystems. The presence or absence of specific soil animal species can modify the structure and functioning of soil systems, such as the turnover of organic matter and nutrient cycling (Bardgett, 2005; Nielsen et al., 2015). Additionally, certain functional types of soil fauna may enhance soil functioning or even modify soil food webs (Brussaard et al., 2007). Soil arthropods are part of any soil but the abundance and diversity varies strongly between different ecosystems, even within small spatial scales (Ettema and Wardle, 2002). This high spatial heterogeneity in the structure of soil communities is likely due to variations in biotic as well as abiotic factors, e.g. climate and litter type (Coûteaux, Marie-Madeleine Bottner and Berg, 1995; Wardle et al., 2006; Berg and McClaugherty, 2008). Soil fauna is highly diverse and can be divided into functional size classes of micro-, meso- and macrofauna (Swift et al., 1979). The trophic differentiation of micro- and macrofauna species has been long accepted and recent evidence based on stable isotope analysis underlined these assumptions (Potapov et al., 2019), whereas mesofauna taxa usually were taken as uniform trophic guild (De Ruiter et al., 1993; Berg and Bengtsson, 2007; Moore and de Ruiter, 2012). Contrasting this assumption, recent studies based on stable isotopes documented a variety of trophic niches and trophic levels within major groups of mesofauna (Schneider et al., 2004; Chahartaghi et al., 2005; Maraun et al., 2011;

Klarner et al., 2013). As Potapov et al. (2019) stated, different species within the same taxonomic group can belong to different trophic levels and may therefore provide different ecosystem services. The most abundant taxa for soil mesofauna are Collembola and Acari (Petersen and Luxton, 1982). Both groups represent a wide range of different life history traits, trophic positions, and therefore are likely to affect ecosystem functions in a variety of ways (Scheu, 2002; Schneider et al., 2004; Nielsen, 2019).

Macrofauna

Macro- and megafauna, due to their larger size, have different and more pronounced effects on ecosystems (Lal, 1988; Folgarait, 1998; Migge-Kleian et al., 2006). They play an important role for litter fragmentation as well as displacement, produce large amounts of faecal pellets and can enhance decomposition processes (David, 2014). Many macro- and megafauna species are considered ecosystem engineers, since they can modify the environment strongly, e.g. by feeding, burrowing, and the production of faecal pellets (Bonachela et al., 2015; Parr et al., 2016; Ashton et al., 2019). Additionally, macro- and megafauna produce lasting imprints on the environment, including the change of soil structure as well as organic matter distribution, and thus influence soil properties, soil biological assemblages, element cycling and ecosystem functioning more than other soil fauna (Migge-Kleian et al., 2006; Parr et al., 2016; Ashton et al., 2019; Nielsen, 2019).

Oribatid mites

With about 11,000 described species (Subías et al., 2018), and the true number of species likely exceeding 50,000 (Walter and Proctor, 2013), oribatid mites are the most diverse soil microarthropods. Oribatid mites colonize a wide range of different habitats, e.g. temperate to tropical regions, deserts, tundras and aquatic habitats (Krantz et al., 2009). Densities of oribatid mites can reach up to 200,000 ind./m^2 in forest soils of temperate regions whereas in tropical regions densities typically are in the range of 30,000-40,000 ind./m^2 (Maraun and Scheu, 2000; Maraun et al., 2007; Scheu et al., 2008). Oribatid mites are trophically highly diverse and span over about three to four trophic levels, including lichen and algae feeders, fungal feeders, primary and secondary decomposer as well as predators/scavengers (Maraun et al., 2004; Schneider et al., 2004; Illig et al., 2005; Erdmann et al., 2007). Different life history traits, e.g. low fertility, slow development and long life cycles, leave oribatid mites sensitive to soil conditions and thereby changes in environmental conditions (Behan-Pelletier, 1999). Due to high population density and species richness oribatid mites have been proposed as indicator organisms for soil health (Bedano et al., 2011) and land use (Zhao et al., 2013), reflecting impacts of land use intensification, especially in tropical rainforest systems (Migge-Kleian et al., 2007; Gan et al., 2014; Hasegawa et al., 2014).

Trophic ecology

Trophic niches

One of the most important concepts in ecology is the niche concept (Hutchinson, 1959; Chase and Leibold, 2003). Niche differentiation is considered to be the basis for species co-existence (Tokeshi, 2009). Organisms not only interact as an ecological ‘guild’, e.g. group of taxa that use the same class of resources in a comparable way (Root, 1967), or due to trophic relations, e.g. predator-prey interactions which can shape the process of evolution but also contributes to the complexity of communities (Tokeshi, 2009), but also due to the use of habitats (Tokeshi, 2009). Therefore, two types of niches are differentiated, the ‘fundamental niche’ (Hutchinson, 1978) and the realized niche, describing the ‘role’ of the species within a community, focusing mainly on its trophic position (Elton, 1927). The fundamental niche is defined as the niche occupied by species in the absence of competition or other biotic interactions, whereas the realized niche is defined as the niche space occupied in presence of competition and biotic factors. Based on the interactions between species and/or populations different mechanisms are responsible for these interactions or effects on other organisms (Abrams, 1987). Six different interaction types are commonly distinguished, i.e. competition, predation, herbivory, parasitism, diseases and mutualism (Krebs, 1994). One of the important factor is the availability of resources for species, forming the basis of competitive interactions (White, 1993). There are two different types of competition as defined by Birch (1957). First, resource competition occurs when organisms (from the same or different species) indirectly interact by using the same resources which is scarce. Second, interference competition occurs when organisms directly interact for access to resources. Competition therefore can lead to changes in the population size of the competing species (Lotka-Volterra equation; Lotka, 1925; Volterra, 1926) or lead to one species ‘winning’ and the extinction of the other or co-existing of species, based on the availability of resources (Tilman, 1977, 1986).

There are different niche-related concepts. The first is environmental filtering, which implies that communities are assembled according to similarity of niches (Vellend, 2010; Kraft et al., 2015). The second is based on competition between species leading to niche differentiation of species within communities (Macarthur et al., 1967; Violle et al., 2011), implying that the structure of communities evolves with the co-existence of species in a stable environment (Korotkevich et al., 2018). The trophic niche as dimension of the ecological niche implies effects of species on other species within communities, thereby being related to the role within the ecosystem of those species (Leibold, 1995; Chase and Leibold, 2003). Species with a broader trophic niche are predicted to more easily invade existing communities than those with a narrower niche, and to survive disturbances more easily (Bommarco et al., 2010; Dammhahn et al., 2017). There are few studies focusing on changes in trophic-niches in disturbed habitats, most of the conducted studies focused on the response of individual species and not the community (Korotkevich et al., 2018). Studies focusing on trophic-niche shifts at the community level are mostly based on aquatic systems (di Lascio et al., 2013; Hansen et al., 2018). One of the few studies analyzing shifts in trophic niches of soil invertebrates to changes in land use systems, regarding the response of individual species is Krause et al. (2019), with the results indicating trophic plasticity in oribatid mite species. Further, focusing on the community level Klarner et al. (2013) investigated the trophic structure of Mesostigmata in beech stands in Central Germany and showed that Mesostigmata predominantly feed on secondary decomposer. Notably, closely related taxa often had very different stable isotope values suggesting that trophic niche partitioning allowed the coexisting of morphological similar species (Klarner et al., 2013).

Trophic plasticity

Trophic plasticity allows animals to react to changing environmental conditions, such as global warming, intensified land use or flooding. Organisms with generalist feeding habits are more flexible regarding their diet and therefore may be less affected by changing environmental conditions as compared to organisms with a more narrow diet. Until today, trophic plasticity mostly has been investigated in aquatic taxa, mainly in fish (Bowen and Allanson, 1982; Almeida et al., 2012; Drymon et al., 2012) and snails (Riera, 2010). Predominantly, these studies focused on changes in morphology and behavior due to changing environmental factors rather than on trophic plasticity. Juvenile *Tilapiu mossumbica* (Cichlidae. Teleostei) move daily from deep offshore waters to shallow littoral areas for feeding and back (Bowen and Allanson, 1982). This movement is linked to changes in physical and biological features of the littoral environment and therefore varies in time. Moreover, with changes in the lake water level there were also changes in the diet and behavior. *Micropterus salmoides* (Percomorphaceae; Teleostei) is known as an invasive species and trophic plasticity likely contributes to the success as invasive species (Almeida et al., 2012). Another important factor for trophic plasticity in one species could be regional variation of diet as shown for *Rhizoprionodon terraenovae* (Carcharhinidae, Selachii) as well as for *Hydrobia ulvae* (Hydrobiidae, Gastropoda) (Riera, 2010; Drymon et al., 2012). Leal et al. (2015) showed that tropic plasticity can also be influenced by symbiosis.

Only few studies investigated the trophic plasticity in the field in soil organisms and very few considered changes in trophic niches with changes in land use. One of the few field studies existing showed that centipede predators are able to switch their diet from feeding on secondary decomposer in rainforest to less ^{13}C enriched prey in oil palm plantations (Klarner et al., 2017). Results of another study on predation of centipedes showed that the management of different forest types in Germany does not affect the prey spectrum, but it varies with the depth of the litter layer and soil pH (Günther et al., 2014). Another study focused on oribatid mites from temperate systems (Gan et al., 2014), where oribatid mites were found to suffer from environmental changes, since those animals are assumed to be specialized regarding their diet (according to their ^{15}N and ^{13}C signature) and therefore likely to go extinct with changes in environmental conditions. Generally, laboratory studies with oribatid mites suggest that their food preferences are innate and little affected by learning (Brückner et al., 2018).

Stable isotopes

It is difficult to study the trophic interactions of soil animals (Pollierer et al., 2009). One major problem is the structure of the soil. Soil structure, e.g. pore size distribution, water infiltration, water holding capacity and/or chemical characteristic have a direct impact on the abundance and distribution of soil animals (Ducarme et al., 2004; Nielsen et al., 2008; Nielsen, 2019). Soil animals are often small, displace complex trophic levels and are not easy to identify (Sunderland et al., 2005; Potapov et al., 2019). Further, the feeding behavior of soil animals is also affected by biotic and abiotic soil conditions (Traugott et al., 2013). Models and simulations can provide insights into dynamics and structure of food webs, however, it is important to validate the trophic position of species/taxa with real-world data (Finlay-Doney and Walter, 2012). Recently, significant methodological advantages have been made studying trophic interactions (Traugott et al., 2013). Some of the important methods for studying trophic interactions are stable isotope and fatty acid analysis which allow to detect resource allocation (Ruess and Chamberlain, 2010; Boecklen et al., 2011), whereas DNA-based techniques allow to link feeding interactions to taxonomic positions (Gariepy et al., 2007; Symondson, 2012). Advantages of DNA-based methods include for example that multiple individual samples can be pooled in e.g., NGS-based techniques (Deagle et al., 2009) or gut-content analysis (Zaidi et al., 1999), however, there also are disadvantages. One of the most critical one is the high sensitivity of PCR, which may not only detect food and predator DNA but also DNA of contaminations (Traugott et al., 2013). Fatty acid analysis can be used to detect different diet due to specific fatty acid signatures of bacteria, fungi, algae and plants which animals are not able to synthesize (Ruess and Chamberlain, 2010). Fatty acids of consumers to a large extent originate from their diet as they are assimilated and incorporated without major change ('dietary routing'; Ruess and Chamberlain, 2010; Traugott et al., 2013). Nevertheless, fatty acid analysis also has disadvantages, one is the intermediate specificity as well as the metabolic modification of fatty acid signatures in the consumer (Traugott et al., 2013). Stable isotope analysis is one of the most valuable tool for studying food webs (Ehleringer et al., 1986; Fry, 2006; Boecklen et al., 2011; Traugott et al., 2013) and has been adopted for long to also study soil food webs (Ponsard and Arditi, 2000; Scheu and Falca, 2000; Scheu, 2002). One of the disadvantages of this method is the rather large amount of material needed hampering the analysis of small species, this, however, has been overcome in part by recent advances in the analytical procedure (Langel and Dyckmans, 2014).

Natural variations in $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios allow to evaluate the trophic structure of animal communities (DeNiro and Epstein, 1978; Minagawa and Wada, 1984; Wada et al., 1991). Stable isotope signatures of animal tissue provide information about the trophic position and trophic links of animals as well as on the basal resource used (Tiunov, 2007; Traugott et al., 2013). The use of stable isotopes for analyzing the structure of food webs started in the 1970s (DeNiro and Epstein, 1978) and increased ever since (Ehleringer et al., 1986; Fry, 2006; Boecklen et al., 2011). ^{13}C ratios are used to trace basal food resources, since $^{13}C/^{12}C$ ratios stay rather constant through food chains (Post, 2002). By contrast, isotopic fractioning leads to an enrichment in ^{15}N from prey to consumer by 3.4 ‰ per trophic level (Post, 2002; Martínez Del Rio et al., 2009), thereby ^{15}N values allow ascribing animals to different trophic levels and reflecting their feeding habits (DeNiro and Epstein, 1978; Kreipe et al., 2015). However, estimation of the trophic position requires an isotopic baseline since $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios vary in primary producers in time and space (Jardine et al., 2006). To establish the appropriate baseline, it is necessary to measure the isotopic signatures of carbon sources within the study site, i.e. by measuring the stable isotope ratio of leaf litter and soil (Casey and Post, 2011). Comparing isotope signatures of animals and the basal resource is a powerful tool to understand trophic interactions and dynamics of organic matter in soil (Potapov et al., 2019), processes otherwise very difficult to study in-situ (Tiunov, 2007). Dead plant material either is used for decomposition or incorporated into soil organic matter, processes which are essentially driven by the activity and/or interactions between soil organisms (De Ruiter et al., 1993; Nielsen et al., 2011; Filser et al., 2016; Potapov et al., 2019).

Stable isotopes cannot only be used to study the structure of food webs, but also to analyze the trophic ecology of specific taxonomic groups (Scheu and Falca, 2000; Halaj et al., 2005; Maraun et al., 2007, 2011; Tiunov, 2007). In soil, stable isotopes have been used to investigate trophic niches of species of earthworms, (Martin et al., 1992), ants (Blüthgen et al., 2003), but also smaller animals such as oribatid mites (Schneider et al., 2004; Erdmann et al., 2007; Maraun et al., 2011), springtails (Chahartaghi et al., 2005) and mesostigmatid mites (Klarner et al., 2013). Blüthgen et al. (2003) showed that stable isotopes analysis is a powerful tool for investigating trophic niche partitioning and plasticity in complex and diverse communities.

Management of oil palm plantations and the 'Biodiversity Enrichment Experiment'

Natural ecosystems are affected by human activities, including conversion into plantations and management of ecosystems (Foley et al., 2005, 2011). Until today, about 40 % of the terrestrial surface has been transformed into agricultural systems (Foley et al., 2011). In part, however, these systems are not managed in a sustainable way. Rather, a considerable proportion of them is degraded; further habitat loss occurs due to construction of infrastructure and desertification processes (Bridges and Oldeman, 1999; Reynolds et al., 2007; Foley et al., 2011; Pavao-Zuckerman and Sookhdeo, 2017; Francini et al., 2018).

Intensification of land use and the associated biodiversity loss affects the structure of ecological communities and therefore the functioning of above- and belowground systems (Sodhi et al., 2004; Erdmann et al., 2007; Wilcove et al., 2013; Barnes et al., 2014;

Edwards et al., 2014; Klarner et al., 2017). Reduced decomposer diversity may compromise decomposition processes as well as carbon and nutrient cycling (Handa et al., 2014). The large scale transformation of rainforests into monoculture plantation systems, such as oil palm and rubber, is one of the main drivers for biodiversity loss, especially in South East Asia (Fitzherbert et al., 2008; Immerzeel et al., 2014; Teuscher et al., 2016). Effects of oil palm plantation management on aboveground biodiversity and ecosystem functioning is receiving increased interest (Nurdiansyah et al., 2016; Syafiq et al., 2016; Teuscher et al., 2016; Ashton-Butt et al., 2018), however, only few studies focused on consequences for the belowground systems (Bessou et al., 2017). As soil communities are linked to the diversity and abundance of plant communities (Eisenhauer et al., 2011; Thakur and Eisenhauer, 2015), conversion of rainforest into monoculture plantations is likely to strongly affect belowground biodiversity. Therefore, to protect biodiversity of tropical regions it is important to integrate the belowground system and to consider the management of plantation systems (Koh et al., 2009; Foster et al., 2011; Luskin and Potts, 2011; Teuscher et al., 2015, 2016). Oil palm plantations may harbor a diverse understory (Foster et al., 2011), however, understory plants often compete with oil palms and therefore commonly are weeded (Tohiran et al., 2017). Removal of understory plants in oil palm plantations may be done by hand, but more commonly by the use of herbicides. However, the extensive use of herbicides may pollute water and thus provides a threat to the already endangered ecosystems (Schiesari and Grillitsch, 2011; Comte et al., 2012). In fact, the use of pesticides in agricultural land-use systems has been linked to the decline in biodiversity (Geiger et al., 2010; Beketov et al., 2013). A number of studies showed that the reduction in herbicide use and the associated increase in the coverage of understory vegetation in oil palm plantations may beneficially affect aboveground invertebrates, but also the decomposer system (Chung et al., 2000; Ashraf et al., 2018; Ashton-Butt et al., 2018; Spear et al., 2018; Darras et al., 2019).

Study site

Studies of the presented theis formed part of the interdisciplinary project “Ecological and socioeconomic functions of tropical lowland rainforest transformation sytems (Sumatra, Indonesia) (Drescher et al., 2016) (Fig. 1).

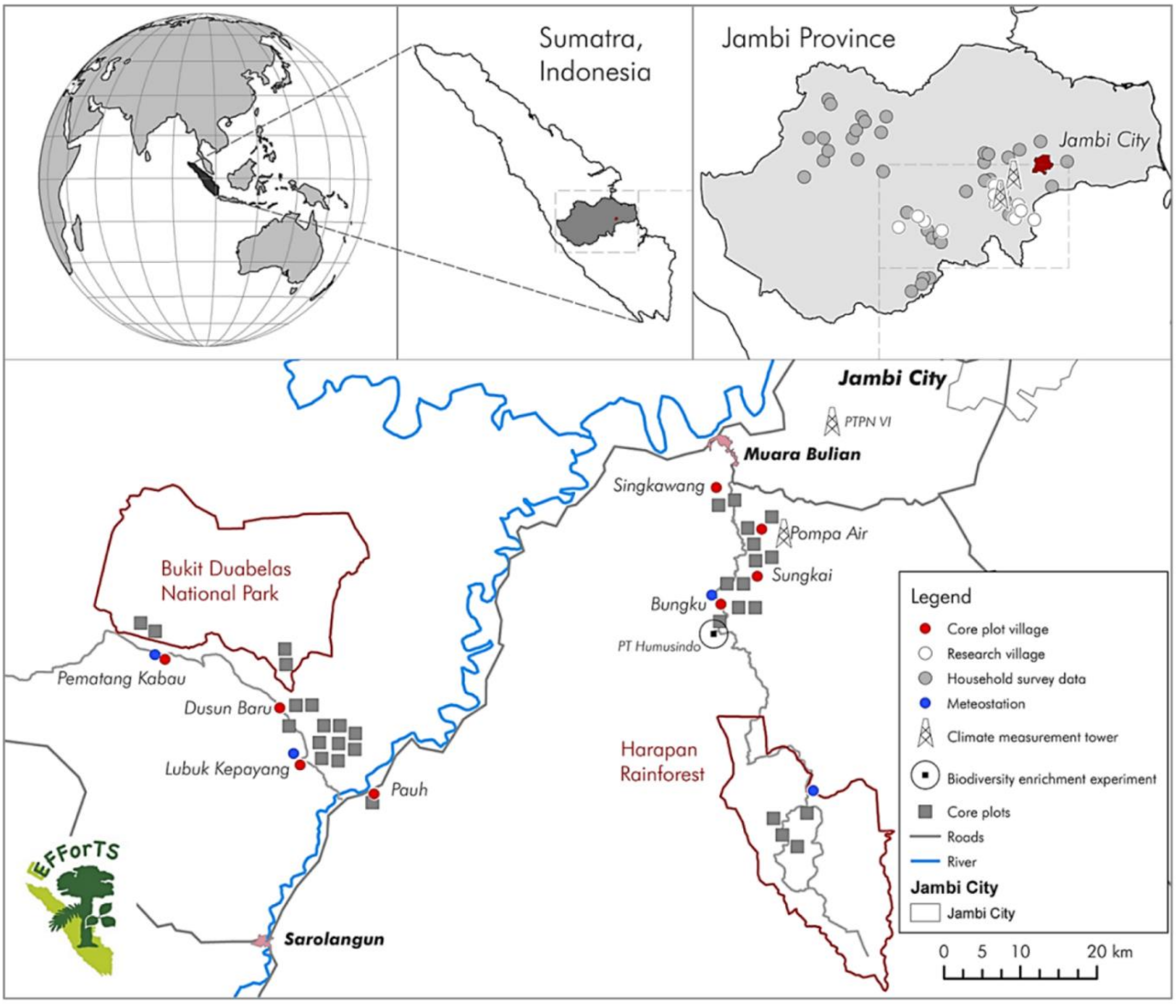

Figure 1. Location of study sites of EFForTS in Sumatra and the Jambi Province (Drescher et al., 2016), core plots are located in the two landscapes near Bukit Duabelas National Park and Harapan Rainforest.

Two (**Chapters 2** and **3**) of the three studies reported were conducted at the EFForTS core plots established 2012 in two landscapes, Bukit Duabelas (2° 0’ 57” S, 120° 45’ 12” E) and Harapan (1° 55’ 40” S, 103° 15’ 33” E). The dominant soil type at both landscapes is Acrisol. At Bukit Duabelas soils with a clay texture predominate whereas Harapan soils are characterized by a sandy loam texture. In total, 32 core plots were established, four plots in each of four different land-use systems: lowland rainforest, jungle rubber, rubber and oil palm monoculture plantations. Rainforest plots represented “primary degraded forest” (classified by Margono et al., 2014), with signs of selective logging as well as extraction of non-timber products. Jungle rubber, represented smallholder rubber agroforest systems comprising previously logged rainforest enriched with rubber trees (*Hevea brasiliensis*). Both, rubber as well as oil palm plots were situated within smallholder monoculture plantations, varying between 7 to 16 years (rubber) and 8 to 15 years (oil palm) in 2012 (Drescher et al., 2016). Each plot was 50 x 50 m and contained 5 x 5 m subplots at random positions within the plot (Drescher et al., 2016). The third study (**Chapter 4**) formed part of the “Biodiversity Enrichment Experiment” established in 2013 in the framework of EFForTS in the oil palm plantation of PT Humusindo Makmur Sejata (01.95° S and 103.25° E, 47±11 m a.s.l.) (Teuscher et al., 2016) (Fig. 2). The experiment was located in the Harapan landscape and the dominant soil type is loamy Acrisol (Allen et al., 2015). In 2016, the average age of planted oil palms was between 6 and 12 years. Management of the plantation contained fertilizer application, regular manual weeding of understory plants as well as removal of epiphytes. Herbicides were only applied if the manual weeding could not conducted due to lack of available workers (Teuscher et al., 2016).

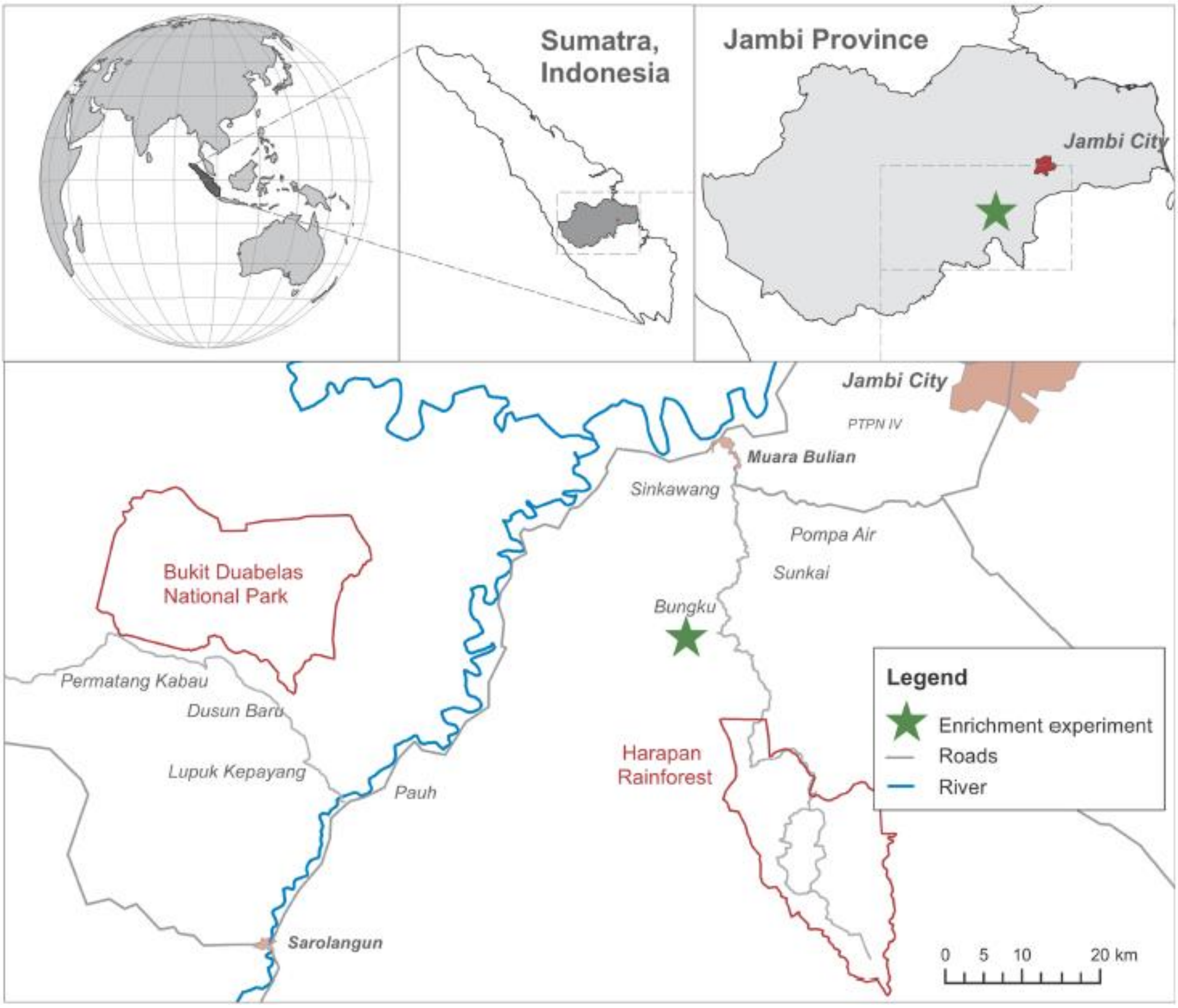

Figure 2. Map of the study area of the EFForTS Project (Drescher et al., 2016, modified from Teuscher et al., 2016). The green star indicates the location of the enrichment experiment in the oil palm plantation of PT Humusindo Makmur Sejata.

Within the oil palm plantation, tree islands of varying species diversity and compositions were established (Fig. 3). 52 plots of different plot size (5 × 5, 10 × 10, 20 × 20 and 40 × 40 m) as well as different tree diversity levels (0, 1, 2, 3 and 6 species) were established, according to the random partitions design of Bell et al. (2009). Each tree species was selected only once at each species diversity level, therefore species composition within the tree islands was random. Additionally, four plots of the same size (10 x 10 m) and management as usual were established as control plots (ctrl) (Teuscher et al., 2016), resulting in 56 plots total. For the enrichment of the tree islands six native trees were selected, i.e. three fruit trees (*Parkia speciosa*, and *Archidendron pauciflorum*, Fabaceae; *Durio zibethinus*, Malvaceae), and three timber trees *(Peronema canescens*, Lamiaceae; *Shorea leprosula*, Dipterocarpaceae), and one known to produces natural latex (*Dyera polyphylla*, Apocynaceae). Prior to tree planting, 40 % of the oil palms were removed from the experimental plots. Management of the established plots contained manual weeding in the first two years (preventing weeds to overgrow planted saplings; every three month) which was stopped after that to allow natural succession, i.e. interaction/competition with each other and oil palms. Application of fertilizers, herbicides and insecticides in the plots were stopped after tree planting. Samples for my thesis were taken in 2016 and therefore were without manual weeding.

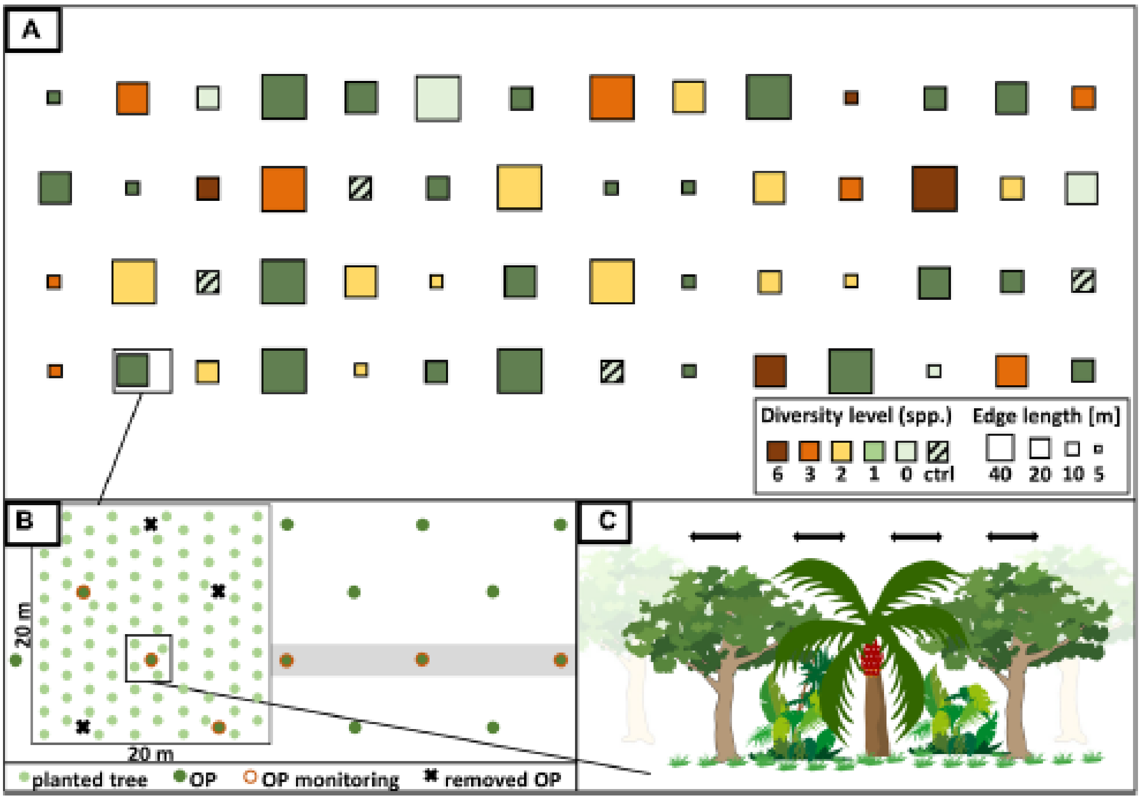

Figure 3. Study design of the biodiversity experiment (Teuscher et al., 2016). (A) Tree island with varying tree diversity levels (0, 1, 2, 3 and 6 species), identity and composition and plot size (5 × 5, 10 × 10, 20 × 20 and 40 × 40 m). Four control plots without treatment and with management as usual are represented by ctrl. In total, there are 56 plots. (B) Oil palms (OP) were cut in the plots to enhance the light conditions, planted trees are in a 2 x 2 m grid. (C) Planted trees interact/compete with each other and the oil palm**s.**

Objectives and chapter outline

This thesis aims at improving the knowledge about the effects of land-use changes in South East Asia, Sumatra (Indonesia), i.e. more specifically the conversion of tropical rainforest to jungle rubber, rubber and oil palm monoculture plantations, on soil arthropod communities, especially oribatid mites, and their trophic ecology. **Chapters 2** to **4** report results from field experiments with **Chapter 2** investigating the shift in trophic niches of individual species of oribatid mites with the conversion of tropical rainforest into plantations, as indicated by stable isotopes (^{15}N, ^{13}C). **Chapter 3** investigates the shift in trophic niches of oribatid mite communities, represented by the species making up 80 % of total oribatid mite individuals in the respective land-use system, as indicated by stable isotopes (^{15}N, ^{13}C). **Chapter 4** investigates the effect of the enrichment of oil palm plantations with native tree species in 'tree islands' as well as varying island size on soil invertebrate communities as part of the 'Biodiversity Enrichment Experiment'.

The main hypotheses of this thesis are as follows:

(1) Oribatid mite species cope with environmental changes in transformed ecosystems by shifting their trophic niches, with land-use system change inducing a shift in trophic levels and/or the use of basal resources indicating trophic plasticity.

(2) The trophic niche of oribatid mite communities changes with land-use system being larger in more natural systems (rainforest, jungle rubber) than in plantation systems (rubber, oil palm).

(3) The enrichment of oil palm plantations with native tree species increases the density and complexity of soil arthropod communities with the effect increasing with plot size.

The content of the three chapters can be summarized as follows:

In **Chapter 2** we investigated shifts in trophic niches of six soil-living oribatid mite species (*Plonaphacarus kugohi*, *Protoribates paracapucinus*, *Scheloribates praeincisus*, *Bischeloribates mahunkai*, *Rostrozetes* cf. *shibai*, and *Rostrozetes* sp. 1) with the conversion of lowland secondary rainforest into plantation systems of different land use intensity (jungle rubber, rubber and oil palm monoculture plantation) in two regions of southwest Sumatra, Indonesia. We measured stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of single oribatid mite individuals and inspected shifts in stable isotope niches with changes in land-use systems. Significant shifts in stable isotope ratios in three of the six studied oribatid mite species (*S. praeincisus*, *R.* cf. *shibai* and *Rostrozetes* sp. 1) indicated that these species in fact shift their trophic niches with environmental changes. The trophic niche of the other three studied species (*B. mahunkai, P. kugohi* and *P. paracapucinus*) did not differ significantly between the land-use systems, but generally followed a similar trend as in the other three species. Overall, the results suggest that colonization of very different ecosystems such as rainforest and intensively managed monoculture plantations by oribatid mite species likely is related to their ability to shift their trophic niches, i.e. to trophic plasticity. Notably, the shift was due to both changes in the use of basal resources as well as trophic levels.

Chapter 3 investigated shifts in the community-level trophic niche of oribatid mites with the conversion of rainforest into rubber and oil palm plantations. We investigated 80 % of oribatid mite communities occurring in lowland secondary rainforest and plantation systems of different land use intensity (jungle rubber, rubber and oil palm monoculture plantation) in two regions of southwest Sumatra, Indonesia. We measured stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of pooled individuals of oribatid mite species and inspected shifts in community-level trophic niche with changes in land-use systems. Our results confirmed that the community-level trophic niche of oribatid mites in fact is wider in rainforest than in plantation systems. Between natural and plantation systems a clear separation of the community-level trophic niche occur, indicating that with natural and plantation systems the community-level trophic niche of oribatid mites is totally different. As indicated by minimum and maximum of litter-calibrated isotopic signatures of oribatid mite community-level trophic niche, only oribatid mite isotopic signatures from oil palm or rubber were significantly different compared to rainforest and jungle rubber. This implies that within oil palm and rubber plantations, there are single species within oribatid mite communities which occupy trophic niches which are not present in rainforest and/or jungle rubber.

The study reported in **Chapter 4** was part of the 'Biodiversity Enrichment Experiment' (see above). This experiment aimed at enhancing biodiversity and ecosystem functioning in oil palm plantations via 'tree islands' with varying diversity level (0, 1, 2, 3 and 6 different tree species) and plot size (5 x 5, 10 x 10, 20 x 20 and 40 x 40 m). We investigated the effect of 'tree islands' on macro- and mesofauna soil invertebrate taxa three years after the experiment was established. Our results demonstrated that neither the diversity level of the planted tree species nor plot size affected the abundance of soil invertebrate taxa but soil invertebrate richness varied with tree diversity. Notably, richness of soil invertebrates peaked at diversity level 2. As soil communities respond with a delay in time to soil forming process, we expect that the observed changes will increase in time.

