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– CENTRE OF BIODIVERSITY AND SUSTAINABLE LAND USE –

Diversity of parasitoid wasps along a tropical land-use gradient

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Abstract

Anthropogenic land-use change is a major contributor to global loss of species and ecosystem functions. Despite being hotspots of biodiversity, tropical rainforests are particularly threatened by rapid conversion to 'cash crop' plantations, such as oil palm (*Elaeis guineensis*) and rubber (*Hevea brasiliensis*) monocultures. Parasitoid wasps provide beneficial ecosystem services as they can effectively control host (and potential pest) populations. Additionally, they are a major component of global biodiversity. However, parasitoid wasps and their sensitivity to land-use change are understudied, especially in the tropics. In this study, the abundance, species richness, diversity, community composition and spatial species turnover rate of six families of parasitoid wasps was investigated along a tropical land-use gradient within two landscapes. Samples from the six parasitoid families (Braconidae, Ceraphronidae, Encyrtidae, Eulophidae, Platygastridae and Scelionidae) were collected via canopy fogging in Jambi province, Sumatra. The investigated land-use systems were primary (degraded) rainforest, Jungle Rubber, rubber monoculture plantations and oil palm monoculture plantations, representing an increasing gradient of management intensity. Sampling was done for equal number of plots and land-use systems in two different regions, which are further referred to as 'Bukit Duabelas landscape' and 'Harapan landscape'. Collected samples had been morphologically identified to the level of 'Morphospecies'. Analyses were conducted based on an abundance dataset of all Morphospecies. Abundance, species richness, diversity and species turnover rate were analyzed using Generalized Linear Models. Community composition was investigated using ordinations based on Detrended Correspondence Analysis. The results show a decline of abundance, species richness and diversity of parasitoid wasps with increasing land-use intensity. Community structure of forest and Jungle Rubber were similar, while those of rubber and oil palm monocultures were distinct from those of other land-use systems. Species turnover was relatively low in forest and rubber monocultures, while being high in Jungle Rubber and oil palm plantations. The Harapan landscape showed lower abundance, species richness, diversity and simultaneously a higher species turnover rate than Bukit Duabelas landscape. The results lead to the conclusion that parasitoid wasps react sensitive to land-use change, and many species and their ecosystem functions are lost with rainforest conversion to monocultures. Additionally, the Harapan landscape seems to be more disturbed than the Bukit Duabelas landscape, regardless of the land-use system. Consequently, policy makers should increase efforts to prevent further rainforest conversion, especially within the Bukit Duabelas landscape, in order to protect parasitoid wasps and their ecosystem functions.

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1 Introduction

Anthropogenic landscape alterations, like deforestation and agricultural intensification are a major driver of global biodiversity loss and degradation of ecosystem services (Foley et al., 2005; Priess et al., 2007). While primarily intended to benefit humankind, these processes may negatively affect ecosystem services important to humans (Díaz et al., 2006). Tropical moist forests 'stand out as highly significant reservoirs of global biodiversity' (Dirzo and Raven, 2003) and primary tropical rainforests have been deemed irreplaceable for the conservation of tropical biodiversity (Gibson et al., 2011). However, these unique ecosystems are severely threatened by deforestation and expansion of agriculture. In particular, the perils of expanding oil palm plantations on biodiversity have been widely addressed (Brühl and Eltz, 2010; Fitzherbert et al., 2008; Turner and Foster, 2009; Yue et al., 2015) and oil palm has even been called 'the greatest immediate threat to biodiversity in Southeast Asia' (Wilcove and Koh, 2010).

While a few vertebrate species gain public attention, and hence conservation efforts, many threatened arthropod species are at risk of being overlooked by conservationists (Kim, 1993). Considering that arthropods account for more than half of the world`s species (Kim, 1993), this poses a problem for protecting global biodiversity. Additionally, the extinction of insects is heavily understudied, mainly because many tropical arthropods still await description, and of those that have Linnaean names, the biology is often unclear (Dunn, 2005). While it has been pointed out that focusing on 'umbrella species' may benefit other species (Wilcox, 1984), doubt remains on the efficiency of focusing on single species for conservation (Simberloff, 1998).

Seven major impediments for the conservation of invertebrate biodiversity have been outlined (Cardoso et al., 2011): 'The public dilemma' describes the problem that invertebrates and their ecological services are largely unknown to the public. 'The political dilemma' is where the same issue applies to policy-makers and stakeholders. Furthermore, research on invertebrates is underfunded and scarce ('the Scientific Dilemma'), a high proportion of species are undescribed ('the Linnean Shortfall'), the distribution of species is widely unknown ('the Wallacean Shortfall') and their abundance and changes in space and time ('the Prehistorian Shortfall') are understudied. Lastly, the biology of the species and their sensitivity to habitat changes are largely unknown ('the Hutchinsonian Shortfall').

The lack of invertebrate conservation is of particular concern because of the ecosystem services they provide: Earthworms, for example, increase soil fertility (Syers et al., 1984). Bees, including the honey bee *Apis mellifera*, play a key role in pollination (Brittain et al., 2013; Greenleaf and Kremen, 2006) and many other invertebrates act as biological control agents, e. g. nematodes (Villani and Wright, 1988), mites (Arthurs et al., 2009), flies (Mays and Kok, 2003), and parasitoid wasps (Smith, 1996). Overall, the global value of ecosystem services has been estimated to be between 16 and 54 trillion US-Dollar per year (Costanza et al., 1997), with wild insects contributing at least 57 billion US-Dollar in the United States alone (Losey and Vaughan, 2006).

When it comes to ecosystem services, some consider the Hymenoptera 'the most important insects for mankind' (Kannagi et al., 2013). Besides bees, it is parasitoid wasps that are particularly beneficial to humans, as they lay their eggs in larvae and eggs of many herbivorous insects. The developing parasitoid consumes the host before it can reproduce, therefore, parasitoid wasps can be extremely efficient in controlling herbivory.

While certain parasitoid taxa, like *Trichogramma* (Trichogrammatidae) are well known and have been used for biological control (Hassan, 1993), the diversity and biology of parasitoid wasps is understudied (Bacher, 2012; Klopfstein et al., 2013). This is a shortcoming, as parasitoid wasps constitute a large fraction of the insect fauna, e.g. at least 25 % in Britain (Shaw and Hochberg, 2001) and are discussed as suitable proxies for general biodiversity (Anderson et al., 2011; Loni and Lucchi, 2014). This Master thesis will focus on investigating the morphological diversity and community structure of six parasitoid wasp families (Braconidae, Ceraphronidae, Encyrtidae, Eulophidae, Platygastridae and Scelionidae) along a land-use transformation gradient from rainforest via Jungle Rubber to monocultures of rubber and oil palm in Jambi, Sumatra.

Since morphology based sorting to families and identification of (morpho-) species is a very time consuming task, possible alternative methods of molecular analyses will be investigated. Those investigations will focus on the possibility of 'DNA metabarcoding` (Taberlet et al., 2012) for pooled samples using a Cytochrome Oxidase C Subunit 1 (COI) marker on the Illumina MiSeq platform.

2 Hypotheses

1) I hypothesize that species richness and inverse Simpson Diversity (Simpson, 1949) will be highest in rainforest, intermediate in Jungle Rubber and lowest in rubber and oil palm. This expectation is based on the fact that the Jungle Rubber vegetation system, albeit poorer in plant diversity than rainforest, consists of additional trees and brush besides the Rubber (Gouyon et al., 1993), presumably allowing for a more diversified canopy arthropod fauna compared to monocultures. Additionally, I expect that abundance follows the same pattern. This is based on reports of higher plant biomass (Barnes et al., 2017) in forest and Jungle Rubber compared to monocultures, which could lead to those systems carrying a higher biomass of herbivores and subsequently parasitoids.

2) I further hypothesize that community composition will be similar between rainforest and Jungle Rubber, but different from that in rubber and oil palm monocultures. This hypothesis is based on the observation that the structure of old Jungle Rubber is comparable to that of secondary forest and that the additional plants in Jungle Rubber from Jambi originate from natural forest (Gouyon et al., 1993). This might allow the establishment of a herbivore and subsequently a predator arthropod community that is similar to the one in natural forests. In contrast, rubber and oil palm monocultures have a high proportion of non-forest plants (Rembold et al., 2017), which subsequently might lead to distinct herbivore and parasitoid communities. Findings in line with this idea were made in canopy ants (Drescher and Rembold, personal observation 2015, as cited in Drescher et al., 2016).

3) For species turnover, defined as the dissimilarity of communities between plots of the same land-use system, I hypothesize a similar pattern as expected in 1): Dissimilarity of species assemblages will be highest in forest and lowest in monocultures, with Jungle Rubber taking an intermediate position. This hypothesis is based on reports of higher plant richness (Kusuma et al., 2018; Rembold et al., 2017) in forest compared to oil palm and rubber monocultures. Higher overall plant diversity might lead to more heterogeneous plant composition and subsequently higher plant species dissimilarity between forest plots. Consequentially, the associated community of herbivore arthropods and their parasitoids would also show higher dissimilarity in forest plots. In contrast, oil palm and rubber monocultures, comprising of only one main tree species and less diverse, albeit more dense understory vegetation (Rembold et

al., 2017) would be spatially homogenous. This would subsequently lead to low dissimilarity in the associated arthropod community and hence parasitoid assemblages between plots.

