Effects of land-use transformations in Indonesia on trophic positions and basal resources of Blattodea, Hemiptera and Collembola in tropical forest canopies using compound-specific isotope analysis of amino acids

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Abstract

Trophic relationships are difficult to determine, especially in the highly diverse habitats of rainforest canopies with complex food web structures. In the lowland rainforest of Jambi province (Indonesia), which is subject to massive landscape transformation for the benefit of rubber and oil palm plantations, it is crucial to examine the trophic structure of food webs and how they are affected by land-use change. Compound-specific analysis of amino acids (CSIA) is a newly emerging tool for disentangling complex food webs, since δ^{13}C and δ^{15}N values of amino acids can be used to determine trophic positions and basal resources. Amino acids of consumers (Blattodea, Hemiptera and Collembola) from different land-use systems (rainforest, jungle rubber, rubber and oil palm) in Harapan and Bukit National Park in Jambi Province were examined to investigate a possible change in basal resources and trophic positions along an increasing land-use gradient. Stable isotope (^{13}C) fingerprinting was used to detect the origin of carbon found in amino acids of consumers to identify the basal resource; ^{15}N values of trophic an source amino acids were used to determine trophic positions. Blattodea and Hemiptera occupied a higher trophic position and shifted in the use of basal resources from plants to microorganisms along an increasing land-use gradient. This suggests a higher proportion of predation and omnivory in the more managed systems and a substitution of missing plant resources with microorganisms, mainly fungi. Trophic positions and basal resources remained stable for Collembola across all land-use systems indicating that they have access to resources not affected by land-use change, as can be found in suspended soils in canopies. These findings suggest that trophic structures and relationships are influenced by land-use change but that there are also groups with feeding strategies that are not as heavily affected as the results of Collembola imply.

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AAs	amino acids
CSIA	compound-specific isotope analysis
eAAs	essential amino acids
Glu	glutamic acid
PDB	Pee Dee Belemnite
Phe	phenylalanine
sAAs	source amino acids
tAAs	trophic amino acids
$\mathbf{TDF_{Glu\text{-}Phe}}$	trophic discrimination factor between Glu and Phe
TP	trophic position
$\mathbf{\Delta^{15}N_{C\text{-}D}}$	difference of δ^{15}N between consumer and diet

1. Introduction

Tropical rainforests cover only 6% of the earth's surface but harbour half of the 1,4 million species that have been identified so far (Seymour & Busch, 2016). Studies on the biodiversity of these ecosystems claim over 900 different plant species per hectare (Balslev et al., 1998) of which 200 were identified as tree species (Turner, 2001). However, these species-rich ecosystems suffer from immense loss of their forest area (Groombridge, 1992). Especially the non-seasonal lowland rainforest, as found in South East Asia, with its abundance of flora and fauna is the most diverse ecosystem of our planet (Brooks et al., 2006), yet, also the most threatened (Koh et al., 2011; Wilcove et al., 2013).
Logging and deforestation have been an ongoing process in South East Asia since the beginning of the second half of the 20th century, resulting in forest clearances for the benefit of crop monocultures such as rubber and oil palm plantations (Koh & Ghazoul, 2008; Wilcove & Koh, 2010). In Indonesia, the globally dominating exporter of rubber and palm oil, vast areas of rainforest have been transformed into arable systems. This created a land-use gradient intensification from rainforest, over jungle rubber to rubber and oil palm monocultures (Gibbs et al., 2010; Margono et al., 2014).

Rainforest represents "primary degraded forest", which is a primary forest that has been subject to selective logging or other human interference leading to a loss of canopies and therefore structural change within the forest (Margono et al., 2014). In the beginning of the 20th century, large areas of the natural tropical rainforest in Indonesia were converted into jungle rubber agroforest systems in which rubber trees were mixed with natural vegetation (Penot, 2004). In terms of biodiversity research, since the ratio of unaffected secondary vegetation is large enough, these jungle rubber gardens may even be regarded as a type of disturbed or secondary forest vegetation (Penot, 2004).
During the past three decades, however, these jungle rubber gardens have progressively been transformed into more productive rubber monoculture plantations (Feintrenie et al., 2010) in order to satisfy the increasing global demand and to improve the local economic situation (Rist et al., 2010). Introduced by Dutch private estates in the 20th century, nat-

ural rubber is one of Indonesia's most important crops and covers around 3.5 million hectares of land by now (Pye-Smith, 2011). Monoculture rubber plantations are intensively cultivated and host over 99% rubber plants and less than 1% natural vegetation (Pye-Smith, 2011).

As another form of agro-cultivation, oil palm plantations have been established at the expense of rainforest and jungle rubber gardens (Pye-Smith, 2011). The area in which oil palms are cultivated in monocultures was five times higher in 2008 than it had been in 1995 (Pye-Smith, 2011). According to Pye-Smith (2011), an amount of 7.65 million hectares of land is estimated to have already been transformed into oil palm plantations and plans are public to develop a further 7 million hectares. According to Carlson et al. (2013), oil palm plantations will be the dominant type of land-use systems in Sumatra and will furthermore intensify the change affecting biodiversity and the whole ecosystem functioning (Laurance et al., 2014).

This intensification of agriculture engenders a severe loss of species, and therefore a decrease of biodiversity (Barnes et al., 2014; Rembold et al., 2017). Habitats such as canopies, which host 40% of extant species, of which 10% are predicted to be canopy specialists, are highly affected by land-use change in terms of biodiversity (Hammond et al., 1997; Watt et al., 1997). They are considered to exhibit one of the most diverse environments on the planet, especially in terms of the variety of arthropod communities (Lowman et al., 2012; Moran & Southwood, 1982; Southwood et al., 1982). However, due to their challenging accessibility, they still represent one of the least explored natural habitats (Lowman et al., 2012). Housing an estimated amount of 6.8 million arthropod species (Hamilton et al., 2013), canopies hold a large share of the total number of terrestrial arthropods, and hence constitute an appealing study object in the field of animal ecology.

Studies targeting arthropods in canopies of tropical rainforests have mainly focused on diversity (Basset et al., 2012; Dial et al., 2006; Perfecto et al., 1997), guild and community structures (Schowalter & Ganio, 1999; Stork, 1987) and herbivory (Lowman, 1984, 1992; Sterck et al., 1992) so far, but there are only a few attempts (e.g. Blüthgen et al. (2003)) to unravel trophic hierarchies and assemble food web structures of arthropods in canopies. Explaining and predicting food web patterns is crucial for a profound understanding of processes within ecosystems (Pimm, 1982). The rates of these processes, such as energy fluxes caused by biomass transfer throughout food webs, are fundamental proxies for ecosystem functioning (Barnes et al., 2014). Therefore, research on trophic interactions and basal resources in canopies along a gradient of increasing land-use intensity can foster an understanding of how the flux of energy is influenced by land-use change and help provide the necessary means to understand how biodiversity affects ecosystem functioning (Duffy et al., 2007).

Compound-specific analysis of amino acids (AAs) in resources and consumers can be applied as a tool for investigating trophic positions within food webs and for determining basal resources of consumers. Amino acids are a major carrier of organic nitrogen and carbon. About half of the total carbon is incorporated in AAs in most organisms, which makes them the most important conductor of carbon through food chains (Larsen et al., 2013). Furthermore, metabolic processing of carbon and nitrogen proceed differently (Larsen et al., 2013). Thus, amino acids present two chemical elements which can indicate crucial dietary resources and trophic positions (Pollierer et al., 2019).

Ecosystem functioning is interwoven with nutrient and biomass transfer (Barnes et al., 2017) as it can be found in food webs of rainforest canopies. Arthropods, especially due to their high abundance, play an important role within the structures of these food webs. Three major arthropod communities in rainforest canopies are Collembola, Blattodea and Hemiptera. Collembola are one of the major soil-living detritivorous arthropods and have been claimed to be one of the most abundant taxa in rainforest canopies (Basset, 2001; Basset et al., 2003; Greenslade et al., 2016; Stork, 1987). Blattodea, with termites colonising canopy ferns in large scales and cockroaches representing 24% of the biomass of the arthropod biomass in rainforest canopies (Basset, 2001), constitute an important factor in rainforest ecosystem functioning (Bell et al., 2007). Among canopy arthropods, Hemiptera are a highly diverse taxa in terms of physiological traits and trophic aspects, colonising various trophic niches and microhabitats and therefore constitute an interesting study object (Vialatte et al., 2010).

The numeric dominance of arthropod communities in canopies, such as that of Collembola, Hemiptera and Blattodea, and the large extent of canopy defoliation has led to the assumption that their nutritious intake is mainly based on herbivory and that they represent a large variety of primary consumers (Lowman, 1984). However, recent studies on food web structures and trophic positions suggest that detritivorous consumers are of major importance for terrestrial (mainly soil) (Hyodo et al., 2015; Steffan et al., 2015) as well as aquatic (Newsome et al., 2011) food webs. Further, their findings implicate a considerable influence of microorganisms on trophic interactions in other habitats, such as rainforest canopies. This leads to the assumption that microbiota potentially function as a major resource for many animals, including canopy-living Blattodea, Hemiptera and Collembola. According to Steffan et al. (2015), microbes are the dominant consumers in most ecosystems, requisitioning a large amount of the heterotrophic biomass circulating through food webs and distributing their trophic patterns throughout the food web.

The aim of this thesis is to use compound-specific isotope analysis (CSIA) in order to unravel trophic positions and basal resources of Blattodea, Hemiptera and Collembola from Jambi's low-land rainforest canopies. Further, it will be tested whether the trophic position and the basal resource of the studied organisms differ between different agricultural land-use types. Arising thereby, the following hypotheses will be tested:

> (1) Besides plants, microorganisms (fungi, bacteria and algae) are part of the diet of the three study organisms. This assumption is based on findings from Hyodo et al. (2015) and Lodge et al. (1996) showing in independent studies the nutritious and digestive contribution of microorganisms to consumers' and predators' diets.
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> (2) Further, basal resources will shift along an intensification of the land-use gradient. Presumably, plants will contribute larger shares to the basal resources of the three arthropod communities in more natural habitats such as rainforest and jungle rubber, whereas the contribution of microbiota as basal resource will increase in the less natural habitats, oil palm and rubber monoculture. This conjecture is based on a decrease in plant diversity along an increasing land-use

gradient intensification and diversity studies that state considerable adaption skills of microorganisms concerning environmental changes (Lodge et al., 1996). Accordingly, it can be assumed that consumers substitute a considerable share of their plant diet for a microbial diet.

(3) Considering the trophic position (TP) of the three studied organisms, an elevation of TP in the more intensely cultivated land-use systems for all of the study organisms can be assumed. This assumption is based on the fact that a decrease in plant diversity along the land-use intensification gradient can be observed which can lead to a substitution of the dietary plant intake. Substituting primary producers, which hold a TP of 1, with decomposing microorganisms or other consumers, that hold a TP higher than 1, will lead to an elevation of the TP of the study organisms.