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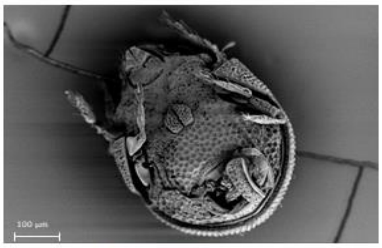
Chapter II

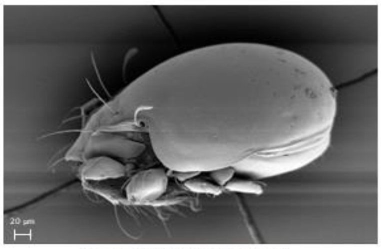
Shift in trophic niches of soil microarthropods with conversion of tropical rainforest into plantations as indicted by stable isotopes (^{15}N, ^{13}C)

Scheloribates praeincisus

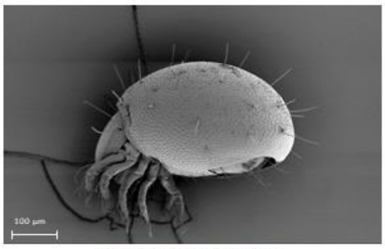


Rostrozetes sp. 1

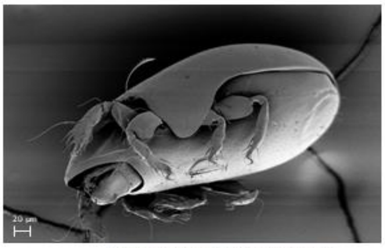
Rostrozetes cf. *shibai*



Bischeloribates mahunkai



Plonaphacarus kugohi



Protoribates paracapucinus

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Abstract

Land-use change is threatening biodiversity worldwide, affecting above and below ground animal communities by altering their trophic niches. However, shifts in trophic niches with changes in land use are little studied and this applies in particular to belowground animals. Oribatid mites are among the most abundant soil animals, involved in decomposition processes and nutrient cycling. We analyzed shifts in trophic niches of six soil-living oribatid mite species with the conversion of lowland secondary rainforest into plantation systems of different land-use intensity (jungle rubber, rubber and oil palm monoculture plantation) in two regions of southwest Sumatra, Indonesia. We measured stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of single oribatid mite individuals and calculated shifts in stable isotope niches with changes in land use. Significant changes in stable isotope ratios in three of the six studied oribatid mite species indicated that these species shift their trophic niches with changes in land use. The trophic shift was either due to changes in trophic level ($\delta^{15}N$ values), to changes in the use of basal resources ($\delta^{13}C$ values) or to changes in both. The trophic shift generally was most pronounced between more natural systems (rainforest and jungle rubber) on one side and monoculture plantations systems (rubber and oil palm plantations) on the other, reflecting that the shifts were related to land-use intensity. Although trophic niches of the other three studied species did not differ significantly between land-use systems they followed a similar trend. Overall, the results suggest that colonization of very different ecosystems such as rainforest and intensively managed monoculture plantations by oribatid mite species likely is related to their ability to shift their trophic niches, i.e. to trophic plasticity.

Introduction

Due to the worldwide growing human population and the associated rising need for food, fuel and fiber, transformation and degradation of landscapes rapidly increased over the last decades (Dirzo and Raven, 2003; Foley et al., 2005; Gibbs et al., 2010; Newbold et al., 2015). This is especially true for tropical regions where rainforest is rapidly and continuously transformed into different land-use systems, such as oil palm and rubber plantations (Sodhi et al., 2010; Wilcove et al., 2013; Meijide et al., 2018). Within the humid tropics Southeast Asia is one of the hotspots of recent deforestation with the highest loss of primary rainforest occurring in Sumatra (Indonesia) on average 0.40 Mha per year between 2009 and 2011 (Laumonier et al., 2010; Miettinen et al., 2011; Margono et al., 2014). Notably, these hotspots of deforestation are located in regions with the highest biodiversity and highest level of endemism worldwide (Myers et al., 2000; Sodhi et al., 2010; Drescher et al., 2016). It has been shown that land-use intensification in the tropics affects diversity and biomass of soil animals including centipedes, earthworms and oribatid mites (Lavelle et al., 1997, 2006; Erdmann et al., 2007; Whalen and Sampedro, 2010; Wilcove et al., 2013; Klarner et al., 2017), which in turn may affect decomposition and nutrient cycling provided by these organisms. Oribatid mites are among of the most abundant soil arthropods worldwide and involved in decomposition processes and nutrient cycling (Maraun and Scheu, 2000; Bardgett, 2005). There are more than 11,000 described species (Subías et al., 2018) with the true number of species likely exceeding 50,000 (Walter and Proctor, 2013). Oribatid mites can reach densities of up to 200,000 ind./m^2 in forest soils of temperate regions whereas in tropical regions densities typically are in the range of 30,000 - 40,000 ind./m^2 (Maraun and Scheu, 2000; Maraun et al., 2007;

Scheu et al., 2008). Oribatid mites are trophically diverse and stable isotope analyses suggest that they span over about four trophic levels including lichen feeders, fungal feeders, primary and secondary decomposers as well as predators/scavengers (Schneider et al., 2004; Illig et al., 2005; Maaß et al., 2015).

Trophic position and trophic interactions characterize species and their role in ecosystem functioning and services. For many ecosystem functions, such as decomposition, nutrient cycling, carbon sequestration, primary production and crop yield, the soil decomposer system is essential (Hooper et al., 2005; Powers et al., 2009). The trophic structure of animal communities can be evaluated by analyzing natural variations in $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios (Wada et al., 1991; Boecklen et al., 2011; Potapov et al., 2019). Animal tissue typically is enriched in ^{15}N as compared to their food resource by about 3 and for ^{13}C by about 1 δ unit per trophic level, however, the enrichment may vary between trophic guilds and also between taxa (Post, 2002; McCutchan et al., 2003; Potapov et al., 2019). Thereby, ^{15}N values allow estimating trophic levels (DeNiro and Epstein, 1978; Kreipe et al., 2015), whereas ^{13}C is used to identify basal food resources since ^{13}C values change little across trophic levels (Wada et al., 1991). Stable isotopes have been used widely to analyze trophic niches of soil invertebrates (Scheu and Falca, 2000; Halaj et al., 2005; Maraun et al., 2007, 2011; Tiunov, 2007) including earthworms (Martin et al., 1992), ants (Rosumek et al., 2018), springtails (Chahartaghi et al., 2005), gamasid mites (Klarner et al., 2013) and oribatid mites (Schneider et al., 2004; Erdmann et al., 2007; Maraun et al., 2011). However, until today stable isotopes rarely have been used to investigate how trophic niches of soil animal taxa are affected by changes in land-use (Lagerlöf et al., 2017; Minor et al., 2017).

Forest transformation and land-use intensification strongly affect animal and plant taxa, and the changes typically are associated by the loss of species (Koh and Wilcove, 2008; Flynn et al., 2009; Barnes et al., 2014). An important mechanism to cope with environmental alterations such as land-use change is to respond in a plastic way by shifting trophic niches and adapt to the resources available locally. Trophic plasticity, therefore, may prevent extinction and thereby support biodiversity in converted ecosystems. Until today ecological plasticity mostly has been investigated in aquatic taxa, such as fish (Bowen and Allanson, 1982; Almeida et al., 2012; Drymon et al., 2012) and gastropods (Riera, 2010). These studies, however, focused on changes in morphology and behavior due to changing environmental factors rather than on trophic plasticity. Few studies investigated trophic shifts in soil animals. Klarner et al. (2017) showed that centipede predators switch their diet from feeding on secondary decomposers in rainforest to less ^{13}C enriched prey in oil palm plantations. Investigating variations in stable isotope ratios in oribatid mites from temperate ecosystems Gan et al. (2014) found oribatid mite species numbers to decline in global change scenarios since trophic specialists will likely go extinct. However, these findings may have been biased as the stable isotope data they used were based on pooled individuals which reduced intraspecific variability. Measuring pooled individuals may reduce the variation in the data and thereby erroneously point to specialist feeding. These restrictions may be circumvented as recent improvements allow to measure stable isotope ratios of small samples (Langel and Dyckmans, 2014) including single individuals of soil microarthropod species.

The current study formed part of the interdisciplinary project “Ecological and socioeconomic functions of tropical lowland rainforest transformation systems”

(EFForTS), established in Jambi Province, southwest Sumatra (Indonesia) (Drescher et al., 2016). By measuring natural variations in $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios of individual specimens, we analyzed trophic niches of six soil living oribatid mite species occurring in rainforest and three major rainforest-transformation systems in Southeast Asia, i.e. rubber agroforest (“jungle rubber”), and rubber and oil palm monoculture plantations. We will further refer to those four system in the following as the four land-use systems (rain forest, jungle rubber, rubber, oil palm). We hypothesized that (1) oribatid mite species adapt to environmental changes in transformed ecosystems by shifting their trophic niche, and that (2) the shifts are more pronounced in ^{13}C than in ^{15}N as changes in land-use systems more strongly affect basal resources (as indicated by ^{13}C) than trophic levels (as indicated by ^{15}N).

Material and Methods

Study sites

Soil samples were taken in two regions of Jambi Province, Bukit Duabelas (2° 0’ 57” S, 120° 45’ 12” E) and Harapan (1° 55’ 40” S, 103° 15’ 33” E). In each region four different land-use systems were investigated: rainforest, jungle rubber, rubber and oil palm plantations (Drescher et al., 2016). Rainforest sites were secondary rainforest which had been selectively logged about 20 - 30 years ago. Jungle rubber originated from enrichment of rainforest with rubber trees (*Hevea brasiliensis*) and includes rainforest trees. Jungle rubber sites were used to represent rainforest conversion systems of low land-use intensity lacking fertilizer input and herbicide application. Rubber as well as oil palm (*Elaeis guineensis*) monocultures were intensively managed plantations of an average age of 13 to 14 years. These systems were chosen to represent high land-use intensity plantation systems. Four replicates of each land-use system (rainforest, jungle rubber, rubber and oil palm plantations) in the two landscapes (Bukit Duabelas, Harapan) were established, resulting in 32 plots; in each plot samples were taken from three subplots, resulting in a total of 96 samples. Each plot spanned 50 x 50 m and the subplots 5 x 5 m (Drescher et al., 2016). For more details of the study site see Drescher et al. (2016). At both landscapes (Bukit Dubaelas, Harapan) acrisols dominated. Soils with a clay texture dominated in Bukit Duabelas, whereas soils with a sandy loam texture dominated in Harapan. All study sites were at similar altitudes varying between 50 and 100 m a.s.l. (Guillaume et al., 2015).

Sampling, extraction and species determination

Samples of 16 x 16 cm comprising the litter layer and the underlying 0 - 5 cm of the mineral soil were taken in October/November 2013. The two layers were separated, transported to the laboratory and extracted by heat (Kempson et al., 1963). Oribatid mites were determined to species/morphospecies level using Balogh & Balogh (Balogh and Balogh, 2012) and ascribed to feeding guilds including lichen feeders, primary decomposer, secondary decomposer/fungal feeders and predators/scavengers based on Maraun et al. (2011). Species and morphospecies were documented by taking pictures, linked with morphological traits and species identification numbers (species ID), and included into Ecotaxonomy database (http://ecotaxonomy.org/). Animals were stored in 70 % ethanol until further analysis.

Stable isotope analysis

The six most abundant oribatid mite species of 220 species overall (D. Sandmann, unpubl. data) occurring in each of the land-use systems in both landscapes were selected for stable isotope analysis, i.e. *Plonaphacarus kugohi* (Aoki, 1959) (Ecotaxonomy species ID 405729), *Protoribates paracapucinus* (Mahunka, 1988) (Ecotaxonomy species ID 405671), *Scheloribates praeincisus* (Berlese, 1910) (Ecotaxonomy species ID 405449), *Bischeloribates mahunkai* Subías, 2010 (Ecotaxonomy species ID 405450), *Rostrozetes* cf. *shibai* (Aoki, 1976) (Ecotaxonomy species ID 405389), und *Rostrozetes* sp. 1 (Ecotaxonomy species ID 405478). In total, 100 individuals of *S. praeincisus*, 75 of *R.* cf. *shibai*, 54 of *P. paracapucinus*, 44 of *B. mahunkai*, 19 of *P. kugohi* and 13 of *Rostrozetes* sp. 1 were analyzed.

For calibration of oribatid mite stable isotope values we measured stable isotope values of leaf litter taken from the dried litter material after extraction of the animals (ca. 2.5 g per sample). Prior to stable isotope analysis the litter was dried at 60°C for 24 h and ground in a ball mill (Retsch Mixer Mill MM200, Haan, Germany). For measuring stable isotope values of Oribatida, single individuals were used. Oribatid mite specimens were dried at 60°C for 24 h and weighed into tin capsules. Between one and three individuals from each of the transformation systems of both landscapes were measured (Table S1). Stable isotope values were determined by a coupled system of an elemental analyzer (NA 1500, Carlo Erba, Milan, Italy) and a mass spectrometer (MAT 251, Finnigan, Bremen, Germany) adopted for the analysis of small sample sizes (Langel and Dyckmans, 2014). The content of ^{13}C and ^{15}N was expressed using the δ notation with δX (‰) = $(R_{sample} - R_{standard}) / R_{standard}$ x 1000, with X representing the target isotope (^{15}N or ^{13}C) and R_{sample} and $R_{standard}$ the

$^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios, respectively. As standard for ^{13}C and ^{15}N analyses Vienna PD Belemnite (Coplen et al., 2002) and nitrogen in atmospheric air were used, respectively. Acetanilid was used as internal standard.

Statistical analysis

Means of $\delta^{13}C$ and $\delta^{15}N$ values of the three litter samples per plot were used as plot-specific litter $\delta^{13}C$ and $\delta^{15}N$ values. Differences between plot-specific litter $\delta^{13}C$ and $\delta^{15}N$ values and the overall mean litter $\delta^{13}C$ and $\delta^{15}N$ values (across all plots, landscapes and land-use systems) were used to adjust individual $\delta^{13}C$ and $\delta^{15}N$ values of oribatid mites per plot which allowed direct comparison of stable isotope values of oribatid mites across plots. The procedure resembles the calculation of Δ values but allows to present data relative to the overall mean litter $\delta^{13}C$ and $\delta^{15}N$ values. Calibrated data were used for all further analysis. Based on these values, average $\delta^{13}C$ and $\delta^{15}N$ values of oribatid mite species across plots, land-use systems and landscapes were calculated. Further variations in $\delta^{13}C$ and $\delta^{15}N$ values within species across the four different land-use systems were inspected using the standard deviation (SD) of stable isotope values within species per plot (Table S2). Oribatid mites were ascribed to trophic levels assuming a trophic enrichment of ^{15}N by 3.4 ‰ per trophic level except for primary decomposers for which we used a value of 1.7 ‰ as they typically are less enriched than consumers of higher trophic level (Vanderklift and Ponsard, 2003; Potapov et al., 2019).

Statistical analyses were performed using R v 3.5.2 (R Core Team, 2018) with R studio interface (RStudio, Inc.). Normality and variance homogeneity were inspected using diagnostic plots. We did not check for overfitting in the model with all species but as we also inspected each species separately and found stable isotope values to vary significantly with land-use systems overfitting in the model with all species is unlikely. Differences in the variation of δ^{13}C and δ^{15}N values across land-use systems were inspected using a linear mixed effects model as implemented in the *lme4* package (Bates et al., 2015). Fixed factors were species identity and land-use system, with 'PlotID' included as random factor. Significant differences between fixed factors were inspected using the *Anova* function. Differences in each δ^{13}C and δ^{15}N values between species were inspected using a linear mixed effects model as implemented in the *nlme* package (Pinheiro et al., 2007). Species identity and land-use systems were used as fixed factors and a random factor 'PlotID' was included to account for multiple sampling per plot. The significance of the fixed factors were inspected using the *Anova* function. Pairwise differences between the different land-use systems were inspected using the *glht* package (Hothorn et al., 2008) with 'Tukey's pairwise contrasts'. Data provided in text and figures are given as means ± 1 SD.

Results

Diagnostic plots of standard deviation against mean δ^{13}C and δ^{15}N showed that the data were distributed normally. Stable isotope values of the combined dataset differed significantly between the six oribatid mite species across land-use systems ($\chi^2_{5,3} = 60.56$, $p < 0.001$ for ^{13}C, and $\chi^2_{5,3} = 78.74$, $p < 0.0001$ for ^{15}N). Variation in stable isotope values within species differed significantly between land-use systems for ^{15}N but not for ^{13}C ($\chi^2_{3,4} = 8.53$, $p = 0.036$ and $\chi^2_{3,4} = 3.85$, $p = 0.279$, respectively; Fig. S3-S4). Variations in δ^{15}N values were similar in rainforest, jungle rubber and rubber plantations (SD of -0.10 ‰, -0.67 ‰ and 0.76 ‰, respectively) but significantly higher in oil palm plantations (SD of

0.62 ‰). Individual mixed effects models for each $\delta^{13}C$ and $\delta^{15}N$ values in these species indicated that these shifts were due to changes in $\delta^{15}N$ values in *S. praeincisus* and *R.* cf. *shibai* ($\chi^2_3 = 17.14$, $p < 0.001$ for *S. praeincisus*, $\chi^2_3 = 10.36$, $p = 0.016$ for *R.* cf. *shibai*), with $\delta^{15}N$ values being lowest in rainforest and highest in rubber plantations in *S. praeincisus*, and being highest in jungle rubber and similarly low in rubber and oil palm plantations as well as in rainforest in *R.* cf. *shibai* (Tukey's HSD test; rubber vs. rainforest $p < 0.001$ for *S. praeincisus,* jungle rubber vs. rainforest $p = 0.025$, jungle rubber vs. oil palm $p = 0.040$, jungle rubber vs. rubber $p = 0.022$ for *R.* cf. *shibai*; Fig. 1).

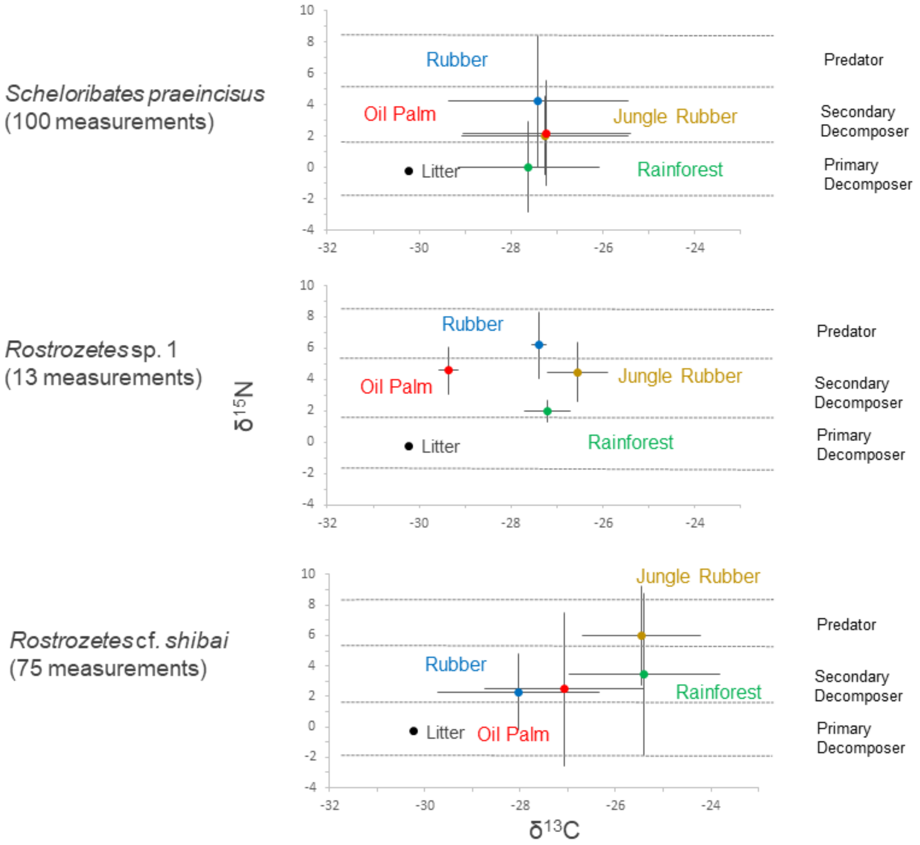

Figure 1: Stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values of oribatid mite species [*Scheloribates praeincisus* (Berlese, 1910), *Rostrozetes* sp. 1 and *Rostrozetes* cf. *shibai* (Aoiki, 1976)] in the four land-use systems studied (rainforest, jungle rubber, rubber and oil palm plantations). Means with standard

deviations; numbers of measurements per species are given in brackets. The average stable isotope value of litter used for calibration (see Methods) is given as reference. Dashed horizontal lines reflect boundaries of trophic levels (primary decomposers, secondary decomposers and predators; see Methods). For statistical analysis see text.

In addition to δ^{15}N, shifts in the trophic niche of *R.* cf. *shibai* with land-use system also was due to changes in δ^{13}C values and this was also true for *Rostrozetes* sp. 1 ($\chi^2_3 = 28.59$, $p < 0.001$ for *Rostrozetes* sp. 1; $\chi^2_3 = 13.77$, $p = 0.003$ for *R.* cf. *shibai*). δ^{13}C values of *Rostrozetes* sp. 1 in oil palm plantations were significantly lower than those in each of the other land-use systems, whereas δ^{13}C values of *R.* cf. *shibai* were significantly lower in oil palm and rubber plantations than in jungle rubber and rainforest (Tukey's HSD test; oil palm vs. rainforest $p = 0.008$, oil palm vs. jungle rubber $p < 0.001$, oil palm vs. rubber $p = 0.012$ for *Rostrozetes* sp. 1; rubber vs. rainforest $p = 0.018$, rubber vs. jungle rubber = 0.018 for *R.* cf. *shibai*). Although not significant, δ^{15}N values for *Rostrozetes* sp. 1 also varied between land-use systems. Mean ^{15}N values classified *Rostrozetes* sp. 1 as secondary decomposer in rainforest, jungle rubber and oil palm plantations, but as predator/scavenger in rubber plantations.

Although stable isotope values of the other three studied oribatid mite species (*B. mahunkai, P. kugohi* and *P. paracapucinus*) did not differ significantly among the four land-use systems (Anova; $p > 0.05$ for all three species), their position varied in isotope space in particular along the δ^{13}C axis, resulting in a separation of rainforest and jungle rubber from rubber and oil palm plantations in each of the species thereby resembling the shift in *Rostrozetes* sp. 1 and *R.* cf. *shibai* (Fig. S1).

Discussion

Based on stable isotope analysis trophic niches of oribatid mites – and soil arthropods in general – have been assumed to vary little at the landscape level (Scheu and Falca, 2000; Schneider et al., 2004; Illig et al., 2005; Erdmann et al., 2007; Pollierer et al., 2009; Fischer et al., 2010; Perdomo et al., 2012; Gan et al., 2014) as well as between forest types (Scheu and Falca, 2000; Schneider et al., 2004). The results of our study are in contrast to these earlier studies where oribatid mite trophic niches were proposed to be rather stable and narrow.

Trophic niches of species

The six studied oribatid mite species which occurred in each of the land-use systems spanned three trophic levels including primary and secondary decomposers as well as predators/scavengers, which is conform to earlier studies (Schneider et al., 2004; Illig et al., 2005; Maraun et al., 2011). Additionally, intraspecific variation in $\delta^{15}N$ values were significantly higher in oil palm plantations than in the other three land-use systems. Presumably, this was due to the lack of primary decomposers in oil palm plantations (which only feed on one trophic level, plant litter) and the presence of only higher trophic level species such as secondary decomposers and predators/scavengers, which are more likely to engage in omnivory and intraguild predation. *Bischeloribates mahunkai* grouped as predator/scavenger in rainforest, rubber and oil palm plantations, but as secondary decomposer in jungle rubber. *Protoribates paracapucinus* grouped as secondary decomposer in rainforest and jungle rubber, but as predator in rubber and oil palm plantations. *Scheloribates praeincisus* and *P. kugohi* uniformly grouped as primary decomposers in rainforest and as secondary decomposers in the other three land-use systems. Although predominantly grouped as secondary decomposers, *Rostrozetes* sp. 1 and *R.* cf. *shibai* were grouped as predators/scavengers in rubber plantations and jungle rubber. Overall, the results confirm that oribatid mites predominantly function as secondary decomposers feeding on microorganisms, in particular fungi, however, they also indicate that in part they feed on animal prey, presumably nematodes (Heidemann et al., 2011, 2014), or live as scavengers. High trophic position in *B. mahunkai* is conform to the suggestion of Rockett (Rockett, 1980) that many species of Scheloribatida live as predators. However, lower trophic position of *S. praeincisus* suggests that this does not apply uniformly to Scheloribatida as indicated previously (Bluhm et al., 2015). Grouping of *Rostrozetes* sp. 1 and *R.* cf. *shibai* as secondary decomposers (and in part as predators) was unexpected since another species of *Rostrozetes*, *R. ovulum*, was shown to live as primary decomposer in a tropical montane rainforest in Ecuador (Illig et al., 2005). *Plonaphacarus kugohi* had the lowest ^{15}N values and in part was grouped as primary decomposer indicating that this species feeds on litter and microorganisms confirming that Phthiracaridae/Euphthiracaridae often function as primary decomposers (Maraun et al., 2011). Primary decomposers are characterized by low fractionation of ^{15}N which likely is related to “protein sparing”, i.e. the retaining of assimilated N in body tissue rather than excreting it due to low nitrogen supply in litter (Swift et al., 1979; Castellini and Rea, 1992; Gannes et al., 2007; Pollierer et al., 2009). However, recent laboratory studies question that this uniformly applies to oribatid mites (Heethoff and Scheu, 2016). Furthermore, high δ^{13}C values of *P. kugohi* indicate that this species incorporates calcium carbonate in their exoskeleton (Norton and Behan-Pelletier, 1991; Pachl et al., 2012).

Shift in trophic niches with land use

Conform to our hypotheses, the studied oribatid mite species shifted their trophic niche with transformation of rainforest into plantation systems, however, this was only significant in three (*S. praeincisus*, *R.* cf. *shibai* and *Rostrozetes* sp. 1) of the six studied species, but in trend it also applied to the other three species. This indicates that the ability of the studied oribatid mite species to colonize very different ecosystems at least in part is due to the fact that they are trophically plastic and adapt to the changed environmental conditions in converted ecosystems by shifting their trophic niche. Δ^{15}N values of *S. praeincisus* and *R.* cf. *shibai* differed between the four land-use systems, e.g. δ^{15}N values of *S*. *praeincisus* in rubber plantations were almost 4 ‰ higher than in rainforest, whereas δ^{15}N values of *R.* cf. *shibai* in jungle rubber were almost 4 ‰ higher than in the other three land-use systems. This indicates that *S*. *praeincisus* as well as *R.* cf. *shibai* alter their resource use with conversion of rainforest/jungle rubber into plantations by shifting its trophic position. *S*. *praeincisus* altered its trophic position from primary decomposer in rainforest to secondary decomposer in plantations, presumably feeding almost exclusively on fungi in the latter. *R.* cf. *shibai* shifted its trophic position from secondary decomposer in rubber, oil palm and rainforest to predator/scavenger in jungle rubber. Notably, *S. praeincisus* and *P. kugohi* were the only species classified as primary decomposers and they only functioned as primary decomposers in rainforest. This is consistent with earlier studies stressing the lack or scarcity of primary decomposers among oribatid mite species in tropical forest ecosystems (Illig et al., 2005). The scarcity of primary decomposers likely is related to the poor litter quality in rainforest ecosystems (Butenschoen et al., 2014; Krashevska et al., 2017; Marian et al., 2017), and the results of this study indicates that this is aggravated by conversion of rainforest into plantations as none of the species studied was classified as primary decomposer in plantations. This suggests that the conversion of rainforest into plantation systems aggravates the shortage and poor quality of litter resources for the decomposer community (Teuscher et al., 2016; Klarner et al., 2017).

Rostrozetes sp. 1 as well as *R.* cf. *shibai* responded in a similar way to the conversion of rainforest into plantation systems as indicated by the shift in $\delta^{13}C$ values, i.e. changes in the basal resources they are using. In both species $\delta^{13}C$ values were similar in rainforest and jungle rubber and different from that in oil palm (*Rostrozetes* sp. 1) and oil palm and rubber plantations (*R.* cf. *shibai*). Soil animals typically are enriched by 3-4 δ units in ^{13}C as compared to litter due to the "detrital shift" (Pollierer et al., 2009; Potapov et al., 2019), and this also was true in the species studied. In *Rostrozetes* sp. 1 and *R.* cf. *shibai* this detrital shift was most pronounced in rainforest and jungle rubber. The more pronounced detrital shift in rainforest and jungle rubber likely reflects a shift in the use of plant litter carbon compounds towards compounds which are easy to access, such as sugars, proteins and (hemi)cellulose, rather than compounds which are difficult to access and have lower $\delta^{13}C$ values such as lignin (Gleixner et al., 1993; Hobbie and Werner, 2004; Bowling et al., 2008; Pollierer et al., 2009; Potapov et al., 2019).

Although stable isotope values in the other three studied oribatid mite species (*B. mahunkai, P. kugohi* and *P. paracapucinus*) also varied, these variations were not significant suggesting that their shifts in trophic niches were less pronounced. Notably, in particular the trophic position of *B. mahunkai*, classified predominantly as predator, varied little between land-use systems suggesting that this species is unable to switch from animal prey (or carcasses) to feeding on litter or microorganisms. Conform to the significant changes in trophic niches in *S. praeincisus*, *Rostrozetes* sp. 1 and *R.* cf. *shibai*, the trophic niches of *B. mahunkai*, *P. kugohi* and *P. paracapucinus* were more similar in rainforest and jungle rubber and separate from those in oil palm and rubber. Also, conform to the former three species, the detrital shift in δ^{13}C in *B. mahunkai, P. kugohi* and *P. paracapucinus* was less pronounced in rubber and oil palm plantations suggesting that detritivores in these systems benefit from high quality litter of the herb layer (see above). Other studies of oribatid mite families and superfamilies showed results similar to our study on species-level (Minor et al., 2017). However, although changes in land use on the trophic structure of soil animals may also be detected at courser taxonomic lever than species, our results indicate that land-use change even affects trophic variability within species, suggesting that to fully appreciate changes in niche space with changes in land use needs high taxonomic resolution and even the level of individuals within species (Somerfield and Clarke, 1995; Hirst, 2006; Heino, 2014; Hanna et al., 2015).

We assumed the shift in trophic niches to be mainly due to changes in the use of basal resources rather than trophic level. Contrary to this hypothesis, the significant shifts in trophic niches in *S. praeincisus* and *Rostrozetes* sp. 1 and *R.* cf. *shibai* were due to both changes in the use of basal resources (*Rostrozetes* sp. 1 and *R.* cf. *shibai*) as well as changes in trophic position (*S. praeincisus* and *R.* cf. *shibai*). Notably, the shift in δ^{15}N values in both of the latter species occurred towards higher trophic positions suggesting that they switched towards including prey of higher trophic levels in converted ecosystems. Overall, this indicates that in particular in primary and secondary decomposers trophic plasticity plays an important role for their ability to colonize a wide range of habitats.

Conclusions

Of the six species studied occurring across the four land-use systems we detected significant shifts in trophic niches in three of them, but trophic niches of the other three species also varied in a similar way. Notably, the shifts were due to both changes in trophic position (δ^{15}N values) as well as changes in the use of basal resources (δ^{13}C values) with the shift in trophic position towards higher trophic levels in transformed ecosystems. The observed shifts in trophic niches are conform to the view that oribatid mites are generalist feeders able to change their diet according to changes in resource availability. Notably, the shifts in trophic niches were most pronounced between more natural systems (rainforest and jungle rubber) and high intensity land-use systems (rubber and oil palm plantations). Overall, the results suggest that the ability of oribatid mite species to colonize a wide range of land-use systems including rainforest and monoculture plantations is likely based on trophic plasticity and the ability to shift both their trophic level and the basal resource they rely on.

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Field work permissions

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Sample collection and determination

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Appendix

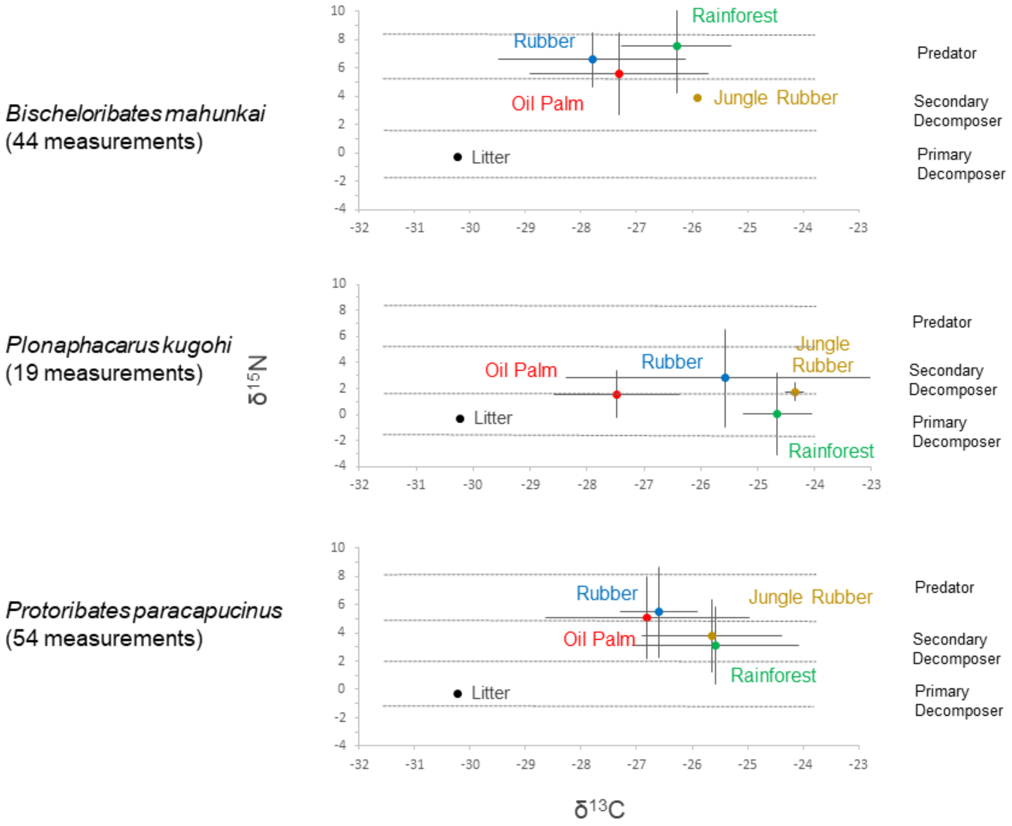

Figure S1: Stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values of oribatid mite species [*Bischeloribates mahunkai* Subías, 2010, *Plonaphacarus kugohi* (Aoki, 1959) and *Protoribates paracapucinus* (Mahunka, 1988)] in the four land-use systems studied (rainforest, jungle rubber, rubber and oil palm plantations). Means with standard deviation; numbers of measurements per species are given in brackets. The average stable isotope value of litter used for calibration (see Methods) is given as reference. Dashed horizontal lines reflect boundaries of trophic levels (primary decomposers, secondary decomposers and predators; see Methods). For statistical analysis see text.