3 Material and Methods

3.1 Study sites and association of the project

The study is part of the DFG-funded collaborative research program CRC990 '*Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems* (EFForTS)' of the University of Göttingen, partnered with Bogor Agricultural University IPB, Jambi University UNJA and Tadulako University UNTAD (Drescher et al., 2016). Indonesia's islands are among the world's major hotspots of biodiversity (Myers et al., 2000), yet their ecosystems are heavily threatened by anthropogenic land-use change. Between 2000 and 2012, Indonesia lost 6.02 Mha of primary forest (Margono et al., 2014) and experienced the largest increase of forest loss worldwide (Hansen et al., 2013).

The study sites of the EFForTS-project are 32 core plots in Jambi province, Sumatra, which are sub grouped into two different regional areas: The Bukit Duabelas landscape, named after the Bukit Duabelas National Park, and the Harapan landscape, named after the Harapan Rainforest. Within each of these landscapes, four plots measuring 50 m * 50 m were established in each of four types of land-use transformation system: Forest, Jungle Rubber, rubber monoculture and oil palm monoculture. The investigated rainforests represent 'primary degraded forest' (Margono et al., 2014). Jungle Rubber is an agro-forest system that consists of rubber trees planted into – often previously logged – forests (Gouyon et al., 1993). Oil palm and rubber monocultures are smallholder plantations, with an age of 7 to 16 years for rubber and 8 to 15 years for oil palm at time of plot selection in 2012 (Drescher et al., 2016). The studied parasitoid wasps were collected in dry seasons 2013 and 2017 as part of two large-scale canopy arthropod sampling campaigns, conducted by teams of students and local assistants under supervision of J. Drescher (Dept. Animal Ecology, University of Göttingen). Canopy arthropod samples were collected by canopy fogging, which is essentially the application of insecticide to tree canopies while catching the stunned or dead arthropods in traps, tarps or funnels. First attempted by Roberts (1973) in Costa Rica, canopy fogging is still widely used in studies targeting arboreal arthropod communities (e.g. Sprick and Floren, 2018; Yusah et al., 2018). There are, however, limitations to the method, e.g. with respect to insect communities that live in epiphytes such as bromeliads (Yanoviak et al., 2003) or medium to large insects Hymenopterans (e.g. Vespidae, Apidae) which seem to be able to detect the approaching fog and escape. Additionally, canopy fogging is biased against very small specimen, which tend to stick to leaves and twigs in the canopy (Drescher, pers. comm). Drescher and team used the Swingfog® SN50 fogger (Swingtec GmbH, Germany) 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.

For the collection of the 2013 samples, target canopies were chosen by identifying three locations per core plot in which the canopy appeared most dense, i.e. the three areas with the highest potential leaf area index. Underneath each selected target canopy, the fogging team placed twelve 1*1m collection funnels, suspended from and each fitted with 250ml wide neck PE-flasks filled with ca. 100ml 96% EtOH. The selection of target canopies and the arrangement of collection funnels differed between the four land-use types. In rainforest, all three target canopies per core plot contained branches and leaves from a random arrangement of unknown trees and epiphytes, and collection funnels were placed in a random pattern underneath the selected target canopy. In Jungle Rubber plots, the three target canopies were chosen to approximately represent the assumed leaf area ratio of rubber trees to unknown tree species. To do that, Drescher and team chose one actively tapped rubber tree as the centroid of a roughly circular arrangement of the twelve collection funnels as the first of three target canopies; the centroids of the second and third target canopies each were different tree species whose canopies were enmeshed with those of neighboring rubber trees. In rubber plantations, the densest canopies were usually found between trees in the same row. Consequently, they placed the collection funnels 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. In the collection campaign of 2017, Drescher and team used only eight collection funnels per core plot, and adapted the funnel arrangement outlined above to the reduced number of collection funnels.

3.2 Study organisms

Parasitoid Hymenoptera of six families were sorted to family-level and Morphospecies-level in facilities of the Department of Plant Protection, Bogor Agricultural University, under supervision of Prof. Dr. Damayanti Buchori. Since the Ichneumonidae proved too difficult, sorting was concentrated on the following six families of parasitoid Hymenoptera: Braconidae, Ceraphronidae, Encyrtidae, Eulophidae, Platygastridae and Scelionidae.

The Braconidae have a cosmopolitan distribution, with approximately 15,000 described species; with estimates suggesting a total species richness two or three times as much (Dolphin and Quicke, 2001). Braconid wasps act as parasitoids towards larvae of a wide range of arthropod taxa, amongst them Lepidoptera (Lei and Camara, 1999), Coleoptera (Loan and Holdaway, 1961), Diptera (López et al., 1999), and Hemiptera (Day et al., 1999).

Ceraphronids have been demonstrated to parasitize cecidomyiid flies (Gilkeson et al., 1993) and one species has even been documented to parasitize Trichoptera pupae (Luhman et al., 1999). Other species are known as hyperparasitoids, attacking other parasitoid Hymenoptera, e.g. bethylid (Jaramillo and Vega, 2009) and braconid (Saethre et al., 2011) species. However, overall little is known about this group that is estimated to include approximately 1,000 species (Masner, 1993a).

With 3,825 species described already in the early 1990s (Gibson, 1993), the Encyrtidae are a particularly large clade of parasitoids. While they parasitize on a wide range of arthropod larvae and eggs, e.g. Coleoptera (Bauer and Liu, 2007), Lepidoptera (Guerrieri and Noyes, 2005) and Diptera (Olton and Legner, 1974), the main hosts for this clade seem to be Coccoidea (Homoptera) (Gibson, 1993).

The Eulophidae are another large taxon, with around 3,900 described species and a diverse range of hosts (Gibson, 1993).

Lastly, the Platygastridae and Scelionidae are part of the ‘superfamily’ Platygastroidea, with around 4,000 described and up to 10,000 species estimated (Masner, 1993b). ‘The Platygastridae are a rather poorly known family of parasitoid wasps that attack a variety of hosts, especially cecidomyiid flies’ (Godfray, 1994). Scelionid wasps are mainly solitary egg endoparasitoids of various insect groups and spiders (Masner, 1993b). Taxonomically, it has to be mentioned that many authors consider the taxa constituting the Scelionidae – the Scelioninae, Teleasinae and Telenominae (Masner, 1993b) – as a subgroup of the Platygastridae (e.g. Madl, 2016; O'connor and Notton, 2013; Rajmohana, 2012). However, since the sorting of Hymenoptera in this project was based on 'Hymenoptera of the world' (Goulet and Huber, 1993), in which Platygastridae and Scelionidae are treated as different taxa (Masner, 1993b), both clades will be treated as separate taxa in this study.

3.3 General structure

This Master thesis consists of two work packages:

1) A statistical analysis of the dataset based on morphological identification to Morphospecies, collected in 2013. These analyses focus on measurements of diversity and community structure.

2) A documentation of molecular experiments for samples of the 2013 and 2017 sampling campaign. These investigations focus primarily on the possible use of samples for DNA-barcoding-approaches.

3.4 Analysis of Morphospecies Dataset

All described analyses were done for the complete parasitoid community and on family level. In Ceraphronidae, no individuals were found in plot HO1. Since the empty plot impeded statistical analysis, it was removed before Generalized Linear Model analysis..

3.4.1 Species-abundance distribution (SAD)

Rank abundance curves

Rank abundance graphs on land-use system level were created in R 3.5.1 (R Core Team, 2018) using the commands *rankabundance* and *rankabunplot* with scale = "logabun" in the package 'BiodiversityR' (Kindt and Coe, 2005).

Species accumulation curves

Species accumulation curves on land-use system level were calculated and plotted in R 3.5.1 (R Core Team, 2018). The command *speccaccum* with method = “random” in the package ‘vegan’ (Oksanen et al., 2018) was used for calculating the data points and standard deviations of the species accumulation curves. Data points and standard deviations were then transferred into a Microsoft Excel 2016 (Microsoft Office 365, Microsoft Corporation) table that was used as data basis for plotting the curves using the command *ggplot* in the package ‘ggplot2’ (Wickham, 2016).

3.4.2 Analysis of biodiversity and community structure

Venn diagrams

Venn diagrams were created in R 3.5.1 (R Core Team, 2018) for land-use systems and landscapes. The command *recast* in the package ‘reshape2’ (Wickham, 2007) and the command *t* for transposing the data matrix were used to re-organize the data in a way that Venn overlaps could be obtained. The commands *vennCounts* and *vennDiagramm* in package ‘limma’ (Ritchie et al., 2015) were used to calculate the classification counts and to create the diagrams.