2. Materials and Methods

2.1 Study site

This master thesis is embedded in the profound research of the interdisciplinary Ecological and Socio-economic Functions of Tropical Rainforest Transformation Systems (EFForTS)-project which takes place in Jambi Province, Indonesia, and will transition into the third phase at the turn of the year (Collaborative Research Center 990 Universität Göttingen, 2016). The so called Collaborative Research Centre 990 is funded by the DFG (German Research Foundation) and examines the socio-economic and ecological changes that come with the current agricultural transformation process in Jambi Province (Drescher et al., 2016) (https://www.uni-goettingen.de/de/310995.html). Its three research foci can be summed up as follows: (i) environmental processes, (ii) biota and ecosystem services, and (iii) human dimension (Drescher et al., 2016). To obtain a better understanding of the codependent effects of the transformation of the land-use systems concerning human well-being, ecosystem functions and biodiversity, the EFForTS-project maintains long-term research projects which cover a wide range of fields (Drescher et al., 2016). The study relevant to this thesis was located in the tropical lowlands of Jambi Province, central Sumatra, Indonesia, in two separate areas, the "Bukit Duabelas National Park" and the "Harapan Rainforest"(Fig. 1).

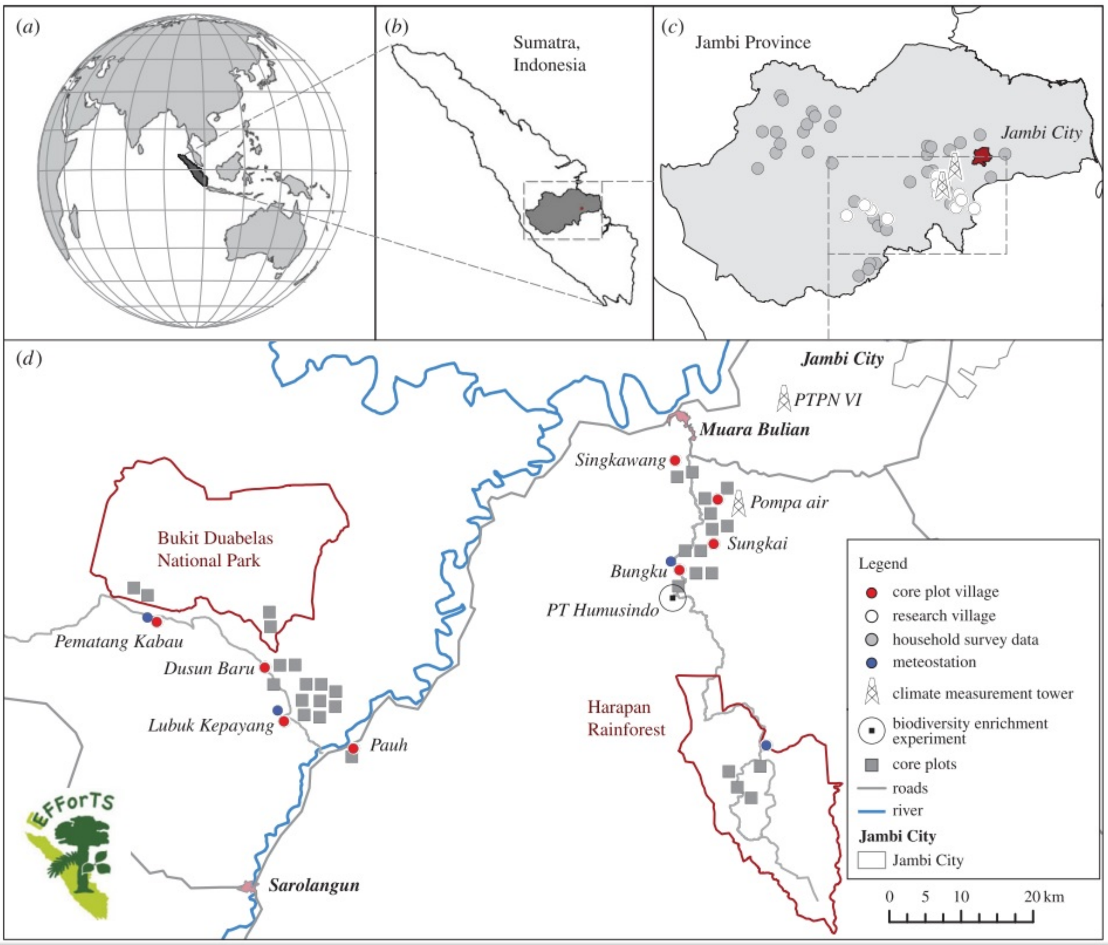


Figure 1: Location of EFForTS study sites in Sumatra (a,b) and Jambi Province (c,d). Socio-economic surveys are carried out all over Jambi Province (c), while the core plot design is located in two landscapes close to Bukit Duabelas National Park and Harapan Rainforest (d). (Drescher et al., 2016).

Jambi province has access to the eastern coast of central Sumatra and covers a land area of 50.160km^2. It stretches from the western Barisan mountain range to the southern Malacca Strait in the east. The climate in Jambi's lowlands can be described as tropical humid, with two rainy seasons peaking in March and December and a dry season during July and August.

The data for environmental processes and biota and ecosystem services presented here were collected in the 'core plot design' by teams of students and local assistants under the supervision of J. Drescher (Dept. Animal Ecology, University of Göttingen). For the core plot design, research core plots were established in the four land-use systems presented earlier: lowland rainforest, jungle rubber, rubber monoculture and oil palm monoculture in Bukit and Harapan (Fig. 1). Sample labels are composed of the studied landscape, Bukit (B) or Harapan (H), followed by the land-use system, lowland rainforest (F), jungle rubber (J), rubber monoculture (R) or oil palm monoculture (O), and finally the core plot number (e.g. BO3 = Bukit Duabelas landscape, oil palm monoculture, core plot 3).

Four core plots were set up in each of the four land-use systems in both of the two landscapes, as described in Drescher et al. (2016), resulting in a total of 32 plots. Each core plot measures 50m x 50m containing three collection areas. At each location, plots with a vegetation structure and species composition typical for each individual land-use system were selected, identifying three specific locations per core plot in which the canopy appeared most dense disregarding the species of the trees. Exact coordinates of each plot are presented in Tabl. 2.

All rubber and oil palm core plots have been established in smallholder monoculture plantations, which varied in age between 7 and 16 years for rubber and between 8 and 15 years for oil palm at the time of plot selection. Each core plot is equipped with a meteorological station which measures air temperature, relative air humidity, soil temperature and soil moisture. All core plots were established on Acrisol soils. While soils in the Harapan landscape contain more even fractions of sand, silt and clay (loam Acrisols), soils in the Bukit Duabelas landscape are clay Acrisols, characterized by higher proportions of clay.

2.2 Sampling

The studied Hemiptera, Collembola and Blattodea were collected during rainy season 2013/2014 as part of a large-scale canopy arthropod sampling campaign as described in Drescher et al. (2016) and J. Drescher (unpublished data). Target canopies (or ’sub-plots’) were chosen based on a preferably high canopy density. Twelve square 1m x 1m collection funnels, each fitted with 250ml wide neck PE-flasks filled with ca. 100ml 96% EtOH, were placed underneath each selected ‘target canopy’.

The selection of ‘target canopies’ and the arrangement of collection funnels differed between the four land-use types: In rainforest core plots, all three target canopies per core plot contained branches and leaves from a random arrangement of unknown trees and epiphytes. In jungle rubber core plots, the three target canopies were chosen to approximately represent the assumed leaf area ratio of rubber trees to unknown tree species. In rubber plantations, the densest canopies were usually between trees on the same row. Consequently, the collection funnels were placed in a roughly rectangular arrangement of two by six funnels between the two trees. In oil palm plantations, maximum leaf area was highest around individual oil palms. Hence, the collection funnels were placed in two rough circles of four and eight funnels, respectively, around the trunk of the palm tree.

The arthropod samples were collected by canopy fogging, a method based on the application of insecticide to tree canopies and subsequently catching the stunned or dead arthropods in traps, tarps or funnels as described by J. Drescher (unpublished data). A Swingfog® SN50 fogger (Swingtec GmbH, Germany) was used to apply a mixture of 50ml DECIS 25 EC® (Bayer Crop Science, active ingredient Deltamethrine, conc. = 25 g/L) dissolved in four liters of petroleum 'white' oil to three target canopies per research plot. Fogging was performed exclusively in the morning since wind currents between the trees tend to increase throughout the day, bearing away the fog and making sampling inaccurate (J. Drescher, pers. comm.). Stunned or dead arthropods were allowed to drop for two hours until the EtOH-containers holding the samples were disconnected from the funnel constructions and stored until further selection and determination.

2.3 Study organisms

Collembola represent one of the major decomposing, soil-living group of insects, however, they can also be found in canopies populating moss, leaf axes, leaf litter suspended in epiphytes or the underside of bark (Dettner & Peters, 2011; Rodgers & Kitching, 2011). They are highly involved in decomposition processes and in the distribution of microorganisms (Dettner & Peters, 2011). Their diet includes fungi, pollen, detritus and microbially decomposed plant components and they have been described as an indicator group for changes in soil quality (Dettner & Peters, 2011); they might potentially show indicator patterns of land-use change.

Blattodea are a highly diverse group representing all termite and cockroach families. Cockraoches are known to be omnivores (Bell et al., 2007), but there are also species that can be described as nutritious specialists only feeding on plants (*Aptera fusca*) or fruit (*Blaptica dubia*) (Bell et al., 2007). Primarily, Blattodea are scavengers, preferring dead organic matter of both, plants and animals, over living organisms. However, cannibalism has also been observed (Bell et al., 2007) and a variety of endosymbiotic gut microbes were found to support the degradation of wood (Nalepa, 1984). Termites are detritivores, preferring dead plant or animal matter (Bignell & Eggleton, 2000) and are considered important for recycling dead matter, even wood, and animal faeces (Freymann et al., 2008). Like cockroaches, they rely on symbiotic microbial breakdown of plant matter such as cellulose so that they can use the nutrients (Ikeda-ohtsubo & Brune, 2009).

Hemiptera are an order of insects comprising several groups such as cicadas, plant- and leafhoppers, aphids and shield bugs. They all share a common type of mouthpart, a piercing or sucking proboscis protruding from the front of the head and all groups, except for Heteroptera, feed exclusively on plant sap (Schuh & Slater, 1995). Among Heteroptera, there are species which are exclusively predatory, sucking blood of vertebrates or lymphatic fluid of other insects, but also species which are strictly herbivorous (Dettner & Peters, 2011).

2.4 Compound-specific isotope analysis

Recently, CSIA, targeting ^{13}C and ^{15}N in AAs, has brought progress to the field of food web ecology (Larsen et al., 2013; Steffan et al., 2013) and is an emerging tool for unraveling food web structures. Compound-specific analysis of AAs provides the means to determine the trophic positions of the studied arthropod samples and reveal their basal resources. The contribution of the analysis of amino acids to trophic ecology is based on the fact that the chemical behaviour of two isotopes is qualitatively similar, yet, the physical behaviour is quantitatively different due to their difference in bond strengths (Hoefs, 2009). This results in a process called “kinetic isotope fractionation”, meaning lighter isotopes such as ^{12}C and ^{14}N show a higher rate constant than heavier isotopes such as ^{13}C and ^{15}N. (Hoefs, 2009). The isotopes ^{12}C and ^{14}N are usually enriched in the product relative to the substrate during processes such as photosythesis and various bacterial processes (Hoefs, 2009).