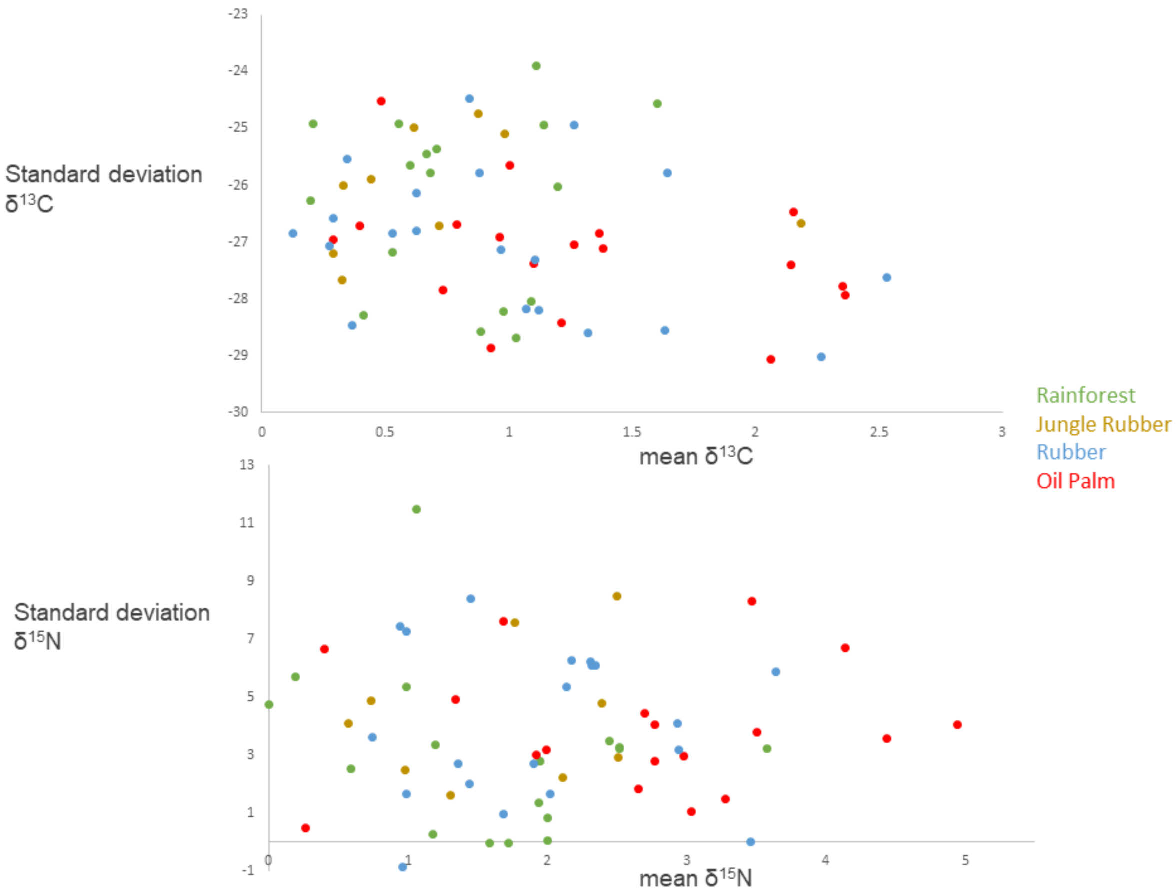

Figure S1: Plotwise standard deviation of mean stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values of oribatid mite species in the four land-use systems studied (rainforest, jungle rubber, rubber and oil palm plantations) plotted against their stable isotope values ($\delta^{13}C$ and $\delta^{15}N$). For details see Table S2 in Appendix.

Table S1: Absolute and calibrated (see methods) stable isotope values of oribatid mite individuals studied. Species ID in Ecotaxonomy database (http://ecotaxonomy.org/), species name, author, landscape, land-use system, absolute values of $\delta^{15}N$ and $\delta^{13}C$ values, and calibrated $\delta^{15}N$ and $\delta^{13}C$ values (all values are rounded to two decimal places). Mean $\delta^{15}N$ and $\delta^{13}C$ values of litter used for calibration of -0.24 and -30.23 ‰, respectively.

species ID	species	author	landscape	land-use system	absolute		calibrated	
					δ15N	δ13C	δ15N	δ13C
405450	*Bischeloribates mahunkai*	Subías, 2010	Bukit Duabelas	jungle rubber	1.97	-26.69	3.90	-25.90
				oil palm	1.68	-25.86	0.60	-25.86

					3.86	-26.23	2.77	-26.22
					4.27	-28.71	3.19	-28.71
					4.72	-27.31	3.64	-27.31
					5.47	-26.96	4.39	-26.96
					8.29	-29.06	7.20	-29.06
					10.37	-27.37	9.29	-27.36
				rainforest	3.68	-27.43	4.10	-26.37
					4.67	-27.62	4.41	-26.05
					6.64	-26.21	6.38	-24.63
				rubber	1.86	-25.67	2.29	-26.34
					1.75	-25.41	3.52	-25.93
					2.80	-26.42	4.58	-26.95
					3.91	-27.45	5.58	-27.92
					6.01	-28.34	6.43	-29.01
					5.05	-26.03	6.72	-26.50
					6.84	-27.79	7.26	-28.46
					5.74	-26.66	7.52	-27.19
					6.11	-25.61	7.79	-26.09
					6.38	-26.04	8.06	-26.52
					6.51	-26.39	8.18	-26.87
					8.00	-28.17	8.43	-28.85
					7.54	-26.72	9.32	-27.24
			Harapan	oil palm	3.44	-25.98	1.56	-26.63
					6.93	-27.15	5.69	-28.55
					6.96	-26.67	5.72	-28.06
					8.57	-25.57	7.33	-26.97
					9.18	-26.57	7.94	-27.96
					9.93	-28.36	8.69	-29.76
					11.76	-21.56	10.51	-22.96
				rainforest	10.89	-27.22	10.45	-26.64
					13.00	-28.27	12.56	-27.70
				rubber	6.48	-30.93	4.32	-31.91
					6.90	-29.64	4.74	-30.62
					7.08	-27.00	4.92	-27.98
					7.17	-25.97	5.01	-26.95
					7.03	-26.71	5.72	-28.12
					7.98	-24.16	5.82	-25.14
					5.07	-25.10	6.12	-26.04
					7.04	-26.23	8.08	-27.16
					7.10	-27.79	8.15	-28.73
					11.06	-30.14	8.90	-31.12
					12.46	-28.40	10.30	-29.38
405729	*Plonaphacarus kugohi*	(Aoki, 1959)	Bukit Duabelas	jungle rubber	-1.42	-23.83	1.07	-24.19
					-0.04	-24.17	2.45	-24.52
				oil palm	1.66	-28.09	0.15	-28.43
					5.60	-27.71	4.09	-28.05

				rainforest	-2.34	-26.70	-3.10	-25.26
				rubber	0.59	-26.03	1.02	-26.71
					2.40	-23.41	2.83	-24.08
					1.82	-23.25	3.59	-23.77
					3.90	-23.30	4.33	-23.97
					4.37	-21.55	6.04	-22.03
			Harapan	oil palm	1.75	-24.54	0.51	-25.93
				rainforest	3.61	-24.62	3.17	-24.05
				rubber	-1.26	-26.42	-3.42	-27.40
					0.41	-22.25	-0.90	-23.66
					-0.52	-25.46	-0.36	-26.89
					1.62	-22.75	0.31	-24.15
					2.07	-22.76	0.76	-24.17
					5.65	-23.14	3.49	-24.12
					4.99	-24.46	3.68	-25.87
					4.90	-32.58	5.06	-34.01
405671	*Protoribates paracapucinus*	(Mahunka, 1988)	Bukit Duabelas	jungle rubber	-0.78	-27.14	1.14	-26.35
					0.13	-26.76	1.54	-25.59
					1.05	-26.30	2.97	-25.52
					2.09	-25.01	3.50	-23.85
					3.83	-26.20	5.75	-25.41
					4.54	-24.22	6.47	-23.44
					4.76	-26.02	7.25	-26.37
					5.71	-25.45	7.63	-24.66
				oil palm	0.75	-26.53	-0.33	-26.52
					4.32	-32.45	3.24	-32.45
					4.57	-26.20	3.49	-26.20
					4.13	-25.75	3.60	-26.40
					4.96	-26.85	3.88	-26.85
					4.95	-23.57	4.41	-24.22
					4.85	-26.58	4.80	-24.67
					6.87	-26.83	5.79	-26.82
					7.29	-25.64	6.76	-26.29
				rainforest	-1.06	-26.53	-1.32	-24.96
					-0.54	-26.48	-1.25	-28.00
					2.79	-28.05	2.54	-26.48
					4.89	-24.53	4.63	-22.95
					5.48	-26.93	5.23	-25.36
					5.60	-26.45	5.34	-24.88
					5.10	-26.16	5.52	-25.10
					5.48	-25.76	5.90	-24.70
				rubber	-1.74	-25.42	-1.32	-26.09
					1.48	-25.86	2.79	-26.08
					2.44	-25.04	3.74	-25.26
					5.25	-26.22	6.92	-26.69

					5.86	-25.92	7.16	-26.14
					5.56	-26.55	7.24	-27.03
					6.47	-26.79	7.77	-27.02
					7.23	-26.39	8.90	-26.86
					8.88	-26.32	10.55	-26.79
				jungle rubber	0.72	-25.57	0.32	-25.69
					0.82	-25.14	0.42	-25.25
					2.87	-26.22	2.47	-26.34
					3.73	-26.12	3.33	-26.24
					7.47	-29.29	6.56	-28.72
				oil palm	3.19	-24.95	1.32	-25.60
					6.66	-26.06	4.79	-26.71
					6.31	-25.79	6.29	-25.76
					7.11	-28.32	7.09	-28.29
					10.09	-26.34	8.21	-26.99
					14.36	-27.65	12.49	-28.30
				rainforest	2.05	-28.26	1.56	-27.73
				rubber	1.82	-23.91	-0.34	-24.89
					1.50	-25.93	1.67	-27.36
					5.84	-25.66	3.68	-26.65
					6.40	-26.08	5.09	-27.48
					5.74	-25.13	5.91	-26.56
					7.04	-25.79	7.20	-27.23
					7.39	-25.61	7.56	-27.04
					8.06	-25.65	8.23	-27.08
405416	*Rostrozetes* cf. *shibai*	(species Aoki, 1976)	Bukit Duabelas	jungle rubber	-2.12	-25.68	-1.10	-23.46
					2.70	-24.73	4.11	-23.57
					3.28	-25.26	5.21	-24.47
					2.85	-26.82	5.34	-27.18
					6.17	-25.37	8.10	-24.58
					6.32	-26.89	8.81	-27.24
					7.51	-26.61	9.44	-25.83
					8.94	-25.34	11.43	-25.69
				oil palm	-1.19	-27.33	-2.27	-27.33
					0.12	-26.45	-0.97	-26.44
					2.13	-26.12	1.05	-26.12
					1.87	-25.69	1.83	-23.78
					2.09	-26.97	2.04	-25.06
					3.16	-30.29	2.08	-30.29
					4.21	-26.81	3.13	-26.80
					4.82	-26.03	3.30	-26.37
					4.75	-26.81	3.67	-26.80
					3.72	-26.68	3.67	-24.78
					5.39	-26.35	4.86	-26.99
					7.26	-25.85	6.18	-25.85

		8.74	-26.30	8.69	-24.40
		12.31	-30.47	11.78	-31.12
	rainforest	-0.53	-26.48	-1.29	-25.04
		-0.98	-24.72	-1.24	-23.15
		-0.77	-26.60	-0.34	-25.54
		1.40	-29.73	1.14	-28.16
		0.81	-27.16	1.23	-26.10
		2.90	-25.66	2.13	-24.22
		2.92	-26.11	2.66	-24.54
		3.28	-24.85	3.02	-23.28
		3.33	-24.27	3.07	-22.70
		4.02	-23.82	3.26	-22.38
		3.20	-26.35	3.62	-25.29
		4.44	-26.59	4.18	-25.01
		4.62	-26.55	4.36	-24.98
		5.45	-26.35	4.74	-27.87
		5.46	-27.17	4.75	-28.69
		4.87	-25.94	5.29	-24.88
		5.68	-26.11	5.42	-24.54
		6.05	-29.33	6.47	-28.28
	rubber	-3.17	-29.85	-1.87	-30.07
		-2.54	-29.92	-0.76	-30.45
		2.24	-28.19	4.02	-28.71
		4.52	-25.94	6.29	-26.46
Harapan	jungle rubber	3.53	-25.70	4.25	-25.67
		3.79	-25.90	4.51	-25.87
		5.20	-26.47	5.92	-26.45
	oil palm	0.50	-25.79	-0.28	-27.06
		1.36	-26.46	0.11	-27.85
		0.89	-27.13	0.11	-28.40
		2.38	-25.87	0.50	-26.52
		1.91	-28.68	0.67	-30.08
		1.91	-25.86	0.67	-27.26
		2.83	-24.83	0.96	-25.48
		4.31	-27.23	3.54	-28.50
		4.34	-25.55	3.56	-26.82
		5.81	-27.25	3.94	-27.90
		6.32	-25.82	4.44	-26.47
		7.13	-26.35	5.26	-27.00
		14.17	-27.11	13.40	-28.38
	rainforest	0.44	-26.19	-0.09	-25.38
		2.46	-26.97	1.96	-26.45
		2.61	-25.62	2.17	-25.04
		3.20	-25.52	2.67	-24.71
		3.18	-26.15	2.91	-25.16
		3.63	-26.58	3.14	-26.06

					4.99	-26.81	4.55	-26.24
					5.65	-26.26	5.11	-25.45
					6.81	-24.90	6.28	-24.08
				rubber	0.45	-25.94	0.61	-27.37
					2.02	-24.86	0.71	-26.27
					2.11	-28.99	2.28	-30.43
					3.98	-25.44	2.67	-26.85
					2.69	-24.78	3.74	-25.72
					5.05	-26.55	5.21	-27.98
405478	*Rostrozetes* sp. 1		Bukit Duabelas	jungle rubber	1.45	-27.95	2.47	-25.74
					1.56	-27.35	3.49	-26.56
					1.06	-26.54	3.55	-26.90
					2.83	-26.85	4.24	-25.68
					2.20	-27.12	4.69	-27.47
				oil palm	4.18	-29.57	3.10	-29.57
					7.56	-28.80	6.05	-29.14
				jungle rubber	7.67	-27.03	8.39	-27.00
				rainforest	1.62	-28.47	1.18	-27.89
					2.33	-27.30	1.89	-26.72
					3.31	-27.59	2.87	-27.01
				rubber	7.03	-27.33	8.34	-27.55
			Harapan	rubber	5.38	-25.82	4.07	-27.23
405449	*Scheloribates praeincisus*	(Berlese, 1910)	Bukit Duabelas	jungle rubber	-2.53	-26.90	-0.04	-27.25
					0.33	-27.30	2.82	-27.65
					2.76	-27.31	4.17	-26.15
					3.60	-27.69	6.09	-28.05
				oil palm	-1.89	-25.56	-2.97	-25.56
					-1.83	-27.84	-2.91	-27.84
					-0.86	-28.79	-0.91	-26.88
					1.18	-29.00	-0.34	-29.34
					0.79	-28.85	-0.29	-28.85
					1.32	-25.11	0.23	-25.11
					2.32	-29.83	0.81	-30.17
					2.32	-25.75	1.23	-25.75
					3.20	-29.27	1.68	-29.62
					3.59	-27.26	2.07	-27.61
					3.93	-29.01	2.84	-29.00
					4.53	-28.97	3.45	-28.97
					3.71	-28.96	3.66	-27.06
					5.10	-23.05	4.02	-23.04
					6.82	-27.63	5.30	-27.97
					5.76	-28.05	5.71	-26.14
					8.93	-23.92	7.85	-23.92
					9.93	-28.05	8.42	-28.39
				rainforest	-9.52	-26.49	-9.78	-24.92

		-1.41	-27.96	-2.17	-26.52
		-2.12	-26.06	-1.69	-25.00
		-1.24	-30.27	-1.50	-28.70
		-1.18	-30.60	-1.44	-29.03
		-1.10	-30.82	-1.36	-29.25
		-0.98	-29.64	-1.24	-28.06
		-0.46	-27.36	-1.23	-25.92
		-0.66	-28.84	-0.92	-27.27
		-0.42	-28.17	-0.68	-26.60
		-0.24	-30.73	-0.50	-29.16
		1.38	-28.14	0.61	-26.70
		1.74	-28.43	1.48	-26.86
		2.75	-26.32	1.98	-24.88
		2.24	-27.99	1.98	-26.42
		3.19	-26.82	2.42	-25.38
		4.20	-26.60	3.43	-25.16
		4.42	-27.42	4.84	-26.36
		5.24	-30.60	4.98	-29.03
		6.20	-25.98	6.63	-24.92
	rubber	-1.46	-25.47	0.22	-25.94
		-1.45	-26.74	0.33	-27.26
		0.46	-24.63	2.14	-25.10
		1.35	-26.87	2.65	-27.09
		2.07	-25.07	3.74	-25.54
		2.56	-27.54	3.87	-27.76
		3.13	-29.50	4.44	-29.72
		3.29	-28.12	5.06	-28.64
		6.62	-25.94	8.39	-26.46
		7.99	-25.62	9.77	-26.14
Harapan	jungle rubber	-1.30	-29.32	-2.21	-28.75
		-1.66	-26.63	-0.93	-26.60
		-0.04	-28.86	0.19	-29.39
		-0.02	-22.01	0.71	-21.98
		0.85	-27.87	1.58	-27.84
		2.05	-26.97	2.77	-26.95
		3.16	-28.39	3.88	-28.36
		4.82	-28.18	5.54	-28.15
	oil palm	-2.70	-25.41	-4.57	-26.06
		-0.09	-25.96	-0.86	-27.23
		1.44	-23.86	-0.44	-24.51
		1.04	-26.92	1.02	-26.89
		2.38	-27.14	1.13	-28.54
		3.07	-27.58	1.20	-28.23
		2.79	-29.04	1.55	-30.44
		4.44	-26.93	2.57	-27.58
		4.53	-27.70	2.66	-28.35

	6.97	-25.57	5.10	-26.22
	8.77	-25.39	8.00	-26.66
	10.01	-23.36	8.77	-24.76
rainforest	-6.15	-29.49	-6.69	-28.67
	-1.71	-29.42	-2.24	-28.60
	-1.75	-29.92	-2.19	-29.34
	-1.38	-28.41	-1.87	-27.89
	-1.30	-28.31	-1.79	-27.78
	-0.89	-30.20	-1.42	-29.39
	-0.29	-30.57	-0.83	-29.75
	0.56	-27.76	0.11	-27.18
	0.71	-30.67	0.21	-30.14
	0.89	-28.15	0.36	-27.33
	0.92	-28.79	0.48	-28.22
	1.33	-28.29	0.89	-27.72
	1.56	-29.59	1.03	-28.78
	1.50	-30.43	1.06	-29.86
	1.81	-30.33	1.36	-29.75
	1.98	-27.93	1.49	-27.41
	2.37	-28.40	1.88	-27.87
	3.51	-28.36	2.98	-27.55
rubber	-0.50	-26.68	-1.81	-28.09
	-1.04	-25.24	-0.88	-26.67
	1.41	-27.41	0.10	-28.81
	2.80	-20.89	2.96	-22.32
	2.83	-27.14	2.99	-28.57
	3.22	-25.80	3.38	-27.24
	3.34	-26.71	3.50	-28.15
	3.62	-28.54	3.79	-29.97
	3.74	-28.48	3.91	-29.91
	4.02	-23.44	4.18	-24.87
	5.58	-30.04	5.75	-31.47
	11.36	-25.42	11.52	-26.86

Table S2: Standard deviation of mean stable isotope (δ13C and δ15N) values of oribatid mite species in the four land-use systems studied. Species ID in Ecotaxonomy database (http://ecotaxonomy.org/), species name, land-use system, plotID, replicate, standard deviation of δ^{13}C and δ^{15}N, mean stable isotope values of δ^{13}C and δ^{15}N.

species ID	species	author	land-use system	plotID	sample size	SD		mean	
						δ15N	δ13C	δ15N	δ13C
405450	*Bischeloribates mahunkai*	Subías, 2010	oil palm	BO3	7	2.696	1.097	4.439	-27.353
				HO3	6	1.686	2.143	7.647	-27.376
			rainforest	BF2	2	0.983	0.706	5.394	-25.339
				HF1	2	1.054	0.529	11.506	-27.172
			rubber	BR1	5	0.987	0.623	7.266	-26.778
				BR2	4	2.304	0.527	6.234	-26.828
				BR4	4	2.315	1.070	6.102	-28.165
				HR2	3	0.942	1.103	7.449	-27.309
				HR3	7	2.168	2.263	6.286	-29.015
405729	*Plonaphacarus kugohi*	(Aoki, 1959)	rubber	BR4	3	1.353	1.264	2.724	-24.921
				HR3	2	3.456	1.640	0.037	-25.757
				HR4	4	1.683	0.837	0.964	-24.461
405671	*Protoribates paracapucinus*	(Mahunka, 1988)	jungle rubber	BJ3	5	2.385	0.979	4.793	-25.076
				BJ4	2	0.981	0.872	2.522	-24.719
				HJ1	4	1.302	0.438	1.635	-25.880
			oil palm	BO2	3	1.339	1.003	4.923	-25.635
				BO3	5	1.986	2.353	3.211	-27.769
				HO1	4	4.136	0.960	6.704	-26.897
				HO4	2	0.399	1.264	6.693	-27.025
			rainforest	BF2	5	2.513	1.138	3.281	-24.926
				BF4	2	0.192	0.203	5.712	-24.901
			rubber	BR1	4	1.450	0.122	8.403	-26.843
				BR3	4	2.139	0.622	5.366	-26.122
				HR1	5	2.347	0.272	6.112	-27.054
				HR3	2	2.013	0.877	1.670	-25.769
405399	*Rostrozetes shibai*	(species Aoki, 1976)	jungle rubber	BJ2	3	2.496	0.714	8.525	-26.703
				BJ3	3	1.766	0.614	7.580	-24.959
				HJ4	3	0.736	0.329	4.896	-25.998
			oil palm	BO2	2	3.462	2.062	8.318	-29.055
				BO3	7	2.654	1.381	1.838	-27.091
				BO4	4	2.769	0.480	4.058	-24.505
				HO1	5	1.921	0.785	3.019	-26.675
				HO2	5	4.942	0.732	4.069	-27.833
				HO3	3	0.261	1.214	0.481	-28.396
			rainforest	BF1	2	0.003	0.410	4.745	-28.281

				BF2	8	1.949	1.598	2.825	-24.543
				BF3	3	1.934	1.111	1.365	-23.881
				BF4	5	2.517	1.197	3.256	-26.016
				HF1	2	1.190	0.596	3.359	-25.639
				HF3	4	2.443	0.554	3.495	-24.904
				HF4	2	0.588	0.194	2.553	-26.252
			rubber	BR2	3	2.940	1.631	3.182	-28.538
				HR1	3	1.901	1.320	2.702	-28.593
				HR4	2	0.982	0.289	1.692	-26.557
405478	*Rostrozetes sp. 1*	(Berlese, 1910)	jungle rubber	BJ2	2	0.569	0.288	4.123	-27.183
405449	*Scheloribates praeincisus*	(Berlese, 1910)	jungle rubber	BJ2	3	2.502	0.323	2.958	-27.650
				HJ4	6	2.111	2.180	2.259	-26.647
			oil palm	BO3	9	3.276	2.150	1.495	-26.449
				BO4	3	2.770	0.396	2.822	-26.694
				BO5	6	2.978	0.923	2.992	-28.849
				HO1	6	3.032	1.366	1.086	-26.825
				HO2	2	4.430	0.286	3.570	-26.947
				HO3	3	3.504	2.362	3.817	-27.910
			rainforest	BF2	10	2.003	1.086	0.080	-28.037
				BF3	6	1.997	0.680	0.840	-25.758
				BF4	3	3.577	0.663	3.258	-25.428
				HF1	6	1.179	1.029	0.284	-28.679
				HF3	6	1.721	0.884	-0.018	-28.567
				HF4	5	1.581	0.978	-0.015	-28.216
			rubber	BR1	3	1.441	0.344	2.034	-25.529
				BR2	4	3.637	0.967	5.887	-27.126
				BR3	3	0.744	1.118	3.653	-28.191
				HR1	10	2.934	2.530	4.111	-27.602
				HR4	2	0.954	0.363	-0.852	-28.452

Chapter III

Variation in community level trophic niches of soil microarthropods with conversion of tropical rainforest into plantations systems as indicted by stable isotopes (^{15}N, ^{13}C)

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Abstract

Land-use change is threatening biodiversity worldwide and is predicted to increase in the next decades, especially in tropical regions. Most studies focused on the response of single or few species to land-use change, only few investigated the response of entire communities. In particular the response of belowground communities to changes in land use received little attention. Oribatid mites (Oribatida, Acari) are among the most abundant soil animals, involved in decomposition processes and nutrient cycling. Oribatid mite species span a wide range of trophic niches and are known to sensitively respond to changes in land use. Here, we investigated shifts in the community-level trophic niche of oribatid mites with the conversion of rainforest into rubber and oil palm plantations. Due to a wider range of resources in more natural ecosystems we expected the community-level trophic niche to shrink with conversion of rainforest into plantations. As the conversion of rainforest into plantations is associated with reduced availability of litter resources we expected the average trophic level (indicated by the $^{15}N/^{14}N$ ratio) to be higher and the role of basal resources (indicated by the $^{13}C/^{12}C$ ratio) to shift towards living plant material in rubber and oil palm plantations. Our results confirm that the community-level trophic niche of oribatid mites in fact is wider in rainforest than in plantation systems. Additionally, the results document that the community-level trophic niche in rainforest and rubber agroforest (“jungle rubber”) is separated from that in monoculture plantation systems, indicating that the trophic niche of oribatid mite communities shifts markedly with conversion of rainforest into plantation systems. Further, $^{15}N/^{14}N$ ratios indicate that oribatid mites in fact shift their diet towards predation and/or scavenging with transformation of rainforest into plantations, presumably due to the limited amount of

litter and its low quality in rubber and oil palm plantations. Exceptionally low $^{13}C/^{12}C$ ratios in rubber plantations suggest that certain oribatid mite species in this land-use system use resources non-existing in the other studied ecosystems. Oribatid mite communities in plantation systems therefore have an unusual high functional richness and uniqueness compared to natural systems.

Introduction

The niche concept forms the basis of concepts explaining the coexistence of species (Hutchinson, 1959; Chase and Leibold, 2003). There are two different niche-related process, i.e. environmental filtering, assuming that the assemblage of communities is based on the similarity of niches of the species coexisting locally, and niche differentiation resulting from competition among species (Macarthur et al., 1967; Vellend, 2010; Violle et al., 2011; Kraft et al., 2015). At stable environmental conditions long-term coexistence of species results in distinct niches of the coexisting species and in predictable community composition with pronounced niche differentiation among coexisting species (Giller, 1996). By contrast, in fragmented habitats or in systems with fluctuating environmental conditions communities are likely to be assembled at least in part at random, and therefore niches of species may overlap (Giller, 1996; Chesson, 2000; Caruso et al., 2012). Trophic niches define the impact of one species on other species based on the use of common resources and therefore are closely related to the role of species in ecosystems (Korotkevich et al., 2018). Species with broader trophic niches likely are able to better cope with disturbances, such as changes in land use or invading species, compared to species with narrower niches (Bommarco et al., 2010; Dammhahn et al., 2017). In contrast to the former, species with narrower niches are more likely to go extinct if environmental conditions and the availability of food resources change (Gan et al., 2014). The complement of trophic niches of coexisting species define the community level trophic niche which is likely to differ between ecosystems due to species turnover and changes in trophic niches of individual species (Tilman, 2004; Salles et al., 2009). These changes are likely to be associated with changes in the functionality of communities (Korotkevich et al., 2018).

Functional diversity, including functional richness, functional evenness and functional divergence, has been shown to increase the ecosystems functioning (Hulot et al., 2000; Pearson, 2001; Bremner et al., 2003). Moreover, it is related to certain characteristics of communities and ecosystems. Mechanisms responsible for diversity - ecosystem functioning relationships are based on the niches of species and their functional space (Tilman, 2001; Adler and Bradford, 2002). If the functional richness is low, part of the available resources remain unused by the local community, resulting in low productivity (Petchey, 2003). By contrast, increased ecosystem functioning due to efficient use of resources is based on high niche differentiation associated with low resource competition (Mason et al., 2005).

The global demand for food, fuel and fiber is associated with the transformation and degradation of ecosystems, and this is increasing rapidly (Sodhi et al., 2010; Wilcove et al., 2013; Meijide et al., 2018). Especially tropical regions are suffering (Sodhi et al., 2010; Wilcove et al., 2013; Meijide et al., 2018). Tropical forest ecosystems, characterized by the highest biodiversity and highest level of endemism worldwide, are shrinking and are transformed into intensively managed monoculture plantations at increasing rates (Myers et al., 2000; Sodhi et al., 2010; Drescher et al., 2016). Biodiversity in plantations typically is strongly reduced compared to rainforest due to reduced diversity of trees as well as more pronounced fluctuating environmental conditions (Wilcove and Koh, 2010). Reduced diversity in plantations may impair the functioning of these systems and this at least in part is likely to be due to changes in trophic interactions and community level trophic niches (Potapov et al., 2019a).

So far, most studies investigating shifts in trophic niches with changes in environmental conditions focused on the response of individual species to disturbances and habitat transformation, whereas changes at the level of communities have been little studied (Korotkevich et al., 2018). Further, only little is known on the effect of land-use change in tropical regions on soil organisms responsible for major ecosystem functions such as decomposition processes and nutrient cycling and this applies in particular to soil mesofauna such as oribatid mites (Maraun and Scheu, 2000; Bardgett, 2005). Oribatid mites are trophically diverse and span over four trophic levels including lichen feeders, fungal feeders, primary and secondary decomposers as well as predators/scavengers (Schneider et al., 2004; Illig et al., 2005; Maraun et al., 2011). Due to their high diversity and wide range of trophic niches oribatid mites are ideal model taxon for studying effects of land-use change on community functioning.

Natural variations in $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios provide insight into the trophic niches of animal species as well as the trophic structure of animal communities (Wada et al., 1991; Newsome et al., 2007; Boecklen et al., 2011), and are increasingly used for characterizing trophic niches of soil animal species (Tiunov, 2007; Potapov et al., 2019b). Animal tissue is enriched by 3.4 ‰ per trophic level in ^{15}N, allowing to study changes in the trophic position of species with environmental changes (DeNiro and Epstein, 1978; Post, 2002; Pollierer et al., 2009; Potapov et al., 2019b). In contrast to ^{15}N, ^{13}C is little enriched in consumers as compared to their diet, allowing to trace basal food resources in food webs (DeNiro and Epstein, 1978; Spence and Rosenheim, 2005; Pollierer et al., 2009; Potapov et al., 2019b). Stable isotopes have been used to analyze trophic niches of a wide range of soil invertebrates (Scheu and Falca, 2000; Halaj et al., 2005; Maraun et al., 2007, 2011; Tiunov, 2007). However, they have rarely been used to investigate how changes in trophic niches of soil organisms are affected by changes in land use (Lagerlöf et al., 2017; Minor et al., 2017; Korotkevich et al., 2018). Additionally, previous metrics for stable isotopes did not account for abundance and/or biomass of the studied species, e.g. all organisms were assumed to have the same importance or impact (Layman et al., 2007; Jackson et al., 2011). Novel techniques allow accounting for these deficiencies but have rarely been used so far (Huxel and McCann, 1998; Cucherousset and Villéger, 2015).

The current study formed part of the interdisciplinary project “Ecological and socioeconomic functions of tropical lowland rainforest transformation systems” (EFForTS), established in Jambi Province, southwest Sumatra, Indonesia (Drescher et al., 2016). By measuring natural variations in $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios, we analyzed changes in the trophic structure of oribatid mite communities with conversion of rainforest into plantation systems. Four major land-use systems in Southeast Asia were investigated, i.e. rainforest, rubber agroforest (“jungle rubber”), rubber and oil palm monoculture plantations. We focused on the niche structure and overall niche position at the level of communities rather than on the changes in trophic niches of individual species, which were addressed in an earlier study (Krause et al., 2019). We hypothesized (1) that the community-level trophic niche of oribatid mites is larger in close to natural ecosystems, such as rainforest and jungle rubber, than in intensively managed agricultural systems, such as rubber and oil palm plantations. Further, we hypothesized (2) that the community-level trophic niche of oribatid mites is shifted in intensively managed agricultural systems towards living plant-based resources due to lower availability of litter resources and more open canopy allowing more pronounced growth of understory plants and algae. In addition, we hypothesized (3) that functional richness and functional redundancy in rainforest are higher compared to plantation systems due to more complex resources and more species rich oribatid mite communities.

Material and Methods

Study sites

Samples were taken in two landscapes of Jambi Province, Bukit Duabelas (2° 0’ 57” S, 120° 45’ 12” E) and Harapan (1° 55’ 40” S, 103° 15’ 33” E). In each landscape, four different land-use systems were investigated: rainforest, jungle rubber, rubber and oil palm plantations (Drescher et al., 2016). Rainforest sites were ‘primary degraded forests’ (classified by Margono et al., 2014) and had been selectively logged at least once. Jungle rubber sites were established by planting rubber trees (*Hevea brasiliensis*) into rainforest and contain rainforest tree species. Jungle rubber sites represent low intensive land-use systems, lacking fertilizer input as well as herbicide application. By contrast, rubber as well as oil palm (*Elaeis guineensis*) monocultures represent high land-use intensity plantation systems managed by the addition of fertilizers as well as herbicides. More details on the study sites are given in Drescher et al. (2016). For each land-use system four replicates were established in each of the two landscapes, resulting in a total of 32 plots. Each plot spanned 50 x 50 m and included three randomly placed subplots of 5 x 5 m (Drescher et al., 2016).

Sampling, extraction and species determination

In October 2013, samples (16 x 16 cm; including the litter layer and 0 – 5 cm of the mineral soil) were taken from each of the subplots, i.e. a total of 96 samples. The samples were transported to the laboratory and extracted by heat (Kempson et al., 1963). Determination of oribatid mites was done to species/morphospecies level using Balogh and Balogh (2012). Species and morphospecies were documented by pictures, linked with morphological traits and species identification numbers (species ID), and included into the Ecotaxonomy database (http://ecotaxonomy.org/). Oribatid mites were ascribed to trophic groups including lichen feeders, primary decomposer, secondary decomposer/fungal feeders and predators/scavengers based on Maraun et al. (2011). Until further analysis, species were stored in 70 % ethanol. For calibration of animal stable isotope values mixed litter samples were taken from the subplots (Klarner et al., 2017).

Stable isotope analysis

For each land-use system in the two landscapes (Bukit Dubaelas and Harapan) species for stable isotope analysis were selected based on their relative abundance; for each land-use system species representing 80 % of total oribatid mite individuals were analyzed (Table S1). These species were assumed to represent the functional niche of the community of oribatid mites of the respective land-use system. Three individuals (if present) were pooled for one sample (sample weight 0.02-0.19 mg). In total, 367 samples including all the species (117) contributing to 80 % of the individuals sampled were analyzed (out of the total of 220 species occurring at the study sites; D. Sandmann, unpubl. data).

Prior to stable isotope analysis samples were dried at 60°C for 24 h. Litter samples were grinded in a ball mill (Retsch Mixer Mill MM200, Haan, Germany) prior to stable isotope measurement. Samples were analyzed using a coupled system of an elemental analyzer (NA 1500, Carlo Erba, Milan, Italy) and a mass spectrometer (MAT 251, Finnigan, Bremen, Germany) adopted for the analysis of small sample sizes (Langel and Dyckmans, 2014). Stable isotope abundance (δX) was expressed using the δ notation with δX (‰) = $(R_{sample}-R_{standard}) / R_{standard} \times 1000$, with X representing the target isotope (^{15}N or ^{13}C) and R_{sample} and $R_{standard}$ the respective target isotope ratio ($^{15}N/^{14}N$ or $^{13}C/^{12}C$). As standard for ^{13}C Vienna PD Belemnite and for ^{15}N atmospheric nitrogen were used. Acetanilid was used for internal calibration.