Abundance

Abundance for each plot was calculated in R 3.5.1 (R Core Team, 2018) using the command *rowSums* . Means and standard deviations for land-use systems and landscapes were calculated using the *tapply* command.

Abundance data were then analyzed using Generalized linear models (GLMs). Best fitting families of distribution were evaluated using the Shapiro-Wilk Normality Test computed with the command *shapiro.test* as well as Quantile-Comparison Plots created with the commands *fitdistr* in the package ‘MASS’ (Venables and Ripley, 2002) and qqp in the package ‘car’ (Fox and Weisberg, 2011) and skewness-kurtosis plots generated with the command *descdist* in the package ‘fitdistrplus’ (Delignette-Muller and Dutang, 2015). Evaluated distribution families were Gaussian, Poisson, negative binomial and Gamma. GLMs were fitted using the *glm* command. If more than one family seemed suitable, GLMs were fitted for each of those families and compared. Non-overdispersed models were preferred over overdispersed ones, and within non-overdispersed models, the one with lowest Akaike Information Criterion (AIC) was chosen. Because some GLMs detected significant interactions between the factors land-use system and landscape, statistical analysis was done for land-use systems within each landscape and for the two landscapes using separate GLMs for each of this analysis. This was also done for datasets where no interaction between the two factors was detected to retain comparability of the results.

Differences between the two landscapes as well as between the land-use systems in each landscape were analyzed by doing multiple comparisons with Tukey's test for the selected fitted GLM using the *glht* command in the package 'multcomp' (Hothorn et al., 2008). P-values were adjusted using the Holm correction method. Additionally, differences between the same land-use systems in different landscapes were analyzed for the complete dataset using Wilcoxon rank sum test with the command *wilcox.test*.

Abundance was plotted using the *ggplot* command in the package 'ggplot2' (Wickham, 2016), with data points being depicted as pirate plots using the (sub-) command *geom_pirate* in the package 'ggpirate' (Braginsky, 2018). Indicators of significance for the land-use systems were added in PowerPoint (Microsoft Office 365, Microsoft Corporation).

Species richness

Species richness for each plot was calculated in R 3.5.1 (R Core Team, 2018) using the command *specnumber* in the package 'vegan' (Oksanen et al., 2018). Means and standard deviations for land-use systems and landscapes were calculated using the *tapply* command.

Analysis of species richness was done as described in detail for abundance. Like with abundance data, statistical differences were analyzed between both landscapes and between land-use systems within each landscape using separate GLMS, because some of the GLMs for the complete data detected an interaction between the two factors landscape and land-use system. As with abundance data, Wilcoxon rank sum test was used to quantify differences between the same land-use systems in the different landscapes for the complete parasitoid community dataset. Plotting of species richness was done as described in detail for abundance.

Diversity

Diversity was calculated as inverse Simpson Diversity (Simpson, 1949) in R 3.5.1 (R Core Team, 2018) for each plot using the *diversity* command with index = "invsimpson" in the package 'vegan' (Oksanen et al., 2018). Means and standard deviations for land-use systems and landscapes were calculated using the *tapply* command.

Analysis of diversity was done using GLMs, as described in detail for abundance. Like with abundance and species richness data, analysis of statistical differences between landscapes and land-use systems within each landscape was done using separate GLMs, because significant interactions between the two factors landscape and land-use system were detected in some GLMs. Differences between the same land-use systems in the Bukit Duabelas landscape and the Harapan landscape were analyzed in the same manner as described for species richness and abundance data. Plotting of diversity was done as described in detail for abundance.

Ordinations

Ordinations were computed in R 3.5.1 (R Core Team, 2018). Data sets were Hellinger-transformed before ordinations using the command *decostand* in the package 'vegan' (Oksanen et al., 2018) as Hellinger distances are suggested to be a suitable and meaningful measure for ordinations in abundance data (Legendre and Gallagher, 2001; Rao, 1995).

Linear or unimodal species response was evaluated by performing a Detrended Correspondence Analysis (DCA) using the *decorana* command in package 'vegan' (Oksanen et al., 2018) and checking the length of the first axis. Because the length of the first axis was > 3 for all datasets, with datasets for Ceraphronidae, Eulophidae and Platygastridae showing a clear unimodal response (axis length > 4), Detrended Correspondence Analysis was chosen as method for ordination.

Environmental information was fitted to the DCA using the *envfit* command in package 'vegan' (Oksanen et al., 2018), and the ordination was graphically depicted using the *plot* command.

Species turnover

Species turnover, the dissimilarity of communities between sampling sites of the same land-use system, was computed in R 3.5.1 (R Core Team, 2018) as a subpart of a dissimilarity matrix calculated with the command *vegdist* in the 'vegan' package (Oksanen et al., 2018). The appropriate index for *vegdist* was chosen by ranking the indices with the command *rankindex* in the 'vegan' package (Oksanen et al., 2018) and selecting the index with highest value. In some cases, Bray-Curtis and Jaccard index turned out the equally highest value. In these cases, Bray-Curtis Dissimilarity Index was chosen.

General statistical properties and possible interactions between the factors land-use system and landscape were investigated using Permutational Multivariate Analysis of Variance with the command *adonis2* in 'vegan' (Oksanen et al., 2018) and multilevel pairwise comparison with the command *pairwise.adonis* (Martinez Arbizu, 2017), adjusting the p-value with the command *p.adjust.m* using the "fdr" correction (Benjamini and Hochberg, 1995).

The distance matrix was converted to a data frame using the command *dist2list* in the ‘metagMisc’ package (Mikryukov, 2018) and modified to keep only rows that compared the same land-use system. As described for abundance, species richness and diversity data, this data frame was then evaluated for the best fitting family of distributions for GLMs using the commands *shapiro.test* and *fitdistr* in package ‘MASS’ (Venables and Ripley, 2002), Quantile-Comparison plots generated by the *qqp* command in package ‘car’ (Fox and Weisberg, 2011) and skewness-kurtosis plots generated with the *descdist* command in ‘fitdistrplus’ (Delignette-Muller and Dutang, 2015). Investigated families of distribution were Gaussian and Gamma. The appropriate GLM was chosen according to the same criteria described in detail in abundance. Because Permutational Multivariate Analysis of Variance suggested significant interactions of the two factors land-use system and landscape in some datasets, separate GLMs were used for statistical analysis of the two landscapes as well as for analysis of land-use systems within the two landscapes. Differences were analyses as described in detail for abundance data.

For plotting turnover, a modified data frame depicting only dissimilarities between plots of the same land-use system within the same landscape was used. Graphical depiction of turnover was done using the *ggplot* command in package ‘ggplot2’ (Wickham, 2016), with data being depicted as pirate plots using the command *geom_pirate* in the package ‘ggpirate’ (Braginsky, 2018).

3.5 Molecular analyses

3.5.1 Preliminary studies

2013 Samples

Samples from 2013 have been examined thoroughly in respect to their suitability for molecular studies. Preliminary project ideas included metabarcoding-approaches on an individual level, comparable to a similar study investigating midges (Meier et al., 2016), or a community-phylogenetics approach.

DNA from 2013 samples was extracted using a total of four different methods of DNA-Extraction – the Genaxxon DNA Purification Mini Spin Column Kit, the DNeasy Blood & Tissue Kit (Qiagen), the QuickExtract DNA Extraction Solution (Lucigen) and the HotSHOT DNA extraction method (Montero-Pau et al., 2008).

To test for the successful extraction of high quality DNA, a polymerase-chain-reaction targeting a highly conserved fragment of about 550bp length within the 28S rDNA marker was applied using the primer pair 28Sa-28Sbout (Tully et al., 2006). Those PCRs, however, resulted in highly insufficient, low amplification success rates for all four methods of DNA extraction. It was concluded that the DNA of most specimen was too degraded for the successful application of molecular techniques, most likely due to handling time at room temperature while specimen were determined. In an effort to use the pre-sorted samples from 2013 for a molecular investigation, up to 10 individuals from a subset of all Morphospecies, i.e. those that accounted for at least 1% of the total abundance where pooled for DNA-extraction using the DNA Purification Mini Spin Column Kit (Genaxxon). While the subsequent PCR targeting the fragment within the 28S-region resulted in an improved amplification success compared to individual samples, the rates of successful amplification overall were still below 50% and could not be deemed promising for further research (Tab. 1), especially given the fact that specimen of many Morphospecies were no longer available.

Table 1. Overview of amplification success for a 550bp 28S-fragment with pooled samples.