Generally, isotopic ratios are referred to by their δ expression and stated in parts per mil (‰). Once used as the C standard, the limestone Pee Dee Belemnite (PDB) was substituted by other carbonates, yet, remains eponym to the widely used ratio scale. Atmospheric N_2 is used as the standard for N stable isotopes. Data of stable isotopes will be based on calculations referring to the following equation presented by Coplen (2011):

$$\delta = \frac{R_{Sample}}{R_{Standard}} - 1 \tag{1}$$

with R constituting the ratio of ^{15}N/^{14}N and ^{13}C/^{12}C, respectively. Positive δ values express a higher isotopic value of the sample compared to the standard or a lower value in case of a negative δ value.

2.4.1 Trophic calculations

Compound specific analysis has been used in the context of two distinct isotope-based methods through which it is possible to (i) identify the basal food resource of an organism and (ii) determine its specific trophic position within a food web. The so called "stable isotope fingerprinting" (Larsen et al., 2013) which functions based on the division of AAs in essential amino acids (eAAs) and non-essential amino acids (neAAs) makes use of distinct δ^{13}C of AAs. In contrast to neAAs, eAAs can only be synthesised by bacteria, plants and fungi and not by higher organisms, therefore they have to be ingested through dietary input. The metabolic diversity among prokaryotes, fungi and plants generates distinct patterns of δ^{13}C of eAAs that can be used to determine the origin of AAs (Larsen et al., 2013). Based on the fact that these patterns are transferred from one species to the other with little or no trophic discrimination, it is possible to use CSIA of AAs to track nutrition movements along food hierarchies and within complex food web structures and to trace carbon flow pathways in terrestrial and marine food webs (Larsen et al., 2013; Pollierer et al., 2019).

The ^{15}N signatures of AAs are enriched at different rates, meaning the enrichment factor per trophic level varies amongst AAs, being significantly high with some, while proving low with others (McClelland et al., 2003). This supports the process of trophic position determination. Since the ^{15}N signature of those amino acids that enrich little throughout the trophic hierarchy is similar to that of the basal food resource, they are called source amino acids (sAAs). Amino acids enriching significantly throughout the trophic hierarchy, have been termed trophic amino acids (tAAs) (Steffan et al., 2013). Trophic amino acids, such as glutamic acid (Glu), hold nitrogen bonds which usually experience cleavage during trophic passing ($\sim$ 6 – 8 ‰), providing potential for isotopic distinction. Therefore, they exhibit higher ^{15}N-enrichment during trophic transfer (Chikaraishi et al., 2007; Ohkouchi et al., 2017). Conversely, sAAs, such as phenylalanine (Phe), exhibit little trophic enrichment due to their resistance to nitrogen-carbon bonding or cleaving (<0.5 ‰) (Chikaraishi et al., 2007; Ohkouchi et al., 2017).

Accordingly, conducting CSIA of AAs allows to gather information concerning basal food resources as well as to determine a specific position within a trophically ranked food web. The latter can be determined by, first, calculating the difference in δ_{15}N between consumer and diet ($\delta^{15}\text{N}_{\text{consumer}}$ - $\delta^{15}\text{N}_{\text{diet mean}}$). A trophic discrimination factor between Glu and Phe ($\text{TDF}_{\text{Glu-Phe}}$) is calculated next, constituting the difference between the ^{15}N enrichment of Glu and Phe from diet to consumer (Chikaraishi et al., 2010, 2011):

$$TDF_{\text{Glu-Phe}} = (\Delta^{15}N_{\text{C-D}})_{\text{Glu}} - (\Delta^{15}N_{\text{C-D}})_{\text{Phe}} \tag{2}$$

According to Post (2002), the $\text{TDF}_{\text{Glu-Phe}}$ can be assumed to be constant and widely applicable. A mean $\text{TDF}_{\text{Glu-Phe}}$ of 7.6 ± 1.2 ‰ (Chikaraishi et al., 2009, 2010) has been established in order to detect a variety of trophic positions and hence, disentangle food web structures in terrestial systems. To calculate a TP the following equation is used:

$$TP_{Glu-Phe} = \frac{\delta^{15}N_{Glu} - \delta^{15}N_{\text{Phe}} - \beta}{TDF_{\text{Glu-Phe}}} + 1 \tag{3}$$

with β representing the isotopic difference between glutamic acid and phenylalanine in the primary producers. Providing various dietary information, stable isotopes of AAs allow to investigate and unravel complex interactions, such as trophic omnivory, and additionally, to trace mass flow through ecological guilds and communities (Kling et al., 1992; Cabana & Rasmussen, 1996).

2.5 Analysis of amino acids

2.5.1 Extraction and derivatisation of amino acids

For CSIA, samples were transferred to Pyrex culture tubes and flushed with N_2 gas, sealed and hydrolyzed in 6 mol/L HCl at 110°C in a heating block for 20h as described in Larsen et al. (2013). After hydrolysis, lipophilic compounds were removed by adding n-hexane/DCM to the Pyrex tubes.Then they were briefly flushed with N2 gas and sealed before vortexing for 30s. The aqueous phase was then filtered through a Pasteur pipette lined with glass wool. Glas wool Pasteur pipettes had been pre-treated at 450°C for four hours for sterilisation purposes. All samples were transferred into 4-mL vials where they were evaporated until dry, while flushing them with N2 gas at 110°C in a heating block for 30min. The samples were then stored at -18°C. To volatize the AAs, I followed the derivatisation procedure of Corr et al. (2007), methylating the dried samples with acidified methanol and subsequently acetylating them with a mixture of acetic anhydride, trimethylamine, and acetone (NACME: N-acetyl methyl ester derivatives). Reaction vials were flushed and sealed with N2 gas to reduce oxidation of AAs during derivatisation, before methylation and acetylation reactions. Pure AAs with known $\delta^{13}C$ and $\delta^{15}N$ values were also derivatised and analyzed to capture carbon that has been added during derivatisation and to detect variability of isotope fractioning during analysis. Nor-leucine was used as internal reference. The N isotopic composition of AAs in samples was expressed relative to atmospheric N by normalizing measured values (vs. reference gas) using scales derived from known $\delta^{15}N$ values of the reference mixture. The C isotopic composition was expressed relative to Vienna Pee Dee Belemnite.

2.5.2 Compound-specific measurements of amino acids

As described in Pollierer et al. (2019), AA derivatives were injected into a Thermo Finnigan Trace GC coupled via a GP interface to a Delta Plus mass spectrometer (Finnigan, Bremen, Germany), located at the Centre for Stable Isotope Research and Analysis, Göttingen, Germany. The GC was equipped with an Agilent J&W VF-35 ms GC column (30 m x 9 0.32 mm x 9 1.00 μm). The heating program started with 80°C held for 1 min, then successively increased by 20°C per minute to 135°C, then by 5°C per minute to 160°C and held for 3 min, then increased again by 8°C per minute to 300°C and held for 3 min. The injection temperature was 280°C and helium was used as carrier gas. The flow rate of helium was 2 mL/min. All samples were analysed in triplicate.

2.6 Statistical analysis

Before analysing the data statistically, it was extracted from chromatograms using Isodat 3.0 (Thermo Fisher Scientific Inc.). Statistical analyses (LDA, ANOVA) were performed using the interface RStudio version 1.2.5019 (RStudio, Inc.) of R (version 3.6.1, R Core Team, 2017). For δ^{13}C fingerprinting, only AAs essential for arthropods (Brodbeck & Strong, 1987) were used: isoleucine (Ile), leucine (Leu), lysine (Lys), methionine (Met), phenylalanine (Phe), threonine (Thr), tryptophan (Try), valine (Val), arginine (Arg), histidine (His). Lys, Trp, His and Arg were excluded due to low peak heights and their insignificance concerning the origin of carbon sources.

Basal resources of the study organisms were determined, predicting biosynthetic origins of eAAs in consumers using a linear discriminant function analysis (LDA, R package MASS; Venables and Ripley 2002). Fungi, bacteria, algae and plants were selected as classifier groups (training data) to determine the basal resources. An LDA was performed using the following AAs: Phe, Leu, Met, Ile, Val and Thr. Their δ_{13}C values proved most significant for tracing original carbon sources of taxonomic groups (Pollierer et al., 2019) and their peak heights were above detection level. Consumer data was added and assigned to a classifier group according to their δ_{13}C values in the eAAs mentioned above.

δ_{15}N values were adjusted by applying measured δ_{15}N values against known values of AAs of standard mixtures. TP was calculated using Eq. (3) with specific β values for each land-use system from both, Bukit and Harapan National Park. β-values were calculated subtracting $\delta_{15}\mathrm{N}_{\mathrm{Phe}}$ from $\delta_{15}\mathrm{N}_{\mathrm{Glu}}$. Using the calculated TP, a multifactorial ANOVA was performed in order to detect interaction effects between the factors *type* (leaves, Blattodea, Hemiptera, Collembola), *area* (Bukit or Harapan) and *management* (rainforest, jungle rubber, rubber monoculture, oil palm monoculture). In addition, a

Tukey HSD test was performed to identify groups with mean values that are significantly different from each other. Glu and Phe were plotted against each other to visualise trophic clustering of leaves and the arthropod communities and to examine enrichment or depletion of Glu and Phe along trophic chains (Fig. 3 and 4). Isoclines were added using Eq. (3) to illustrate trophic levels in the graph.

3. Results

3.1 Trophic positions based on ^{15}N analysis of amino acids

TP of Blattodea, Hemiptera and Collembola differed significantly. Blattodea had a mean TP of 2.3 ± 0.5, Hemiptera around a mean TP of 2.4 ± 0.3 and Collembola around a mean TP of 2.7 ± 0.4) (ANOVA, $F_{2,83} = 6.275$, $p < 0.0029$). Further, TP of the three consumer groups (Blattodea, Hemiptera and Collembola) differed significantly between land-use types (rainforest, jungle rubber, rubber, oil palm) (ANOVA, *land-use type* × *area*, $F_{3,63} = 3.758, p = 0.015$) (Fig. 2). Mean TP of Blattodea from Bukit ranged from 1.7 (rainforest) to 2.5 (oil palm), whereas TP of Blattodea ranged from 2.0 (rainforest) to 2.6 (jungle rubber) in Harapan (Tabl. 1). This pattern of range was also true for Hemiptera but not for Collembola. For Collembola, the difference in TP between the land-use systems was bigger in Harapan than in Bukit. Mean TP of Blattodea and Hemiptera gradually increased with intensifying land-use, being lowest in rainforest (Bla = 2,3; Hem = 2,4) and highest in oil palm (Bla = 2,6; Hem = 2,5). Mean TP of Collembola was relatively stable across land-use systems with a slight decrease in oil palm.

Table 1: Mean TP of consumers (Blattodea, Collembola and Hemiptera) in land-use types (rainforest, jungle rubber, rubber, oil palm) in the areas Bukit and Harapan, as calculated using Eq. (3) with the standard TDF of 7.6 ± 0.1 ‰ (Chikaraishi et al., 2014).