Statistical analysis

Means of $\delta^{13}C$ and $\delta^{15}N$ values of litter samples across subplots were used for calibration of stable isotope values of oribatid mites of the respective plot. Calibrated $\delta^{13}C$ and $\delta^{15}N$ values were calculated as difference between the plot-specific litter $\delta^{13}C$ and $\delta^{15}N$ values, and the mean $\delta^{13}C$ and $\delta^{15}N$ value of oribatid mite species, and given as $\Delta^{13}C$ and $\Delta^{15}N$ values, respectively. Calibrated values were used for statistical analyses.

For characterizing the trophic structure of communities we calculated ‘isotopic metrics’ (Layman et al., 2007; Cucherousset and Villéger, 2015). These metrics describe the position of species of a studied community within two-dimensional space, represented by $\delta^{15}N$ and $\delta^{13}C$ values and included, among others, the convex hull area, which is the ‘smallest area’ that is filled by all species within the studied community (Layman et al., 2007). Cucherousset and Villéger (2015) further developed metrics based on the ones from Layman et al. (2007), by merging them with the functional diversity metrics suggested by Villéger et al. (2008) and Laliberté and Legendre (2010). These metrics are mathematically independent of the number of species and account for the abundance or biomass of the studied species (Cucherousset and Villéger, 2015). Additionally, they provide a process for scaling stable isotope axes, which allows to quantify isotopic diversity as well as the levels of potential isotopic overlap between species.

Statistical analyses were performed using R v 3.5.2 (R Core Team, 2018) with R studio interface (RStudio, Inc.). We used the R script provided by Cucherousset and Villeger (2015) to scale two stable isotope axes and calculate isotopic metrics for each community. Δ^{13}C and Δ^{15}N values were scaled between 0 and 1 based on maximum and minimum across communities to ensure equal contribution of two isotopes in the multidimensional metric calculation. Before calculating community mean values and multidimensional metrics, species were weighted according to their contribution to the total community biomass per plot and therefore, those metrics were adjusted according to the functional relevance of the species. Individual body mass of oribatid mite species were calculated from individual measurements of body length and width (D. Sandmann, unpubl. data) using the allometric regression $\log P = 1.53 \times \log L + 1.53 \times \log l - 6.67$, with P body mass, L body length and l body width (Lebrun, 1971). First, we calculated single-dimensional metrics – minimum, maximum, range and mean for Δ^{13}C and Δ^{15}N values for each community. Maximum as well as minimum Δ^{13}C and Δ^{15}N values were represented by one species with the most extreme values within the community. Second, we calculated five multidimensional metrics including isotopic divergence ('IDiv'), isotopic dispersion ('IDis'), isotopic evenness ('IEve'), isotopic uniqueness ('IUni') and isotopic richness ('IRic')

(Cucherousset and Villéger, 2015). In addition to the convex hull area (Layman et al., 2007) ‘IDiv’ is weighting stable isotope values according to the biomass of species and showing the distance between all species as well as the center of the convex hull area. ‘IDiv’ values close to 0 indicate that species with the most extreme stable isotope values, e.g. primary decomposers and predators, are rare, whereas ‘IDiv’ values close to 1 indicate that species with the most extreme stable isotope values are among the dominant species. 'IDis’ reflects the convex hull area but also isotopic divergence and therefore can be interpreted as scaled multidimensional variance. ‘IDis’ is a generalized version of the ‘centroid distance’ (Layman et al., 2007) but accounts for the relative contribution of species to community biomass. 'IDis' approaches 1 when most stable isotope values are fare from the center of the group, i.e. species with contrasting stable isotope values but similar abundance, e.g. primary and high-level consumers, whereas ‘IDis’ approaches 0 if stable isotope values of the species differ little. In contrast to ‘IDiv’ and ‘IDis’, which do not consider the distance between species, ‘IEve’ quantifies the distribution of species in stable isotope space weighted by biomass. 'IEve' values close to 1 indicate that the isotope values of the species of the studied community are evenly distributed. By contrast, 'IEve' values close to 0 indicate that most stable isotope values of the studied species cluster together indicating e.g., that there are mostly herbivore and only few predator species. 'IUni', is defined as the inverse of the average isotopic redundancy, which reflects the closeness of stable isotope values of the studied species within the community. 'IUni' equals 0 if stable isotope values of species among communities are similar indicating, e.g. that species of different communities occupy a similar isotope range. By contrast, 'IUni' is close to 1 if stable isotope values of species differ among communities indicating that e.g., the isotope values of species with high biomass are very different from those of the other species of the community. Contrary to the latter, 'IRic' calculates community properties based on the size and position of isotope niches among species. ‘IRic’ represents the functional richness i.e., the functional space filled by the community (Villéger et al., 2008). For single trait approaches functional richness reflects the difference between the maximum and minimum trait values of the community (Mason et al., 2005). To calculate functional richness for multiple traits the convex hull area occupied by a community is used as multidimensional measure (Cornwell et al., 2006; Layman et al., 2007; Villéger et al., 2008). Functional richness does not have an upper limit as it represents a volume, which depends on the number of traits and their units, however, functional richness values may be limited by 0 and 1 due to standardization of the hull volume, e.g. the volume occupied by all studied species (Mason et al., 2005; Villéger et al., 2008).

Data were analyzed using the *aov* (analysis of variance) function with landscape and land-use system as factors followed by post-hoc comparison of means using *HSD.test* function to inspect differences between land-use systems. Results were displayed using the *ggplot2* package (Wickham, 2016). The baseline was represented by zero (Figs. 2, 3). Communities were represented by points in graphs. Oribatid mites were ascribed to trophic levels assuming an enrichment of ^{15}N by 3.4 ‰ per trophic level except for primary decomposer which were assumed to be only enriched in ^{15}N by a maximum of 1.7 ‰ compared to litter (Vanderklift and Ponsard, 2003; Potapov et al., 2019b).

Results

Trophic structure

As indicated by ^{15}N values, rainforest, jungle rubber and rubber plantations harbored species spanning over three trophic levels including primary and secondary decomposers as well as predators (Fig. S1a-c). By contrast, oil palm plantations lacked primary decomposers and only comprised secondary decomposers and predators (Fig. S1d). Additionally, rainforest and rubber plantations harbored species with stable isotope values lower than those of litter (Fig. S1a and S1c). In rubber plantations some oribatid mite species were highly depleted in ^{13}C relative to the litter baseline (up to 6 ‰; Fig. S1c).

Calibrated stable isotope values of oribatid mite communities of the four land-use systems separated the two more natural systems from the two monoculture plantations (Fig. 1). Notably, rainforest and jungle rubber as well as oil palm and rubber plantations overlapped widely.

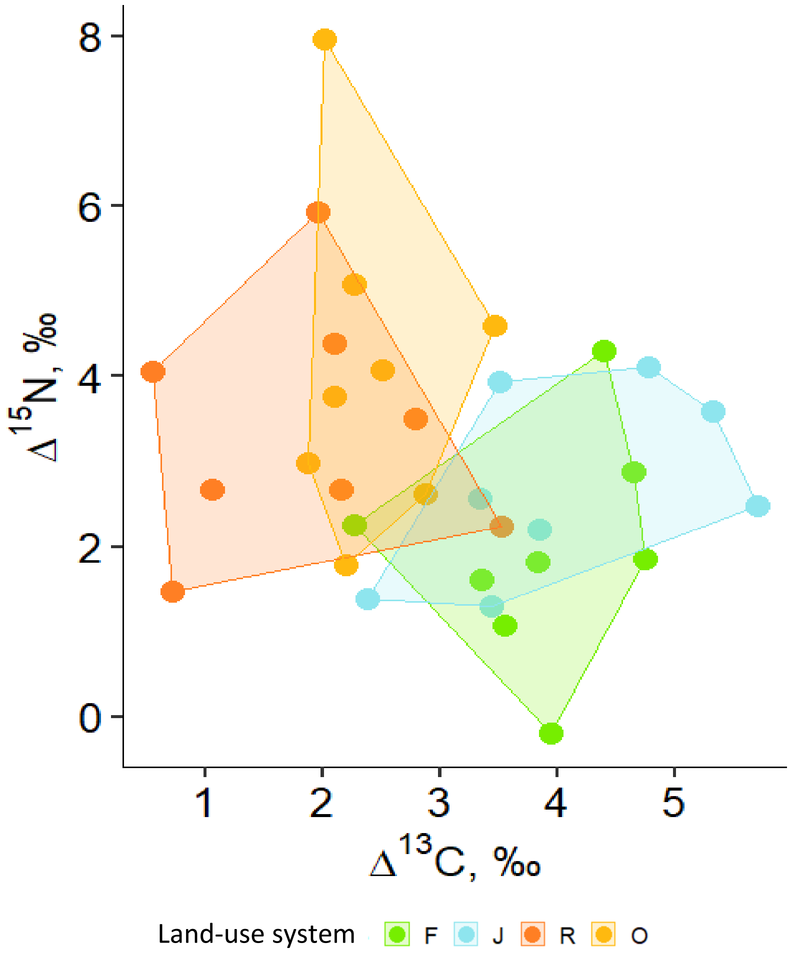

Figure 1: Average $\Delta^{13}C$ and $\Delta^{15}N$ stable isotope values of oribatid mite communities in rainforest (green), jungle rubber (blue), rubber (red) and oil palm plantations (orange) (eight replicates each). Each point represent the average position of oribatid mite communities per replicate land-use system; for each land-use system eight replicates were studied (four in each of two landscapes).

One-dimensional metrics

Similar to the calibrated stable isotope values, the average community positions of $\Delta^{13}C$ and $\Delta^{15}N$ values ('IPos') indicated separation of more natural systems and plantation systems (Figs. 2a - e). The average community positions of both $\Delta^{13}C$ and $\Delta^{15}N$ values varied significantly between the land-use systems ($F_{3,27}$= 7.09, p < 0.001 for $\Delta^{13}C$ and $F_{3,27}$=

7.93, $p = < 0.001$ for $\Delta^{15}N$). Average community positions of $\Delta^{13}C$ were similar in rainforest and jungle rubber, but significantly lower in rubber and oil palm plantations, on average by 1.58 ‰ (Fig. 2a; Table S2). By contrast, average community positions of $\Delta^{15}N$ were similar in rubber and oil palm plantations, but significantly lower in jungle rubber, on average by 1.79 ‰, and in rainforest, on average by 3.03 ‰ (Fig. 2e; Table S2).

Maximum $\Delta^{13}C$ values, but not maximum $\Delta^{15}N$ values, varied significantly with land-use system ($F_{3,27} = 7.22$, $p = 0.001$ for $\Delta^{13}C$ and $F_{3,27} = 0.41$, $p = 0.74$ for $\Delta^{15}N$). Maximum $\Delta^{13}C$ values were similar in rainforest, jungle rubber and rubber plantations, but significantly lower in oil palm plantations, on average by 2 ‰ (Fig. 2b; Table S2). Further, minimum $\Delta^{13}C$ and $\Delta^{15}N$ values varied significantly with land-use system ($F_{3,27} = 19.51$, $p < 0.001$ for $\Delta^{13}C$ and $F_{3,27} = 10.56$, $p = <0.001$ for $\Delta^{15}N$). Minimum $\Delta^{13}C$ were similar in rainforest, jungle rubber and oil palm plantations, but significantly lower in rubber plantations, on average by 4.46 ‰. By contrast, minimum $\Delta^{15}N$ values were similar in rainforest, jungle rubber and rubber plantations, but significantly higher in oil palm plantations, on average by 4.15 ‰ (Fig. 2g; Table S2).

Similar to the previous metrics, the range between maximum and minimum $\Delta^{13}C$ and $\Delta^{15}N$ values varied significantly between land-use system ($F_{3,27} = 16.31$ $p = 0.005$ for $\Delta^{13}C$ and $F_{3,27} = 5.18$ $p = 0.006$ for $\Delta^{15}N$). The range in $\Delta^{13}C$ values was similar in rainforest, jungle rubber and oil palm plantations, but significantly higher in rubber plantations, on average by 4.87 ‰ (Fig. 2d; Table S2). By contrast, the range in $\Delta^{15}N$ values was similar in rainforest and rubber plantations, but significantly lower in jungle rubber, on average by 2.52 ‰, and in oil palm plantations, on average by 4.94 ‰ (Fig. 2h) (Table S2).

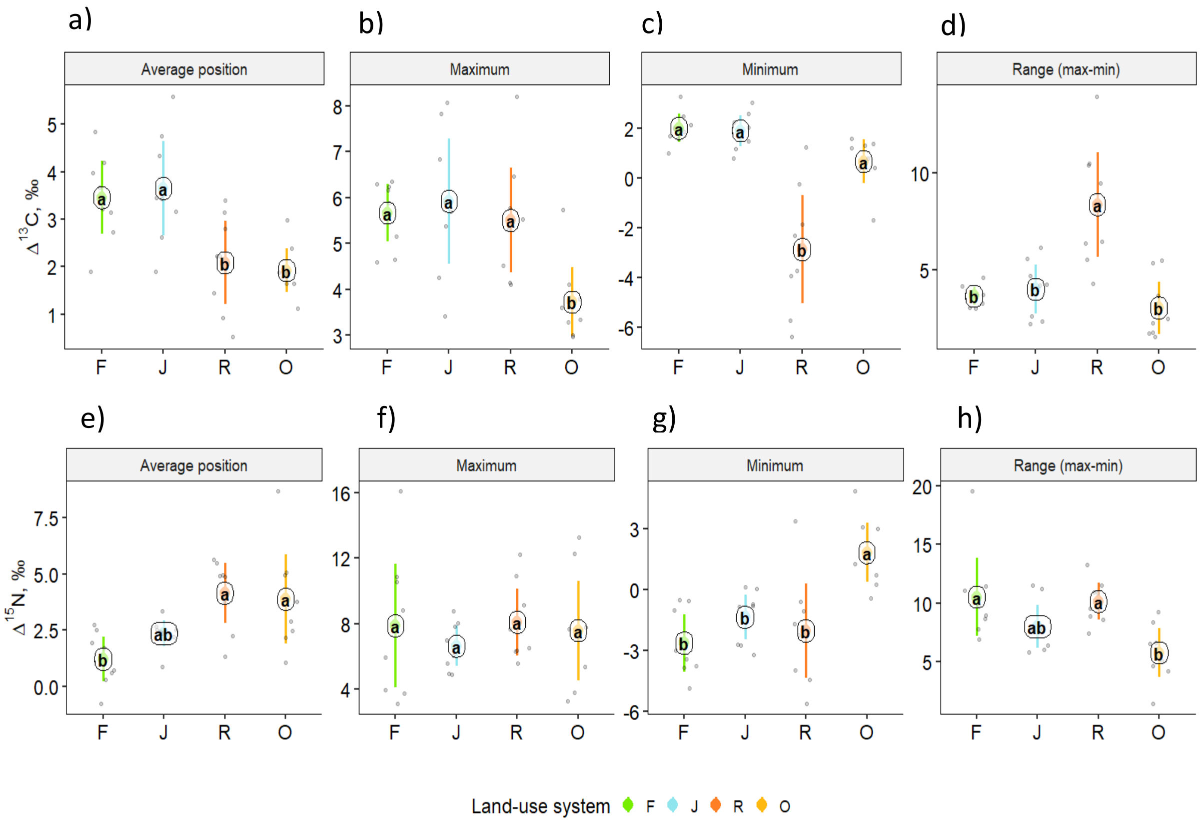

Figure 2. One-dimensional metrics for $\Delta^{13}C$ (upper panel) and $\Delta^{15}N$ values (lower panel) of oribatid mite communities. Average position (a, e), maximum (b, f), minimum (c, g) and range between minimum and maximum (d, h); means (circles) and confidence intervals. Each point represents one community. For the calculation of the metrics see Methods and Table S2. For the calculation of the average positions, species were weighted according to their contribution to the total community biomass per plot. Means, sharing the same letter are not significantly different (Tukey's HSD test, $P < 0.05$).

Multidimensional metrics

For the multidimensional metrics $\Delta^{13}C$ and $\Delta^{15}N$ values were scaled between 0 and 1 (without units). Isotopic dispersion ('IDis'), isotopic divergence ('IDiv') and isotopic evenness ('IEve') did not differ significantly between the four land-use systems (Figs. 3a-c)

('IDis' $F_{3,27} = 1.65$ $p = 0.201$; 'IDiv' $F_{3,27} = 0.46$ $p = 0.714$; 'IEve' $F_{3,27} = 1.53$ $p = 0.228$). By contrast, isotopic richness ('IRic') varied significantly between the land-use systems ($F_{3,27} = 8.1$ $p = < 0.001$); it was similar in rainforest, jungle rubber and oil palm plantations, but significantly higher in rubber monoculture plantations, on average by 0.11 (Fig. 3d; Table S3). Further, isotopic uniqueness ('IUni') varied significantly with land-use system ($F_{3,27}= 5.33$ $p = 0.005$); it increased from rainforest to jungle rubber and rubber plantations to oil palm plantations, in total by 0.3 (Fig. 3e; Table S3). For detailed information on plot level metrics values see Appendix (Figs S2 – S9).

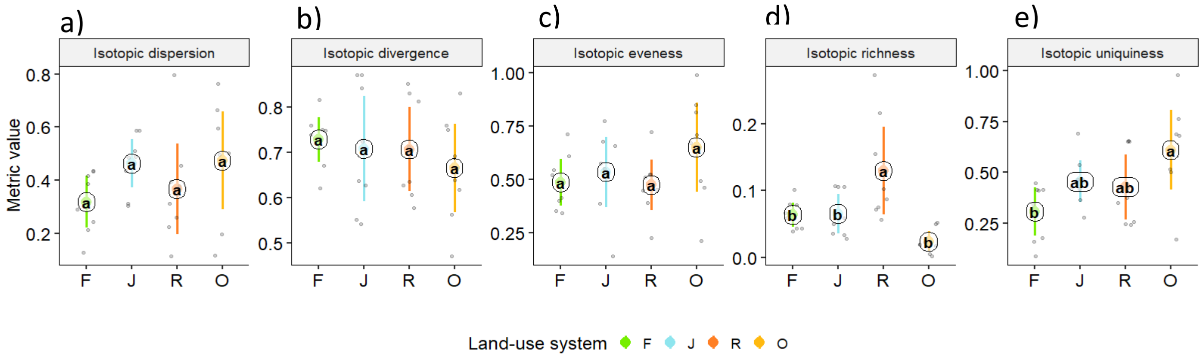

Figure 3: Multidimensional isotopic metrics of oribatid mite communities of four land-use systems, rainforest (F), jungle rubber (J), rubber (R) and oil palm plantations (O) – (a) isotopic dispersion ('IDis'), (b) isotopic divergence ('IDiv'), (c) isotopic evenness ('IEve'), (d) isotopic richness ('IRic') and (e) isotopic uniqueness ('IUni') Each point represents one community, means (circles) and confidence intervals. For calculations see Methods and Table S3. For the calculation of the metrics, species were weighted according to their contribution to the total community biomass per plot. Means sharing the same letter are not significantly different (Tukey's HSD test, $P < 0.05$).

Discussion

We investigated effects of land-use change on the trophic ecology of oribatid mite communities as model taxon of soil invertebrates and the decomposer food web. The study adds to the few existing studies investigating changes in community trophic niches and energy fluxes (Korotkevich et al., 2018; Susanti et al., 2019). We investigated shifts in the community-level trophic niche of oribatid mites with the conversion of rainforest into rubber and oil palm plantations. Oribatid mite communities were represented by the species accounting for 80 % of total oribatid mite individuals as functional community. The results indicate that the community niche of oribatid mites differs most between more natural (rainforest and jungle rubber) and monoculture plantation systems (rubber and oil palm plantations). Further, the results indicate that in rubber monoculture plantations oribatid mites use basal resources not existing in any of the other studied land-use systems. In addition, the results indicate that in oil palm plantations trophic chains are shorter than in the other land-use systems.

One-dimensional metrics

Generally, both $\Delta^{13}C$ and $\Delta^{15}N$ values were similar in rainforest and jungle rubber and distant from those in oil palm and rubber plantations, indicating that trophic niches in the more natural systems are similar and markedly different from those in the two plantation systems with trophic niches in the more natural as well as the two monoculture plantation systems differing little. This supports findings of Krause et al. (2019) who analyzed individual oribatid mite species and showed that trophic niches shifted most from rainforest to monoculture plantation systems. These changes were due to both changes in the use of basal resources as well as trophic level and indicated trophic plasticity of oribatid mite species. Using fatty acids as trophic markers Susanti et al. (2019) found strong changes in the flux of energy through soil food webs with the conversion of rainforest into rubber and oil palm plantations. Changes in energy channels with land-use intensity suggest that soil fauna communities are able to response in a flexible way to changes in the availability of resources. In rainforest energy in soil food webs is channeled mainly to higher trophic levels via the bacterial energy channel, whereas in oil palm plantations the plant-based channel is more important (Susanti et al., 2019). Results of the study of Susanti et al. (2019) further suggest that in tropical ecosystems algae play an important role as food resource for Collembola and Oribatida. Furthermore, generalist predator such as centipedes (Chilopoda) have been shown to switch from decomposer prey to other prey, predominantly herbivore species, in monoculture plantations, presumably due to reduced or lacking litter layer in the latter two systems (Klarner et al., 2017). The amount of leaf litter in the litter layer in natural ecosystems typically is higher than in planation systems (Hyodo et al., 2015), and this also applies to the ecosystems investigated the present study (Krashevska et al., 2017). In our study the litter layer in oil palm plantations was lacking or poorly developed, whereas in oil palm a dense herb layer of mostly introduced weeds was present (Drescher et al., 2016). Similar to the results of Susanti et al. (2019) the shift towards lower $\Delta^{13}C$ values in oribatid mite communities in our study indicates that conversion of rainforest into plantation systems is associated with a strengthening of the plant-based energy channel in plantation systems. By contrast, high $\Delta^{13}C$ values in rainforest and jungle rubber indicated that soil food webs in the natural systems are predominantly based on microbial energy channels (Potapov et al., 2013, 2019b).

Maximum $\Delta^{13}C$ values of oribatid mite communities (reflecting one species with the most extreme values from the community) were significantly lower in oil palm plantations compared to the other three land-use systems, indicating that compared to the other land-use systems oribatid mites in oil palm plantations lack certain basal resources and trophic niches. Presumably, this reflects the virtual absence of litter in oil palm plantations associated with the lack of primary decomposers, which is supported by the absence of species with low $\Delta^{15}N$ values. Soil animals typically are enriched in ^{13}C by 3-4 δ units compared to litter (“detrital shift”; (Pollierer et al., 2009; Potapov et al., 2019) and therefore, the lower maximum $\Delta^{13}C$ values and associated less pronounced detrital shift in oribatid mites in oil palm plantations presumably again reflect that oribatid mites (as well as other detritivores, see above) predominantly rely on freshly fixed plant carbon rather than microbial energy channels. Labile litter compounds which are easy to digest, such as sugars and proteins, are more abundant in fresh plant material (including algae) than in litter, and are often enriched in ^{13}C (Gleixner et al., 1993), whereas structural compounds which are difficult to digest, such as lignin and cellulose, are more depleted (Benner et al., 1987).

Minimum $\Delta^{13}C$ values of oribatid mite communities were significantly lower (reflecting one species with the most extreme values from the community) in rubber plantations (up to 6 ‰) than in the other three land-use systems, indicating that oribatid mites in rubber plantations use some basal resources with exceptionally low $\delta^{13}C$ values not available in the other land-use systems. Potentially, this reflects the use of carbon from understory plants and algae which assimilated CO_2 originating from decomposing organic matter (canopy effect; (Van der Merwe and Medina, 1991). However, this is unlikely to explain the difference in minimum $\Delta^{13}C$ values of oribatid mite communities between rubber plantations and the other land-use systems studied as neither the abundance of algae nor of understory plants is higher in rubber monoculture plantations than in the other land-use systems studied (Rembold et al., 2017; Schulz et al., 2019; Susanti et al., 2019). Another possibility might be that low $\Delta^{13}C$ values of oribatid mite communities reflect the use of plant compounds depleted in ^{13}C such as lignin (Bowling et al., 2008; Pollierer et al., 2009). However, the use of lignin as carbon source is also unlikely since - with very few exceptions - animals are unable to digest lignin (Berg and Ryszard, 2005).

Due to the very low minimum $\Delta^{13}C$ values in oribatid mites of rubber plantations the range of $\Delta^{13}C$ values was significantly higher as compared to the other three land-use systems, again reflecting that in rubber plantations certain oribatid mite species use resources depleted in ^{13}C which are not available in the other land-use systems. Very high ^{13}C values in jungle rubber and rubber such as in *Plonaphacarus kugohi* presumably are due to the incorporation of calcium carbonate in their exoskeleton (Norton and Behan-Pelletier, 1991; Maraun et al., 2011; Pachl et al., 2012).

In contrast to maximum and minimum ^{13}C values, maximum $\Delta^{15}N$ values of oribatid mites did not significantly differ between land-use systems. However, minimum $\Delta^{15}N$ values were significantly higher in oil palm plantations compared to the other three land-use systems reflecting the lack of primary decomposers in oil palm plantations (see above). Earlier studies also showed that in tropical ecosystems primary decomposers are scarce or lacking (Illig et al., 2005) and this likely is related to litter of poor quality (Butenschoen et al., 2014; Marian et al., 2017).

Generally, trophic level enrichment in ^{15}N in primary decomposers is lower than in secondary decomposers and predators (Scheu and Falca, 2000; Vanderklift and Ponsard, 2003). Potentially, this is due to nitrogen limitation of primary decomposers (Yoneyama et al., 1997) and low litter quality (Cornejo et al., 1994). Oribatid mites may switch from feeding on detritus to scavenging or predation, e.g. by feeding on nematodes (Heidemann et al., 2011, 2014). For centipedes it has been shown that they switch from decomposer prey in rainforest to herbivore prey in oil palm presumably due to the rich understory in oil palm plantations, indicating that diet switching contributes to the colonization of very different land-use systems by soil animals (Klarner et al., 2017).

Multidimensional metrics

Isotopic dispersion (‘IDis’), isotopic divergence ('IDiv') and isotopic evenness ('IEve') did not differ significantly between the four land-use systems indicating that the oribatid mite communities in the studied land-use systems are rather balanced and lack species occupying extreme trophic positions. Presumably, at least in part this reflects the ability of oribatid mite species to adapt to local resources (Krause et al., 2019).

In contrast to the three metrics above, isotopic richness ('IRic') was significantly higher in rubber plantations than in the three other land-use systems studied, confirming the results of isotopic ranges and reflecting a more tight functional space filling by oribatid mite communities of this system (Cucherousset and Villéger, 2015). Further, isotopic uniqueness ('IUni') in oil palm plantations exceeded that in the other three land-use systems, with jungle rubber and rubber plantations being intermediate between oil palm plantations and rainforest. High ‘IUni’ values indicate that the community harbors species with very different stable isotope values, e.g. feeding exclusively on certain resources not or little consumed by other species (Cucherousset and Villéger, 2015). High values in oil palm plantations and low values in rainforest therefore suggest low functional redundancy in the former and high functional redundancy in the latter. This indicates that the loss of species is more likely to be associated with a loss of functions in oil palm plantations than in rainforest.

Conclusions

Our results document that oribatid mites in tropical ecosystems occupy a wide range of trophic niches allowing insight into changes in the structure and functioning of decomposer systems with changes in land use. Changes in community-level trophic niches with conversion of rainforest into plantation systems were due to both changes in trophic position ($\Delta^{15}N$ values) as well as the use of basal resources ($\Delta^{13}C$ values). Notably, changes in the use of basal resources were more prominent and consistent than those in trophic positions, indicating that changes in resource use with transformation of rainforest into plantations are more pronounced than changes in trophic level. Oribatid mite communities in both monoculture plantation systems studied had lower $\Delta^{13}C$ values indicating that the decomposer food web in these systems relies more heavily on plant-based resources, whereas the decomposer food web in rainforest and jungle rubber is based predominantly on microorganisms and litter-based resources. Further, higher average $\Delta^{15}N$ values in oribatid mites of monoculture plantation systems compared to rainforest and jungle rubber indicate the scarcity or lack of primary decomposers in the former. High isotopic richness (‘IRic’) and exceptionally low $\Delta^{13}C$ values in rubber plantations indicate that oribatid mite communities in this system are functionally diverse and use carbon resources not existing in the other land-use systems studied, but the identity of these resources remains enigmatic. High isotopic uniqueness (‘IUni’) in oil palm plantations suggest that in particular these plantations are susceptible to losses of function with the loss of species. Overall, the results document that conversion of rainforest into plantation systems is associated with pronounced shifts in community level trophic niches of detritivores, which are likely associated with changes in the functioning of the decomposer system and the channeling of energy through the decomposer food web.

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Field work permissions

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no. S.07/KKH-2/2013 issued by the Ministry of Forestry of the Republic of Indonesia. Sample export for analysis in Germany was based on permit no. 125/KKH-5/TRP/2014 issued by the Ministry of Forestry of the Republic of Indonesia.

Sample collection and determination

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Appendix

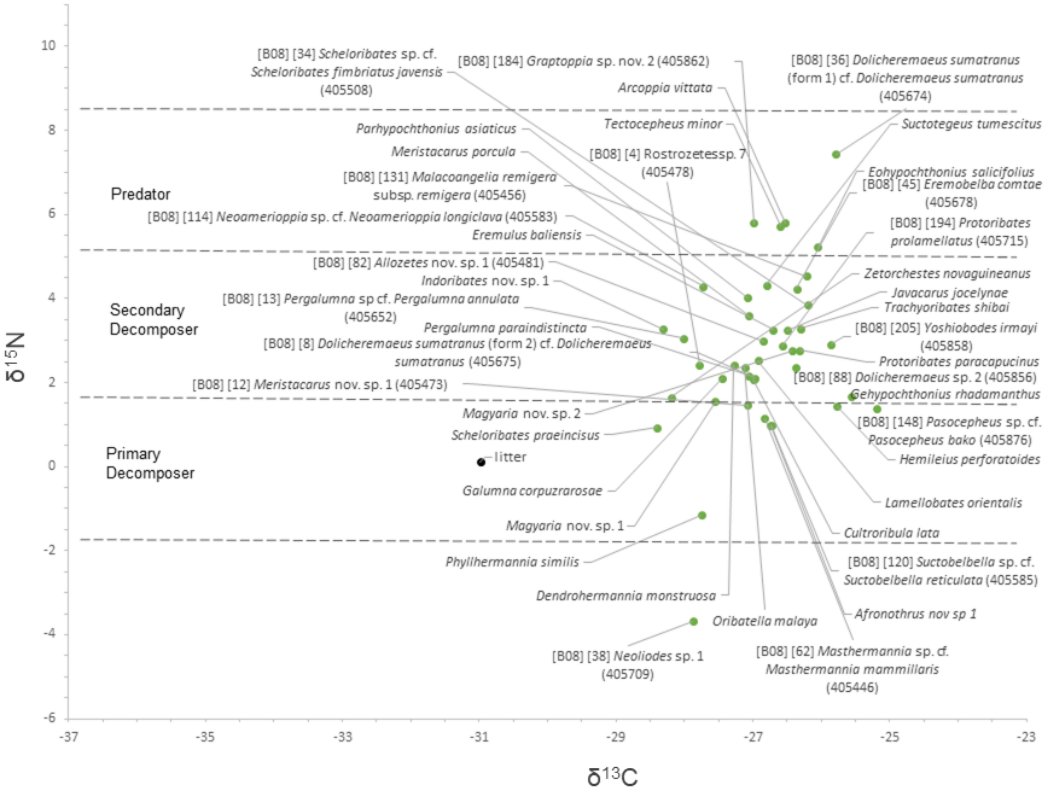


Figure S1a: Mean stable isotope values of oribatid mite species of the four land-use systems studied: rainforest (a), jungle rubber (b), rubber (c) and oil palm (d). The average stable isotope value of litter used for calibration (see Methods) is given as reference. Dashed horizontal lines reflect boundaries of trophic levels (primary decomposers, secondary decomposers and predators; see Methods). For statistical analysis see text.

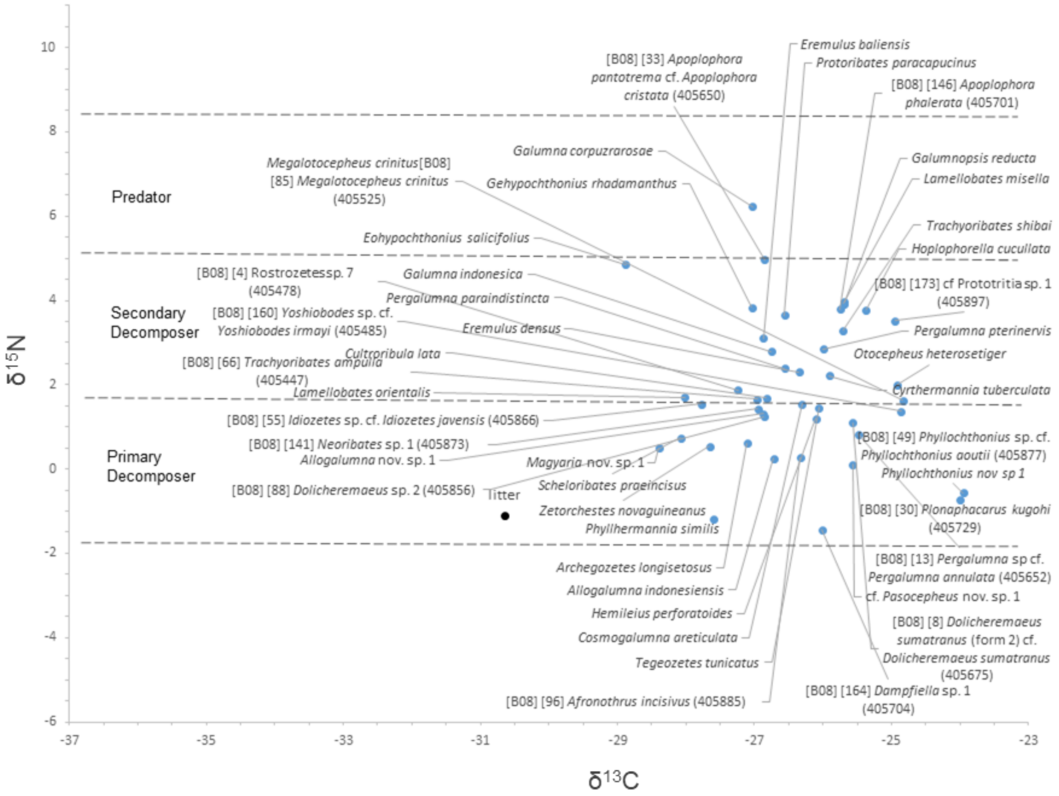


Figure S1b: Mean stable isotope values of oribatid mite species of the four land-use systems studied: rainforest (a), jungle rubber (b), rubber (c) and oil palm (d). The average stable isotope value of litter used for calibration (see Methods) is given as reference. Dashed horizontal lines reflect boundaries of trophic levels (primary decomposers, secondary decomposers and predators; see Methods). For statistical analysis see text.