Taxon	Morphospecies in total	Morphospecies accounting for at least 1% of total abundance	Successfully amplified Morphospecies in first trial	Morphospecies with no more specimen available
Braconidae	309	22	9	0
Ceraphronidae	153	33	14	12
Encyrtidae	170	26	2	2
Eulophidae	168	29	21	4
Platygastridae	189	18	5	7
Scelionidae	193	19	6	1
Total	**1,182**	**147**	**57**	**26**

2017 Samples

With specimen from the 2013 collection not suitable for advanced molecular investigations, it was decided that samples from 2017 – likely containing less degraded DNA – should be used for this purpose. In order to test the assumption of the fresh samples containing better-quality DNA, ten specimen from the 2017 samples belonging to the plot BF1 were used for DNA extraction with the DNA Purification Mini Spin Column Kit (Genaxxon Bioscience) and the extracted DNA was subjected to PCR targeting the highly conserved 28S-fragment for control of quality. An amplification and subsequent sequencing success of 100% indicated that the DNA quality of the fresh samples was sufficient for their use in molecular studies (Fig. 1).

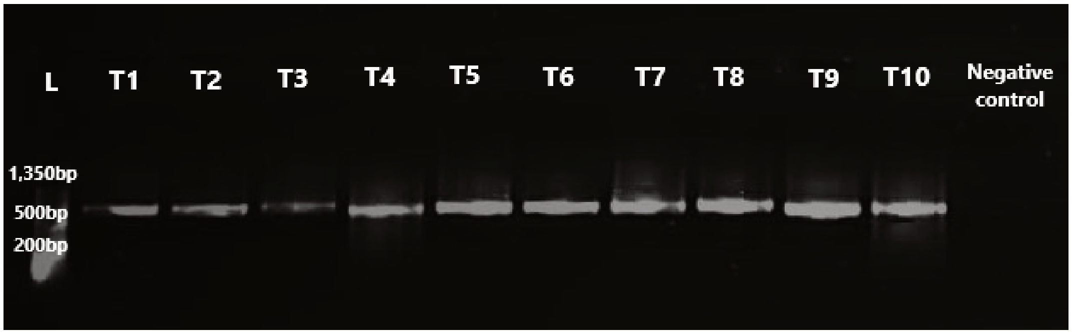

Figure 1. Amplification success of 10 test samples from BF1 (T1 -T10) targeting a 550bp 28S-fragment.

However, given the fact that sorting the 2017 samples to Morphospecies level was a task too time-consuming for a master thesis, a plan was developed to sort out only those specimen corresponding to the six major taxa (Braconidae, Ceraphronidae, Encyrtidae, Eulophidae, Platygastridae and Scelionidae) that had been sorted to Morphospecies level in the 2013 samples, and to investigate the possibility of metabarcoding with these samples.

Since the standard barcoding fragment from the Cytochrome-C-Oxidase Subunit 1 (COI) (Folmer et al., 1994; Hebert et al., 2003) is too long for MiSeq sequencing with the Illumina-technology, a shorter fragment of approximately 313bp length within the classic COI barcoding region (Leray et al., 2013) was chosen. This fragment was selected because it had already proven to be a suitable contender for metabarcoding among different arthropod groups (Brandon-Mong et al., 2015).

Preliminary tests with this fragment using the extracted DNA from the 2017 samples resulted in high amplification success (Fig. 2) and sequencing using the Sanger method yielded appropriate sequences in 90% of tested samples. In the light of these promising findings, this fragment was chosen for further investigation.

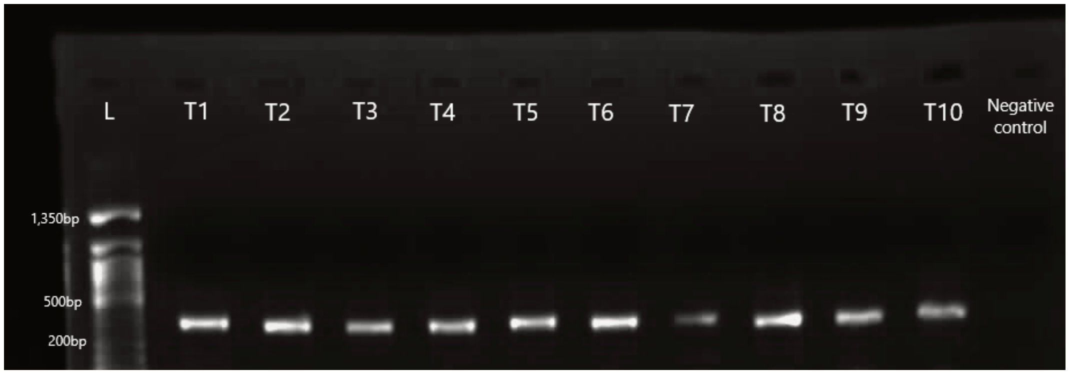

Figure 2. Amplification success of 10 test samples from BF1 (T1 – T10) targeting a 313bp fragment within the COI-region.

3.5.2 Sampling and subsampling

From the unsorted parasitoid wasps collected in 2017, individuals of 24 plots, comprising the forest, rubber monoculture and oil palm monoculture land-use systems were imported to Göttingen. The samples had been sorted to order level in spring 2018. Subsequently, all individuals from the families Braconidae, Ceraphronidae, Encyrtidae, Eulophidae, Platygastridae and Scelionidae had been separated from the rest of the mixed canopy arthropods by Nurul Novianti and Rizky Nazarreta (EFForTS interns from Bogor Agricultural University). From samples obtained this way, ≤50 individuals per plot were randomly selected. This way, a total amount of 987 specimen was selected for molecular analysis.

3.5.3 Sample preparation

DNA-extraction was carried out using the Agencourt DNAdvance Genomic DNA Isolation Kit (Beckman Coulter). After incubation in Lysis Buffer and Proteinase K, the rest of the extraction was performed using the Biomek 4000 automated platform (Beckman Coulter), with DNA eluted in 50 µl of water.

3.5.4 Polymerase chain reactions

PCR reagents were mixed in the ratio presented in Tab. 2. Primers targeted a 313 bp sub fragment (Leray et al., 2013) of the classic COI barcoding region (Folmer et al., 1994; Hebert et al., 2003) and were modified with Illumina-adaptors and plot-specific barcodes on both ends. The PCR-program (Tab. 3) was run in the Biometra TAdvanced Thermal Cycler (Analytik Jena).

Table 2. Mastermix for first step PCR per 2.5 µl of DNA template.

Reagent	Amount (µl)
H_2O	12.55
5x Phusion HF Buffer	5
dNTP Mix	0.5
Primer forward	2
Primer reverse	2
Phusion DNA Polymerase (2U/µl)	0.25

Table 3. PCR program for first-step PCR.

Step	Temperature (°C)	Duration (seconds)	Loop
Initial denaturation	98	30	
Denaturation	98	15	39x
Annealing	48	15	
Elongation	72	30	
Final elongation	72	600	
Cooling	4	∞	

3.5.5 Purification of PCR product

PCR products were purified using the Agencourt AMPure XP PCR purification kit (Beckman Coulter) together with the Biomek 4000 automated platform (Beckman Coulter) according to the manufacturers protocol with two changes: 1. One additional pause after the final ethanol washing step to check for complete removal of ethanol; 2. eluting the purified products in a final volume of 20 µl H_2O.

3.5.6 Measurement of concentration

Concentration of PCR product was measured at the Institute of Microbiology and Genetics of the University of Göttingen using the Synergy 2 Microplate Reader (BioTek) with the QuantiFluor dsDNA System (Promega). Target DNA concentration was > 10 ng/µl. PCR products belonging to the same land-use system within the same landscape were then pooled equimolarly.

4 Results

4.1 Morphospecies dataset

The Morphospecies dataset is based on a total of 10,070 specimen identified to 1,182 Morphospecies (Msp). The Braconidae account for 309 Msp., the Ceraphronidae for 153, Encyrtidae for 170, Eulophidae for 168, Platygastridae for 189 and Scelionidae for 193 MSp.

4.1.1 Species-abundance distribution (SAD)

Rank abundance curves

The maximum number of Msp (914) was found in forest, followed by 742 Msp in Jungle Rubber. Total number of Msp for rubber plantations was 413 and 410 Msp in oil palm plantations (Fig. 3). Starting point of the species accumulation curve was highest in Jungle Rubber and lowest in oil palm.

In individual parasitoid families, the highest number of Msp was always found in forest, the lowest number in monocultures. Height of starting points of the curves varied between families (Fig. A1, A10, A19, A28, A37 and A46 in appendix).