Type	Area	Land-use type	TP	SD
Blattodea	Bukit	rainforest	1,9	0,4
		jungle rubber	2,5	0,3
		rubber	1,7	0,3
		oil palm	2,7	0,1
	Harapan	rainforest	2,6	0,2
		jungle rubber	2,6	0,3
		rubber	2,0	0,6
		oil palm	2,4	0,2
Collembola	Bukit	rainforest	2,5	0,0
		jungle rubber	2,6	0,3
		rubber	2,6	0,2
		oil palm	2,6	0,1
	Harapan	rainforest	2,9	0,2
		jungle rubber	2,8	0,1
		rubber	2,5	1,2
		oil palm		
Hemiptera	Bukit	rainforest	2,2	0,3
		jungle rubber	2,5	0,1
		rubber	2,0	0,1
		oil palm	2,6	0,3
	Harapan	rainforest	2,5	0,3
		jungle rubber	2,4	0,1
		rubber	2,4	0,2
		oil palm	2,4	0,2
Leaves	Bukit	rainforest	1,0	0,0
		jungle rubber	1,0	0,2
		rubber	1,0	0,1
		oil palm	1,0	0,2
	Harapan	rainforest	1,0	0,1
		jungle rubber	1,0	0,2
		rubber	1,0	0,5
		oil palm	1,0	0,1

TP of the consumers differed significantly, with differences depending on land-use type (ANOVA, *group* × *land-use type*, $F_{6.63} = 2.376, p = 0.039$). Collembola in rainforest and jungle rubber had a significantly higher TP than Blattodea from rainforest, whereas TP of Blattodea from all other land-use systems did not differ significantly from that of Collembola or Hemiptera (Fig. 2). Blattodea, Collembola and Hemiptera did not differ significantly between land-use types within their own group (ANOVA; Tukey HSD, p = 0.015).

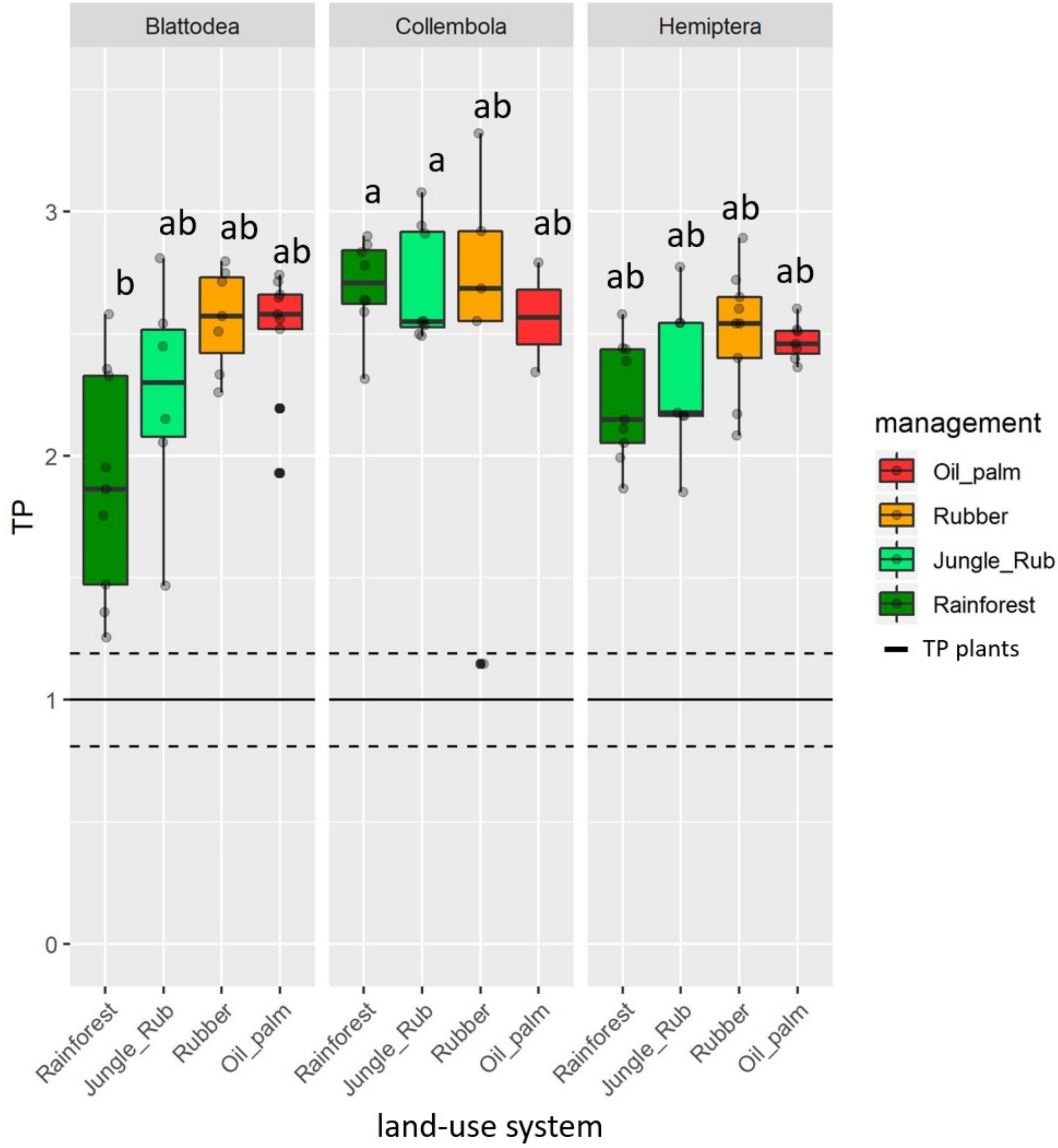


Figure 2: Trophic positions of Blattodea, Hemiptera and Collembola from Harapan and Bukit in four different land-use systems (rainforest, jungle rubber, rubber and oil palm, n = 4 core-plots per system). Boxes indicate second and third quartile, whiskers the upper and lower quartile, bold vertical line shows median, grey dots represent sample positions. Letters a and b indicate significant differences between land-use systems (ANOVA results/Tukey's all pairwise comparison of means, p = 0.015).

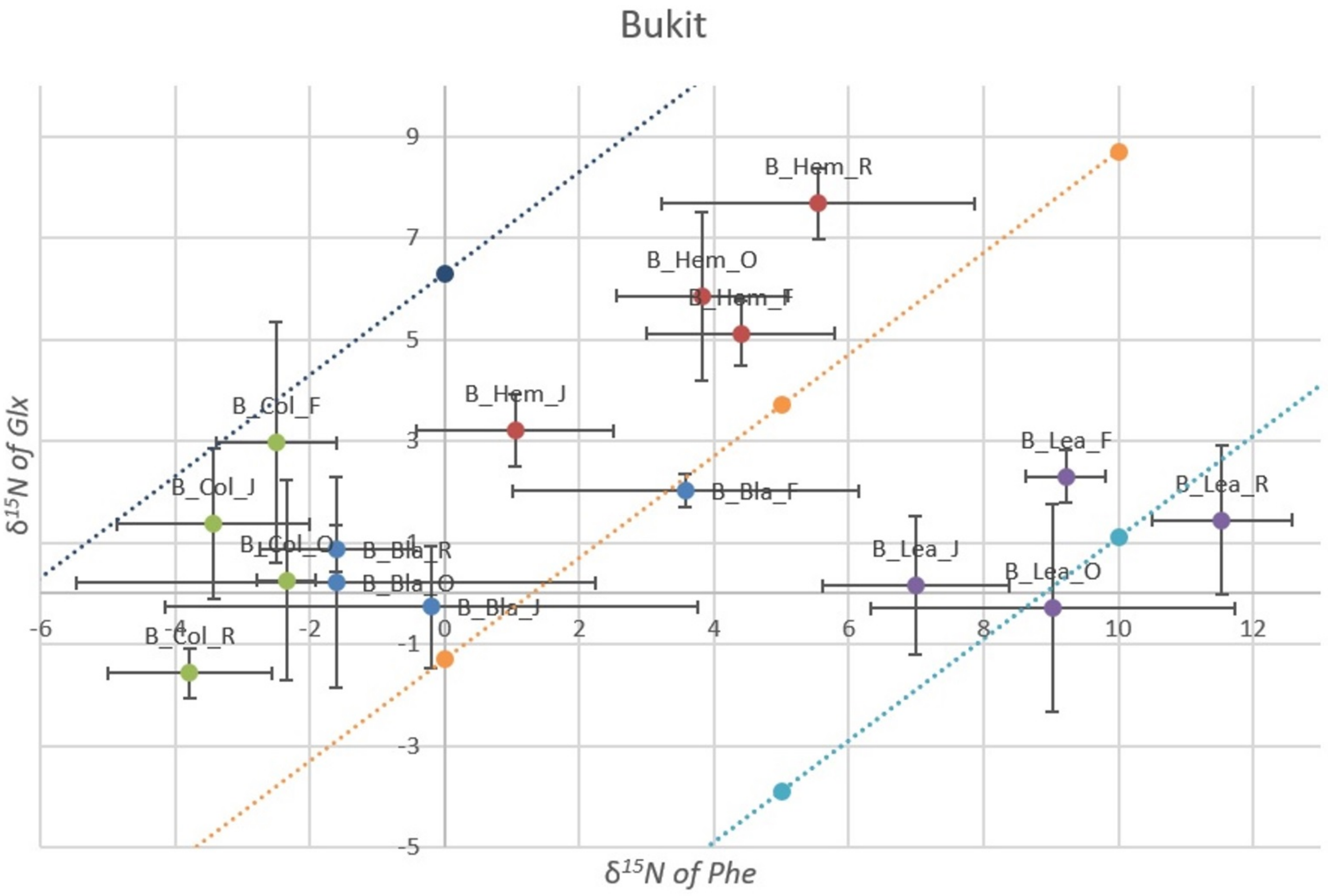


Figure 3: Crossplot of $\delta^{15}N_{Glu}$ against $\delta^{15}N_{Phe}$ for trophic positions of leaves (purple dots), Blattodea (light blue dots), Hemiptera (red dots) and Collembola (green dots) in Bukit Duabelas. N-enrichment and -depletion of Glu and Phe for consumers (Blattodea, Collembola, Hemiptera) in comparison to the resource (leaves) is visualised. Isoclines for trophic positions 1-3 were inserted using Eq. (3).