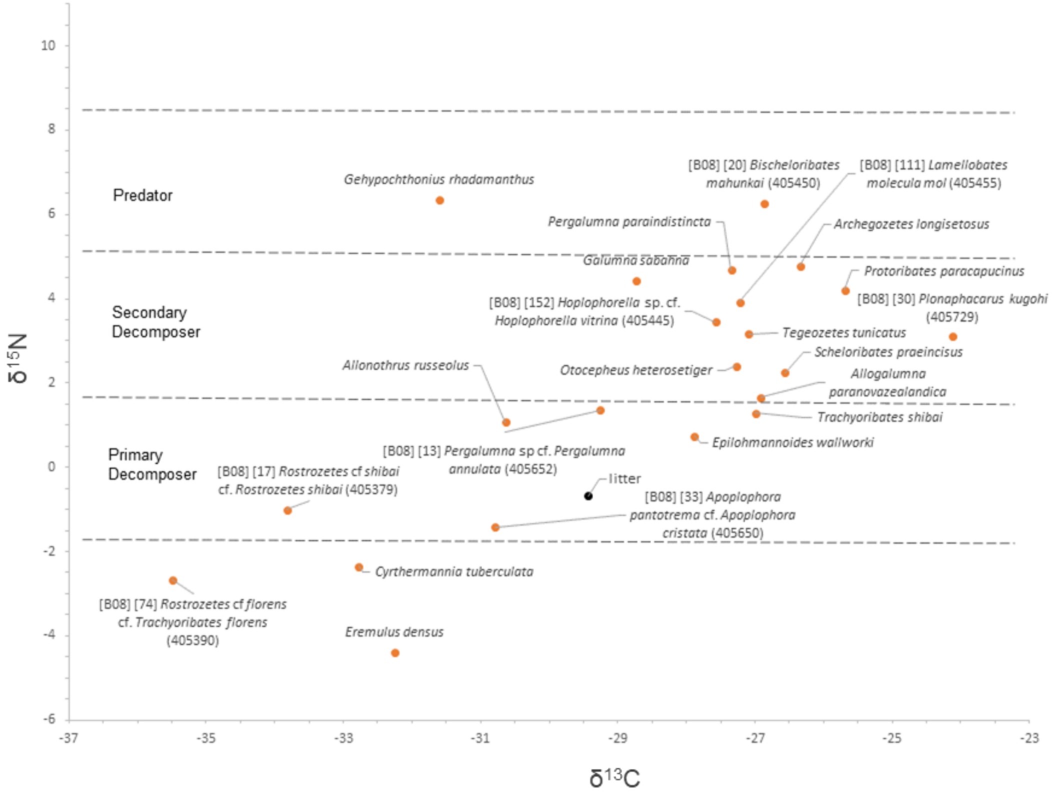


Figure S1c: Mean stable isotope values of oribatid mite species of the four land-use systems studied: rainforest (a), jungle rubber (b), rubber (c) and oil palm (d). The average stable isotope value of litter used for calibration (see Methods) is given as reference. Dashed horizontal lines reflect boundaries of trophic levels (primary decomposers, secondary decomposers and predators; see Methods). For statistical analysis see text.

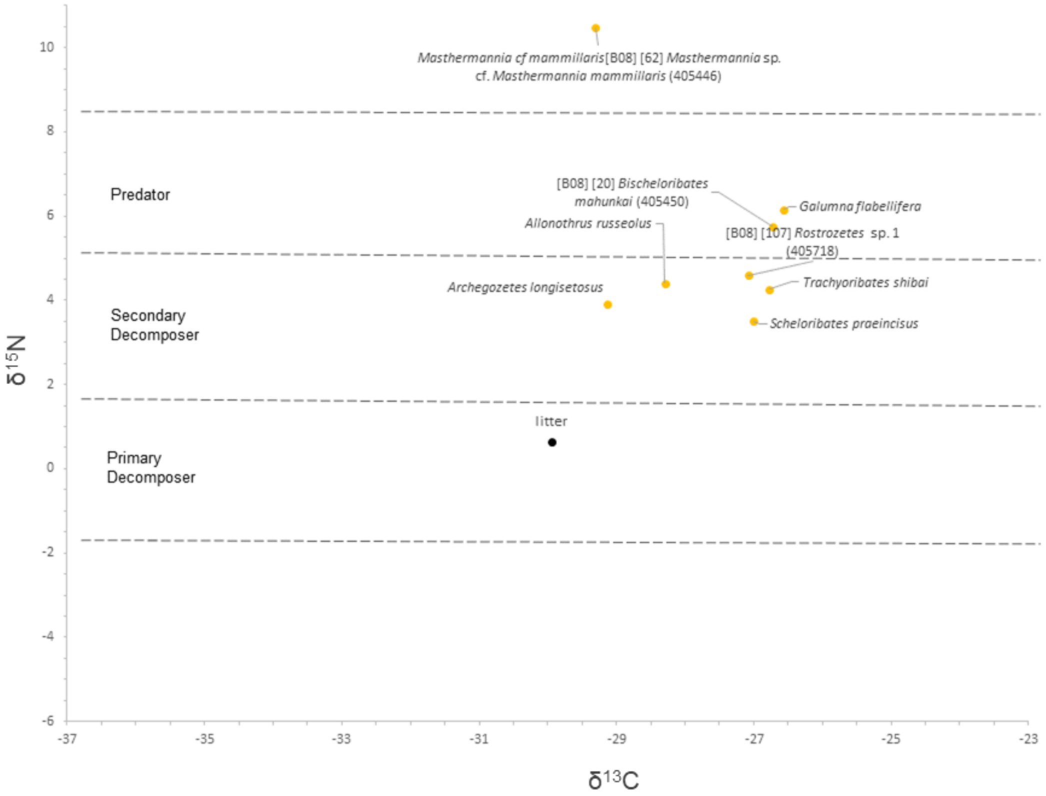
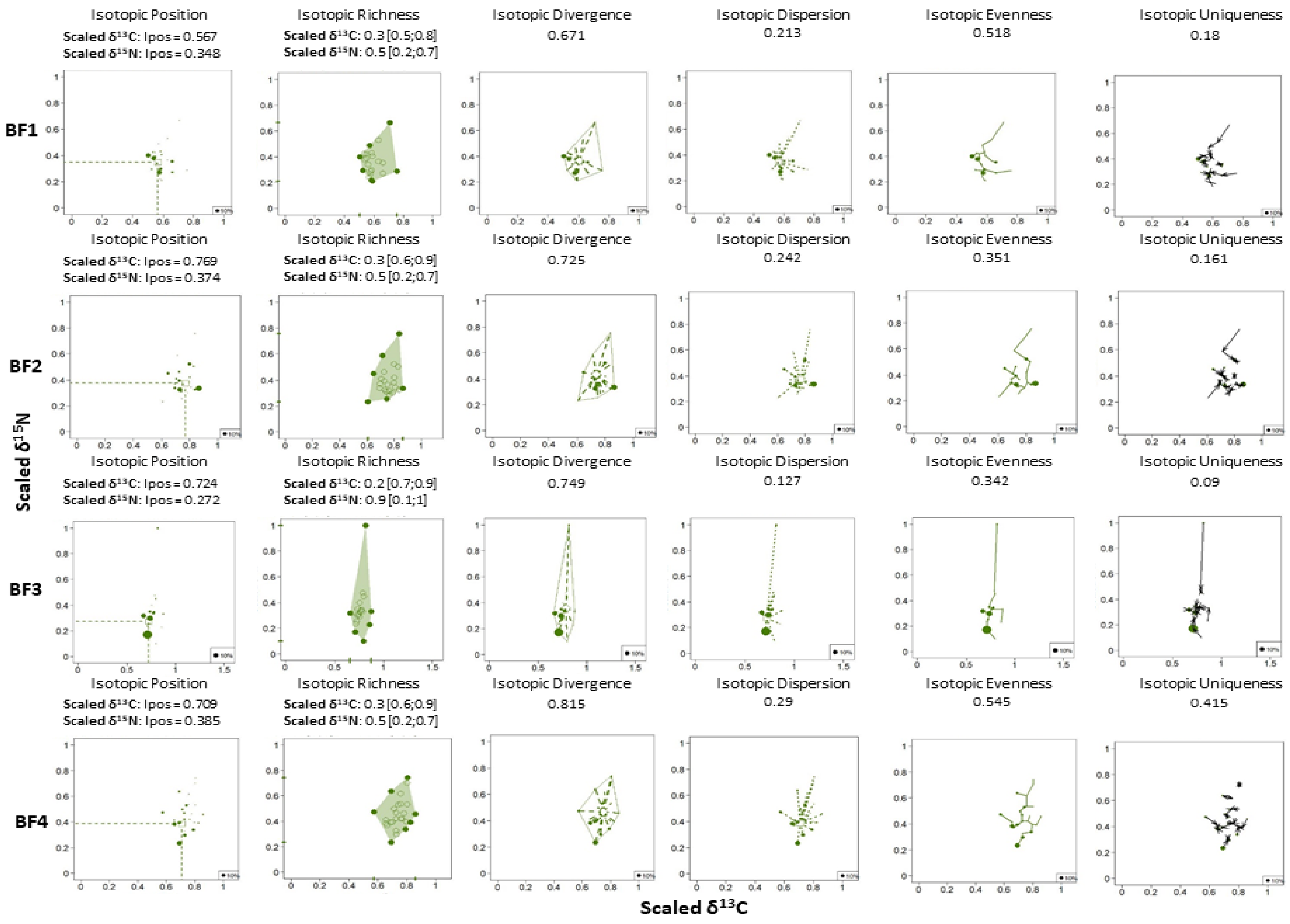
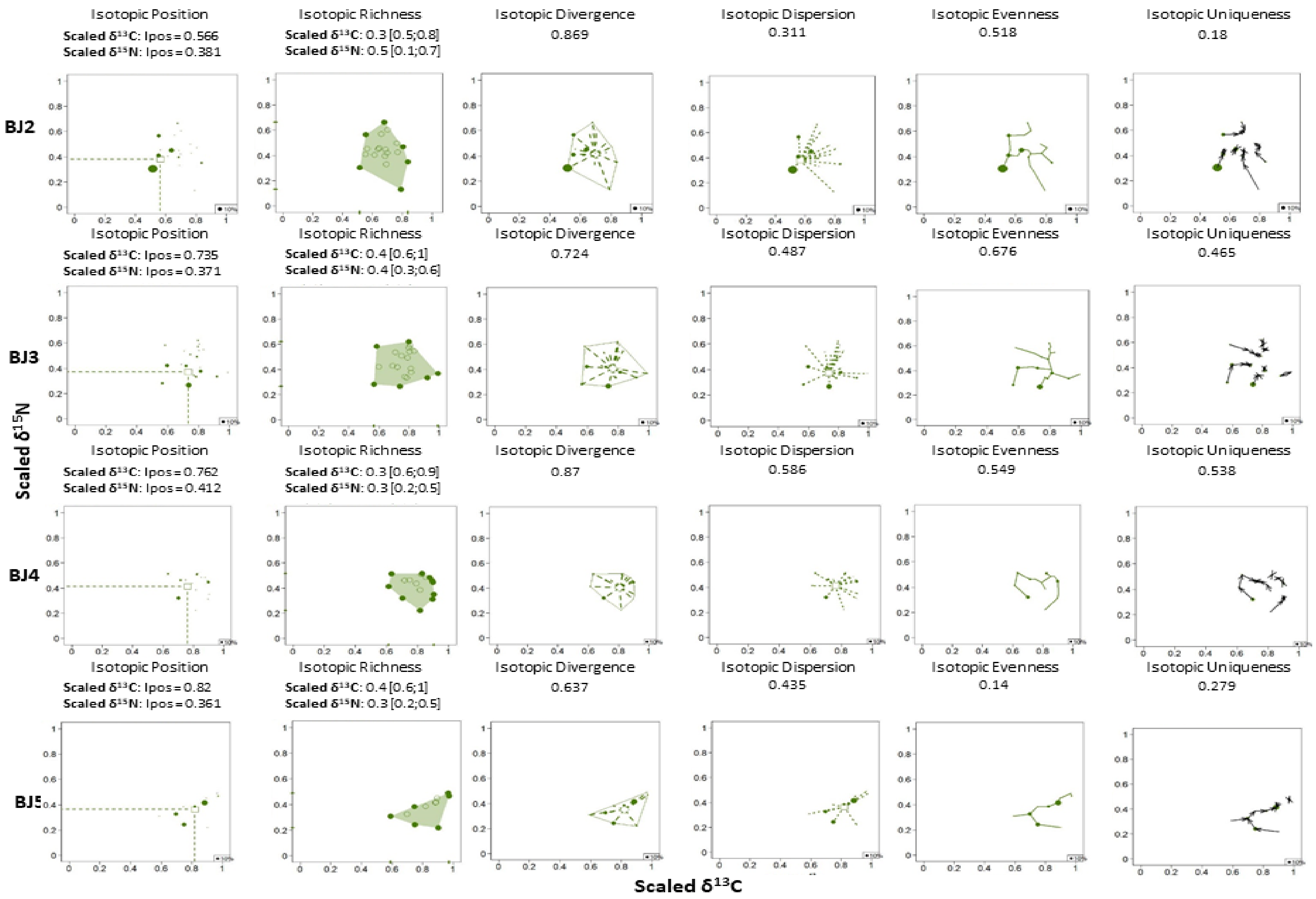


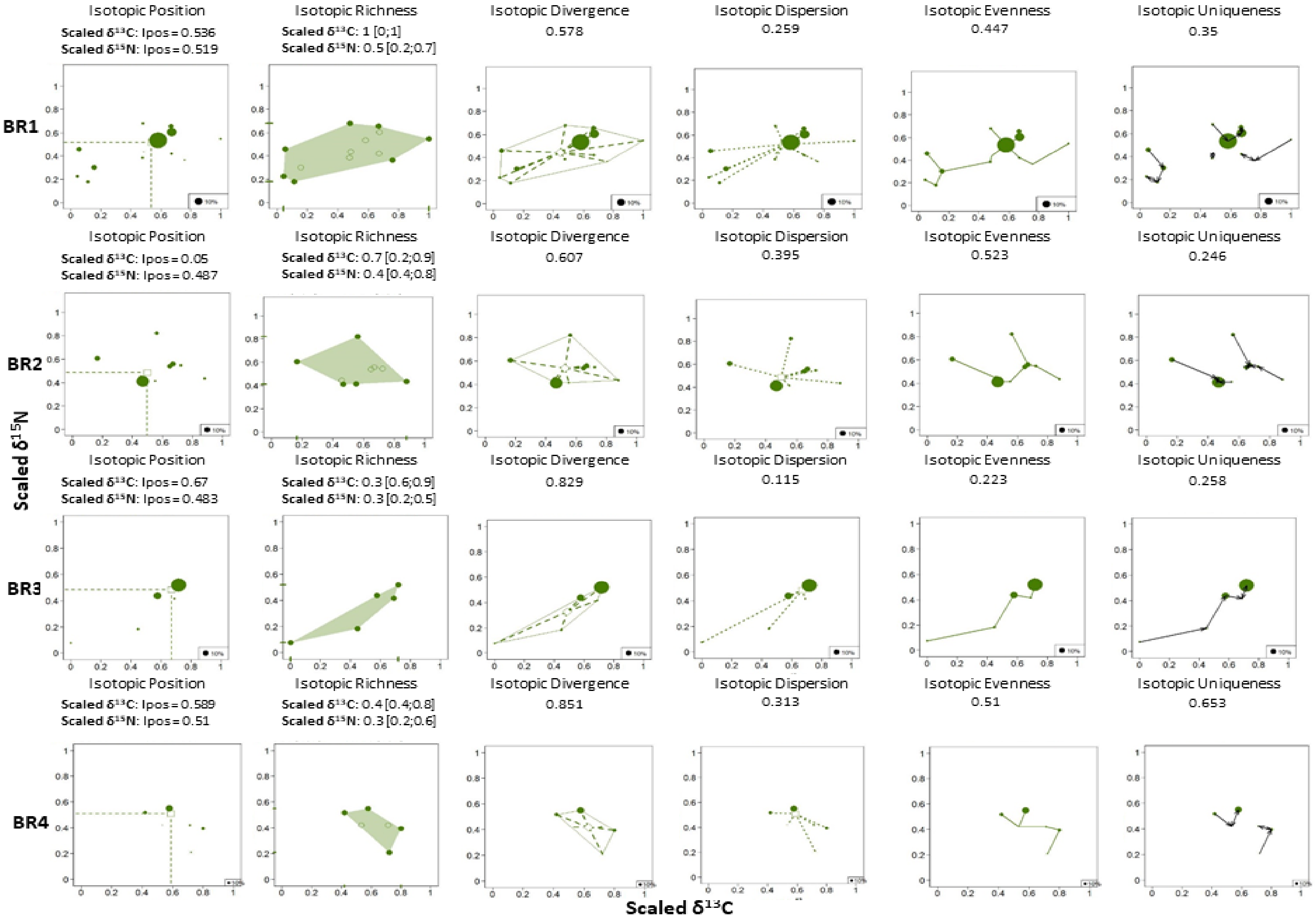
Figure S1d: Mean stable isotope values of oribatid mite species of the four land-use systems studied: rainforest (a), jungle rubber (b), rubber (c) and oil palm (d). The average stable isotope value of litter used for calibration (see Methods) is given as reference. Dashed horizontal lines reflect boundaries of trophic levels (primary decomposers, secondary decomposers and predators; see Methods). For statistical analysis see text.



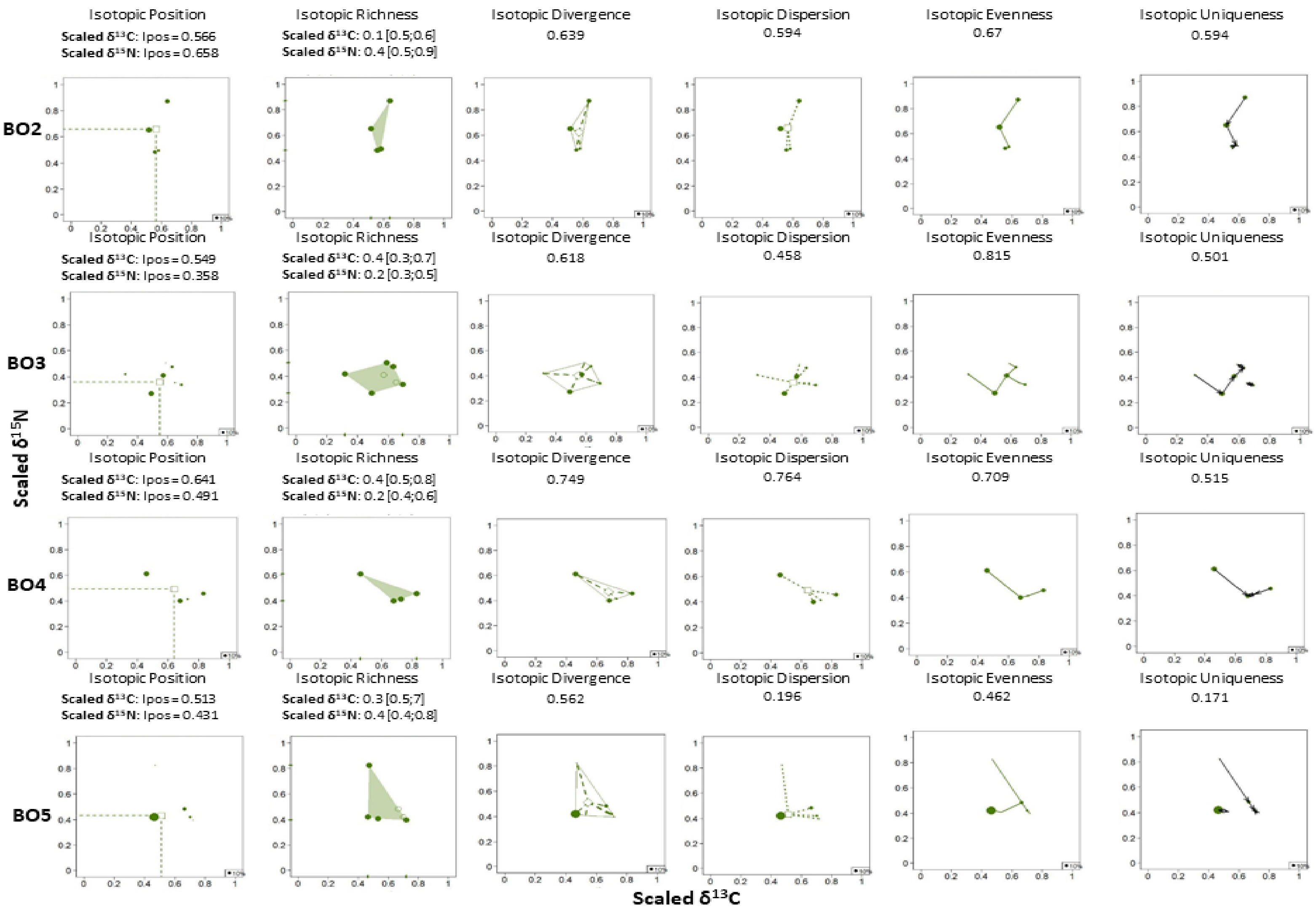
Figures S2: Stable isotope values of oribatid mite communities according to the land use-systems BF (Bukit Duabelas/rainforest) per plot. The two axes (scaled $\delta^{13}C$ and scaled $\delta^{15}N$) have the same range (values ranging from 0 to 1). For more details see statistical analysis.



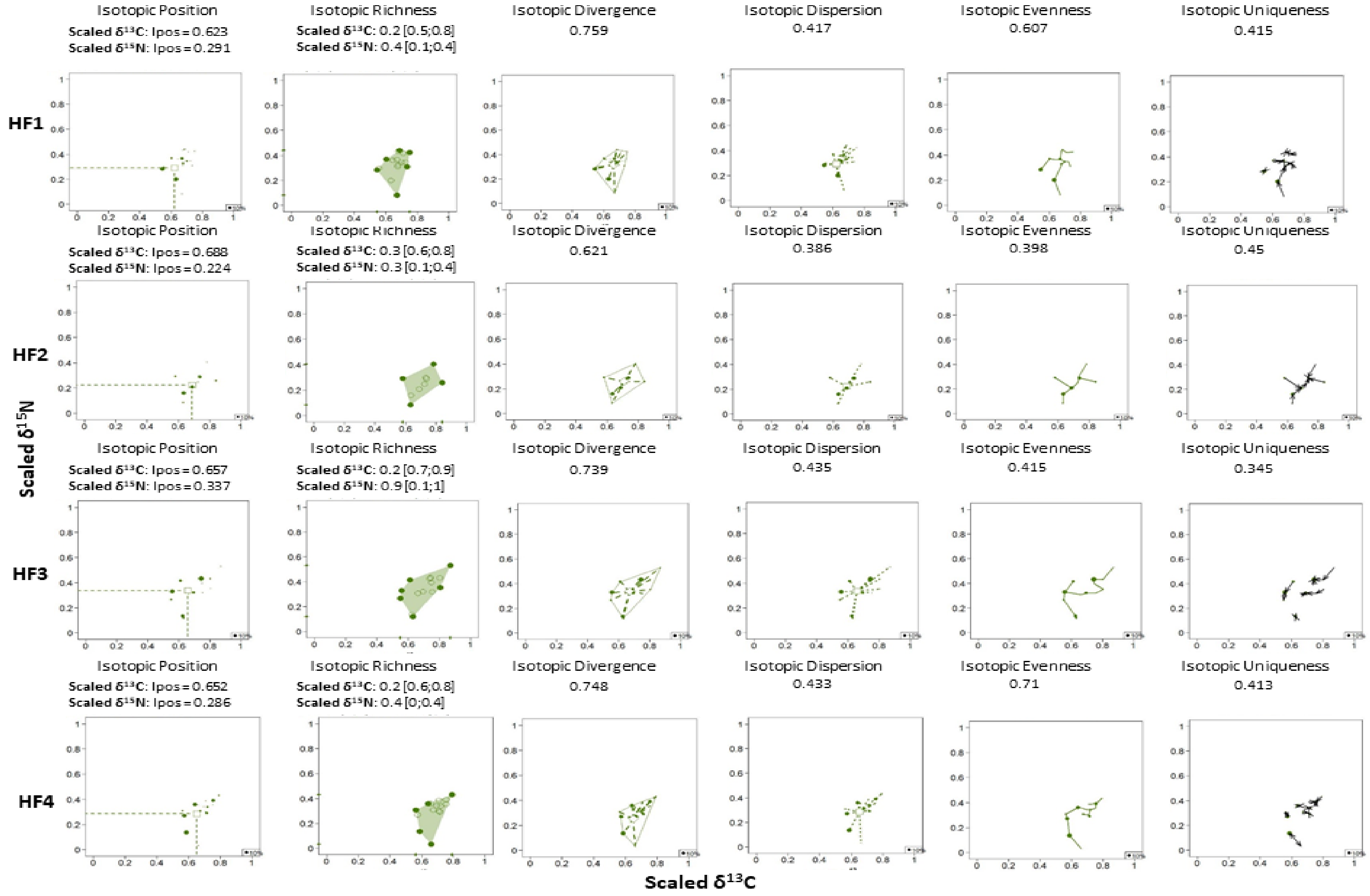
Figures S3: Stable isotope values of oribatid mite communities according to the land use-systems BJ (Bukit Duabelas/jungle rubber) per plot. The two axes (scaled $\delta^{13}C$ and scaled $\delta^{15}N$) have the same range (values ranging from 0 to 1). For more details see statistical analysis.



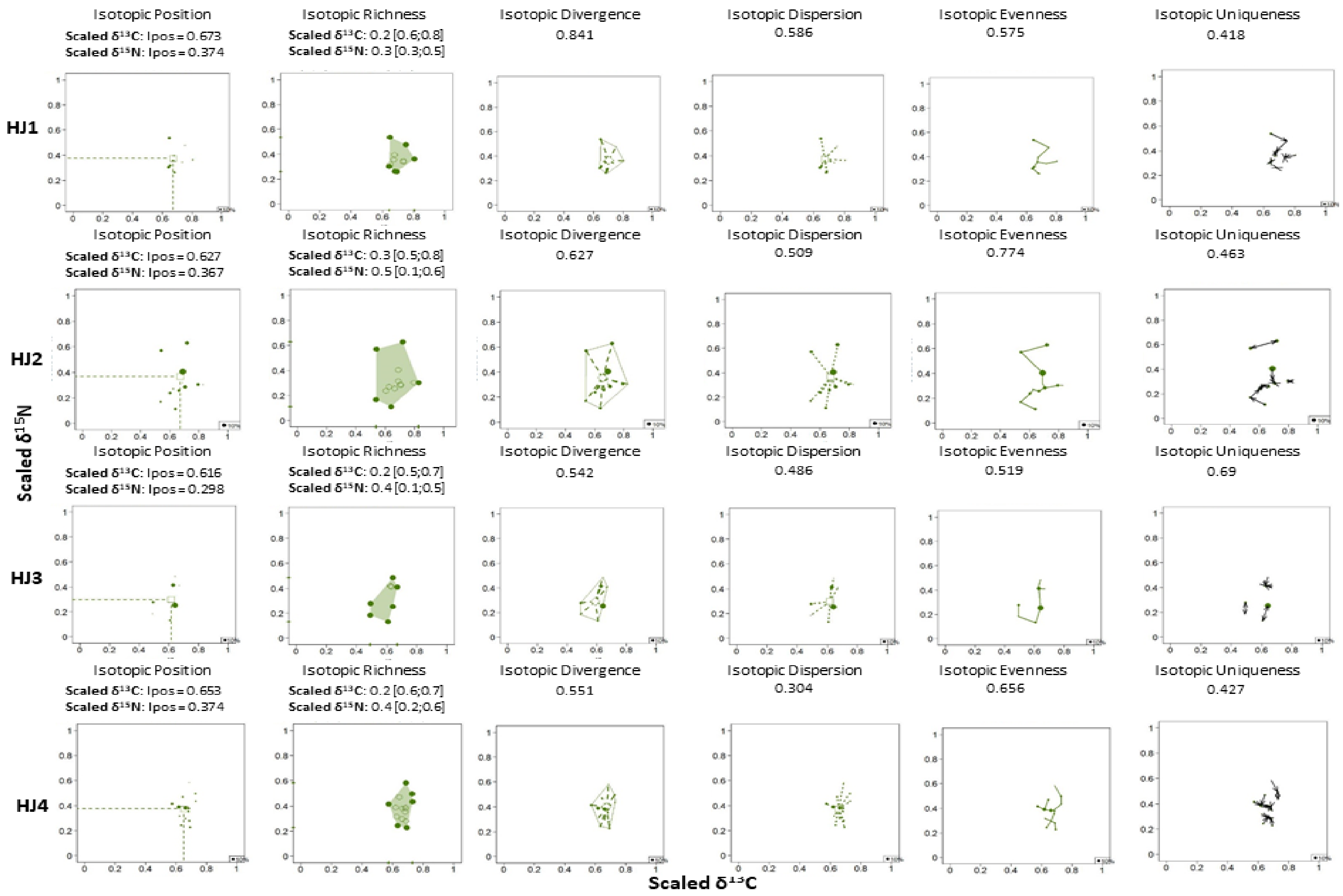
Figures S4: Stable isotope values of oribatid mite communities according to the land use-systems BR (Bukit Duabelas/rubber plantation) per plot. The two axes (scaled δ^{13}C and scaled δ^{15}N) have the same range (values ranging from 0 to 1). For more details see statistical analysis.



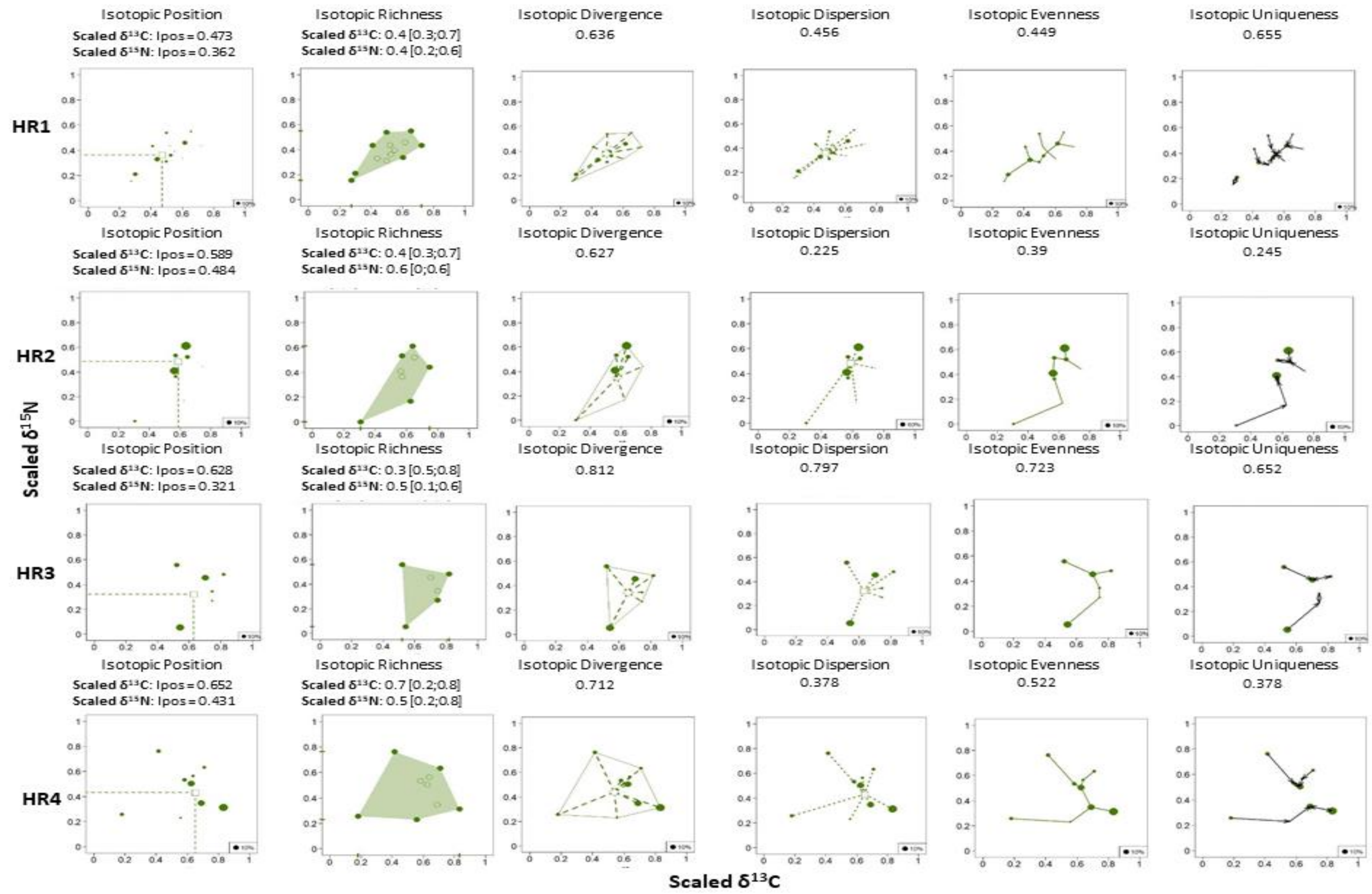
Figures S5: Stable isotope values of oribatid mite communities according to the land use-systems BO(Bukit Duabelas/oil palm plantation) per plot. The two axes (scaled $\delta^{13}C$ and scaled $\delta^{15}N$) have the same range (values ranging from 0 to 1). For more details see statistical analysis.



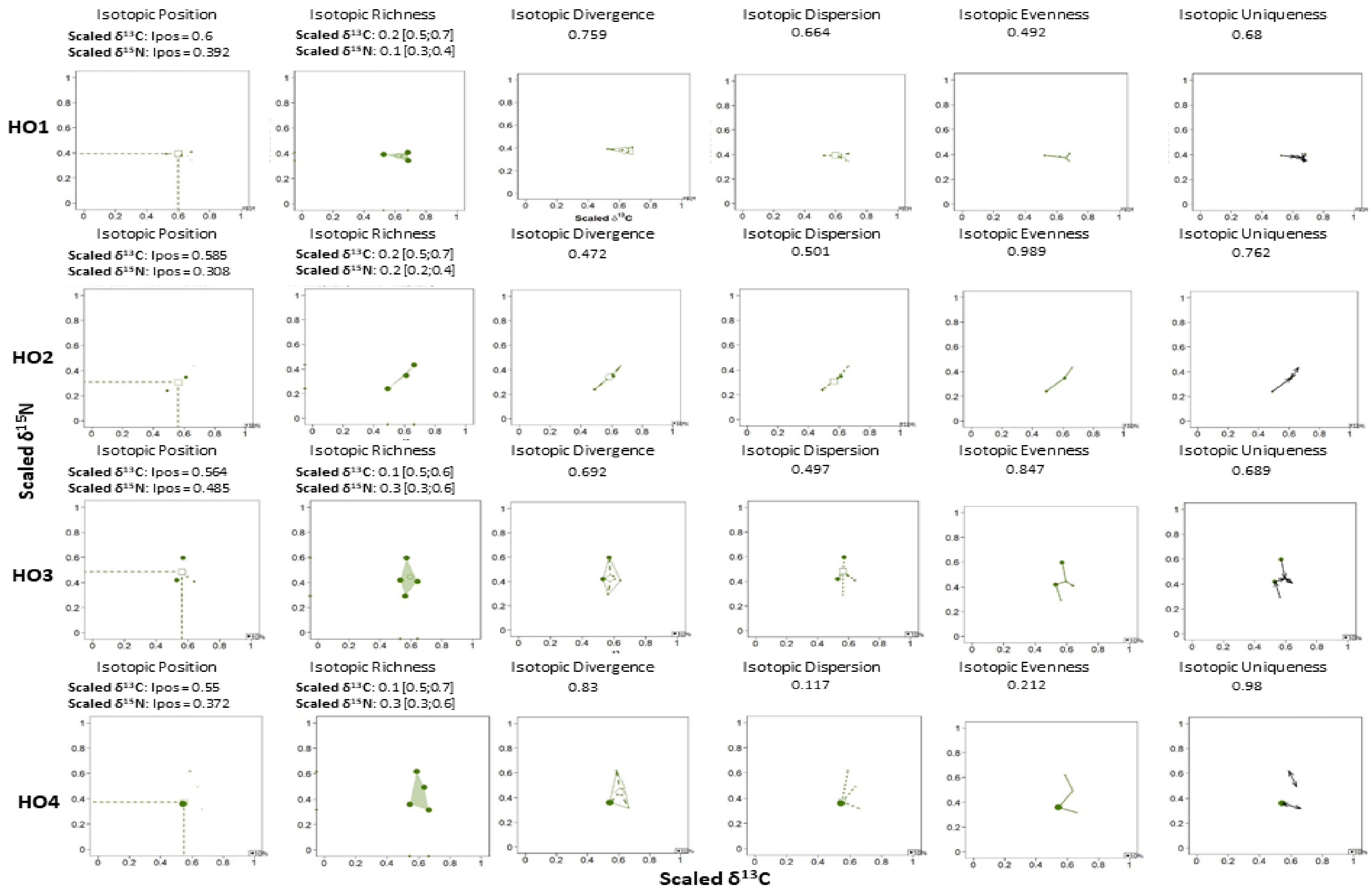
Figures S6: Stable isotope values of oribatid mite communities according to the land use-systems HF (Harapan/rainforest) per plot. The two axes (scaled $\delta^{13}C$ and scaled $\delta^{15}N$) have the same range (values ranging from 0 to 1). For more details see statistical analysis.