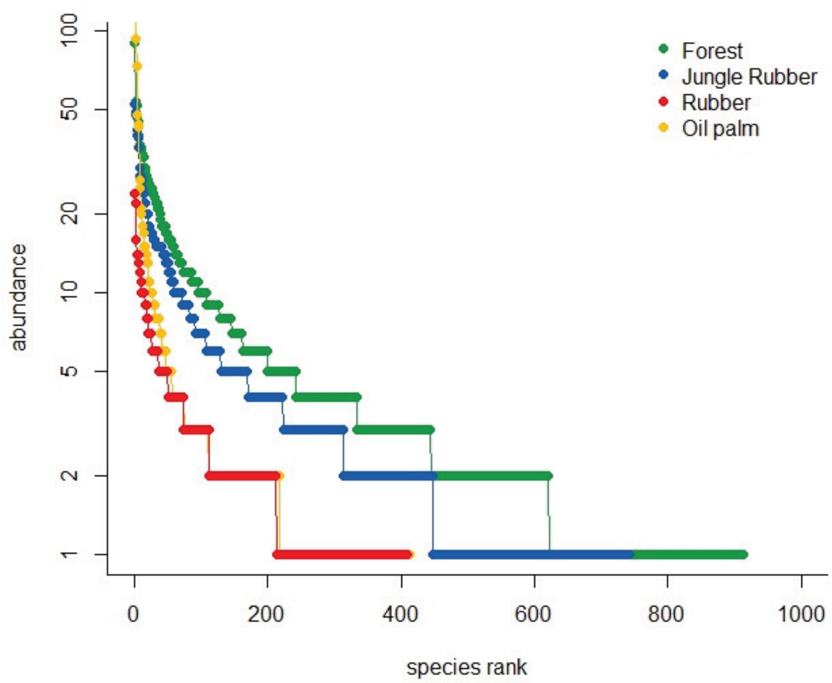

Figure 3. Rank-abundance curves for parasitoid wasps in four land-use systems. Abundance is shown as logarithm of abundance using base 10.

Species Accumulation curves

Curves indicate maximum number of Msp after a single sampling in forest (279.52) with number in the monocultures being lowest (oil palm: 84.61, rubber: 89.81) and intermediate in Jungle Rubber (175.78). Steepness of forest and Jungle Rubber curves was higher than in both monocultures (Fig. 4). These aspects indicate greater species richness in forest and Jungle Rubber compared to rubber and oil palm plantations. In addition, none of the four land-use systems reached saturation after eight sampling sites (Fig. 4), indicating undersampling.

The individual parasitoid families showed the same patterns: After one sampling, the highest number of Msp were captured in forest with the lowest numbers found in monocultures (Fig. A2, A11, A20, A29, A38 and A47 in appendix). In Encyrtidae, growth of the curves was similar for all four land-use systems (Fig. A20 in appendix), however, in all other families species accumulation curves for forest and Jungle Rubber showed higher steepness than those for monocultures.

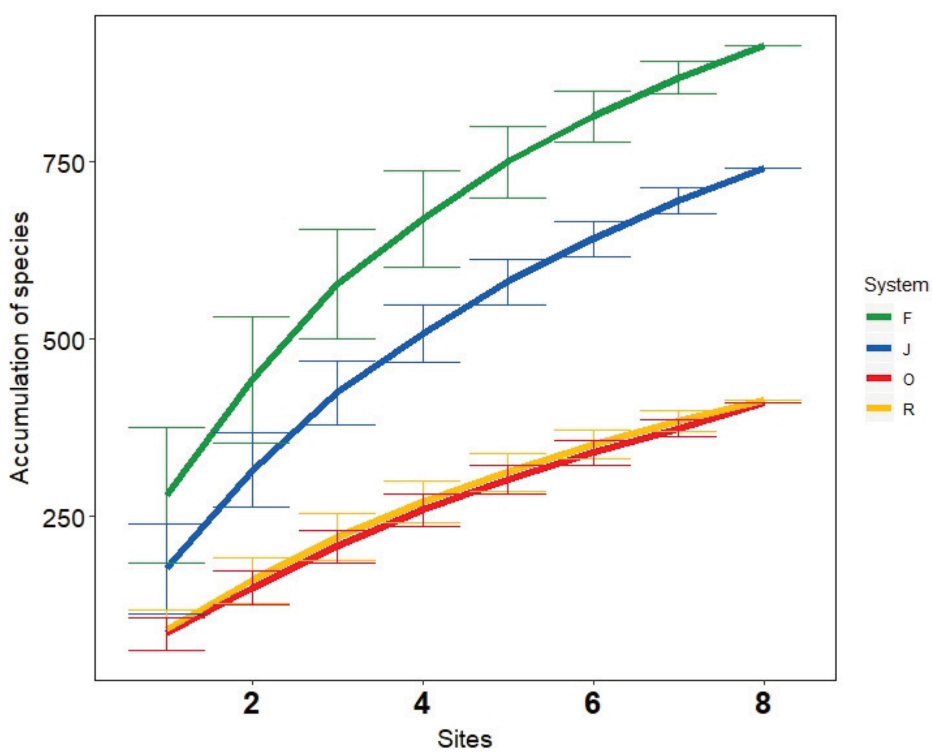

Figure 4. Species accumulation curves for parasitoid wasps in four land-use systems. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Error bars represent standard deviation.

4.1.2 Analysis of biodiversity and community structure

Venn diagrams

Approximately 46% of Msp (551 out of 1182) were found exclusively in forest and/or Jungle Rubber with 8.9% of Msp (106 out of 1182) found exclusively in monocultures. In comparison, 11% (136 out of 1182) of all Morphospecies were found in all four land-use systems (Fig. 5). Furthermore, 34% (405 out of 1182) Msp were found exclusively in the Bukit Duabelas landscape (henceforth referred to as Bukit Duabelas) and only 14% of Msp (161 out of 1182) were found only in the Harapan landscape (henceforth referred to as Harapan). 52% (616 out of 1182) of Msp were observed in both landscapes (Fig. 6).

At the family level, the proportion of Msp found in forest and/or Jungle Rubber ranged from 18% (in Encyrtidae) to 64% (in Platygastridae); in contrast, the proportion of Msp found only in monocultures ranged from 4.5% (in Ceraphronidae) to 11.3% (in Scelionidae). Between 1% (in Platygastridae) and 24% (in Encyrtidae) of Msp were found in all four land-use systems (Fig. A3, A12, A21, A30, A39, and A48 in appendix). The percentage of Msp found exclusively in Bukit Duabelas ranged from 18.8% (in Encyrtidae) to 52.9% (in Platygastridae), with between 5.9% (in Eulophidae) and 20% (in Braconidae) of Msp present only in Harapan. Between 35.9% (in Platygastridae) and 70.5% (in Encyrtidae) of Msp were found in both landscapes (Fig. A4, A13, A22, A31, A40 and A49 in appendix).

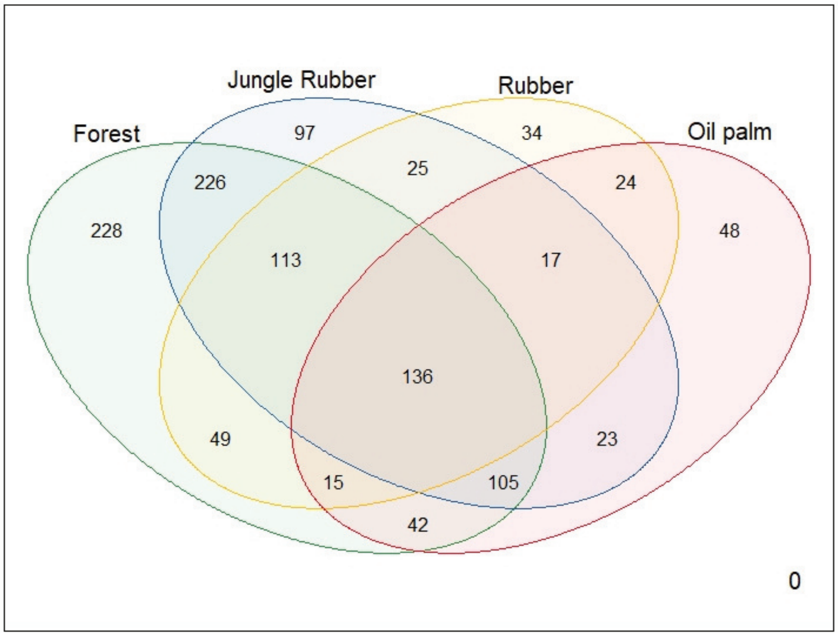

Figure 5. Venn diagram for parasitoid wasps in four different land-use systems. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated land-use systems.

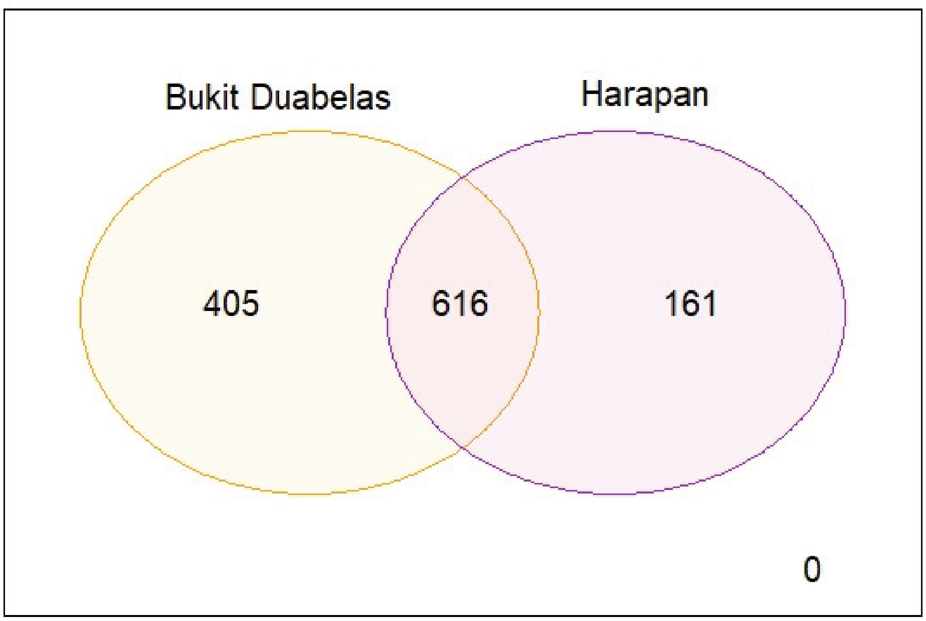

Figure 6. Venn diagram for parasitoid wasps in the two landscapes. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated landscapes.