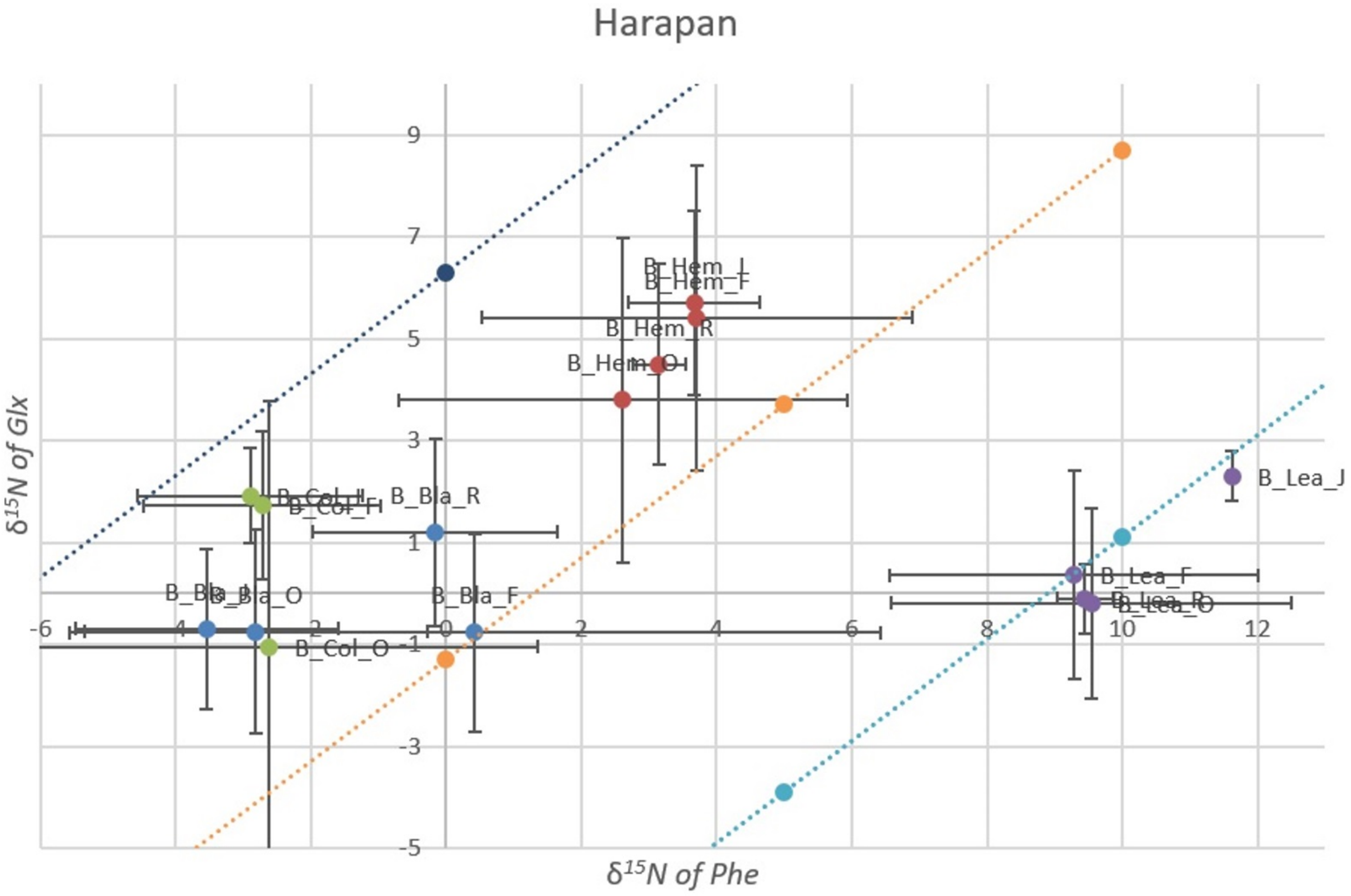


Figure 4: Crossplot of $\delta^{15}N_{Glu}$ against $\delta^{15}N_{Phe}$ for trophic positions of leaves (purple dots), Blattodea (light blue dots), Hemiptera (red dots) and Collembola (green dots) in Harapan. N-enrichment and -depletion of Glu and Phe for consumers (Blattodea, Collembola, Hemiptera) in comparison to the resource (leaves) is visualised. Isoclines for trophic positions 1-3 were inserted using Eq. (3).

Visualising a $\delta^{15}N_{Glu}$-$\delta^{15}N_{Phe}$ dependency, allowed to reveal and reconstruct trophic chains leading from the basal resource (leaves) to consumers (Blattodea, Hemiptera and Collembola) (Fig. 3 and 4).

All consumers were depleted in Phe, with the highest depletion in Collembola, followed by Blattodea and Hemiptera for samples from Bukit. In Harapan, Blattodea were most depleted in Phe, followed by Collembola and Hemiptera. Blattodea were only slightly enriched in ^{15}N of Glu, with $\delta^{15}N_{Glu}$ of samples > -1 and < 2.2. Collembola with a TP < 2.5 were also not enriched in $\delta^{15}N_{Glu}$, or even depleted compared to $\delta^{15}N_{Glu}$ of leaves, whereas Collembola with a TP > 2.5 had ^{15}N values of Glu between 2 and 4, demonstrating enrichment in ^{15}N of Glu compared to leaves. Hemiptera were most enriched in ^{15}N values of Glu, with values between 3 and 8%. Hemiptera, Collembola and leaves from Harapan clustered close together in contrast to samples from Bukit.

3.2 ^{13}C stable isotope fingerprinting

Running an LDA with training and consumer data, biosynthetic origins of Blattodea, Hemiptera and Collembola were predicted. Phe (0.36) and Val (0.27) constituted the highest absolute coefficients for LD1 and Leu (0.28) and Phe (0.22) the highest absolute coefficients for LD2. Group means, further coefficients and the proportion of trace are listed in Fig. 8 (appendix). False classifications occurred when applying LDA to the training data itself, classifying bacteria, fungi or plants in the wrong group. Out of 230 samples, six were classified in the wrong group, resulting in a classification accuracy of 0.974. Out of three observations that belong to the class algae, two were classified as fungi and one as plants. Furthermore, three observations belonging to the class fungi were falsely predicted with two observations classified as algae and one as bacteria.

3.2.1 Blattodea

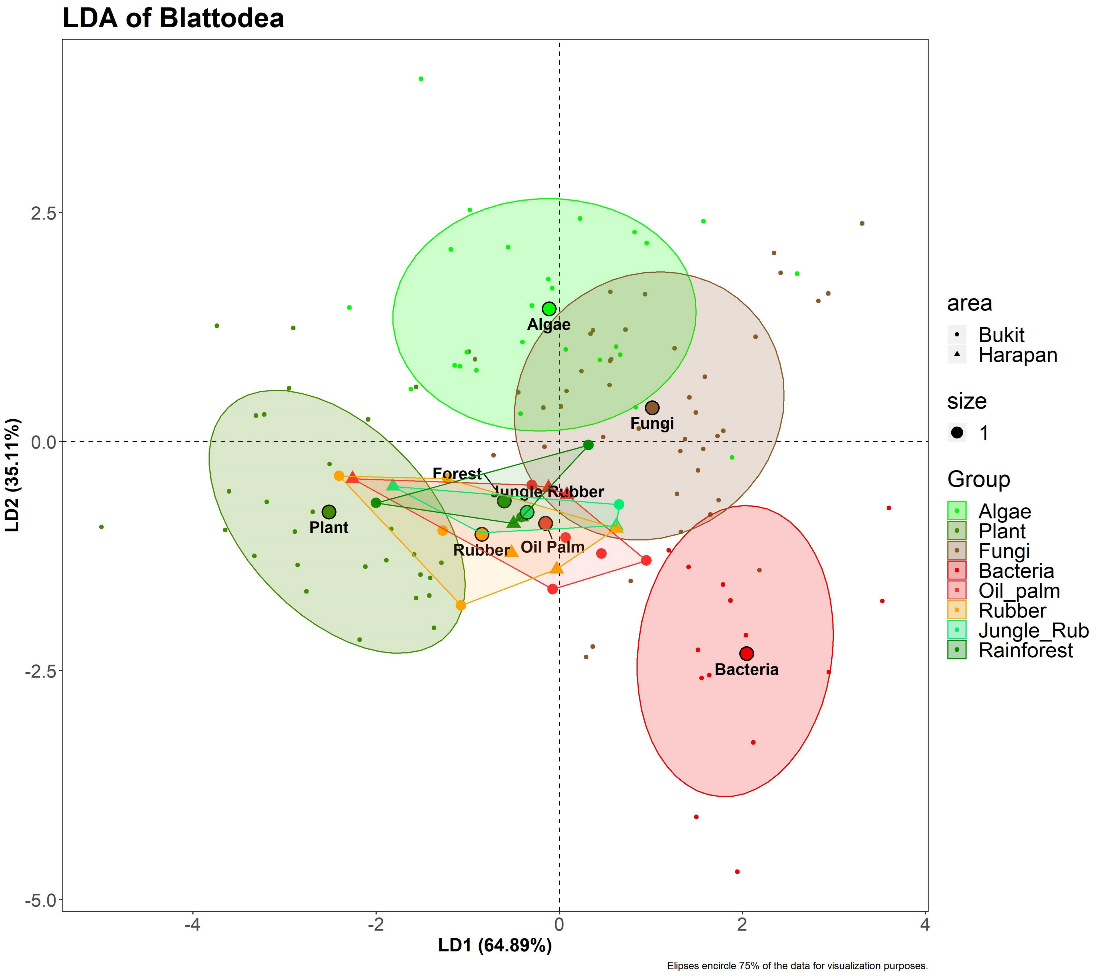
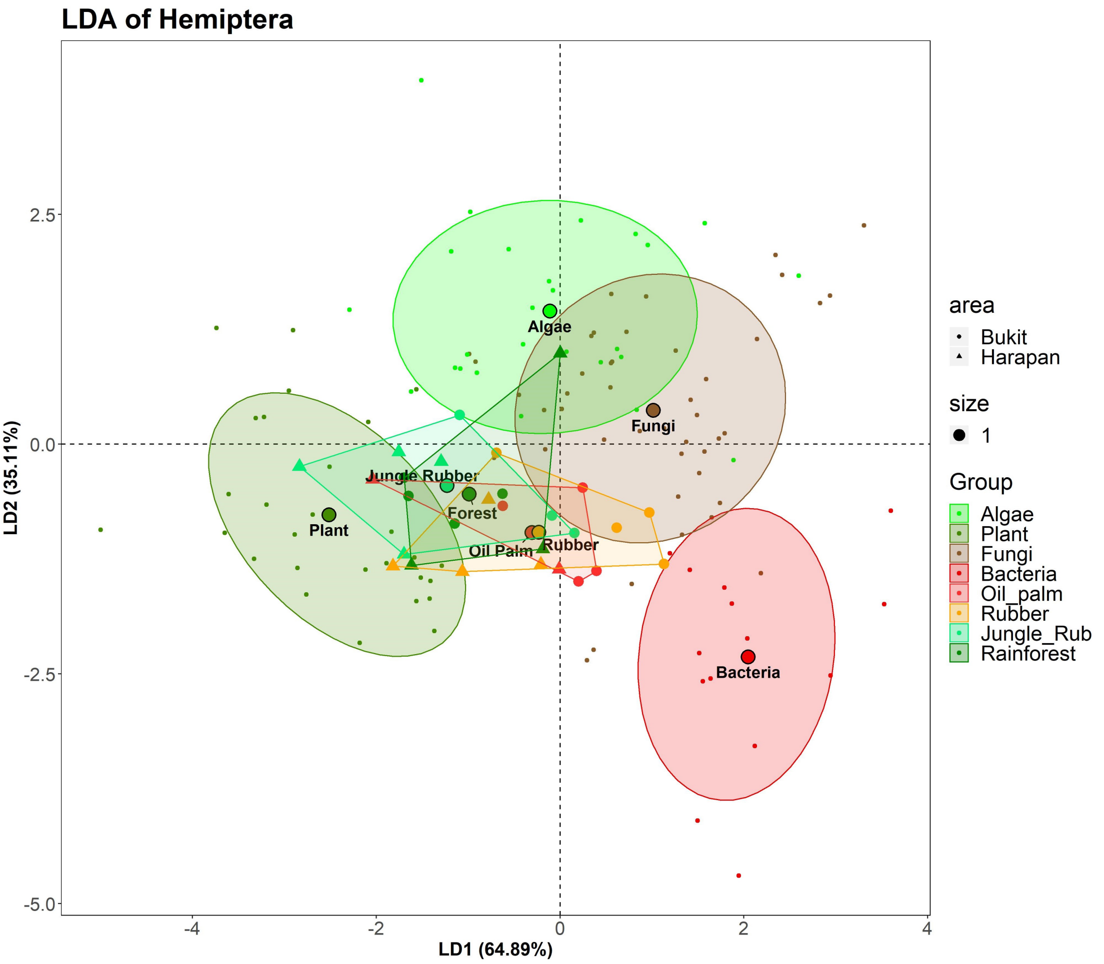


Figure 5: Linear discriminant analysis (LDA) with δ^{13}C values of amino acids of Blattodea collected from rainforest, jungle-rubber, rubber plantations and oil-palm plantations in Bukit Duabelas National Park and Harapan Rainforest. Classifiers (plants, bacteria, algae and fungi) were grouped according to specific δ^{13}C patterns. Hulls around the classifiers constitute 75% of the data for visualisation purposes.