Figures S7: Stable isotope values of oribatid mite communities according to the land use-systems HJ (Harapan/jungle rubber) per plot. The two axes (scaled $\delta^{13}C$ and scaled $\delta^{15}N$) have the same range (values ranging from 0 to 1). For more details see statistical analysis.



Figures S8: Stable isotope values of oribatid mite communities according to the land use-systems HR (Harapan/rubber plantations) per plot. The two axes (scaled $\delta^{13}C$ and scaled $\delta^{15}N$) have the same range (values ranging from 0 to 1). For more details see statistical analysis.



Figures S9: Stable isotope values of oribatid mite communities according to the land use-systems HO (Harapan/oil palm plantation) per plot. The two axes (scaled $\delta^{13}C$ and scaled $\delta^{15}N$) have the same range (values ranging from 0 to 1). For more details see statistical analysis.

Table S1: Absolute and calibrated (see methods) stable isotope values of oribatid mite individuals studied. Species ID in Ecotaxonomy database (http://ecotaxonomy.org/), sample, species name, author, landscape, land-use system, absolute values of δ^{15}N and δ^{13}C values, biomass per species percentage and Δ^{15}N and Δ^{13}C per community (weighted values accordingly to the percentage of species per plot).

sample	species	species	author	absolute		litter-calibrated		Biomass	community	
	ID			δ13C	δ15N	mean δ15N	mean δ13C	species %	Δ15N	Δ13C
Bukit Duabelas rainforest										
BF1	405583	[B08] [114] *Neoamerioppia* sp. cf. *Neoamerioppia longiclava* (405583)		-27.30	4.03	0.47	-28.72	0.02	0.10	-0.67
BF2				-28.75	4.22	0.02	-31.81	0.08	0.34	-2.32
BF3				-27.32	1.40	0.53	-31.67	0.17	0.24	-4.70
BF4				-27.56	7.53	-0.67	-31.29	0.04	0.33	-1.22
BF2				-27.62	4.46	0.02	-31.81	0.03	0.14	-0.84
BF4	405652	[B08] [13] *Pergalumna* sp cf. *Pergalumna annulata* (405652)	Mahunka, S., 1973	-27.05	3.93	-0.67	-31.29	0.04	0.15	-1.02
BF1	405456	[B08] [131] *Malacoangelia remigera* subsp. *remigera* (405456)		-25.91	6.36	0.47	-28.72	0.01	0.08	-0.32
BF2				-26.53	2.69	0.02	-31.81	0.00	0.01	-0.10
BF4	405876	[B08] [148] *Pasocepheus* sp. cf. *Pasocepheus bako* (405876)		-25.39	1.90	-0.67	-31.29	#N/A	#N/A	#N/A
BF2	405862	[B08] [184] *Graptoppia* sp. nov. 2 (405862)		-28.08	1.71	0.02	-31.81	0.06	0.11	-1.75
BF4				-25.90	9.87	-0.67	-31.29	0.00	0.00	-0.01
BF4	405715	[B08] [194] *Protoribates prolamellatus* (405715)	Ermilov, Sandmann & Scheu, 2019	-26.57	2.87	-0.67	-31.29	0.01	0.03	-0.25
BF3	405858	[B08] [205] *Yoshiobodes irmayi* (405858)		-26.58	2.13	0.53	-31.67	0.00	0.00	-0.03
BF4				-25.14	3.70	-0.67	-31.29	0.02	0.06	-0.39
BF1	405674	[B08] [36] *Dolicheremaeus sumatranus* (form 1) cf. *Dolicheremaeus sumatranus* (405674)		-25.46	2.54	0.47	-28.72	0.09	0.22	-2.24
BF2				-25.95	10.87	0.02	-31.81	0.00	0.01	-0.03
BF4				-25.95	8.91	-0.67	-31.29	0.01	0.05	-0.15
BF3	405678	[B08] [45] *Eremobelba comtae* (405678)		-26.44	4.64	0.53	-31.67	0.01	0.05	-0.26
BF4				-26.27	3.82	-0.67	-31.29	0.00	0.00	0.00
BF1	405868	[B08] [47] *Haplozetes bayartogtokhi* (405868)	Ermilov, Sandmann & Scheu, 2019	-26.79	0.16	0.47	-28.72	0.01	0.00	-0.36
BF2				-26.08	5.34	0.02	-31.81	0.02	0.08	-0.40
BF1	405446	[B08] [62] *Masthermannia* sp. cf. *Masthermannia mammillaris* (405446)		-26.68	1.11	0.47	-28.72	0.01	0.02	-0.37

BF2				-26.69	0.93	0.02	-31.81	0.00	0.00	-0.04
BF3				-27.50	0.44	0.53	-31.67	0.02	0.01	-0.42
BF4				-27.07	0.81	-0.67	-31.29	0.01	0.01	-0.26
BF1	405481	[B08] [82] *Allozetes* nov. sp. 1 (405481)		-26.46	3.67	0.47	-28.72	0.02	0.06	-0.46
BF2				-27.23	2.30	0.02	-31.81	0.02	0.04	-0.51
BF3	405856	[B08] [88] *Dolicheremaeus* sp. 2 (405856)		-26.70	2.40	0.53	-31.67	0.04	0.10	-1.09
BF4				-26.05	2.31	-0.67	-31.29	0.01	0.03	-0.35
BF1	405885	[B08] [96] *Afronothrus incisivus* (405885)		-25.88	2.80	0.47	-28.72	0.00	0.01	-0.07
BF2				-27.29	-0.07	0.02	-31.81	0.00	0.00	-0.05
BF4				-27.05	0.20	-0.67	-31.29	0.10	0.02	-2.60
BF2	405633	*Arcoppia vittata*	Hammer, 1979	-26.53	5.79	0.02	-31.81	0.09	0.52	-2.40
BF1	405384	*Dendrohermannia monstruosa*	Aoki, 1977	-27.05	3.27	0.47	-28.72	0.05	0.18	-1.48
BF3				-26.82	2.27	0.53	-31.67	0.04	0.09	-1.02
BF4				-27.96	1.72	-0.67	-31.29	0.01	0.01	-0.16
BF1	405618	*Eohypochthonius salicifolius*	Hammer, 1979	-24.73	9.29	0.47	-28.72	0.01	0.05	-0.13
BF2				-27.37	1.17	0.02	-31.81	0.03	0.04	-0.94
BF1	405626	*Eremulus baliensis*	Hammer, 1982	-26.55	4.19	0.47	-28.72	0.02	0.08	-0.49
BF3				-26.42	-2.93	0.53	-31.67	0.01	-0.02	-0.20
BF4				-26.62	7.12	-0.67	-31.29	0.01	0.10	-0.36
BF1	405547	*Galumna corpuzrarosae*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-26.92	2.25	0.47	-28.72	0.03	0.07	-0.86
BF4				-28.10	2.68	-0.67	-31.29	0.02	0.05	-0.50
BF2	405638	*Gehypochthonius rhadamanthus*	Jacot, 1936	-25.56	1.68	0.02	-31.81	0.27	0.45	-6.82
BF1	405627	*Hemileius perforatoides*	(Hammer, 1979)	-24.06	1.16	0.47	-28.72	0.01	0.01	-0.21
BF2				-25.96	1.44	0.02	-31.81	0.04	0.06	-1.03
BF3				-25.55	-0.13	0.53	-31.67	0.00	0.00	-0.06
BF4				-26.11	1.07	-0.67	-31.29	0.08	0.09	-2.11
BF3				-27.00	3.57	0.53	-31.67	0.00	0.01	-0.07
BF4				-25.64	2.22	-0.67	-31.29	0.01	0.03	-0.37
BF3	405471	*Indoribates hauseri*	(Mahunka, 1997)	-27.31	2.53	0.53	-31.67	0.04	0.10	-1.09
BF4				-29.30	4.01	-0.67	-31.29	0.05	0.21	-1.50
BF1	405530	*Lamellobates orientalis*	Csiszár, 1961	-27.42	1.24	0.47	-28.72	0.02	0.02	-0.51
BF2				-28.05	2.44	0.02	-31.81	0.02	0.05	-0.59
BF3				-27.61	0.03	0.53	-31.67	0.01	0.00	-0.39
BF4				-27.43	2.27	-0.67	-31.29	0.04	0.08	-1.00
BF1	405472	*Magyaria leonilae*	Ermilov, Sandmann & Scheu, 2019	-27.73	3.51	0.47	-28.72	0.19	0.67	-5.32
BF2				-27.53	1.43	0.02	-31.81	0.17	0.24	-4.64
BF3				-28.40	1.85	0.53	-31.67	0.04	0.08	-1.22
BF4				-27.60	2.24	-0.67	-31.29	0.07	0.16	-1.96
BF1	405578	*Meristacarus porcula*	Grandjean, 1934	-26.56	1.32	0.47	-28.72	0.08	0.10	-2.10
BF2				-27.91	3.33	0.02	-31.81	0.03	0.10	-0.86
BF3				-26.53	5.21	0.53	-31.67	0.00	0.01	-0.06
BF4				-27.28	4.57	-0.67	-31.29	0.03	0.14	-0.85
BF3	405439	*Oribatella malaya*	Balogh & Mahunka, 1974	-27.01	1.22	0.53	-31.67	0.02	0.02	-0.49

BF4				-26.86	5.26	-0.67	-31.29	0.05	0.29	-1.46
BF1	405672	*Parhypochthonius asiaticus*	Mahunka, 1997	-27.08	4.01	0.47	-28.72	0.00	0.01	-0.04
BF1	405548	*Pergalumna paraindistincta*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-27.22	3.05	0.47	-28.72	0.18	0.54	-4.79
BF2				-27.55	2.95	0.02	-31.81	0.08	0.24	-2.22
BF3				-26.99	1.95	0.53	-31.67	0.00	0.01	-0.11
BF2	405470	[B08] [2] *Phyllhermannia similis* (405470)		-27.01	0.62	0.02	-31.81	0.01	0.01	-0.24
BF3				-27.64	-1.38	0.53	-31.67	0.39	-0.54	-10.90
BF4				-27.58	-1.20	-0.67	-31.29	0.20	-0.23	-5.40
BF1				-26.67	0.70	0.47	-28.72	0.18	0.13	-4.87
BF1	405671	*Protoribates paracapucinus*	(Mahunka, 1988)	-26.48	-0.54	0.47	-28.72	0.01	-0.01	-0.28
BF2				-26.50	3.54	0.02	-31.81	0.02	0.06	-0.48
BF4				-25.96	5.29	-0.67	-31.29	0.01	0.05	-0.26
BF2	405449	*Scheloribates praeincisus*	(Berlese, 1910)	-29.33	-0.56	0.02	-31.81	0.01	-0.01	-0.34
BF3				-27.20	1.61	0.53	-31.67	0.04	0.06	-1.00
BF4				-26.49	2.83	-0.67	-31.29	0.01	0.03	-0.32
BF2	405668	*Suctotegeus tumescitus*	Mahunka, 1987	-27.77	7.15	0.02	-31.81	0.00	0.02	-0.08
BF1	405457	*Tectocepheus minor*	Berlese, 1903	-26.59	-0.39	0.47	-28.72	0.01	0.00	-0.19
BF2				-27.03	1.27	0.02	-31.81	0.00	0.00	-0.05
BF3				-26.16	16.63	0.53	-31.67	0.02	0.37	-0.58
BF4				-26.63	5.39	-0.67	-31.29	0.01	0.05	-0.25
BF1	405389	*Trachyoribates shibai*	(Aoki, 1976)	-26.76	5.45	0.47	-28.72	0.01	0.04	-0.19
BF2				-26.42	1.86	0.02	-31.81	0.01	0.02	-0.22
BF3				-25.32	2.13	0.53	-31.67	0.01	0.03	-0.35
BF4				-27.07	2.83	-0.67	-31.29	0.03	0.08	-0.73
BF1	405642	*Zetorchestes novaguineanus*	Krisper, 1987	-25.45	0.79	0.47	-28.72	0.03	0.03	-0.87
BF3				-28.26	1.84	0.53	-31.67	0.12	0.22	-3.44
BF4				-28.09	2.02	-0.67	-31.29	0.14	0.28	-3.82
jungle rubber										
BJ2	405652	[B08] [13] *Pergalumna* sp cf. *Pergalumna annulata* (405652)	Mahunka, S., 1973	-28.01	1.48	-2.73	-29.88	0.01	0.01	-0.18
BJ3				-22.96	0.18	-2.17	-31.02	0.01	0.00	-0.20
BJ2	405873	[B08] [141] *Neoribates* sp. 1 (405873)		-26.95	1.42	-2.73	-29.88	0.16	0.23	-4.30
BJ4	405701	[B08] [146] *Apoplophora phalerata* (405701)		-25.75	3.79	-1.65	-31.40	0.11	0.42	-2.89
BJ2				-24.49	1.85	-2.73	-29.88	0.00	0.00	-0.03
BJ3				-25.52	0.42	-2.17	-31.02	0.11	0.05	-2.77
BJ4				-24.71	-0.47	-1.65	-31.40	0.00	0.00	-0.06
BJ5				-24.74	3.70	-1.26	-32.45	0.00	0.00	-0.03
BJ3	405704	[B08] [164] *Dampfiella* sp. 1 (405704)		-26.17	-0.39	-2.17	-31.02	0.03	-0.01	-0.78
BJ4				-25.85	-2.47	-1.65	-31.40	0.02	-0.05	-0.47
BJ3	405897	[B08] [173] cf *Prototritia* sp. 1 (405897)		-25.24	4.07	-2.17	-31.02	0.00	0.01	-0.07
BJ4				-24.97	3.25	-1.65	-31.40	0.01	0.04	-0.27
BJ5				-24.63	3.26	-1.26	-32.45	0.04	0.12	-0.88
BJ2	405729	[B08] [30] *Plonaphacarus kugohi* (405729)	Aoki, 1959	-24.00	-0.73	-2.73	-29.88	0.03	-0.02	-0.80
BJ2	405478	[B08] [4] *Rostrozetes* sp. 7 (405478)		-26.83	1.63	-2.73	-29.88	0.00	0.00	-0.07
BJ3				-27.35	1.56	-2.17	-31.02	0.00	0.00	-0.04

BJ4				-26.85	2.83	-1.65	-31.40	0.02	0.06	-0.54
BJ5				-27.95	1.45	-1.26	-32.45	0.00	0.00	-0.02
BJ3	405877	[B08] [49] *Phyllochthonius* sp. cf. *Phyllochthonius aoutii* (405877)		-23.96	-0.57	-2.17	-31.02	0.06	-0.03	-1.34
BJ4	405866	[B08] [55] *Idiozetes* sp. cf. *Idiozetes javensis* (405866)		-25.32	3.28	-1.65	-31.40	0.01	0.03	-0.24
BJ5				-30.23	-0.21	-1.26	-32.45	0.00	0.00	-0.12
BJ3	405675	[B08] [8] *Dolicheremaeus sumatranus* (form 2) cf. *Dolicheremaeus sumatranus* (405675)		-25.57	1.09	-2.17	-31.02	0.01	0.01	-0.33
BJ2	405525	[B08] [85] Megalotocepheus crinitus (405525)	(Berlese, 1905)	-25.01	0.89	-2.73	-29.88	0.00	0.00	-0.01
BJ4				-24.66	2.38	-1.65	-31.40	0.19	0.44	-4.61
BJ3	405885	[B08] [96] *Afronothrus incisivus* (405885)		-25.95	-0.56	-2.17	-31.02	0.04	-0.02	-1.06
BJ2	405539	*Allogalumna indonesiensis*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-26.12	-1.13	-2.73	-29.88	0.00	0.00	-0.06
BJ3	434473	*Allogalumna* nov. sp. 2		-26.88	1.32	-2.17	-31.02	0.08	0.11	-2.27
BJ2	405541	*Cosmogalumna areticulata*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-26.04	0.81	-2.73	-29.88	0.00	0.00	-0.10
BJ5	405393	*Cyrthermannia tuberculata*	Balogh, 1958	-25.91	2.22	-1.26	-32.45	0.06	0.14	-1.58
BJ3	405618	*Eohypochthonius salicifolius*	Hammer, 1979	-28.88	4.86	-2.17	-31.02	0.02	0.11	-0.66
BJ2	405620	*Eremulus densus*	Hammer, 1979	-26.23	1.36	-2.73	-29.88	0.00	0.00	-0.01
BJ3				-26.47	3.25	-2.17	-31.02	0.02	0.08	-0.61
BJ2	405544	*Galumna indonesica*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-26.62	4.08	-2.73	-29.88	0.00	0.01	-0.03
BJ5				-26.89	1.49	-1.26	-32.45	0.08	0.12	-2.12
BJ4	405679	*Galumnopsis reducta*	(Mahunka, 1995)	-25.69	3.96	-1.65	-31.40	0.01	0.06	-0.38
BJ3	405638	*Gehypochthonius rhadamanthus*	Jacot, 1936	-27.04	3.84	-2.17	-31.02	0.00	0.02	-0.13
BJ2	405627	*Hemileius perforatoides*	(Hammer, 1979)	-26.27	0.25	-2.73	-29.88	0.02	0.01	-0.62
BJ5				-25.94	2.15	-1.26	-32.45	0.43	0.92	-11.10
BJ2	405573	*Hoplophorella cucullata*	(Ewing, 1909)	-25.11	2.47	-2.73	-29.88	0.01	0.01	-0.15
BJ3				-25.63	5.09	-2.17	-31.02	0.01	0.06	-0.31
BJ4	405875	*Kalloia gerdweigmanni*	Ermilov, Sandmann & Scheu, 2019	-24.56	0.38	-1.65	-31.40	0.01	0.00	-0.23
BJ3	405454	*Lamellobates misella*	(Berlese, 1910)	-25.70	3.92	-2.17	-31.02	0.01	0.05	-0.33
BJ2	405530	*Lamellobates orientalis*	Csiszár, 1961	-28.13	3.94	-2.73	-29.88	0.10	0.38	-2.73
BJ3				-29.13	-1.69	-2.17	-31.02	0.06	-0.11	-1.88
BJ4				-28.54	3.92	-1.65	-31.40	0.08	0.33	-2.42
BJ5				-28.64	0.15	-1.26	-32.45	0.17	0.03	-4.84

BJ2	405472	*Magyaria leonilae*	Ermilov, Sandmann & Scheu, 2019	-28.18	0.59	-2.73	-29.88	0.13	0.08	-3.61
BJ3				-28.67	1.34	-2.17	-31.02	0.13	0.18	-3.86
BJ4				-28.83	1.70	-1.65	-31.40	0.04	0.06	-1.08
BJ5				-27.89	-1.62	-1.26	-32.45	0.22	-0.35	-6.08
BJ2	405470	[B08] [2] *Phyllhermannia similis* (405470)		-28.73	-1.70	-2.73	-29.88	0.51	-0.87	-14.68
BJ3	405470			-26.64	-2.04	-2.17	-31.02	0.29	-0.59	-7.75
BJ4	405470			-27.52	-0.29	-1.65	-31.40	0.33	-0.10	-9.20
BJ2	405671	*Protoribates paracapucinus*	(Mahunka, 1988)	-26.02	4.76	-2.73	-29.88	0.00	0.01	-0.04
BJ3				-25.86	2.87	-2.17	-31.02	0.04	0.12	-1.05
BJ4				-25.88	1.11	-1.65	-31.40	0.03	0.04	-0.86
BJ2	405449	*Scheloribates praeincisus*	(Berlese, 1910)	-27.30	0.47	-2.73	-29.88	0.01	0.00	-0.22
BJ4				-27.31	2.76	-1.65	-31.40	0.11	0.30	-2.96
BJ2	405524	*Tegeozetes tunicatus*	Berlese, 1913	-24.68	-5.48	-2.73	-29.88	0.00	0.00	-0.01
BJ3				-25.76	4.62	-2.17	-31.02	0.02	0.09	-0.52
BJ4				-26.20	2.25	-1.65	-31.40	0.01	0.02	-0.27
BJ5				-25.80	2.88	-1.26	-32.45	0.00	0.00	-0.04
BJ2	405389	*Trachyoribates shibai*	(Aoki, 1976)	-26.35	6.03	-2.73	-29.88	0.01	0.08	-0.35
BJ3				-25.75	5.65	-2.17	-31.02	0.03	0.16	-0.71
BJ4				-24.73	2.70	-1.65	-31.40	0.01	0.02	-0.16
BJ5				-25.68	-2.12	-1.26	-32.45	0.00	0.00	-0.06
rubber plantation										
BR2	405455	[B08] [111] *Lamellobates molecula mol* (405455)		-33.63	5.54	-2.02	-29.71	0.10	0.57	-3.47
BR2	405639	[B08] [13] *Pergalumna* sp cf. *Pergalumna annulata* (405652)		-29.25	1.35	-2.02	-29.71	0.51	0.69	-15.04
BR1	405379	[B08] [17] *Rostrozetes* cf *shibai* cf. *Rostrozetes shibai* (405379)		-33.82	-1.00	-1.92	-29.76	0.06	-0.06	-1.87
BR1	405450	[B08] [20] *Bischeloribates mahunkai* (405450)	Subías 2010	-26.30	5.59	-1.92	-29.76	0.17	0.94	-4.41
BR2				-26.31	4.46	-2.02	-29.71	0.10	0.45	-2.64
BR4				-27.49	5.68	-0.67	-29.56	0.62	3.52	-17.03
BR1	405729	[B08] [30] *Plonaphacarus kugohi* (405729)	Aoki, 1959	-21.55	4.37	-1.92	-29.76	0.01	0.04	-0.22
BR2				-23.25	1.82	-2.02	-29.71	0.03	0.05	-0.65
BR4				-24.25	2.30	-0.67	-29.56	0.14	0.31	-3.30
BR1	405390	[B08] [74] *Rostrozetes* cf *florens* cf. *Trachyoribates florens* (405390)	(Balogh, 1970)	-35.49	-2.67	-1.92	-29.76	0.02	-0.05	-0.66
BR1	405381	*Archegozetes longisetosus*	Aoki, 1965	-27.63	4.07	-1.92	-29.76	0.58	2.36	-16.03
BR4				-28.16	2.88	-0.67	-29.56	0.00	0.01	-0.13
BR1	405393	*Cyrthermannia tuberculata*	Balogh, 1958	-29.18	0.80	-1.92	-29.76	0.01	0.01	-0.36
BR3				-36.38	-5.51	-1.55	-30.01	0.02	-0.11	-0.75
BR1	405620	*Eremulus densus*	Hammer, 1979	-34.45	-3.62	-1.92	-29.76	0.02	-0.08	-0.80
BR1	405664	*Galumna sabahna*	Mahunka, 1995	-29.12	7.25	-1.92	-29.76	0.01	0.09	-0.37
BR2				-29.39	2.06	-2.02	-29.71	0.06	0.13	-1.85
BR4				-29.80	4.99	-0.67	-29.56	0.18	0.88	-5.27
BR1	405638	*Gehypochthonius rhadamanthus*	Jacot, 1936	-35.33	2.45	-1.92	-29.76	0.05	0.12	-1.70
BR2				-27.86	10.24	-2.02	-29.71	0.05	0.51	-1.38
BR1	405386	*Otocepheus heterosetiger*	Aoki, 1965	-29.04	1.94	-1.92	-29.76	0.00	0.01	-0.08
BR4				-25.51	2.88	-0.67	-29.56	0.04	0.11	-1.01

BR1	405671	*Protoribates paracapucinus*	(Mahunka, 1988)	-26.37	6.73	-1.92	-29.76	0.05	0.33	-1.29
BR3				-25.90	4.06	-1.55	-30.01	0.75	3.06	-19.51
BR4				-25.42	-1.74	-0.67	-29.56	0.02	-0.04	-0.59
BR1	405449	*Scheloribates praeincisus*	(Berlese, 1910)	-25.06	0.36	-1.92	-29.76	0.00	0.00	-0.11
BR2				-26.60	4.11	-2.02	-29.71	0.09	0.38	-2.44
BR3				-27.97	2.35	-1.55	-30.01	0.19	0.44	-5.28
BR1	405524	*Tegeozetes tunicatus*	Berlese, 1913	-26.36	1.59	-1.92	-29.76	0.02	0.03	-0.41
BR2				-25.53	4.23	-2.02	-29.71	0.03	0.15	-0.89
BR3				-26.33	1.87	-1.55	-30.01	0.01	0.02	-0.33
BR2	405389	*Trachyoribates shibai*	(Aoki, 1976)	-28.02	1.41	-2.02	-29.71	0.01	0.02	-0.42
BR3				-29.85	-3.17	-1.55	-30.01	0.02	-0.08	-0.73
oil palm plantation										
BO2	405718	[B08] [107] *Rostrozetes* sp. 1 (405718)		-27.83	5.15	0.29	-29.59	0.19	0.99	-5.33
BO3				-27.98	6.20	0.84	-30.24	0.00	0.01	-0.06
BO4				-27.89	3.14	-0.19	-32.14	0.05	0.16	-1.39
BO5				-25.78	4.28	1.27	-29.89	0.02	0.07	-0.42
BO3	405450	[B08] [20] *Bischeloribates mahunkai* (405450)	Subías 2010	-27.36	5.52	0.84	-30.24	0.11	0.61	-3.03
BO2	405446	[B08] [62] *Masthermannia* sp. cf. *Masthermannia mammillaris* (405446)		-26.59	13.55	0.29	-29.59	0.26	3.58	-7.03
BO3				-31.95	4.33	0.84	-30.24	0.07	0.32	-2.39
BO5				-29.39	13.53	1.27	-29.89	0.00	0.06	-0.13
BO2	405506	*Allonothrus russeolus*	Wallwork, 1960	-27.48	5.42	0.29	-29.59	0.12	0.64	-3.26
BO3				-28.28	4.13	0.84	-30.24	0.31	1.28	-8.77
BO5				-29.48	4.83	1.27	-29.89	0.76	3.69	-22.52
BO3	405381	*Archegozetes longisetosus*	Aoki, 1965	-29.42	1.11	0.84	-30.24	0.35	0.39	-10.39
BO4				-31.78	7.51	-0.19	-32.14	0.36	2.70	-11.43
BO5	405634	*Galumna flabellifera*	Hammer, 1979	-26.56	6.16	1.27	-29.89	0.13	0.82	-3.52
BO3	405449	*Scheloribates praeincisus*	(Berlese, 1910)	-26.45	2.58	0.84	-30.24	0.12	0.30	-3.05
BO4				-28.60	2.87	-0.19	-32.14	0.34	0.97	-9.68
BO5				-28.51	4.51	1.27	-29.89	0.01	0.06	-0.39
BO2	405389	*Trachyoribates shibai*	(Aoki, 1976)	-28.41	8.85	0.29	-29.59	0.43	3.77	-12.09
BO3				-27.09	2.92	0.84	-30.24	0.03	0.10	-0.91
BO4				-26.41	4.11	-0.19	-32.14	0.25	1.03	-6.66
BO5				-26.03	4.82	1.27	-29.89	0.07	0.33	-1.80
Harapan rainforest										
HF1	405473	[B08] [12] *Meristacarus* nov. sp. 1 (405473)		-26.59	2.11	0.20	-30.81	0.00	0.01	-0.09
HF2				-26.89	0.90	0.03	-31.22	0.03	0.03	-0.78
HF3				-27.75	1.35	0.29	-31.05	0.01	0.01	-0.15
HF4	405585	[B08] [120] *Suctobelbella* sp. cf. *Suctobelbella reticulata* (405585)		-26.73	0.99	0.25	-30.76	0.08	0.08	-2.22
HF1	405652	[B08] [13] *Pergalumna* sp cf. *Pergalumna annulata* (405652)	Mahunka, S., 1973	-28.36	2.61	0.20	-30.81	0.08	0.20	-2.21
HF3				-29.29	1.85	0.29	-31.05	0.23	0.43	-6.76
HF4				-27.76	2.41	0.25	-30.76	0.18	0.44	-5.06
HF1	405508	[B08] [34] *Scheloribates* sp. cf. *Scheloribates fimbriatus javensis* (405508)		-26.80	3.69	0.20	-30.81	0.01	0.02	-0.16
HF4				-25.60	4.00	0.25	-30.76	0.02	0.10	-0.64
HF1	405709	[B08] [38] *Neoliodes* sp. 1 (405709)		-27.40	-3.64	0.20	-30.81	0.01	-0.02	-0.16

HF2				-28.36	-3.74	0.03	-31.22	0.04	-0.17	-1.27
HF3				-28.24	-2.71	0.29	-31.05	0.04	-0.10	-1.07
HF4				-27.50	-4.63	0.25	-30.76	0.01	-0.07	-0.39
HF1	405478	[B08] [4] *Rostrozetes* sp. 7 (405478)		-27.78	2.42	0.20	-30.81	0.00	0.01	-0.13
HF3	405446	[B08] [62] *Masthermannia* sp. cf. *Masthermannia mammillaris* (405446)		-26.42	1.59	0.29	-31.05	0.01	0.01	-0.21
HF4				-26.65	2.04	0.25	-30.76	0.06	0.11	-1.50
HF1	405675	[B08] [8] *Dolicheremaeus sumatranus* (form 2) cf. *Dolicheremaeus sumatranus* (405675)		-26.97	2.11	0.20	-30.81	0.05	0.11	-1.43
HF4	434366	*Cultroribula lata*	Aoki, 1961	-27.00	2.08	0.25	-30.76	0.02	0.03	-0.41
HF1	405626	*Eremulus baliensis*	Hammer, 1982	-27.27	3.98	0.20	-30.81	0.01	0.04	-0.28
HF3				-26.67	3.95	0.29	-31.05	0.00	0.00	-0.03
HF1	405547	*Galumna corpuzrarosae*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-27.32	1.37	0.20	-30.81	0.01	0.02	-0.38
HF1	405627	*Hemileius perforatoides*	(Hammer, 1979)	-26.46	1.34	0.20	-30.81	0.02	0.03	-0.53
HF2				-25.34	0.06	0.03	-31.22	0.08	0.00	-2.00
HF3				-26.57	4.13	0.29	-31.05	0.27	1.11	-7.12
HF4				-26.13	2.39	0.25	-30.76	0.01	0.01	-0.15
HF3	405641	*Javacarus jocelynae*	Judson, 1991	-26.50	3.25	0.29	-31.05	0.01	0.04	-0.34
HF1	405530	*Lamellobates orientalis*	Csiszár, 1961	-27.16	4.16	0.20	-30.81	0.03	0.12	-0.77
HF2				-26.84	0.72	0.03	-31.22	0.21	0.15	-5.62
HF3				-24.75	6.22	0.29	-31.05	0.02	0.10	-0.41
HF4				-26.14	3.15	0.25	-30.76	0.15	0.46	-3.82
HF1	405472	*Magyaria leonilae*	Ermilov, Sandmann & Scheu, 2019	-27.26	1.70	0.20	-30.81	0.06	0.11	-1.75
HF2				-27.54	-1.04	0.03	-31.22	0.25	-0.26	-6.98
HF4				-26.81	1.17	0.25	-30.76	0.01	0.01	-0.15
HF3	405439	*Oribatella malaya*	Balogh & Mahunka, 1974	-27.28	1.68	0.29	-31.05	0.11	0.19	-3.08
HF4				-27.32	1.30	0.25	-30.76	0.04	0.06	-1.16
HF1	405548	*Pergalumna paraindistincta*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-27.40	2.56	0.20	-30.81	0.12	0.32	-3.41
HF2				-27.01	-0.18	0.03	-31.22	0.02	0.00	-0.59
HF3				-25.69	2.35	0.29	-31.05	0.00	0.00	-0.04
HF4				-27.53	2.43	0.25	-30.76	0.01	0.03	-0.35
HF3	405470	[B08] [2] *Phyllhermannia similis* (405470)		-28.31	-2.39	0.29	-31.05	0.13	-0.31	-3.65
HF1				-27.96	-1.05	0.20	-30.81	0.29	-0.31	-8.16
HF2				-28.34	-2.09	0.03	-31.22	0.27	-0.56	-7.54
HF4				-28.54	-2.43	0.25	-30.76	0.22	-0.54	-6.40
HF1	405449	*Scheloribates praeincisus*	(Berlese, 1910)	-29.25	0.73	0.20	-30.81	0.25	0.18	-7.33
HF3				-29.38	0.51	0.29	-31.05	0.05	0.02	-1.34
HF4				-28.74	0.48	0.25	-30.76	0.15	0.07	-4.38
HF1	405389	*Trachyoribates shibai*	(Aoki, 1976)	-26.21	3.80	0.20	-30.81	0.01	0.04	-0.24
HF2				-26.15	3.18	0.03	-31.22	0.01	0.03	-0.28

HF3				-25.72	4.03	0.29	-31.05	0.03	0.12	-0.76
HF4				-26.78	3.04	0.25	-30.76	0.00	0.01	-0.12
HF1	405642	*Zetorchestes novaguineanus*	Krisper, 1987	-29.07	1.01	0.20	-30.81	0.04	0.04	-1.06
HF2				-29.11	0.76	0.03	-31.22	0.09	0.06	-2.50
HF3				-28.51	3.72	0.29	-31.05	0.10	0.38	-2.89
HF4				-28.90	1.34	0.25	-30.76	0.03	0.04	-0.89
jungle rubber										
HJ2	405650	[B08] [33] *Apoplophora pantotrema* cf. *Apoplophora cristata* (405650)		-27.10	3.86	0.67	-30.80	0.31	1.20	-8.39
HJ4				-26.61	6.06	-0.97	-30.26	0.01	0.04	-0.16
HJ4	405447	[B08] [66] *Trachyoribates ampulla* (405447)		-26.96	1.66	-0.97	-30.26	0.20	0.33	-5.38
HJ2	405856	[B08] [88] *Dolicheremaeus* sp. 2 (405856)		-26.86	1.24	0.67	-30.80	0.11	0.14	-2.92
HJ4	405885	[B08] [96] *Afronothrus incisivus* (405885)		-26.71	1.09	-0.97	-30.26	0.05	0.05	-1.34
HJ2	405539	*Allogalumna indonesiensis*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-27.85	-2.54	0.67	-30.80	0.06	-0.15	-1.67
HJ3				-26.29	2.85	-0.47	-29.70	0.01	0.02	-0.14
HJ4				-26.63	1.86	-0.97	-30.26	0.01	0.02	-0.32
HJ1	405381	*Archegozetes longisetosus*	Aoki, 1965	-26.68	2.31	0.16	-30.12	0.07	0.17	-1.98
HJ2				-28.05	0.90	0.67	-30.80	0.02	0.01	-0.44
HJ3				-26.73	-0.59	-0.47	-29.70	0.49	-0.29	-13.12
HJ4				-26.98	-0.15	-0.97	-30.26	0.04	-0.01	-0.95
HJ1	405541	*Cosmogalumna areticulata*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-25.75	1.93	0.16	-30.12	0.01	0.03	-0.36
HJ2				-27.13	1.90	0.67	-30.80	0.00	0.01	-0.08
HJ2	434366	*Cultroribula lata*	Aoki, 1961	-26.69	8.70	0.67	-30.80	0.11	0.98	-3.01
HJ3				-27.18	-3.19	-0.47	-29.70	0.07	-0.22	-1.88
HJ4				-26.63	-0.45	-0.97	-30.26	0.06	-0.03	-1.49
HJ1	405626	*Eremulus baliensis*	Hammer, 1982	-26.59	3.09	0.16	-30.12	0.05	0.14	-1.23
HJ2				-26.93	1.29	0.67	-30.80	0.03	0.04	-0.89
HJ3				-26.73	4.43	-0.47	-29.70	0.02	0.10	-0.61
HJ4				-27.24	3.59	-0.97	-30.26	0.06	0.21	-1.60
HJ1	405547	*Galumna corpuzrarosae*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-27.03	6.23	0.16	-30.12	0.23	1.43	-6.21
HJ2	405875	Kalloia gerdweigmanni	Ermilov, Sandmann & Scheu, 2019	-25.59	1.61	0.67	-30.80	0.07	0.12	-1.83
HJ4				-26.54	-1.67	-0.97	-30.26	0.05	-0.08	-1.24
HJ1	405530	*Lamellobates orientalis*	Csiszár, 1961	-26.53	0.27	0.16	-30.12	0.11	0.03	-2.89
HJ3				-26.88	2.89	-0.47	-29.70	0.24	0.69	-6.40
HJ4				-28.24	2.45	-0.97	-30.26	0.09	0.22	-2.52
HJ1	405386	*Otocepheus heterosetiger*	Aoki, 1965	-24.73	2.41	0.16	-30.12	0.07	0.17	-1.72
HJ2				-25.10	1.60	0.67	-30.80	0.01	0.01	-0.20