Abundance

The abundance of parasitoid wasps was significantly lower in Harapan than in Bukit Duabelas (Fig. 7, $p < 0.05$). In general, forest produced greatest abundance, monocultures the lowest abundance with Jungle Rubber having an intermediate abundance (Tab. 4). Differences between land-use systems were more pronounced and statistically significant in Bukit Duabelas. In Bukit Duabelas, forest had significantly higher abundance of parasitoid wasps than Jungle Rubber (Fig. 7, $p < 0.01$) and monocultures (both $p < 0.0001$). Additionally, parasitoid wasps were significantly more abundant in Jungle Rubber than in the monocultures (Fig. 7, all $p < 0.001$). Lastly, abundance of parasitoid wasps was significantly higher in forest of Bukit Duabelas than in forest of Harapan ($p < 0.05$).

On family level, parasitoid wasp abundances in Bukit Duabelas were significantly higher than in Harapan for the Ceraphronidae ($p < 0.05$) (Fig. A14 in appendix,) and the Eulophidae ($p < 0.01$) (Fig. A32 in appendix); however, no significant abundance differences between the two landscapes were found in the remaining four families, indicating that the overall pattern was strongly influenced by Ceraphronidae and Eulophidae. With exception of the Encyrtidae and Scelionidae, highest abundance was found in forest and lowest abundance in the monocultures, regardless of landscape (Tab. A1, A5, A13, A17 and Fig. A5, A14, A32 and A41 in appendix). In the Encyrtidae, abundance in Harapan was highest in rubber monocultures and second highest in Jungle Rubber (Tab. A9 and Fig. A23 in appendix), while highest abundance of Scelionidae in Harapan was observed in Jungle Rubber (Tab. A21 and Fig. A50 in Appendix).

Table 4. Abundance of parasitoid wasps in four land-use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	544.62 ± 307.43	371 ± 128.88	215.37 ± 121.22	127.75 ± 47.427
Bukit Duabelas Landscape	787.75 ± 204.44	449.5 ± 71.94	203 ± 71.72	150.75 ± 35.22
Harapan Landscape	301.5 ± 145.28	292.5 ± 130.96	227.75 ± 169.52	104.75 ± 50.95

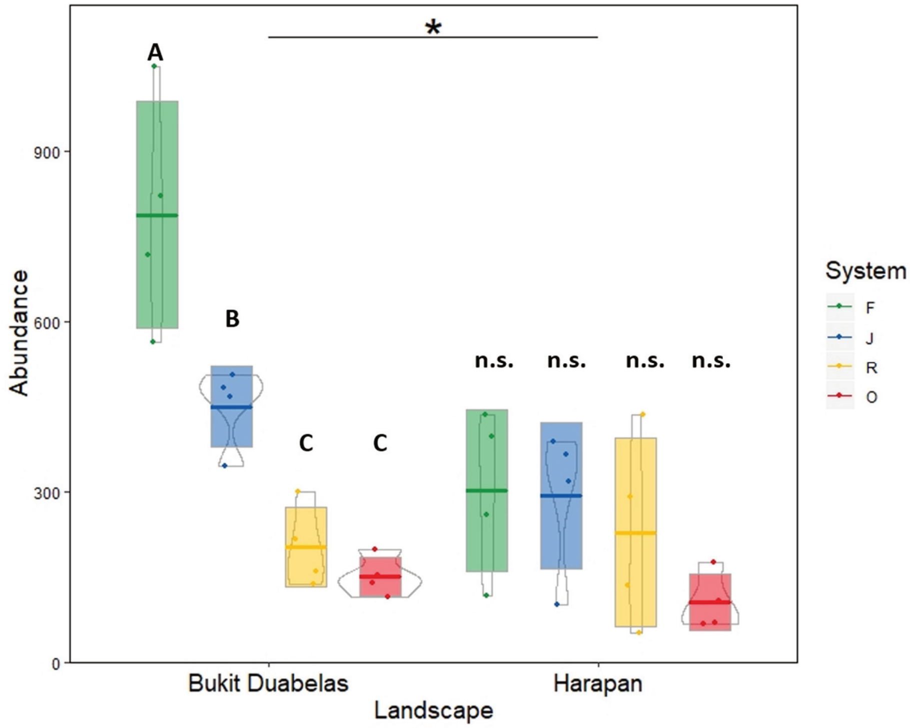

Figure 7. Pirate plots of parasitoid wasp abundance in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Species richness

Species richness of the parasitoid community was significantly lower in Harapan than in Bukit Duabelas ($p < 0.05$, Fig. 8). In both landscapes, parasitoids showed highest species richness in forest and lowest in the monocultures (Tab. 5). In Bukit Duabelas, species richness in forest was significantly higher than in Jungle Rubber ($p < 0.01$) and monocultures (all $p < 0.001$). Additionally, species richness in Jungle Rubber was significantly higher than in monocultures (all $p < 0.001$). In Harapan, species richness in forest was significantly higher than in monocultures (all $p < 0.05$) and significantly more species were found in Jungle Rubber than in oil palm ($p < 0.05$). Forest in Bukit Duabelas had significantly more species than forest in Harapan ($p < 0.05$).

At the family level, species richness was significantly higher in Bukit Duabelas compared to Harapan in Ceraphronidae, Encyrtidae, Eulophidae, Platygastridae and Scelionidae (all p <0 .05) (Fig. A15, A24, A33, A42 and A51 in appendix), but not in Braconidae (Fig. A6 in appendix). With exception of the Encyrtidae and Scelionidae, the highest species richness was found in forest and the lowest in monocultures, regardless of the landscape (Tab. A2, A6, A14, and A18 in appendix). In Encyrtidae and Scelionidae, the highest number of species in Harapan was found in Jungle Rubber (Tab. A10 and A22 in appendix).

Table 5. Species richness of parasitoid wasps in four land-use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	263 ± 108.87	184.5 ± 59.53	89.37 ± 30.58	85.62 ± 24.42
Bukit Duabelas Landscape	355 ± 42.37	223 ± 28.99	101 ± 32.14	99.75 ± 14.46
Harapan Landscape	171 ± 57.38	146 ± 58.96	79 ± 29.35	70.25 ± 23.5

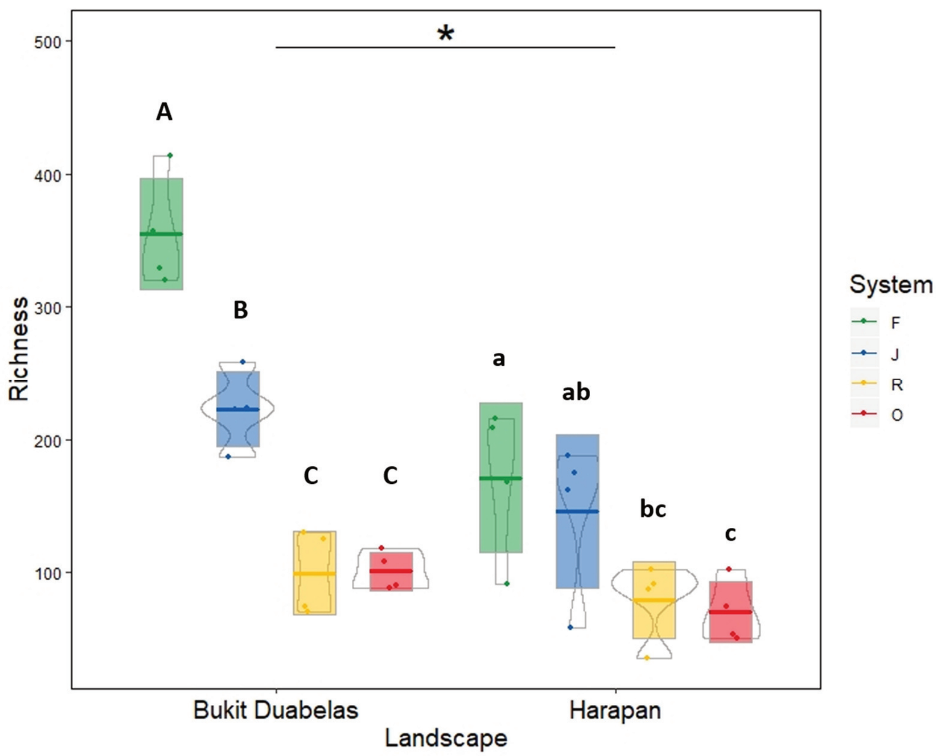

Figure 8. Pirate plots of parasitoid wasp species richness in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Diversity

Inverse Simpson Diversity of the parasitoid wasp community was significantly higher in Bukit Duabelas than in Harapan ($p < 0.01$) (Fig. 9). Diversity was highest in forest and lowest in monocultures for both landscapes (Tab. 6), however, statistically significant differences were only found in Bukit Duabelas. In Bukit Duabelas, diversity of parasitoid wasps in forest was significantly higher than in monocultures (all $p < 0.001$) and parasitoid wasps were significantly higher in diversity in Jungle Rubber than in rubber monocultures ($p < 0.001$). Additionally, diversity of parasitoid wasp was significantly higher in forest of Bukit Duabelas than in forest of Harapan ($p < 0.05$).