In the LDA, Blattodea of oil palm plantations all positioned close to fungi, except one sample from Harapan, which was classified as having plants as their basal resource (Fig. 5). The centroid of Blattodea from oil palm plantations positioned close to the fungal cluster. Most Blattodea samples from Harapan rubber plantations positioned between fungi and plants, however, due to closer vicinity to fungi they were classified as having fungi as their basal resource. Blattodea from Bukit rubber plantations all positioned within the confidence interval of plants. The centroid of Blattodea from rubber plantations positioned between the fungal and the plant cluster. Blattodea from

Bukit jungle rubber positioned one sample each in plants and fungi. Those from Harapan jungle rubber also positioned one sample each in plants and fungi. The centroid of Blattodea from jungle rubber clustered close to fungi. Blattodea samples from Bukit rainforest positioned in and between fungi and plants which led to a classification of one sample having plants and two samples having fungi as their basal recourse. Blattodea from Harapan rainforest positioned between fungi and plants and were all classified as having fungi as their basal recourse. The centroid of Blattodea from the rainforest fell between the plant and the fungi cluster with a slight drive towards fungi.

3.2.2 Hemiptera



Elipses encircle 75% of the data for visualization purposes.

Figure 6: Linear discriminant analysis (LDA) with δ^{13}C values of amino acids of Hemiptera collected from rainforest, jungle-rubber, rubber plantations and oil-palm plantations in Bukit Duabelas National Park and Harapan Rainforest. Classifiers (plants, bacteria, algae and fungi) were grouped according to specific δ^{13}C patterns. Hulls around the classifiers constitute 75% of the data for visualisation puposes.

Positions of samples of Hemiptera varied and were highly dispersed throughout all management types (Fig. 6). Hemiptera from Bukit oil palm plantations positioned close to or within the fungi and the bacteria cluster and were all classified as having fungi as their basal resource. Hemiptera from Harapan oil palm plantations positioned close to plants and fungi at equal shares and were classified accordingly. The centroid of Hemiptera from oil palm plantations fell close to the fungi cluster. Positions of Hemiptera from Bukit rubber plantations varied from being close to fungi, algae and bacteria; however, all were classified as having fungi as their basal resource.

Hemiptera samples from Harapan rubber plantations showed a shift towards plants and and three out of four samples were classified accordingly. However, 34HR2Hem was classified as having fungi as their basal resource. Whereas Hemiptera from jungle rubber in Bukit positioned close to fungi and algae, samples from Harapan positioned close to plants. Two out of three Hemiptera samples from Bukit jungle rubber were classified as having fungi and one as having plants as their basal resource. All of the Hemiptera samples from Harapan jungle rubber were classified as having plants as their basal resource. The centroid of Hemiptera from jungle rubber fell close to the plant cluster. Hemiptera from Bukit rainforest positioned close to plants and between fungi and plants, with three samples being classified as having plants and one sample as having fungi as their basal resource. Hemiptera from Harapan rainforest positioned close to fungi, algae and plants with no detectable pattern and were classified accordingly. Therefore, the centroid of Hemiptera from the rainforest fell between plants, fungi and algae with a slight drive towards plants. It can be noted that none of the samples were classified as having bacteria as their basal resource and only one of the samples (HF2Hem) was classified as having algae as their basal resource.

3.2.3 Collembola

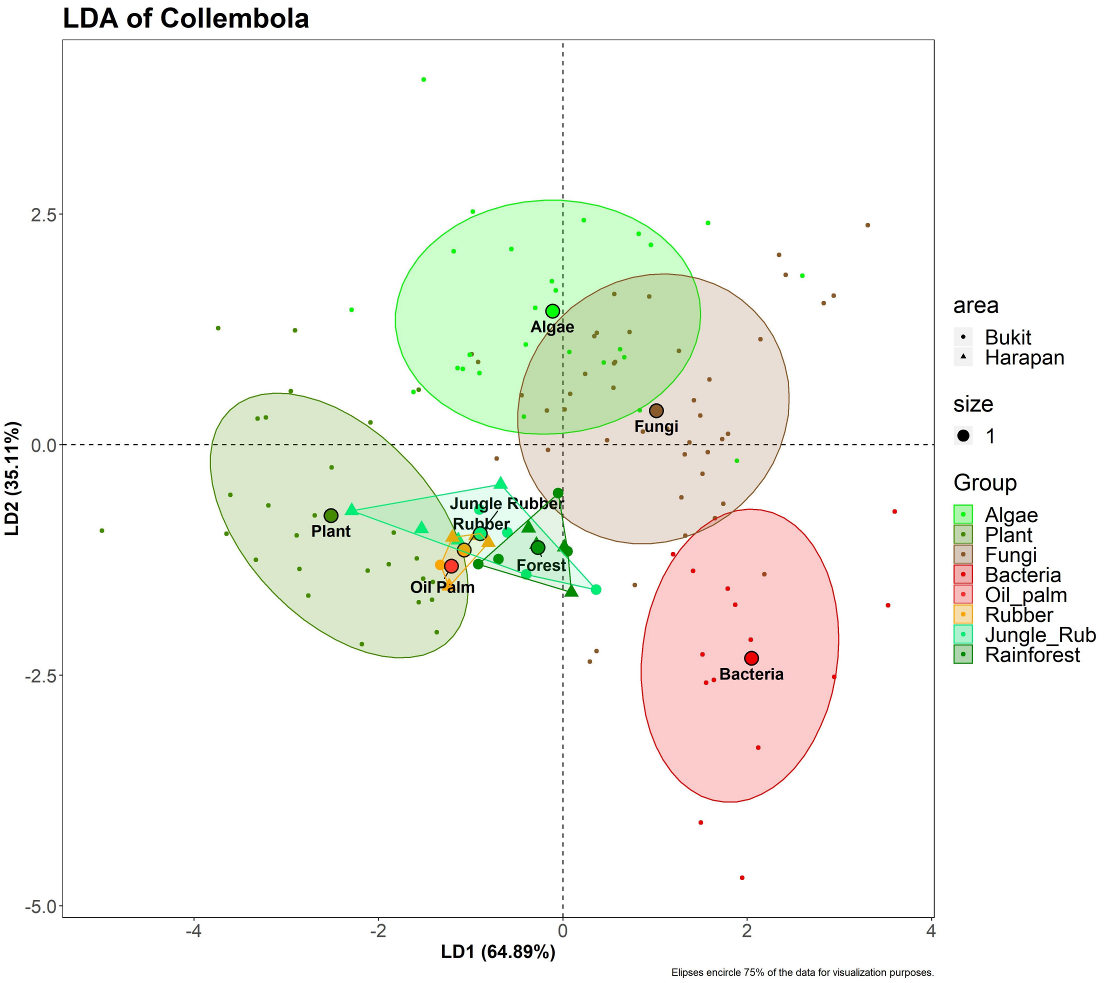


Figure 7: Linear discriminant analysis (LDA) with δ^{13}C values of amino acids of Collembola collected from rainforest, jungle-rubber, rubber plantations and oil-palm plantations in Bukit Duabelas National Park and Harapan Rainforest. Classifiers (plants, bacteria, algae and fungi) were grouped according to specific δ^{13}C patterns. Hulls around the classifiers constitute 75% of the data for visualisation purposes.

Due to many measurements of Collembola samples from oil palm plantations with concentrations below the peak detection point, only one Collembola sample (Bukit) was analysed which positioned within the plant cluster (Fig. 7). Collembola from Bukit rubber plantations positioned within the plant cluster. Collembola from Harapan rubber plantations positioned within or close to plants and were all classified as having plants as their basal resource except one (87HR3Col) which was classified as having fungi as their basal recourse. Collembola samples from Bukit jungle rubber positioned between fungi and plants with sample 84BJ5Col showing a shift towards bacteria. Three of them were classified as having fungi and one as having plants as their basal resource. Collembola from Harapan jungle rubber positioned close to plants and one between plants and fungi. The centroid of Collembola from jungle rubber fell close to the plant cluster. Collembola from rainforest positioned between fungi and plants with a slight shift towards fungi and bacteria. Collembola from Harapan rainforest were all classified as having fungi as their basal resource. The centroid of Collembola from rainforest fell between plants and fungi, with a slight drive towards fungi.

4. Discussion

4.1 Trophic positions based on ^{15}N analysis of amino acids

By combining δ^{13}C and δ^{15}N analysis of amino acids, we investigated basal resources and trophic positions of Blattodea, Hemiptera and Collembola as indication of trophic changes along an increasing land-use intensification gradient. Consumers were classified according to carbon isotopic patterns characteristic for one of the basal resources (bacteria, algae, fungi and plants).

To calculate TP of the consumers, plot-specific β values of leaves were used. Applying these resource-specific β values, TP of leaves was approximately 1, using Eq. (3). TP of consumers was, as expected, between 2 and 3, suggesting that they all represent primary or secondary consumers. Mean TP of Hemiptera was 2.4, higher than expected for pure herbivores, which should occupy a TP around 2. Hemiptera constitute a highly diverse group, including pure herbivorous families (Cicadellidae) (Dietrich, 2005), omnivorous families (Miridae) (Wheeler, 2001) and predacious families (Reduviidae) (Weirauch, 2008), representing a range of TP from pure herbivores (2) to pure predators (3). Since 15 individuals per core plot were randomly selected for analysis, each sample contains Hemiptera with different feeding habits. This results in a mean TP over all Hemiptera tested, which should approximate the mean TP of Hemiptera at the order level.

Intermediate TPs suggest further, that either omnivores represent a large share of the sampled Hemiptera or that it results from a balance of herbivores, predators and omnivores. The latter is supported by collection records of Hemiptera from each core plot (J. Drescher et al., unpublised data) revealing that herbivorous, omnivorous and predatory families were among the sampled individuals. Collection records of Hemiptera also reveal a change in community composition, providing an explanation for an increasing TP of Hemiptera with an increase in land-use intensity. The relative abundance of purely herbivorous families such as Cicadillidae, Flatidae and Issidae compared to abundance predacious families such as Reduviidae and Anthocoridae was higher in rainforest and jungle rubber than in rubber and oil palm. Accordingly, predacious families are relatively more abundant in rubber and oil palm than in rainforest and jungle rubber, compared to purely herbivorous families.