HJ1	405548	*Pergalumna paraindistincta*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-25.52	4.89	0.16	-30.12	0.03	0.17	-0.89
HJ2				-27.50	0.61	0.67	-30.80	0.07	0.04	-1.91
HJ4				-26.67	1.65	-0.97	-30.26	0.06	0.10	-1.61
HJ4	405529	*Pergalumna pterinervis*	(Canestrini, 1898)	-26.00	2.85	-0.97	-30.26	0.04	0.11	-1.04
HJ1	405470	[B08] [2] *Phyllhermannia similis* (405470)		-26.39	0.19	0.16	-30.12	0.02	0.00	-0.45
HJ3				-28.93	-2.08	-0.47	-29.70	0.01	-0.02	-0.34
HJ4				-27.39	-1.27	-0.97	-30.26	0.05	-0.06	-1.40
HJ1	405671	*Protoribates paracapucinus*	(Mahunka, 1988)	-25.76	2.03	0.16	-30.12	0.02	0.04	-0.44
HJ2				-29.29	7.47	0.67	-30.80	0.09	0.68	-2.65
HJ2	405449	*Scheloribates praeincisus*	(Berlese, 1910)	-29.32	-1.30	0.67	-30.80	0.04	-0.05	-1.23
HJ3				-28.86	-0.04	-0.47	-29.70	0.12	-0.01	-3.42
HJ4				-27.61	1.85	-0.97	-30.26	0.22	0.40	-5.94
HJ1	405524	*Tegeozetes tunicatus*	Berlese, 1913	-26.96	1.49	0.16	-30.12	0.17	0.25	-4.47
HJ3				-26.97	2.99	-0.47	-29.70	0.04	0.13	-1.18
HJ4	405389	*Trachyoribates shibai*	(Aoki, 1976)	-26.02	4.17	-0.97	-30.26	0.05	0.22	-1.39
HJ1	405642	*Zetorchestes novaguineanus*	Krisper, 1987	-27.09	1.10	0.16	-30.12	0.22	0.25	-6.03
HJ2				-28.37	0.25	0.67	-30.80	0.08	0.02	-2.15
HJ4				-27.52	0.28	-0.97	-30.26	0.03	0.01	-0.75
rubber plantation										
HR1	405455	[B08] [111] *Lamellobates molecula mol* (405455)		-24.65	3.39	-0.41	-28.80	0.01	0.02	-0.15
HR2				-26.54	-3.24	-1.29	-29.30	0.01	-0.02	-0.14
HR3				-25.39	6.22	1.92	-29.25	0.31	1.92	-7.84
HR4				-25.90	7.71	1.07	-28.83	0.04	0.34	-1.15
HR1	405445	[B08] [152] *Hoplophorella* sp. cf. *Hoplophorella vitrina* (405445)		-27.57	3.46	-0.41	-28.80	0.01	0.05	-0.38
HR2	405450	[B08] [20] *Bischeloribates mahunkai* (405450)	Subías 2010	-26.37	6.40	-1.29	-29.30	0.38	2.42	-9.97
HR3				-28.03	8.45	1.92	-29.25	0.16	1.39	-4.61
HR4				-26.71	7.03	1.07	-28.83	0.08	0.58	-2.20
HR1	405729	[B08] [30] *Plonaphacarus kugohi* (405729)	Aoki, 1959	-27.90	5.68	-0.41	-28.80	0.07	0.39	-1.93
HR3				-24.78	2.20	1.92	-29.25	0.03	0.06	-0.71
HR4				-23.05	2.27	1.07	-28.83	0.29	0.66	-6.67
HR1	405650	[B08] [33] *Apoplophora pantotrema* cf. *Apoplophora cristata* (405650)		-30.79	-1.42	-0.41	-28.80	0.17	-0.24	-5.29
HR1	405540	*Allogalumna paranovazealandica*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-26.39	1.31	-0.41	-28.80	0.00	0.00	-0.04
HR2				-27.44	2.00	-1.29	-29.30	0.31	0.62	-8.54
HR1	405506	*Allonothrus russeolus*	Wallwork, 1960	-28.74	1.14	-0.41	-28.80	0.22	0.25	-6.34
HR4				-32.54	1.01	1.07	-28.83	0.06	0.06	-2.06
HR2	405381	*Archegozetes longisetosus*	Aoki, 1965	-27.33	0.98	-1.29	-29.30	0.06	0.06	-1.68
HR3				-23.73	6.79	1.92	-29.25	0.09	0.62	-2.17
HR4				-24.86	9.19	1.07	-28.83	0.05	0.46	-1.25
HR1	405619	*Epilohmannoides wallworki*	Hammer, 1979	-27.89	0.75	-0.41	-28.80	0.09	0.06	-2.39

HR1	405620	*Eremulus densus*	Hammer, 1979	-31.13	-2.65	-0.41	-28.80	0.02	-0.06	-0.73
HR2				-31.18	-6.90	-1.29	-29.30	0.05	-0.35	-1.58
HR1	405664	*Galumna sabahna*	Mahunka, 1995	-29.19	3.44	-0.41	-28.80	0.07	0.24	-2.05
HR2				-26.19	4.38	-1.29	-29.30	0.10	0.45	-2.67
HR2	405548	*Pergalumna paraindistincta*	Ermilov, Sandmann, Klarner, Widyastuti & Scheu, 2015	-27.35	4.68	-1.29	-29.30	0.09	0.42	-2.46
HR1	405671	*Protoribates paracapucinus*	(Mahunka, 1988)	-25.62	5.95	-0.41	-28.80	0.03	0.17	-0.71
HR3				-24.79	3.83	1.92	-29.25	0.05	0.18	-1.18
HR4				-26.08	6.40	1.07	-28.83	0.18	1.15	-4.67
HR1	405449	*Scheloribates praeincisus*	(Berlese, 1910)	-26.17	3.95	-0.41	-28.80	0.19	0.75	-4.94
HR4				-27.04	0.46	1.07	-28.83	0.02	0.01	-0.53
HR1	405524	*Tegeozetes tunicatus*	Berlese, 1913	-27.49	1.82	-0.41	-28.80	0.11	0.20	-3.08
HR3				-27.72	-2.52	1.92	-29.25	0.36	-0.90	-9.95
HR4				-29.15	11.99	1.07	-28.83	0.08	0.98	-2.39
HR1	405389	*Trachyoribates shibai*	(Aoki, 1976)	-27.16	2.54	-0.41	-28.80	0.01	0.02	-0.25
HR2				-24.78	2.69	-1.29	-29.30	0.00	0.00	-0.03
HR4				-25.15	3.00	1.07	-28.83	0.19	0.57	-4.77
oil palm plantation										
HO1	405718	[B08] [107] *Rostrozetes* sp. 1 (405718)		-26.91	4.28	1.63	-29.59	0.22	0.94	-5.92
HO3				-25.87	4.25	1.00	-28.84	0.09	0.38	-2.34
HO4				-27.35	4.89	-0.22	-30.27	0.03	0.15	-0.86
HO1	405450	[B08] [20] *Bischeloribates mahunkai* (405450)	Subías 2010	-25.98	3.44	1.63	-29.59	0.01	0.05	-0.34
HO3				-26.86	8.32	1.00	-28.84	0.41	3.40	-11.00
HO2	405506	*Allonothrus russeolus*	Wallwork, 1960	-28.17	0.12	0.53	-28.96	0.40	0.05	-11.14
HO4				-28.05	7.55	-0.22	-30.27	0.04	0.29	-1.07
HO1	405381	*Archegozetes longisetosus*	Aoki, 1965	-28.28	4.52	1.63	-29.59	0.43	1.95	-12.21
HO3				-27.46	4.48	1.00	-28.84	0.39	1.73	-10.59
HO4				-28.70	1.94	-0.22	-30.27	0.92	1.79	-26.48
HO1	405449	*Scheloribates praeincisus*	(Berlese, 1910)	-26.33	4.09	1.63	-29.59	0.04	0.16	-1.03
HO2				-25.67	4.34	0.53	-28.96	0.03	0.11	-0.64
HO3				-26.51	5.06	1.00	-28.84	0.07	0.33	-1.75
HO4				-26.92	1.04	-0.22	-30.27	0.01	0.01	-0.21
HO1	405389	*Trachyoribates shibai*	(Aoki, 1976)	-26.02	4.89	1.63	-29.59	0.30	1.45	-7.70
HO2				-26.42	2.51	0.53	-28.96	0.58	1.45	-15.31
HO3				-27.00	1.72	1.00	-28.84	0.05	0.08	-1.30

Table S2: Single-dimensional metrics of oribatid mite community - average position ('IPos'), maximum, minimum and range (max-min). Variable ($\Delta^{13}C$ and $\Delta^{15}N$), land-use system, value and the letter (a/b/ab) representing the significances. $\Delta^{13}C$ and $\Delta^{15}N$ values were scaled between 0 and 1 based on maximum and minimum across communities to ensure equal contribution. Maximum as well as minimum of $\Delta^{13}C$ and $\Delta^{15}N$ values were represented by one species with the most extreme values within the whole community. For calculation see Materials and Methods, for statistical analysis see text.

	variable	land-use system	value	letter
average position	$\Delta^{13}N$	jungle rubber	0.69	a
average position	$\Delta^{13}N$	rainforest	0.67	a
average position	$\Delta^{13}N$	rubber plantation	0.58	b
average position	$\Delta^{13}N$	oil palm plantation	0.57	b
average position	$\Delta^{15}N$	rubber plantation	0.45	a
average position	$\Delta^{15}N$	oil palm plantation	0.44	a
average position	$\Delta^{15}N$	jungle rubber	0.37	ab
average position	$\Delta^{15}N$	rainforest	0.31	b
maximum	$\Delta^{13}N$	jungle rubber	0.84	a
maximum	$\Delta^{13}N$	rainforest	0.83	a
maximum	$\Delta^{13}N$	rubber plantation	0.81	a
maximum	$\Delta^{13}N$	oil palm plantation	0.69	b
maximum	$\Delta^{15}N$	rubber plantation	0.63	a
maximum	$\Delta^{15}N$	rainforest	0.62	a
maximum	$\Delta^{15}N$	oil palm plantation	0.61	a
maximum	$\Delta^{15}N$	jungle rubber	0.56	a
minimum	$\Delta^{13}N$	rainforest	0.57	a
minimum	$\Delta^{13}N$	jungle rubber	0.57	a
minimum	$\Delta^{13}N$	oil palm plantation	0.48	a
minimum	$\Delta^{13}N$	rubber plantation	0.24	b
minimum	$\Delta^{15}N$	oil palm plantation	0.34	a
minimum	$\Delta^{15}N$	jungle rubber	0.20	b
minimum	$\Delta^{15}N$	rubber plantation	0.16	b
minimum	$\Delta^{15}N$	rainforest	0.14	b
range (max-min)	$\Delta^{13}N$	rubber plantation	0.57	a
range (max-min)	$\Delta^{13}N$	jungle rubber	0.28	b
range (max-min)	$\Delta^{13}N$	rainforest	0.25	b

range (max-min)	Δ^{13}N	oil palm plantation	0.21	b
range (max-min)	Δ^{15}N	rainforest	0.48	a
range (max-min)	Δ^{15}N	rubber plantation	0.47	a
range (max-min)	Δ^{15}N	jungle rubber	0.37	ab
range (max-min)	Δ^{15}N	oil palm plantation	0.27	b

Table S3: Multi-dimensional metrics of oribatid mite community - isotopic dispersion (‘IDis’), isotopic divergence (‘IDiv’), isotopic evenness (‘IEve’), isotopic richness (‘IRic’), isotopic uniqueness (‘IUni’). Land-use system, value and the letter (a/b/ab) representing the significances. Δ^{13}C and Δ^{15}N values were scaled between 0 and 1 based on maximum and minimum across communities to ensure equal contribution. Maximum as well as minimum of Δ^{13}C and Δ^{15}N values were represented by one species with the most extreme values within the whole community. For calculation see Materials and Methods, for statistical analysis see text.

multidimensional metrics	land-use system	value	letter
‘IDis’	oil palm plantation	0.47	a
‘IDis’	jungle rubber	0.47	a
‘IDis’	rubber plantation	0.37	a
‘IDis’	rainforest	0.32	a
‘IDiv’	rainforest	0.73	a
‘IDiv’	jungle rubber	0.71	a
‘IDiv’	rubber plantation	0.71	a
‘IDiv’	oil palm plantation	0.67	a
‘IEve’	oil palm plantation	0.65	a
‘IEve’	jungle rubber	0.53	a
‘IEve’	rainforest	0.49	a
‘IEve’	rubber plantation	0.47	a
‘IRic’	rubber plantation	0.13	a
‘IRic’	jungle rubber	0.07	b
‘IRic’	rainforest	0.06	b
‘IRic’	oil palm plantation	0.02	b
‘IUni’	oil palm plantation	0.61	a
‘IUni’	jungle rubber	0.46	ab
‘IUni’	rubber plantation	0.43	ab
‘IUni’	rainforest	0.31	b

Chapter IV

Response of soil animal communities to tree diversity enrichment of oil palm plantations

Alena Krause, Anton Potapov, Stefan Scheu and Mark Maraun

Abstract

The transformation and degradation of landscapes is rapidly increasing worldwide. Due to the increase in the human population and increased resource demand, pressure on ecosystems is increasing strongly. Especially tropical regions are suffering. In south East Asia rainforest is increasingly transformed into cash crop monoculture plantations such as rubber, oil palm and acacia. In particular oil palm is one of the fasted expanding crops, and therefore, effects of oil palm plantation management on biodiversity and ecosystem functioning are of increasing interest. However, in particular studies on the belowground system are rare. The structure and functioning of soil systems are essential for the functioning of ecosystems. This study formed part of the 'Biodiversity Enrichment Experiment' within the interdisciplinary project "Ecological and socioeconomic functions of tropical lowland rainforest transformation systems" (EFForTS), located in southwest Sumatra, Indonesia. In this experiment 'tree islands' of varying species diversity (0, 1, 2, 3 and 6 tree species) and plot sizes (5 x 5, 10 x 10, 20 x 20 and 40 x 40 m) were established in oil palm plantations. We investigated the effect of these 'tree islands' on the soil macro- and mesofauna three years after the experiment started. Neither the different diversity levels of trees nor plot size significantly affected the abundance of soil invertebrate taxa. However, the richness of soil invertebrate taxa was increased in plantations with two tree species. Overall, the results indicate that diversity and abundance of plant communities little affects the structure and diversity of soil invertebrates in the short term. However, soil animal communities are likely to respond to the enrichment of plantations by trees at later stages and this needs further investigation.

Introduction

Transformation as well as degradation of landscapes is rapidly increasing worldwide. This is driven predominantly by the growing human population and increased use of resources; by 2050 the worldwide population size will increase to 9.7 billion people (UN, 2015). This in turn will lead to an increase in the demand of food, fuel and fiber (Dirzo and Raven, 2003; Foley et al., 2005; Gibbs et al., 2010; Newbold et al., 2015). Such demands, however, lead to high pressure on ecosystems worldwide regarding the production and yield of agricultural landscapes (Godfray et al., 2010; Lambin and Meyfroidt, 2011; Tscharntke et al., 2012). Until today 40 % of the terrestrial surface is managed for agricultural purposes or transformed into agricultural systems; (Bridges and Oldeman, 1999; Reynolds et al., 2007; Foley et al., 2011; Pavao-Zuckerman and Sookhdeo, 2017; Francini et al., 2018).

Especially tropical regions suffer from degradation and transformation into different land-use systems, e.g. oil palm or rubber plantations (Sodhi et al., 2010; Wilcove et al., 2013; Meijide et al., 2018). Those transformations are threatening ecosystems with the highest rates of biodiversity and endemism worldwide (Jones, 2013). One of the rapidly increasing agricultural land-use system are vegetable oils (Clay, 2013), in particular oil palm. This is not only one of the fastest expanding crops but also one of the most versatile oils (Carter et al., 2007; Fitzherbert et al., 2008; Zimmer, 2010; Ashraf et al., 2018). In consequence of its versatility, palm oil is widely used, beyond that it is the oil seed crop that produces the highest yield of oil per land area (Zimmer, 2010; Ashraf et al., 2018). In Indonesia, transformation of rainforest into agricultural systems strongly increased in the last decades. Oil palm plantations were often established on rainforest sites which were previously logged or degraded by fire (Curran et al., 2004; Dennis et al., 2005; Fitzherbert et al., 2008; Drescher et al., 2016). In 2012, 0.84 million hectares of rainforest were converted into agricultural systems in Indonesia; the highest rate worldwide (Margono et al., 2014; Drescher et al., 2016).

Conversion of rainforest into plantations and intensification of land use are known to affect diversity and biomass, and therefore ecosystem functioning of above- and belowground animals and plants (Sodhi et al., 2004; Fitzherbert et al., 2008; Wilcove et al., 2013; Barnes et al., 2014; Edwards et al., 2014; Klarner et al., 2017). In particular, the reduction of decomposer diversity may reduce decomposition rates as well as carbon and nutrient cycling (Handa et al., 2014). Decomposition is one of the most important processes for terrestrial ecosystems, since about 90 % of the primary production of plants enters the soil system as leaf and wood detritus or rhizodeposits (McNaughton et al., 1989; Bardgett, 2005). Soil structure and thereby the functioning of soil systems, e.g. the turnover of organic matter and nutrient cycling, can be modified by the presence of soil animal species (Bardgett, 2005; Nielsen et al., 2015). Soil animals contribute to soil functioning and energy fluxes (Brussaard et al., 2007). Even within small spatial scales the abundance and diversity of soil arthropods varies, since organisms are not distributed uniformly due to environmental gradients (Legendre and Fortin, 1989; Ettema and Wardle, 2002). Additionally, active dispersal and movement of soil organisms is limited, depending on the species from few millimeters to centimeters per day (Ettema and Wardle, 2002). Variations in abiotic as well as biotic factors, e.g. climate and litter type, are major determinants of the high spatial variability of the structure of soil communities (Coûteaux et al., 1995; Wardle et al., 2006; Berg and McClaugherty, 2008). Spatial variability of soil animals also is related to the variability in the composition and diversity of plant communities (Scherber et al., 2010; Eisenhauer et al., 2011; Thakur and Eisenhauer, 2015). This might be due to variations in plant species richness but also to the identity of individual plant species (Spehn et al., 2000; Wardle et al., 2006; Viketoft et al., 2009; Eisenhauer et al., 2010, 2011). The decline in plant diversity and thereby the loss of litter and root resources negatively impacts the density, diversity and functioning of soil organisms (Hooper et al., 2000; Scherber et al., 2010; Eisenhauer et al., 2011). However, studies investigating the response of soil biota to changes in plant diversity and identity for longer periods of time (Eisenhauer et al., 2009, 2011; Viketoft et al., 2009) and considering a wide range of taxonomic and functional groups are scare (Hedlund et al., 2003; Scherer-Lorenzen and Leadley, 2003; Milcu et al., 2008; Viketoft et al., 2009; Eisenhauer et al., 2011).

An option for restoring the diversity and functioning of decomposer communities is the planting of native trees (Chazdon, 2008; Teuscher et al., 2016). Planted tree islands form, among others, local areas of recovery which then might enhance or initiate natural succession not only within the tree islands but also for the surrounding environment (Yarranton and Morrison, 1974; Corbin and Holl, 2012; Teuscher et al., 2016). Increased diversity in tree islands may be due to the fact that larger area is associated with increased species richness (MacArthur and Wilson, 1963, 1967; Jonsson et al., 2009). However, the most effective island size (economically and ecologically) is still debated (Mendenhall et al., 2014; Teuscher et al., 2016). Generally, management strategies of intensively managed oil palm plantations targeting at increasing biodiversity but maintaining productivity are virtually lacking until today (Teuscher et al., 2016).

To protect biodiversity of tropical regions it is important to integrate the belowground system and to consider the management of plantation systems (Koh et al., 2009; Foster et al., 2011; Luskin and Potts, 2011; Teuscher et al., 2015, 2016). The effects of oil palm plantation management on aboveground biodiversity and ecosystem functioning is receiving increased interest (Nurdiansyah et al., 2016; Syafiq et al., 2016; Teuscher et al., 2016; Ashton-Butt et al., 2018), however, so far studies on belowground systems are scarce (Bessou et al., 2017; Krause et al., 2019; Potapov et al., 2019; Susanti et al., 2019). The current study formed part of the interdisciplinary project “Ecological and socioeconomic functions of tropical lowland rainforest transformation systems” (EFForTS), established in Jambi Province, southwest Sumatra, Indonesia (Drescher et al., 2016). The aim of the ‘Biodiversity Enrichment Experiment’ was to enhance biodiversity and ecosystem functioning in oil palm plantations by ‘tree islands’ of varying diversity level of planted tree species and plot size. We hypothesized that the abundance, diversity and community of belowground soil invertebrate taxa will increase with both increasing plot size and increasing diversity of planted tree species.

Material and Methods

Study sites

The ‘Biodiversity Enrichment Experiment’, was established in 2013 in the oil palm plantation of PT Humusindo Makmur Sejata (01.95° S and 103.25° E, 47±11 m a.s.l.; see also paragraph “study design” of the general introduction; Fig. 2) (Teuscher et al., 2016). Loamy Acrisol is the dominant soil type (Allen et al., 2015). Within the existing oil palm plantation, ‘tree islands’ of varying diversity level (0, 1, 2, 3 and 6 planted tree species) and plot size (5 × 5, 10 × 10, 20 × 20, 40 × 40 m) were established (see Fig. 3 of the paragraph "study design" of the General Introduction). Following the random partitions design of Bell et al. (2009), 52 'tree island' were established. Additionally, four control plots ("ctrl", 10 x 10 m) without any experimental treatment, i.e. with management-as-usual, were established resulting in 56 'tree islands' in total. Species composition within the 'tree island' was random and each tree species was selected only once at each species diversity level (Teuscher et al., 2016). Prior to the tree planting, 40 % of the oil palms within the 'tree islands' were cut. For the enrichment of the 'tree islands' six native trees were selected including three fruit trees (*Parkia speciosa*, and *Archidendron pauciflorum*, Fabaceae; *Durio zibethinus*, Malvaceae), two timber trees *(Peronema canescens*, Lamiaceae; *Shorea leprosula*, Dipterocarpaceae), and one tree used for the production of latex (*Dyera polyphylla*, Apocynaceae). Management of the 'tree island' plots contained manual weeding in the first two years (preventing weeds to overgrow planted saplings; done every three months). Manual weeding was stopped thereafter to allow natural succession as well as interaction/competition of native trees with each other and oil palms. Application of fertilizer, herbicides and pesticides in 'tree island' plots was stopped after tree planting. More details on the study sites and experimental design are given in Teuscher et al. (2016). Samples for soil invertebrate extraction were taken in 2016 after manual weeding was finished.

Sampling, extraction and species determination

In October to November 2016, four soil samples (16 x 16 cm, litter layer and 0 – 5 cm of mineral soil) were taken randomly from a 5 x 5 m subplot established in each plot, i.e. a total of 224 samples were taken. In the 5 x 5 m plot the full plot area was used for taking samples. The samples were transported to the laboratory and extracted by heat (Kempson et al., 1963). Soil invertebrates were transferred into ethanol (70 %) and sorted to high rank taxa including Oribatida, Collembola, Annelida and Chilopoda (Table S1). The taxa were assigned to size classes of meso- and macrofauna (Table S1 and S2).

Statistical analysis

The numbers of individuals of the four samples per subplot were summed up and given as number of individuals per square meter. Further, the number of meso- and macrofauna taxa of the four samples per subplot were summed up to obtain the total number of meso- and macrofauna taxa of the area sampled, i.e. 1024 cm². Meso- and macrofauna were analyzed separately due to large differences in density. Statistical analyses were performed using R v 3.5.2 (R Core Team, 2018) with R studio interface (RStudio, Inc.). Normality and homogeneity of variance were inspected using diagnostic plots and this indicated that preconditions for parametric data analysis were met. Effects of diversity level of planted tree species and plot size were assessed using linear models (Wilkinson and Rogers, 1973; Chambers and Hastie, 1992). Significance was evaluated using the *anova* function (Chambers and Hastie, 1992). Data were visualized using *ggplot* in the ggplot2 package (Wickham, 2016).

Additionally, principal components analysis (PCA) was used to analyze and present graphically the response of the different taxa to tree diversity levels. Here, the response variables (different taxa) were log-transformed to improve homogeneity of variances. The different tree diversity levels (0, 1, 2, 3, 6 planted tree species) were included as passive/supplementary variables not affecting the ordination. PCA was performed using CANOCO 5 (Microcomputer Power, Ithaca, USA, 2012).

Results

The abundance of mesofauna was higher than the abundance of macrofauna with an overall averages of 3645 ind./m^2 and 828 ind./m^2, respectively. Additionally, the richness of mesofauna was higher than the richness of macrofauna with overall averages of 160 ± 26 ind./m^2 and 153 ± 45 ind./m^2, respectively. Among macrofauna groups, Diplopoda and Coleoptera (larve) had the highest abundance with averages of 223 and 166 ind./m^2, respectively. Among mesofauna taxa, Collembola and Oribatida had the highest abundance with averages of 1706 and 1339 ind./m^2, respectively. For more detailed information see Table S1.

Abundance of total macro- and mesofauna

Tree diversity neither significantly affected the abundance of macro- nor mesofauna ($F_{1,50} = 1.53$, $p = 0.2219$ and $F_{1,50} = 0.68$, $p = 0.4122$, respectively). Although not significant, macrofauna abundance was similar at diversity level 0, 1 and 2 and lower at diversity level 3 and 6 (Figure 1a; for detailed information see Table S3). Abundance of mesofauna was highest at diversity level 2, 3 and 6 and lowest at diversity level 0 (Figure 1b; for detailed information see Table S3).

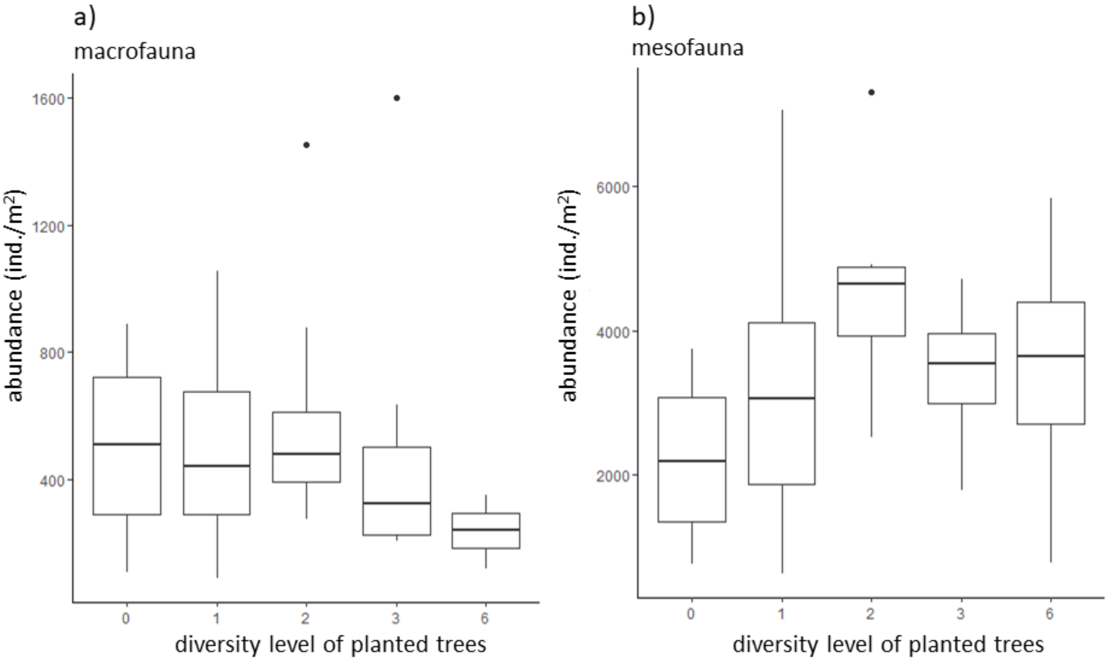


Figure 1: Abundance of macrofauna (a) and mesofauna (b) at the five tree diversity levels (0, 1, 2, 3 and 6). Note the different scales. Differences between means in both analyses were not significant, *anova* $p > 0.05$.

Plot size also did not significantly affect the abundance of macro- and mesofauna ($F_{3,48} = 1.19$, $p = 0.3244$ and $F_{3,48} = 1.23$, $p = 0.3092$, respectively). Although not significant, macrofauna abundance was similar in 20 x 20 and 40 x 40 m and lower in 10 x 10 and 5 x 5 m plots (Figure 2a; for detailed information see Table S4). Mesofauna abundance was similar in each of the plots of different size (Figure 2b; for detailed information see Table S4).

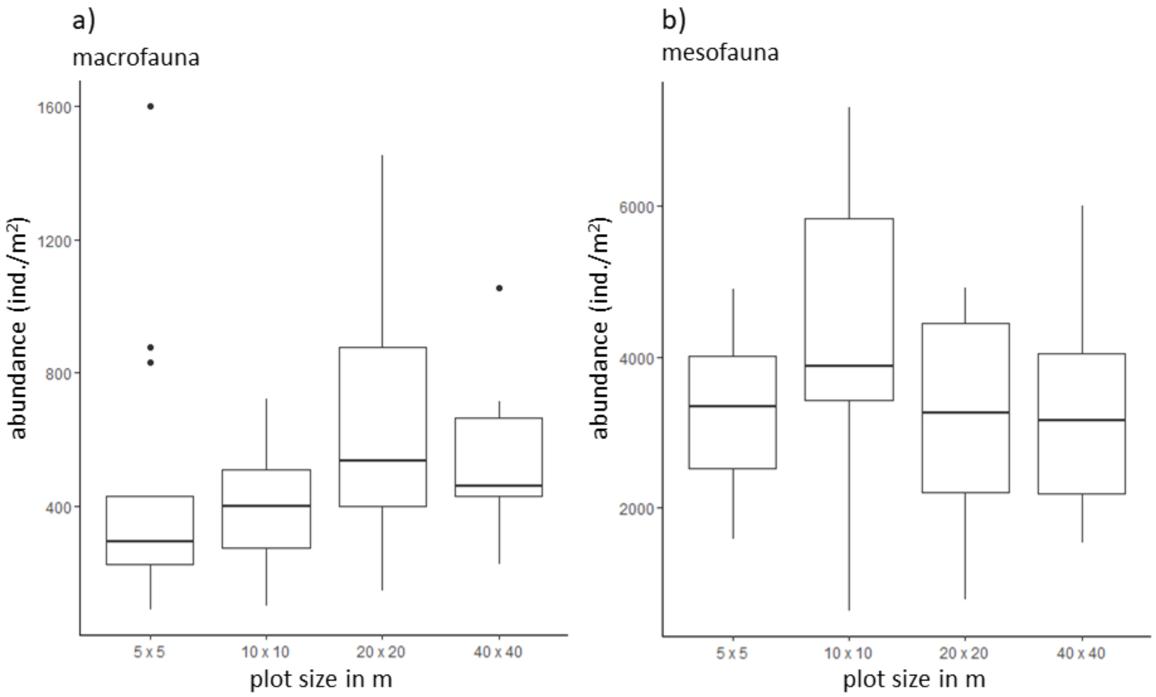


Figure 2: Abundance of macrofauna (a) and mesofauna (b) at the four plot sizes (5 x 5, 10 x 10, 20 x 20 and 40 x 40 m). Note the different scales. Differences between means in both analyses were not significant, *anova* $p > 0.05$.

Richness of macro- and mesofauna taxa

Richness of macrofauna taxa varied significantly with tree diversity ($F_{1,50} = 4.29$; $p = 0.027$), whereas richness of mesofauna taxa were not significant (Figure 3; for detailed information see Table S5). Macrofauna richness was highest at diversity level 2, lowest at diversity level 6 and intermediate at diversity levels 0, 1 and 3 (Figure 3a). Mesofauna richness was similar at all diversity levels (Figure 3b).

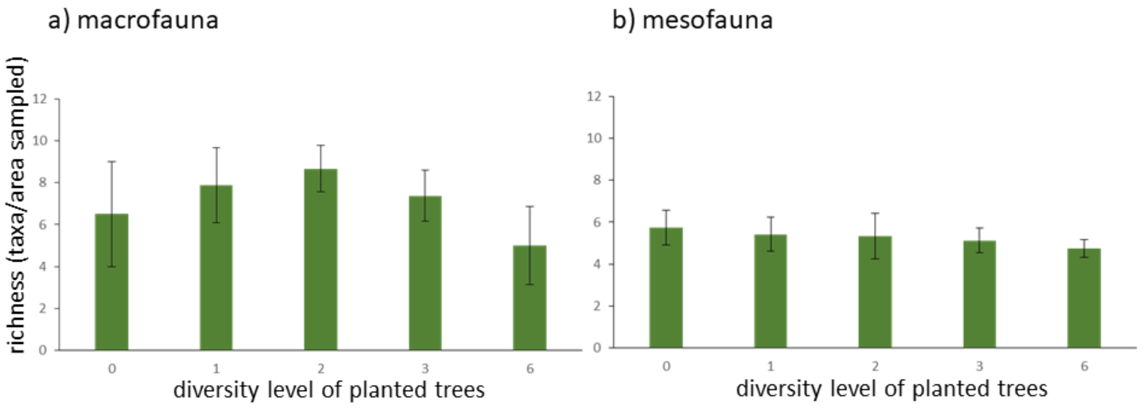


Figure 3: Richness of macrofauna (a) and mesofauna (b) at five tree diversity levels (0, 1, 2, 3 and 6) of the area sampled per plot, i.e. 1024 cm². Means with standard deviation.

Macro- and mesofauna richness did not vary significantly with plot size ($F_{3,48}$ = 0.71, p = 0.55 and $F_{3,48}$ = 1.53, p = 0.219, respectively) (Figure 4; for detailed information see Table S6). Although not significant, macrofauna richness was highest at plot size 20 x 20 m, similar at plot size 40 x 40 m, 10 x 10 m and 5 x 5 m (Figure 4a). Mesofauna richness of soil invertebrate taxa was similar at plot size 5 x 5 m and 20 x 20 m and slightly lower at plot size 10 x 10 m and 40 x 40 m (Figure 4b).

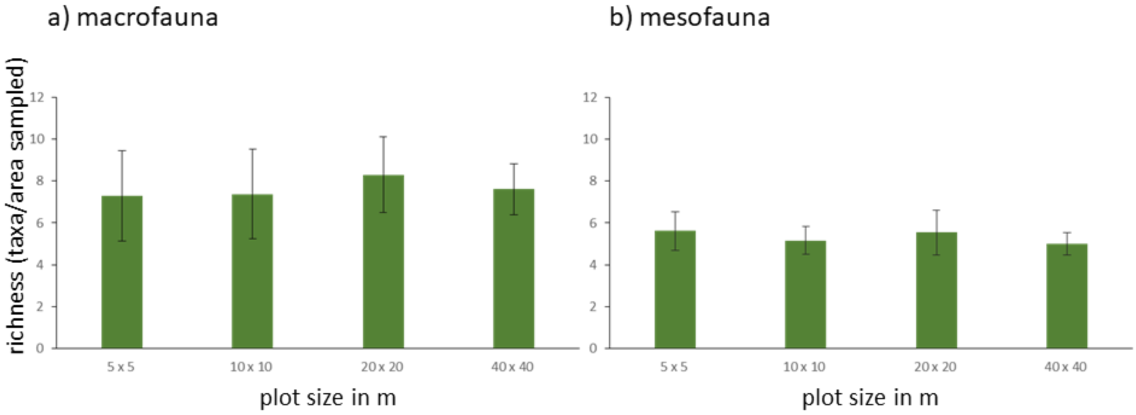


Figure 4: Richness of macrofauna (a) and mesofauna (b) at the four plot sizes (5 x 5, 10 x 10, 20 x 20 and 40 x 40 in m) of the area sampled per plot, i.e. 1024 cm². Means with standard deviation.