The inverse Simpson index values of the families Encyrtidae, Eulophidae, Platygastridae and Scelionidae were significantly higher in Bukit Duabelas than in Harapan (Fig. A25, A34, A43 and A52 in appendix, all $p < 0.05$). In the Braconidae and Ceraphronidae, no significant differences between the landscapes were found (Fig. A7 and A16 in appendix). With exception of the Encyrtidae, inverse Simpson Diversity of parasitoid wasps was highest in forest and lowest in monocultures in both landscapes (Tab. A3, A7, A15, A19 and A23 in 23ppendix). The Encyrtidae showed highest diversity in Jungle Rubber and second highest diversity in oil palm within Harapan (Tab. A11 in appendix).

Table 6. Inverse Simpson Diversity of parasitoid wasps in four land-use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	124.92 ± 55.04	87.88 ± 37.14	34.88 ± 21.98	59.17 ± 13.86
Bukit Duabelas Landscape	170.15 ± 31.4	108.72 ± 35.02	43.05 ± 15.87	69.53 ± 9.96
Harapan Landscape	79.69 ± 25.06	67.05 ± 28.91	26.7 ± 26.41	48.81 ± 7.93

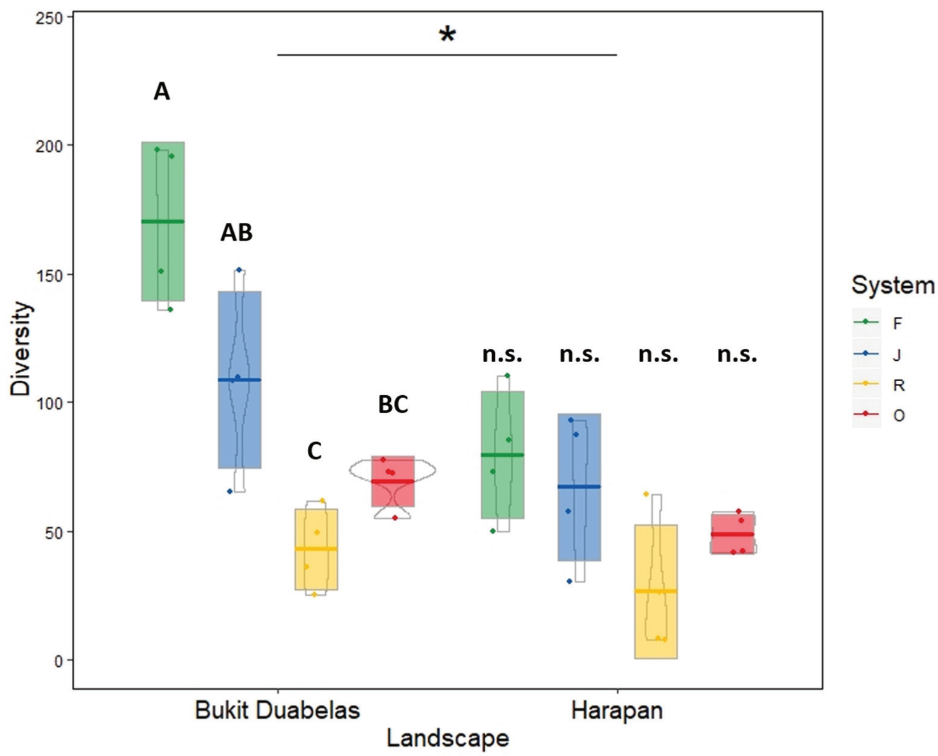

Figure 9. Pirate plots of parasitoid wasp inverse Simpson Diversity in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Community structure

While parasitoid wasp communities of forest and Jungle Rubber overlapped to a degree, communities of oil palm and rubber were distinct (Fig. 10). This indicates that parasitoid wasp communities of forest and Jungle Rubber had similar species composition compared to the communities of oil palm and rubber. In addition, forest plots showed little variation in the ordination compared to the other three land-use systems. Overall, the DCA showed 58.8% of the total variance in the plots.

Analyzed at the family level, ordinations differed considerably from those of the overall dataset. DCAs showed a stronger overlap between communities of different land-use systems (Fig. A8, A17, A26, A35, A44 and A53 in appendix), with the only distinct land-use systems being oil palm in Braconidae and Encyrtidae (Fig. A8 and A26 in appendix). The percentage of variance depicted by the DCAs ranged from 55.08% (in Eulophidae, Fig. A35 in appendix) to 61.12% (in Braconidae, Fig. A8 in appendix).

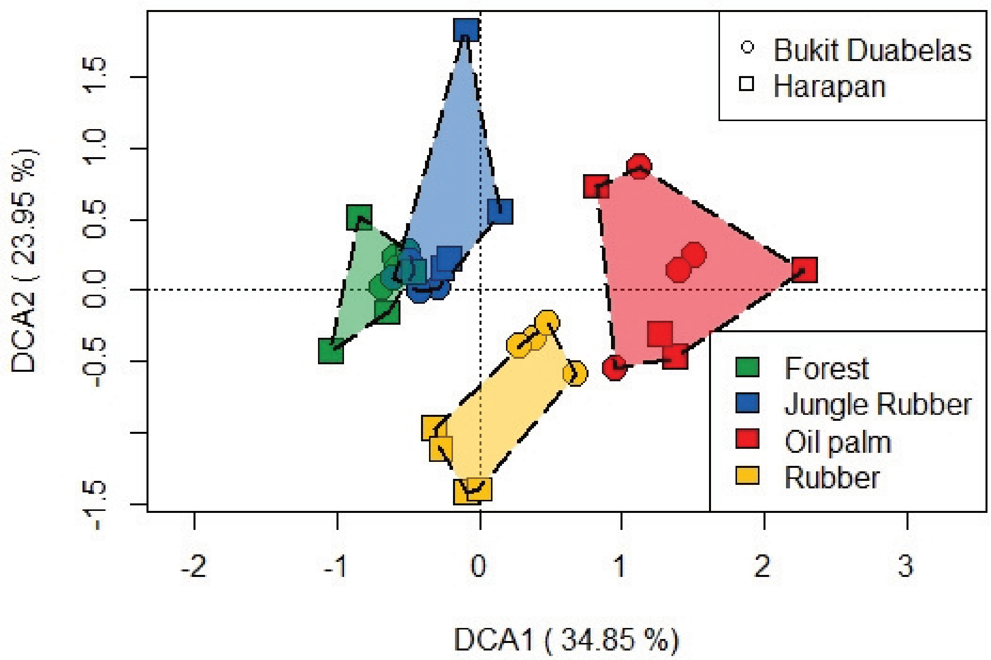

Figure 10. Detrended Correspondence Analysis for parasitoid wasps in four land-use systems based on a matrix of Hellinger-transformed data. Percentages on axes represent the proportion of total variation shown in the ordination.

Species Turnover

Species turnover, i.e. the dissimilarity of community composition between plots of the same land-use system, was overall significantly higher in Harapan than in Bukit Duabelas ($p < 0.001$). In Harapan, species turnover was highest in Jungle Rubber and lowest in oil palm, while in Bukit Duabelas, species turnover was highest in oil palm monocultures and lowest in forest (Fig 11, Tab. 7). Statistically significant differences in species turnover between land-use systems were only found in Bukit Duabelas. Here, oil palm had a significantly higher species turnover than Jungle Rubber ($p < 0.05$), forest and rubber (both $p < 0.001$). Additionally, Jungle Rubber in Bukit Duabelas had a higher turnover than forest ($p < 0.01$) and rubber ($p < 0.05$). Moreover, forest, Jungle Rubber and rubber plantations showed significantly higher turnover rates in Harapan than in Bukit Duabelas (all $p < 0.05$).