Blattodea showed similar trophic patterns as Hemiptera, having a lower TP in the more natural landscapes (rainforest and jungle rubber) and a higher TP in the more intensely managed landscapes (rubber and oil palm). The mean TP of Blattodea was 2.3, positioning them between pure herbivores and purely predacious insects, which was expected for this omnivorous group. Higher TP in the more intensely managed landscapes suggests that, similar to Hemiptera, the proportion of generalist and predacious Blattodea increases, while abundance of purely herbivorous Blattodea decreases due to loss of specific host plants. Usually, herbivorous populations influence the carnivore population via bottom-up control, keeping the number of predators lower than their own (Terborgh & Estes, 2013). A reason, why this does not seem to apply to Hemiptera and Blattodea in rubber an oil palm, might be a strong dependence of predators on detritivores (Hyodo et al., 2010) suggesting that they constitute a considerable substitute prey for predacious Hemiptera and Blattodea.

A lower TP of Blattodea and Hemiptera in the more natural landscapes suggests that the degree of herbivory in rainforest and jungle rubber is higher than in rubber and oil palm. This may be due to energetic constraints of predation, such that herbivory is more energetically favourable in ecosystems with high plant diversity (Carbone et al., 1999). Therefore, the hypothesis concerning higher TP in more intensively managed landscapes is supported for Hemiptera and Blattodea, however, not for Collembola.

TP of Collembola was relatively stable across all land-use systems, only slightly lower in Harapan rubber, suggesting that Collembola feed from a consistent and stable food resource which does not change qith forest transformation. Collembola colonise various areas of the canopy, including bark, moss and suspended soils supporting epiphytes mostly found in frond axils (Potapov et al., 2020; Rodgers & Kitching, 2011). The latter are considered microhabitats offering a particularly stable microclimate (Paoletti et al., 1991; Rodgers & Kitching, 2011). Organisms colonising these "epiphyte islands" are exposed to less environmental change and have access to similar food resources despite changes in their macrohabitat. More epiphytes are found in oil palm plantations than in rainforest and jungle rubber (Böhnert et al., 2016; Turner & Foster, 2009). Further, Potapov et al. (2020) demonstrated a great contribution of suspended soils to Collembola density and diversity in the course of land-use change. The stable environment of these microhabitats presumably contributes to a relatively constant TP of Collembola in rainforest, jungle rubber and oil palm. Accordingly, a lower TP of Collembola in rubber suggests reduced food quality, which could be due to lower abundance of suspended soils in rubber plantations.

For Blattodea, Hemiptera and Collembola, Phe was depleted compared to the diet, resulting in a strongly negative difference of δ^{15}N between consumer and diet ($\Delta^{15}\mathrm{N}_{\text{C-D}}$). Negative trophic fractionation of Phe in primary consumers feeding from leaves has also been observed in springtails and oribatid mites (Pollierer et al., 2019) and other arthropods including lacewings, bettles and aphids (Chikaraishi et al., 2011; Steffan et al., 2013, 2015). The reason for these depleted $\delta^{15}\mathrm{N}_{\mathrm{Phe}}$ values is presumed to be rather selective feeding from N-depleted Phe pools within plants (Pollierer et al., 2009, 2019) than metabolic cleavage of Phe (McMahon & McCarthy, 2016). In plants, the phenylpropanoid pathway involves the biosynthesis of polyphenol compounds such as lignin, phenylpropanoids and flavonoids (Fritz et al., 1976). As presumed by Pollierer et al. (2019), the studied consumers may have only consumed specific N-depleted pools of Phe, object to a specific metabolic pathway. Furhter, the high N-depletion of Phe in Collembola presumably caused their calculated TP to be higher than that of Hemiptera and Blattodea.

4.2 ^{13}C stable isotope fingerprinting

Results of δ^{13}C fingerprinting demonstrated a great dietary contribution of fungi and plants for all consumers, with the highest contribution of eAAs originating from fungi for Blattodea. For Hemiptera and Collembola, fungi and plants as basal resource were relatively balanced and only one Hemitpera plot-sample was classified as having algae as basal resource. Consequently, my hypothesis that, besides plants, fungi, bacteria and algae function as basal resource for the three consumers can only be confirmed for fungi and algae. However, shifts towards bacteria were notable for Hemiptera and Blattodea from rubber and oil palm, and Collembola from jungle rubber and rainforest, suggesting a bacterial contribution to the consumers' diet, which is lower than that of fungi and plants.

High contributions of eAAs originating from fungi can be a proximate cause of (i) feeding on fungi, (ii) indirectly ingesting fungi, which grow in and on plant material, (iii) consuming detritivorous invertebrates, which feed on fungi. For Hemiptera, with a dominance of herbivorous families in rainforest and jungle rubber and a dominance of predacious and omnivorous families in rubber and oil palm, all possibilities of fungi intake are possible but tendencies can be noted: Presumably, Hemiptera from rubber and oil palm, where TP was higher than in rainforest and jungle rubber, mainly feed on invertebrates and detritivores, which feed on fungi, whereas Hemiptera from rainforest and jungle rubber presumably prefer feeding directly on fungi or ingest fungal particles with plant intake, resulting in a lower TP.

Since there are no collection records of Blattodea, assumptions are more speculative. Blattodea constitute a diverse group, including Blattidae (cockroaches) and Isoptera (termites). Cockroaches are a mainly omnivorous group, while termites are purely detritivorous, consuming dead plant material, even bark (Freymann et al., 2008). Additionally, Macrotermitinae, a termite subfamily with approximately 330 species and a high abundance in the tropics (Eggleton & Tayasu, 2001), have a symbiotic relationship with basidiomycete fungi of the genus *Termitomyces*, benefiting from fungal breakdown of wooden parts of plants (Aanen et al., 2002; Mueller & Gerardo, 2002). Symbiotic relationships like this and fungivorous or predacious cockroaches consuming fungivores may explain the high proportion of fungi as basal resource for Blattodea.

Contribution of plants, fungi and bacteria as basal resources was more equally distributed among Collembola than among Hemiptera and Blattodea. Relatively consistent basal resources are in line with the relatively stable TP of Collembola, supporting the previous assumption of constant access to certain resources due to suspended soils associated with epiphytes. The balanced contribution of fungi and plants as basal resource to the diet of Collembola and their mean TP of 2.6 suggest a higher degree of predation than for Hemiptera and Blattodea in all land-use systems. However, considering the high N-depletion of Phe in Collembola, it is more likely that this is the main cause of a higher TP of Collembola, rather than a higher proportion of predators. Although studies such as gut-content analyses conducted by (Anderson & Healey, 1972), found relatively large amounts of plants, it is possible that those plants have been infested with fungi which reflects the detected fungal carbon patterns by LDA and explains the high

TP.

Hemiptera and Blattodea shifted the use of basal resources across land-use systems, with a higher degree of plants as basal resources in rainforest and jungle rubber and a shift towards fungi and bacteria in rubber and oil palm (Fig. 5, Fig. 6). This supports the second hypothesis that the proportion of microorganisms as basal resource increases with increasing land-use intensity and plants dominate in rainforest and jungle rubber. As plant diversity and, hence, food quality for primarily herbivorous consumers decreases with increasing land-use intensity (Turner et al., 2007; Turner & Foster, 2009), plant based nutritious intake has to be substituted. The potential of microorganisms, especially fungi and bacteria, to constitute a substitute resource has been highlighted in previous studies (Pollierer et al., 2019; Steffan et al., 2015) and also provides an explanation for the higher TP of Hemiptera and Blattodea in rubber and oil palm. Further, trophic contribution of gut microbes was proven for Hemiptera and Blattodea in previous studies (Hongoh, 2010; Hussin et al., 2018; Indiragandhi et al., 2010; Zhou et al., 2015). Living in a symbiotic relationship with their host, gut microbes produce eAAs which can be detected using δ^{13}C fingerprinting. Tendencies of Hemiptera and Blattodea to shift towards bacteria as a basal resource in rubber and oil palm suggest microbial support of their metabolism.

5. Conclusion

By using compound-specific isotope analysis of amino acids, basal resources and trophic positions of Blattodea, Hemiptera and Collembola were determined. Comparing basal resources and trophic positions of rainforest, jungle rubber, rubber plantations and oil palm plantations, allowed to infer trophic changes along an increasing land-use intensification. Plants and fungi dominated as basal resource for all consumers, whereas only one sample was classified as having algae as basal resource. Additionally, a shift towards bacteria and fungi in rubber and oil palm was detectable for Hemiptera and Blattodea. These findings suggest that, although some species are known and described as herbivores, they consume plant material in order to feed from fungi, growing on it. Further, the shift towards bacteria and fungi suggests that Hemiptera and Blattodea substitute plants with microorganisms in the case of decreasing resource availability or quality. The hypothesis that microorganisms serve as basal resources for all consumer groups can therefore be confirmed but not as pronounced as assumed for algae and bacteria. The next hypothesis assuming a shift towards microorganisms as basal resource with increased land-use can be confirmed for Hemiptera and Blattodea but not for Collembola. Basal resources of Collembola remained relatively stable which was also reflected in a relatively constant TP for Collembola across all land-use systems. Increasing TP of Hemiptera and Blattodea along an intensification of land-use is supported by changes in community composition, with an increasing proportion of predacious families in rubber and oil palm, presumably causing the elevation of TP. A possible goal of further studies could be to investigate which resources are not available for Hemiptera and Blattodea in rubber and oil palm plantations. For this purpose, identification of communities at species level is necessary. Futher methods, such as the molecular gut content analysis, can help unravel more about feeding habits and basal resources of Collembola. This, combined with further investigations concerning the stable TP of Collembola, has the potential to suggest innovative cultivation methods, like additional understories, to improve biodiversity and ecosystem functioning in rubber and oil palm plantations.