Community structure

In total, 21,270 individuals of 25 taxa (Table S2) were identified. Only Collembola and Oribatida occurred at each diversity level of planted trees and plot size. None of the taxa occurred exclusively at only one tree diversity level.

The first two axes of the PCA accounted for a total of 39.2 % of the variation in taxa data (Figure 5). The first axis (PC1) accounted for the majority of the variability (21.0 %) and separated diversity level 2 from the other four diversity levels (0, 1, 3 and 6). The second axis (PC2) accounted for 18.2 % and separated diversity levels 2 and 1 from diversity levels 0, 3 and 6. Taxa associated with diversity level 2 were mostly decomposers, including Collembola, Oribatida, Symphyla and Diplopoda, and two predatory taxa, i.e. Mesostigmata and Chilopoda. Taxa associated with the other four diversity levels of planted tree species (0, 1, 3 and 6) were mostly predators, including predatory Coleoptera, Opiliones and Schizomida, and one decomposer taxon, i.e. Annelida. Along the second axis diversity level 1 was mostly associated with predators, including Pseudoscorpiones, Araneae and Diplura (Campodidae) and one decomposer taxon, i.e. Annelida. By contrast, diversity level 2 was mostly associated with decomposer taxa, including Oribatida, Collembola and Symphyla. Taxa associated with diversity level 3 were Opiliones and Schizomida, with diversity level 6 it was predatory Coleoptera and with diversity level 0 is was Thysanoptera.

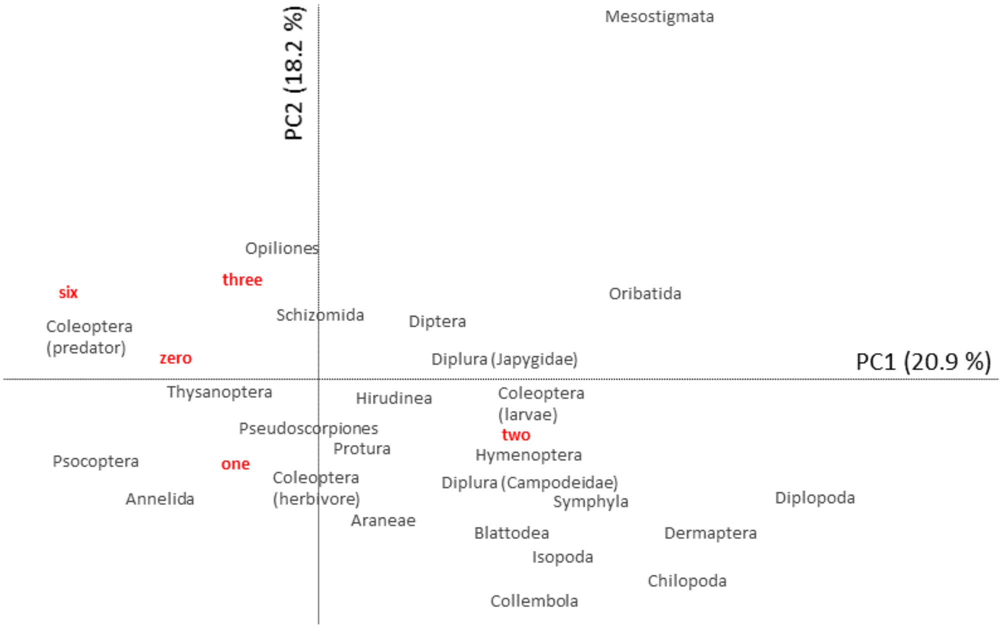


Figure 5: Principal components analysis (PCA) of the community composition of soil invertebrate taxa. Tree diversity levels (0, 1, 2, 3 and 6) were included as passive variables (red). The first axis (PC1) represents 20.9 % and the second (PC2) 18.2 % of the variability in taxa data; the length of gradient is 1.2. Data were log-transformed prior to the analysis.

Discussion

Abundance of macro- and mesofauna

Neither the diversity of planted tree species nor plot size significantly affected the abundance of macro- and mesofauna taxa. These findings contrast results of earlier studies showing that increased coverage of plants, due to a reduction of herbicide use, beneficially affects aboveground invertebrates (Chung et al., 2000; Ashton-Butt et al., 2018; Spear et al., 2018; Darras et al., 2019). In contrast to these results, bird diversity and bird abundance have been shown to increase with increasing number of planted trees in oil palm plantations (Teuscher et al., 2015). However, plant diversity effects have been found to dampen at higher trophic level and with the degree of omnivory of consumers, and this was true for both abundance and richness of above- and belowground organisms (Scherber et al., 2010). Results of the study of Scherber et al. (2010) further showed the response of belowground organisms to plant diversity to be less pronounced compared to that of aboveground organisms. In particular herbivore species responded more strongly to changes in plant diversity than predator and omnivore species. Also, alley-cropping, i.e. planting a mosaic of tree, grass and/or shrubs species into cropland (Gold and Garrett., 2009), has been shown to impact aboveground arthropod diversity; larger numbers of predators and decomposers occurred at sites with alley-cropping (Ashraf et al., 2018). Plant diversity effects on soil biota have been shown to strongly depend on time and only occur after a pronounced time lag of four to six years after manipulating plant species diversity (Eisenhauer et al., 2011). This suggests that three years after the establishment of plant communities of different diversity in the present study might have been too short for macro- and mesofauna soil invertebrate taxa to respond to the established experimental treatments. Castillo et al. (2018) showed that abundance and species richness of oribatid mites changed due to reforestation of pastureland in tropical montane forest in Ecuador after seven years, but the changes still were little pronounced. Supporting the conclusion that soil invertebrates respond to changes in plant community composition with a pronounced lime lag, Teuscher et al. (2016) found significant effects of planting trees as well as plot size on bird and aboveground invertebrate species one year after the establishment of the experiment. Aboveground invertebrates associated with the herb-layer increased slightly compared to the control plots. Further, contrasting the findings of the present study, aboveground invertebrates also responded to plot size already one year after the establishment of the experiment (Teuscher et al., 2016). This likely reflects the more close association of aboveground animals, in particular herbivores, with plant species and associated changes in environmental factors and habitat structure (Tscharntke et al., 2011; Pywell et al., 2012; Teuscher et al., 2016). Supporting our findings, earlier studies showed that physical habitat characteristics might be more important drivers for belowground soil invertebrate communities than the diversity and identity of planted trees (Ducarme et al., 2004; Nielsen et al., 2010; Bluhm et al., 2019). However, physical habitat characteristics also change with changes in tree diversity and identity but these changes are slow and need to be investigated in long-term studies (Bluhm et al., 2019).

Richness of macro- and mesofauna taxa

Confirm to our hypothesis, the richness of macrofauna taxa varied with the diversity of planted tree species; it was at a maximum at diversity level 2, whereas it was at a minimum at diversity level 6. Similar to these findings, it has been demonstrated that aboveground arthropod diversity and richness increase in oil palm plantations with alley-cropping (Azhar et al., 2014; Ashraf et al., 2018). Alley-cropping includes a variety of crop plants and trees which increase habitat heterogeneity, soil fertility, water quality as well as carbon and nutrient cycling (Fahrig et al., 2011; Torralba et al., 2016; Ashraf et al., 2018). Additionally, it enhances the complexity of the vegetation and thereby the number and size of microhabitats (Lawton, 1983; Jose, 2009). Oil palm plantations generally lack a diverse understory, and herbicides as well as fertilizer use is high (Ismail et al., 2009). Similar to Alley-cropping, the enrichment of oil palm plantations with native tree species and the reduced fertilizer and herbicide use may increase resource availability and thereby increase the diversity of micohabitats.

Richness as well as abundance of macro- and mesofauna taxa did not significantly respond to variations in plot size. These findings are consistent with results of earlier studies indicating that species richness may not vary in a consistent way with island area (Brose, 2003; Báldi, 2008; Jonsson et al., 2009). The study of Brose (2003) demonstrated that habitat area did not affect species richness of wetland carabid beetle communities in agricultural landscapes in northern Germany. Báldi (2008) demonstrated that habitat heterogeneity may in fact decrease with habitat size and species-area relationship were not significant for nine out of eleven studied taxa including Collembola, Oribatida and Chilopoda. Jonsson et al. (2009) also found the diversity of belowground invertebrates of the boreal zone of northern Sweden to be rather insensitive to changes in island size or isolation.

Community structure

Community analysis showed that taxa associated with diversity level 2 and 1 were primarily decomposers, whereas taxa associated with diversity levels 0, 3 and 6 were primarily predators. This suggests that decomposer invertebrates benefitted from increased litter input and the formation of a litter layer in plantations of low tree species richness. Potentially, higher tree diversity counteracted the accumulation of litter in the litter layer by facilitating litter decomposition. In fact, it has been shown that litter mixtures may decompose much faster than single litter species or mixtures of low species richness (Hättenschwiler et al., 2005; Benbow et al., 2015). On the contrary, predator taxa such as cursorial spiders may benefit from more open habitats facilitating prey capture (Wise, 1995; Lawrence and Wise, 2000). If true, this implies that low diversity levels of tree species are associated with low nutrient recycling hampering primary production with important feedbacks to the belowground system. Potentially, in the long-term tree plantations of low diversity may be associated by a depauperated soil biota community (Wardle, 2006; Wardle et al., 2006). However, the traits of plant and litter species responsible for changes in soil animal communities associated with changes in plant species are little understood (Wardle, 2006), but the changes are likely driven by changes in litter quality (Díaz et al., 2004; Wardle, 2006) but also by changes in the physical structure of litter (Hansen, 1999; Wardle, 2006; Wardle et al., 2006). Supporting our conclusion that predators may benefit from more open habitats with shallow litter layers, results of earlier studies on Oribatida and Chilopoda indicate that monoculture plantations, such as rubber and oil palm, favor predators and/or scavengers (Klarner et al., 2017; Krause et al., 2019, A. Krause unpublished data 2020). Another study showed that soil porosity and pH are the main drivers of oribatid mite abundance and richness, indicating that physical habitat characteristics might override food resources as driving factors for soil animal communities (Ducarme et al., 2004).

Overall, the results of the present study indicate that the enrichment of oil palm plantation with native trees may contribute to the formation of more complex decomposer communities, but further long-term studies with a wider range of tree species are needed to explore the factors responsible for changes in soil communities increasing the functioning of plantation systems. Enrichment of oil palm plantations with native trees is a promising option to enhance biodiversity of existing monoculture plantations and to develop more sustainable management strategies.

Conclusions

The decline in biomass of arthropod species in temperate and tropical regions are driven in the first place by changes in land use. Alternative management practices of agricultural systems therefore are receiving increased attention. However, since soil formation processes are slow, effects of the enrichment of plantation systems with native trees for soil invertebrate taxa are likely to be delayed. Three years after the establishment of enrichment planting soil invertebrate abundance did not change significantly. However, soil invertebrate richness increased at intermediate tree diversity level, indicating that resource availability peaks at intermediate diversity level. Presumably, additive mixture effects increase litter decomposition thereby increasing food quality for litter feeding macrofauna. Long-term experiments are needed to more fully explore the response of soil animal communities to the enrichment of plantation systems with native trees species and the feedbacks to the functioning of the plantations.

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Appendix

Table S1: Size class of soil taxa and their mean abundance per m^2.

size class	soil taxa	mean abundance per m^2
macrofauna	Annelida	20
macrofauna	Araneae	13
macrofauna	Blattodea	15
macrofauna	Chilopoda	62
macrofauna	Coleoptera (herbivore)	29
macrofauna	Coleoptera (larvae)	166
macrofauna	Coleoptera (predator)	45
macrofauna	Dermaptera	30
macrofauna	Diplopoda	223
macrofauna	Diptera	57
macrofauna	Hirudinea	10
macrofauna	Hymenoptera	43
macrofauna	Isopoda	56
macrofauna	Opiliones	15
macrofauna	Schizomida	11
macrofauna	Thysanoptera	33
mesofauna	Collembola	1706
mesofauna	Diplura (Campodea)	32
mesofauna	Diplura (Japygidae)	88
mesofauna	Mesostigmata	212
mesofauna	Oribatida	1339
mesofauna	Protura	10
mesofauna	Pseudoscorpiones	29
mesofauna	Psocoptera	18
mesofauna	Symphyla	211

Table S2: Size class and numbers of individuals summed up for the four samples taken, i.e. per 1024 cm². Plot ID, diversity level of planted tree species (0, 1, 2, 3 and 6), plot size (5 x 5, 10 x 10, 20 x 20, 40 x 40) in m, size class (meso-, macrofauna) and number of individuals.

plotID	diversitylevel	plot size in m	size class	abundance
1	1	40 x 40	macrofauna	108
			mesofauna	324
2	3	20 x 20	macrofauna	41
			mesofauna	226

3	2	20 x 20	macrofauna	59
			mesofauna	503
4	1	10 x 10	macrofauna	45
			mesofauna	723
5	1	40 x 40	macrofauna	73
			mesofauna	299
6	1	5 x 5	macrofauna	37
			mesofauna	171
7	3	40 x 40	macrofauna	23
			mesofauna	183
8	1	5 x 5	macrofauna	9
			mesofauna	163
9	3	10 x 10	macrofauna	65
			mesofauna	398
10	0	20 x 20	macrofauna	91
			mesofauna	292
11	1	10 x 10	macrofauna	10
			mesofauna	65
12	1	20 x 20	macrofauna	42
			mesofauna	303
13	1	10 x 10	macrofauna	28
			mesofauna	710
14	1	10 x 10	macrofauna	74
			mesofauna	535
15	1	20 x 20	macrofauna	55
			mesofauna	403
16	3	5 x 5	macrofauna	23
			mesofauna	426
17	1	20 x 20	macrofauna	90
			mesofauna	455
18	2	5 x 5	macrofauna	28
			mesofauna	301
19	6	20 x 20	macrofauna	21
			mesofauna	80
20	1	10 x 10	macrofauna	52
			mesofauna	235
21	6	10 x 10	macrofauna	36
			mesofauna	597
22	2	5 x 5	macrofauna	90
			mesofauna	258
23	6	40 x 40	macrofauna	28
			mesofauna	402
24	2	40 x 40	macrofauna	37
			mesofauna	421
25	1	5 x 5	macrofauna	30

			mesofauna	192
26	2	40 x 40	macrofauna	51
			mesofauna	415
27	2	10 x 10	macrofauna	41
			mesofauna	363
28	1	5 x 5	macrofauna	26
			mesofauna	410
29	3	40 x 40	macrofauna	47
			mesofauna	361
30	1	20 x 20	macrofauna	15
			mesofauna	93
31	1	5 x 5	macrofauna	85
			mesofauna	393
32	2	10 x 10	macrofauna	31
			mesofauna	748
33	3	20 x 20	macrofauna	21
			mesofauna	333
34	2	10 x 10	macrofauna	52
			mesofauna	465
35	0	40 x 40	macrofauna	68
			mesofauna	158
36	2	20 x 20	macrofauna	73
			mesofauna	487
37	0	10 x 10	macrofauna	11
			mesofauna	79
38	1	20 x 20	macrofauna	99
			mesofauna	456
39	2	5 x 5	macrofauna	44
			mesofauna	502
40	0	5 x 5	macrofauna	36
			mesofauna	384
41	1	10 x 10	macrofauna	43
			mesofauna	351
42	1	5 x 5	macrofauna	21
			mesofauna	338
43	1	40 x 40	macrofauna	44
			mesofauna	224
44	3	5 x 5	macrofauna	164
			mesofauna	482
45	1	40 x 40	macrofauna	68
			mesofauna	260
46	2	40 x 40	macrofauna	47
			mesofauna	499
47	2	20 x 20	macrofauna	149
			mesofauna	497

48	3	10 x 10	macrofauna	25
			mesofauna	366
49	1	40 x 40	macrofauna	45
			mesofauna	174
50	6	5 x 5	macrofauna	12
			mesofauna	343
51	1	20 x 20	macrofauna	53
			mesofauna	188
52	1	40 x 40	macrofauna	55
			mesofauna	615

Table S3: Mean and standard deviation (sd) of the abundance of macro- and mesofauna per square meter in plots varying in planted tree species (0, 1, 2, 3 and 6).

diversitylevel	size class	mean m^2	sd m^2
0	macrofauna	503	298
	mesofauna	2229	1151
1	macrofauna	491	262
	mesofauna	3288	1713
2	macrofauna	571	313
	mesofauna	4443	1159
3	macrofauna	499	440
	mesofauna	3387	909
6	macrofauna	237	86
	mesofauna	3472	1804

Table S4: Mean and standard deviation (sd) of abundance of macro- and mesofauna (size class) per square meter varying with plot size (5 x 5, 10 x 10, 20 x 20, 40 x 40 m).

plot size in m	size class	mean m^2	sd m^2
5 x 5	macrofauna	454	404
	mesofauna	3277	1060
10 x 10	macrofauna	385	178
	mesofauna	4233	2125
20 x 20	macrofauna	608	356
	mesofauna	3242	1410
40 x 40	macrofauna	521	208
	mesofauna	3256	1282

Table S5: Variations in mean and standard deviation (sd) of soil invertebrate taxa richness per sampled area (1024 cm²) with diversity level of planted tree species (0, 1, 2, 3 and 6).

diversit ylevel	size class	mean taxa per area sampled	sd taxa per area sampled
0	macrofauna	6.50	2.50
	mesofauna	5.75	0.83
1	macrofauna	7.88	1.79
	mesofauna	5.42	0.81
2	macrofauna	8.67	1.11
	mesofauna	5.33	1.11
3	macrofauna	7.38	1.22
	mesofauna	5.13	0.60
6	macrofauna	5.00	1.87
	mesofauna	4.75	0.43

Table S6: Variations in mean and standard deviation (sd) of soil invertebrate taxa richness per sampled area (1024 cm²) with plot size (5 x 5, 10 x 10, 20 x 20, 40 x 40 m).

diversit ylevel	size class	mean taxa per area sampled	sd taxa per area sampled
5 x 5	macrofauna	7.31	2.16
	mesofauna	5.62	0.92
10 x 10	macrofauna	7.38	2.13
	mesofauna	5.15	0.66
20 x 20	macrofauna	8.31	1.81
	mesofauna	5.54	1.08
40 x 40	macrofauna	7.62	1.21
	mesofauna	5.00	0.55

Chapter V

General Discussion


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The human population is rapidly growing worldwide and in parallel the demand for food, fuel and fibre (Dirzo and Raven, 2003; Foley et al., 2005; Gibbs et al., 2010; Newbold et al., 2015). Satisfying these demands puts high pressure on ecosystems worldwild (Dirzo and Raven, 2003; Foley et al., 2005; Gibbs et al., 2010; Newbold et al., 2015) and results in increased conversion of natrual ecosystems into plantations as well in more intensively managed production systems (Godfray et al., 2010; Lambin and Meyfroidt, 2011; Tscharntke et al., 2012). In the past decades, especially tropical regions suffered from the transformation of landscapes (Sodhi et al., 2010; Wilcove et al., 2013; Meijide et al., 2018; see **Chapter 1**). This thesis aimed at improving understanding how the conversion of rainforest and jungle rubber into monoculture plantation systems (rubber and oil palm monoculture plantations) affects soil arthropods, especially oribatid mites and their trophic ecology in tropical lowland regions in South East Asia. The investigated land-use systems represented a gradient of different intensively managed systems, from more natural systems, represented by secondary rainforest and jungle rubber, to intensively managed systems, represented by rubber and oil palm monoculture plantations. Further, we investigated if the enrichment of oil palm plantations with native tree species planted in ‘tree islands’ of varying tree diversity and plot size beneficially affects soil invertebrates.

In **Chapter 2** we investigated shifts in the trophic niches of six soil-living oribatid mite species (*Plonaphacarus kugohi*, *Protoribates paracapucinus*, *Scheloribates praeincisus*, *Bischeloribates mahunkai*, *Rostrozetes* cf. *shibai*, and *Rostrozetes* sp. 1). Therefore, we measured stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of single oribatid mite individuals. For three of the six studied species (*S. praeincisus*, *R.* cf. *shibai* and *Rostrozetes* sp. 1) significant shifts of the trophic level (represented by ^{15}N) and of the use of basal resources (represented by ^{13}C) were shown, indicating that at least these species change their trophic niches with changing environment. The other three studied species (*B. mahunkai, P. kugohi* and *P. paracapucinus*) did not differ significantly, however, their trophic shifts followed the same trend. Additionally, the trophic niches of all species separated between more natural systems, i.e. rainforest and jungle rubber, and monoculture plantation systems, i.e. rubber and oil palm plantation. These results contrast earlier studies, which assumed trophic niches of oribatid mite species to be stable and narrow. The investigated oribatid mite species spanned over three trophic levels, including primary and secondary decomposers and predators/scavengers, which is conform to earlier studies (Schneider et al., 2004; Illig et al., 2005; Maraun et al., 2011). Notably, changes in trophic niches of species were due to both changes in the trophic position (indicated by ^{15}N values) as well as the use of basal resources (indicated by ^{13}C values) with the shifts in transformed ecosystems occurring towards higher tropic levels. This indicates that oribatid mite species switched towards prey of higher trophic levels in converted ecosystems, presumably to animal prey such as nematodes (Heidemann et al., 2011, 2014). Decomposer species were virtually lacking in oil palm plantations, but were also scarce in the other land-use systems, which is conform to another study in tropical ecosystems (Illig et al., 2005). By contrast, higher tropic level species, such as secondary decomposers and predators/scavengers, were present in each of the land-use systems. The scarcity of primary decomposer likely is related to poor litter quality (Butenschoen et al., 2014; Krashevska et al., 2017; Marian et al., 2017) and this is aggravated by the conversion of rainforest into plantation systems (Teuscher et al., 2016; Klarner et al., 2017). In fact, none of the studied oribatid mite species were identified as primary decomposer in plantation systems. Typically soil animals are enriched by 3-4 δ units in ^{13}C compared to litter and this has been termed "detrital shift" (Pollierer et al., 2009; Potapov et al., 2019); this also was true in the present study. However, the detrital shift was more pronounced in rainforest and jungle rubber than in monoculture plantations, which likely reflects changes in the usage of plant litter carbon compounds, i.e. form difficult accessible ones with lower $\delta^{13}C$ values, e.g. lignin, towards easy accessible ones, e.g. sugar and proteins (Gleixner et al., 1993; Hobbie and Werner, 2004; Bowling et al., 2008; Pollierer et al., 2009; Irawan et al., 2019). Additionally, primary decomposer are characterized by low fractionation of ^{15}N, presumably related to "protein sparing", i.e. the retaining of assimilated N in body tissue rather than excreting it due to low nitrogen supply in litter (Swift et al., 1979; Castellini and Rea, 1992; Gannes et al., 2007; Pollierer et al., 2009). In conclusion, our results indicate that oribatid mites predominantly function as secondary decomposers feeding on microorganisms, in particular fungi, however, they also indicate that in part they feed on animal prey or live as scavengers. Results of this study further indicate that oribatid mite species are able to colonize different ecosystems and this at least in part is due to trophic plasticity and the shift in the use of basal resources with conversion of rainforest into plantation systems.

Chapter 3 investigated shifts in the community-level trophic niche of oribatid mites. Here, we investigated 80 % of oribatid mite communities of rainforest and monoculture plantation systems of oil palm and rubber. Different to the first study, we measured stable isotopes ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of pooled individuals. Results of this study confirmed that the community-level trophic niche of oribatid mites is broader in rainforest than in plantation systems. The results further indicated that community-level trophic niche are clearly separated between natural and plantation systems. Further, confirming results of the study presented in **Chapter 1**, $^{15}N/^{14}N$ ratios indicated that oribatid mites shift their diet towards predation and/or scavenging in monoculture plantation systems, presumably due to low amounts and low quality of litter in plantations. Additionally, very low $^{13}C/^{12}C$ ratios in rubber plantations indicated that certain oribatid mite species in these systems use resources which do not exist in the other systems. However, the identity of those resources used remained unclear as neither the abundance of algae nor of understory plants is higher in rubber plantations than in the other three land-use systems studied (Rembold et al., 2017; Schulz et al., 2019; Susanti et al., 2019). Additionally, it is unlikely that oribatid mite communities use plant compounds depleted in ^{13}C such as lignin (Bowling et al., 2008; Pollierer et al., 2009), as animals in general are unable to digest lignin (Berg and Ryszard, 2005). However, the results in general suggest that oribatid mite communities in rubber plantations are functionally more diverse than in the other three land-use systems studied. The high uniqueness in oil palm plantations, however, suggested that the loss of species in these systems is associated with a loss of function. Additionally trophic chains in oil palm plantations were shorter as in the other three land-use systems. Again, primary decomposer were lacking supporting the conclusion of the study presented in **Chapter 2,** that the quality of litter in the studied ecosystems is poor (Butenschoen et al., 2014; Krashevska et al., 2017; Marian et al., 2017). Additionally, parallel to the results presented in **Chapter 2**, the use of resources of oribatid mite communities changed with changing land-use systems. Changes in the flux of energy trough soil food webs with changes in land-use demonstrate that soil fauna communities are able to respond in a flexible way to changes in the availability of resources (Susanti et al., 2019). The study of Susanti et al. (2019) further indicated that in tropical ecosystems algae play an important role as food resource for Collembola and Oribatida. Similar to the results of Susanti et al. (2019), results of this study indicate that the conversion of rainforest into plantation systems likely is associated with the strengthening of the plant-based energy channel in plantation systems. Moreover, high ^{13}C values in rainforest and jungle rubber indicate that in these systems soil food webs are predominantly based on the microbial energy channel (Potapov et al., 2013, 2019). Further, generalist predators, such as Chilopoda, have been shown to switch from decomposer prey to predominantly herbivore prey in monoculture plantations (Klarner et al., 2017). These shifts predominantly were due to reduced or lacking litter layer in plantation systems (Klarner et al., 2017). In natural ecosystems the thickness of the litter layer generally is higher than in plantation systems (Hyodo et al., 2015). As in the study presented in **Chapter 2**, the trophic niche of communities of oribatid mites differed most between more natural systems, i.e. rainforest and jungle rubber, and monoculture plantations, i.e. rubber and oil palm plantations. ^{13}C and ^{15}N values further indicated that community-level trophic niches of oribatid mites are similar in more natural ecosystems, and markedly different from those in plantation systems. Notably, oribatid mite communities showed similar trends as in the study presented in **Chapter 2**, indicating that the conversion of rainforest into plantation systems is associated with pronounced shifts in the decomposer system and the channeling of energy trough the decomposer food web.

Results of the first two studies indicated that soil-living oribatid mites are able to adapt to changing environmental conditions with changes in land-use contrasting most species of the aboveground system (Teuscher et al., 2015; Darras et al., 2019). The study presented in **Chapter 4** investigated the response of meso- and macrofauna species in ‘tree islands’ with varying diversity level planted native tree species (0, 1, 2, 3 and 6) and plot size (5 x 5, 10 x 10, 20 x 20 and 40 x 40 m^2). Three years after the establishment of the experiment we found little evidence that the enrichment of oil palm plantations in ‘tree islands’ affected the abundance of meso- and macrofauna soil invertebrates. However, the richness of soil invertebrate taxa benefited from ‘tree islands’ of diversity level 2. The results contrast earlier studies reporting that a more pronounced understory in plantation systems beneficially impacts aboveground invertebrates (Chung et al., 2000; Ashton-Butt et al., 2018; Spear et al., 2018; Darras et al., 2019). Additionally, bird diversity and bird abundance were increasing with increasing numbers of planted trees at the experimental site (Teuscher et al., 2015). However, it has been demonstrated that the response of belowground organisms to variations in plant diversity generally are less pronounced than the response of aboveground species (Scherber et al., 2010). Another management strategy beneficially affecting aboveground arthropod diversity is Alley-cropping, i.e. planting trees, grasses and/or shrubs into monoculture crop plantations (Gold and Garrett., 2009; Ashraf et al., 2018). Further, arthropod habitat size may be enhanced by increasing the complexity of vegetation and therefore microhabitat diversity (Lawton, 1983; Jose, 2009), which in turn may benefit arthropod diversity. Increased diversity of crop plants and trees might result in an increase in habitat heterogeneity, soil fertility, water quality as well as carbon and nutrient cycling (Fahrig et al., 2011; Torralba et al., 2016; Ashraf et al., 2018). However, decomposer species of grassland ecosystems have been shown to respond to changes in the diversity of plant communities with a delay of four to six years (Eisenhauer et al., 2011). This might explain why we did not find changes in the abundance of macro- and mesofauna three years after establishment of the ‘Enrichment experiment’. Additionally, physical habitat characteristics, such as pH and soil porosity, have been assumed to more strongly affect soil communities than plant diversity (Ducarme et al., 2004; Nielsen et al., 2010; Bluhm et al., 2019). Again, changes in physical habitat characteristics are slow and might be difficult to detect in short term experiments (Bluhm et al., 2019). Further, the use of herbicides and the associated reduced herb layer in oil palm plantations may affect animal communities (Ismail et al., 2009), even after treatments have has been terminated (Teuscher et al., 2016). However, the enrichment of oil palm plantations with 'tree islands' and the reduced fertilizer and herbicide use likely increased resource availability and habitat diversity. An earlier study at the experimental site demonstrated that aboveground invertebrate species were less affected by 'tree islands' than vertebrate species, such as birds (Teuscher et al., 2016). Presumably, the planted trees and the associated new habitats, and the parallel ceasing of fertilizer and pesticide application exerted positive effects on birds (Tscharntke et al., 2011; Pywell et al., 2012; Teuscher et al., 2016).

Plot size of the 'tree islands' generally did not significantly affect the richness and abundance of soil invertebrate taxa. This is consistent with results of earlier studies demonstrating that species richness and abundance may vary little with island size or connectivity (Brose, 2003; Báldi, 2008; Jonsson et al., 2009). However, in most studies plant diversity and habitat heterogeneity were identified as major drivers of the richness and abundance of species (Báldi, 2008; Jonsson et al., 2009).

The analysis of the community structure showed that taxa associated with diversity level 1 and 2 were mostly decomposers, whereas taxa associated with the other diversity level were mainly predators. It has been shown that the response of belowground animal species to variations in plant species is less pronounced than that of aboveground species (Wardle et al., 2006; Scherber et al., 2010; Eisenhauer et al., 2011). Until now, however, effects of plant species on soil animal species are little understood, but the differential response is likely to be related to different traits of plant species in particular those affecting plant litter quality (Díaz et al., 2004; Wardle, 2006).

Conclusions

Overall, our studies confirmed our hypothesis that at least some oribatid mite species are able to cope with environmental changes in transformed ecosystems by shifting their tropic niches, i.e. by trophic plasticity. Additionally, the community-level trophic niche of oribatid mite changed with changing land-use systems. This, however, contradicted our hypothesis that oribatid mite communities are trophically broader in more natural ecosystems. Especially in rubber plantations oribatid mite communities are functionally diverse and use carbon resources not occurring in the other land use systems studied. The results further indicate that in particular in oil palm plantations the loss of species is associated with a loss of function. Notably, results of the studies presented in **Chapter 2** and **3** indicated that changes in the use of basal resources (indicated by ^{13}C) were more prominent and consistent than those in trophic position (indicated by ^{15}N). This suggests that the transformation of rainforest into plantations changes the resource use of soil invertebrate species but in part also their tropic level. Furthermore, it indicates that colonization of different land-use systems by oribatid mites in part is due to trophic plasticity.

Three years after the enrichment of oil palm plantations with ‘tree islands’ the density and complexity of soil invertebrate communities was little affected. Presumably, this was due to the delayed response of soil invertebrate communities to changes in plant community composition and tree planting. The diversity and abundance of plant communities will likely have stronger effects later in time, but this needs further investigation in particular in tropical ecosystems.

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List of publications

Krause A, **Pachl P, Schulz G, Lehmitz R, Seniczak A, Schaefer I, Scheu S, Maraun M.** 2016. Convergent evolution of aquatic life by sexual and oribatid mites. *Experimental and Applied Acarology* 70: 439-453.

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Thesis declaration

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

The experiment presented in **Chapter 2** and **3** was set up at the first phase of German-Indonesian research project "Ecological and socio-economic functions of tropical lowland rainforest transformation systems" (EFForTS) whereas **Chapter 4** was set up at the second phase of the EFForTS project. Samples of the experiments in **Chapter 2** and **3** were collected, extracted and exported in the first phase by Bernhard Klarner based on the research permits no. 332/SIP/FRP/SM/IX/2012, 389/SIP/FRP/SM/X/2013 and 145/SIP/FRP/SM/V/2013, collection permit no. S.07/KKH-2/2013 and export permit no. 125/KKH-5/TRP/2014 issued by by the State Ministry of Research and Technology of the Republic of Indonesia (RISTEK), by the Indonesian Ministry of Forestry (PHKA) and issued by the Ministry of Forestry of the Republic of Indonesia. Oribatid mite species were identified by Dorothee Sandmann and Svenja Meyer, Kristina Richter, Anneliese Beckendorff and Melissa Jüds. Samples of the experiments in **Chapter 4** were collected, extracted and exported by myself, based on the research permits no. 343/SIP/FRP/E5/Dit.KI/X/2016, collection permit no. S.1006/KKH/SDG/KSA.2/10/2016 and exported on permit no. SK.337/KSDAE/SET/KSA.2/7/2019, issued by the State Ministry of Research and Technology of the Republic of Indonesia (RISTEK), Indonesian Ministry of Forestry (PHKA) and by the Ministry of Forestry of the Republic of Indonesia. Measurements of the stable isotopes were performed by the Kompetenzzentrum Stabile Isotope Göttingen (KOSI).

I am first author of all manuscripts; I have analyzed the data, written the manuscripts, developed the main ideas, and created tables, figures and appendices. All persons contributing to the manuscripts have been named. All co-authors contributed to finalizing the manuscripts.

The cover-photographs were all taken by me or my colleagues and helpers in Indonesia (see acknowledgments) except for the EM pictures of Oribatida used on the cover page for **Chapter 2**, which were taken by Mark Maraun under the supervision of Dorothea Hause-Reitner from the Faculty of Geoscience and Geography, University of Göttingen.

I confirm that the electronical and printed version of this thesis are identical.

Plagiarism declaration

I, Alena Krause, declare that I have written this doctoral thesis independently. All persons contributing to the manuscripts have been named (see above). All sentences or passages quoted from other people's work have been specifically acknowledged by clear cross-referencing.

I have not submitted this thesis in any form for another degree at the university or institution.

Alena Krause

Hamburg, November 2020

Poster and oral presentation

Milbenkundliches Kolloquium in Bozen 07.-09.09.2017

Krause A, Pachl P, Schulz G, Lehmitz R, Seniczak A, Schaefer I, Scheu S, Maraun M. 2016. Convergent evolution of aquatic life by sexual and oribatid mites. *Experimental and Applied Acarology* 70: 439-453. (Talk)

International symposium on socio - ecological transformation of tropical lowland rainforest in Bali 07.-11.10.2018

Krause A, Sandmann D, Bluhm S L, Ermilov S, Widyastuti R, Farikhah Haneda N, Scheu S, Maraun M. 2019. Shift in trophic niches of soil microarthropods with conversion of tropical rainforest into plantations as indicated by stable isotopes (^{15}N, ^{13}C). *PLOS ONE* 14(10): e0224520 (Talk)

GTÖ conference in Edinburgh 08.-15.04.2019

Krause A, Sandmann D, Bluhm S L, Ermilov S, Widyastuti R, Farikhah Haneda N, Scheu S, Maraun M. 2019. Are soil animals able to change their diet in the changing world? – Changes in trophic niches of oribatid mites with rainforest transformation (Poster)