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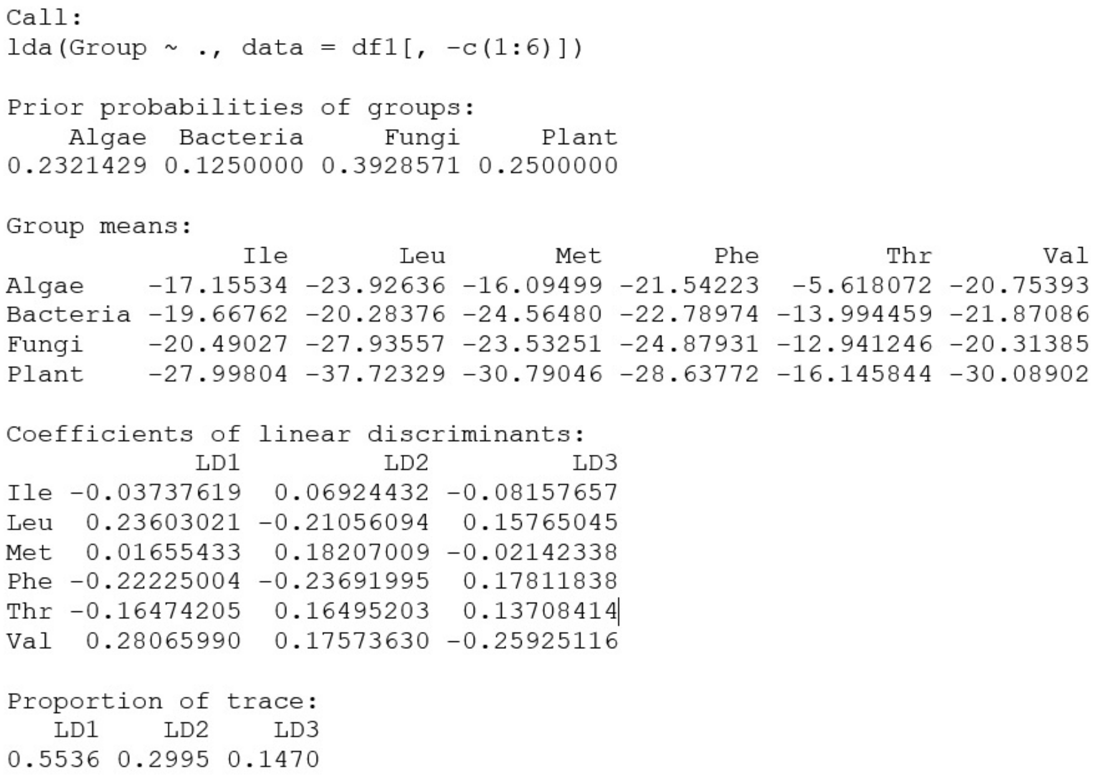
Appendices



```
Call:
lda(Group ~ ., data = df1[, -c(1:6)])

Prior probabilities of groups:
    Algae  Bacteria     Fungi     Plant 
0.2321429 0.1250000 0.3928571 0.2500000 

Group means:
               Ile       Leu       Met       Phe        Thr       Val
Algae    -17.15534 -23.92636 -16.09499 -21.54223  -5.618072 -20.75393
Bacteria -19.66762 -20.28376 -24.56480 -22.78974 -13.994459 -21.87086
Fungi    -20.49027 -27.93557 -23.53251 -24.87931 -12.941246 -20.31385
Plant    -27.99804 -37.72329 -30.79046 -28.63772 -16.145844 -30.08902

Coefficients of linear discriminants:
            LD1         LD2         LD3
Ile -0.03737619  0.06924432 -0.08157657
Leu  0.23603021 -0.21056094  0.15765045
Met  0.01655433  0.18207009 -0.02142338
Phe -0.22225004 -0.23691995  0.17811838
Thr -0.16474205  0.16495203  0.13708414
Val  0.28065990  0.17573630 -0.25925116

Proportion of trace:
   LD1    LD2    LD3 
0.5536 0.2995 0.1470 
```

Figure 8: Summary output of the LDA after model training showing the prior probabilities of groups, group means, coefficients of linear discriminants and proportion of trace for the individual LDs.

Table 2: Coordinates of core plots from all four land-use systems, rainforest (F), jungle rubber (J), rubber (R) and oil palm (O), in Harapan (H) and Bukit Duabelas (B).

Plot Code	**Management**	**Landscape**	**Latitude**	**Longitude**
BF1	Forest	BukitDuabelas	S 01°59’42.5”	E 102°45’08.1”
BF2	Forest	BukitDuabelas	S 01°58’55.1”	E 102°45’02.7”
BF3	Forest	BukitDuabelas	S 01°56’33.9”	E 102°34’52.7”
BF4	Forest	BukitDuabelas	S 01°56’31.0”	E 102°34’50.3”
BJ3	JungleRubber	BukitDuabelas	S 02°03’46.7”	E 102°48’03.5”
BJ4	JungleRubber	BukitDuabelas	S 02°00’57.3”	E 102°45’12.3”
BJ5	JungleRubber	BukitDuabelas	S 02°08’35.6”	E 102°51’04.7”
BJ6	JungleRubber	BukitDuabelas	S 02°01’49.3”	E 102°46’15.0”
BO2	Oil palm	BukitDuabelas	S 02°04’32.0”	E 102°47’30.7”
BO3	Oil palm	BukitDuabelas	S 02°04’15.2”	E 102°47’30.6”
BO4	Oil palm	BukitDuabelas	S 02°03’01.5”	E 102°45’12.1”
BO5	Oil palm	BukitDuabelas	S 02°06’48.9”	E 102°47’44.5"
BR1	Rubber	BukitDuabelas	S 02°05’30.7”	E 102°48’30.7”
BR2	Rubber	BukitDuabelas	S 02°05’06.8”	E 102°47’20.7”
BR3	Rubber	BukitDuabelas	S 02°05’43.0”	E 102°46’59.6”
BR4	Rubber	BukitDuabelas	S 02°04’36.1”	E 102°46’22.3”
HF1	Forest	Harapan	S 02°09’09.9”	E 103°21’43.2”
HF2	Forest	Harapan	S 02°09’29.4”	E 103°20’01.5”
HF3	Forest	Harapan	S 02°10’30.1”	E 103°19’57.8”
HF4	Forest	Harapan	S 02°11’15.2”	E 103°20’33.4”
HJ1	JungleRubber	Harapan	S 01°55’40.0”	E 103°15’33.8”
HJ2	JungleRubber	Harapan	S 01°49’31.9”	E 103°17’39.2”
HJ3	JungleRubber	Harapan	S 01°50’56.9”	E 103°17’59.9”
HJ4	JungleRubber	Harapan	S 01°47’07.3”	E 103°16’36.9”
HO1	Oil palm	Harapan	S 01°54’35.6”	E 103°15’58.3”
HO2	Oil palm	Harapan	S 01°53’00.7”	E 103°16’03.6”
HO3	Oil palm	Harapan	S 01°51’28.4”	E 103°18’27.4”
HO4	Oil palm	Harapan	S 01°47’12.7”	E 103°16’14.0”
HR1	Rubber	Harapan	S 01°54’39.5”	E 103°16’00.1”
HR2	Rubber	Harapan	S 01°52’44.5”	E 103°16’28.4”
HR3	Rubber	Harapan	S 01°51’34.8”	E 103°18’02.1”
HR4	Rubber	Harapan	S 01°48’18.2”	E 103°15’52.0”

Table 3: LDA-predicted basal resources (fungi and algae) for each sample of the three consumers, Blattodea (Bla), Hemiptera (Hem) and Collembola (Col) from all four land-use systems, rainforest (F), jungle rubber (J), rubber (R) and oil palm (O), in Harapan (H) and Bukit (B). The number in front of the sample code represents sequence number. Proportion of trace: LD1 = 0.6489, LD2 = 0.3511.

sample	**predicted**
29BJ5Bla	Fungi
32BJ3Bla	Plant
19BO5Bla	Fungi
28BO3Bla	Fungi
50BO4Bla	Fungi
51BO2Bla	Fungi
61BO3-2Bla	Fungi
11BF4Bla	Fungi
33BF3Bla	Fungi
41BF2Bla	Plant
37BR3Bla	Plant
53BR3-2Bla	Plant
54BR3-3Bla	Plant
55BR3-4Bla	Plant
9HJ2Bla	Fungi
39HJ3Bla	Plant
18HO4Bla	Plant
43HO3Bla	Fungi
47HO4Bla	Fungi
12HF2Bla	Fungi
24HF1Bla	Fungi
10HR4Bla	Fungi
25HR3Bla	Fungi
42HR2Bla	Fungi
66BJ6Col	Plant
72BJ3Col	Fungi
80BJ4Col	Fungi
84BJ5Col	Fungi
89BO4Col	Plant
65BF2Col	Fungi
68BF1Col	Plant
76BF3Col	Fungi
85BF4Col	Plant
75BR1Col	Plant
77BR4Col	Plant
67HJ3Col	Plant
69HJ1Col	Fungi
88HJ2Col	Plant

sample	**predicted**
90HJ4Col	Plant
70HF3Col	Fungi
71HF1Col	Fungi
81HF2Col	Fungi
86HF4Col	Fungi
63HR2Col	Plant
64HR4Col	Plant
79HR1Col	Fungi
87HR3Col	Plant
2BJ5Hem	Plant
20BJ6Hem	Fungi
40BJ4Hem	Fungi
14BO4Hem	Fungi
26BO3Hem	Fungi
30BO2Hem	Fungi
38BO5Hem	Fungi
1BF2Hem	Plant
15BF1Hem	Fungi
27BF4Hem	Plant
57BF2-2Hem	Plant
35BR4Hem	Fungi
58BR4-2Hem	Fungi
59BR4-3Hem	Fungi
60BR4-4Hem	Fungi
3HJ1Hem	Plant
4HJ2Hem	Plant
23HJ4Hem	Plant
45HJ3Hem	Plant
36HO2Hem	Plant
44HO1Hem	Fungi
13HF3Hem	Fungi
16HF1Hem	Plant
31HF2Hem	Algae
17HR4Hem	Plant
34HR2Hem	Fungi
52HR4-2Hem	Plant
62HR4-2Hem	Plant

Table 4: δ^{13}C values of essential amino acids leucine (leu), isoleucine (Ile), metionine (Met), phenylalanine (Phe), threonine (Thr) and valine (Val) of consumers (Blattodea, Hemiptera and Collembola) from all four land-use systems (rainforest, jungle rubber, rubber and oil palm) measured via gas chromatography.

Type in land-use system	**mean δ^{13}C Ile**	**mean δ^{13}C Leu**	**mean δ^{13}C Met**	**mean δ^{13}C Phe**	**mean δ^{13}C Thr**	**mean δ^{13}C Val**
Blattodea	-27,575	-32,692	-28,455	-31,374	-18,198	-30,184
jungle rubber	-26,421	-32,167	-28,541	-31,016	-16,997	-29,550
oil palm	-27,983	-32,664	-29,044	-33,249	-19,837	-30,351
rainforest	-27,971	-32,525	-27,160	-29,388	-17,914	-29,931
rubber	-27,490	-33,198	-28,872	-31,226	-17,021	-30,613
Hemiptera	-24,010	-33,086	-26,200	-26,203	-18,687	-26,961
jungle rubber	-23,583	-32,840	-25,961	-25,601	-17,644	-26,603
oil palm	-22,466	-28,385	-26,699	-22,790	-11,161	-25,239
rainforest	-23,486	-32,066	-26,127	-26,245	-18,791	-26,184
rubber	-25,534	-35,560	-26,534	-27,518	-21,193	-28,759
Collembola	-26,935	-33,329	-27,909	-30,122	-17,603	-29,527
jungle rubber	-25,135	-33,383	-26,164	-28,125	-15,922	-28,512
oil palm	-27,763	-32,828	-28,621	-30,574	-19,353	-30,252
rainforest	-26,682	-33,038	-27,909	-29,530	-15,365	-28,813
rubber	-27,916	-33,936	-28,712	-31,991	-19,538	-30,386

Statement of Authorship

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Semester: WS19/20
Degree Course: Education
Module: Masterarbeit im Fach Biologie
Exam: Masterarbeit - Education
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Declaration

I hereby declare that I have produced this work independently and without outside assistance, and have only used the sources and tools stated.

I have clearly identified the sources of any sections from other works that I have quoted or given in essence.

I have complied with the guidelines on good academic practice at the University of Göttingen.

I am aware that failure to comply with these principles will result in the examination being graded "nicht bestanden", i.e. failed.

Göttingen, 11th March 2020 Camilla Schmidt