Family based turnover rates in Harapan were significantly higher than in Bukit Duabelas in Encyrtidae, Eulophidae and Scelionidae (Fig. A27, A36 and A54 in appendix, all $p < 0.05$), while Braconidae, Ceraphronidae and Platygastridae showed no significant differences in species turnover between the two landscapes (Fig. A9, A18, A45 in appendix). Within each landscape, turnover rates were highest in one of the monocultures (Tab. A8, A12, A16, A20 and A24 in appendix), with the exception of the Braconidae, where turnover rates in Harapan were highest in Jungle Rubber (Tab. A4 in appendix). In all six families, forest had either the lowest or the second lowest turnover rate, regardless of the landscape.

Table 7. Species turnover rate of parasitoid wasps measured as Morisita-Horn dissimilarity index in four land-use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	**Jungle Rubber**	**Rubber**	**Oil Palm**
Overall	0.69 ± 0.12	0.75 ± 0.09	0.7 ± 0.11	0.78 ± 0.06
Bukit Duabelas Landscape	0.51 ± 0.05	0.63 ± 0.07	0.53 ± 0.06	0.73 ± 0.04
Harapan Landscape	0.73 ± 0.09	0.79 ± 0.09	0.7 ± 0.1	0.76 ± 0.06

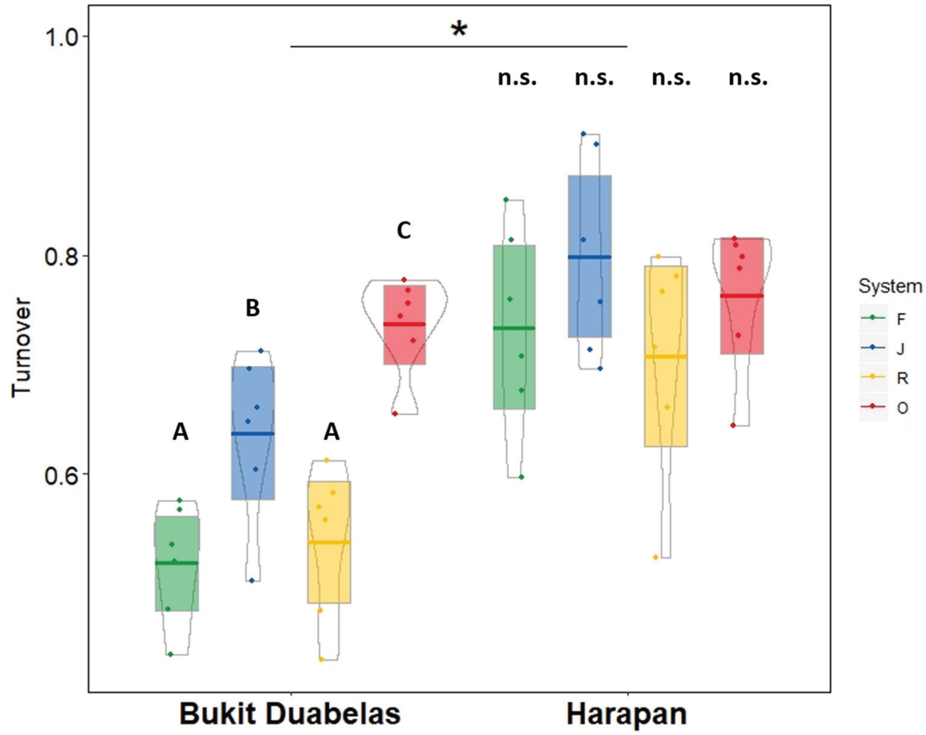

Figure 11. Pirate plots of parasitoid wasp species turnover rate in four land-use systems in two landscapes calculated as Morisita-Horn dissimilarity index. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

4.2 Molecular analyses

While individual-based PCRs yielded products, the concentration varied heavily between individuals. Concentration measurement done for the samples of HF1 showed that only 36% of PCR products had a final concentration of 10 ng/µl or more, the minimum concentration for next generation sequencing on the MiSeq platform (Poehlein, personal communication). The proportion of failed PCRs – hereby defined by a concentration < 1 ng/ µl – was 34%. As a result of the low success rate it was decided to terminate the individual-based experiments and to proceed by pooling the DNA of specimen corresponding to one plot before PCR (see chapter “Molecular experiments with pooled DNA” in appendix). Results from those experiments indicate that high variability of concentration and high amount of failed PCR product might have been avoided by standardizing the concentration of template DNA. This was however impeded by the fact that no reliable equipment for measuring genomic DNA concentrations was at our disposal.

5 Discussion

5.1 Response of biodiversity along the land-use-transformation gradient in two landscapes

I hypothesized that abundance, species richness and inverse Simpson Diversity would be highest in forest, intermediate in Jungle Rubber and lowest in rubber and oil palm monocultures. Despite the aforementioned observations in Encyrtidae and Scelionidae, the results for all families combined confirm this hypothesis.

Overall parasitoid wasp abundance decreases from forest to oil palm and rubber monocultures, indicating that forest habitats have the capacity to host more individuals of parasitoids than monocultures. A possible explanation for this phenomenon might be a reduction in plant biomass that comes with land-use (Barnes et al., 2017). Knops et al. (1999) reported a correlation between plant biomass and abundance of herbivore insects. Given this correlation, it might be concluded that increased plant biomass of trees and non-wooden vascular plants like epiphytes and understory vegetation could lead to higher carrying capacity for herbivorous insects in forest, and subsequently to more individuals of parasitoid wasps.

Abundance of parasitoid wasps is higher in Bukit Duabelas than Harapan. This finding is mainly due to the higher parasitoid abundance in forest of Bukit Duabelas (BF) compared to the Harapan forest (HF). Additionally, this finding seems to be strongly influenced by the families Ceraphronidae and Eulophidae, being the only families that showed significantly lower abundance in Harapan. Similar to the overall parasitoid community, lower abundance in Ceraphronidae and Encyrtidae in Harapan seem mainly due to lower abundance in HF compared to BF. The interpretation of this observations could be that plant biomass and consequently abundance of herbivore insects might be lower in Harapan forest compared to Bukit Duabelas forest, especially for host organisms of Ceraphronidae and Eulophidae. However, because abundance values can be influenced by single, individual-rich species, they have to be interpreted with caution. A good example to demonstrate influence of single species are the Encyrtidae in plot HR4. Here the weight of Morphospecies (MSp) *Enc011* (91 individuals) and *Enc029* (104 individuals) is so strong that overall, mean values for rubber monocultures are the highest for all four land-use systems. Without those two MSp, mean values for forest are highest (and rubber only second-highest).

Species richness and inverse Simpson Diversity decline from forest over Jungle Rubber to monocultures on level of the complete parasitoid community. This trend is also apparent in all families except the Encyrtidae and Scelionidae in Harapan. Since canopy fogging usually manages to cover the canopy in monocultures (Drescher, personal communication), but cannot completely cover the canopies of forest and Jungle Rubber which are higher (Kotowska et al., 2015), differences in species richness between forest, Jungle Rubber and monocultures have likely been underestimated. The negative impact of conversion from rainforest to monocultures like rubber and oil palm plantations on biodiversity has been observed across all domains of life, e.g. vascular plants (Beukema et al., 2007), birds (Aratrakorn et al., 2006), bats (Phommexay et al., 2011), moths (Alonso-Rodríguez et al., 2017) and even testate amoebae (Krashevska et al., 2016). With that in mind, the decline in parasitoid species richness might be explained by the parasitoids dependency on host organisms. Novotny et al., (2006) suggested that plant diversity is the main factor contributing to the general higher diversity of herbivore insects in the tropics, and Hunter and Price (1992) suggested that higher heterogeneity in plants may support a higher heterogeneity in herbivores, which can lead to increased diversity in their natural enemies. Losses in plant species richness as well as reduction in diversity of understorey plants with rainforest conversion to monocultures have been documented for the investigated plots (Kusuma et al., 2018; Rembold et al., 2017). Species richness and diversity loss in parasitoids over the land-use gradient from forest over Jungle Rubber to the monocultures could therefore be interpreted as a bottom-up effect, with loss in plant biodiversity (Beukema et al., 2007; Drescher et al., 2016) and subsequently herbivore diversity leading to a decline in parasitoid diversity. The relatively high species richness and diversity in Jungle Rubber also falls in line with this interpretation of the findings, as plant diversity in this agro ecosystem is considerably higher than in monocultures (Beukema et al., 2007) and plants coexisting in Jungle Rubber in Jambi originate from natural forest (Gouyon et al., 1993). Therefore, it is unsurprising that the transition from forest to Jungle Rubber does not affect parasitoid biodiversity as severely as transition to monocultures.

Overall, Harapan shows lower species richness and diversity Bukit Duabelas. The main contributing factor for this phenomenon are the forest systems, which are significantly higher in parasitoid wasp species richness and diversity in Bukit Duabelas than in Harapan. Following the aforementioned relation of plant biodiversity influencing parasitoid diversity, this observation might indicate that plant species diversity is less in HF compared BF, leading to a reduction in herbivore diversity. However, it is also possible that HF has a higher host richness and subsequently lower individual density per host species, resulting in a decline of specialist parasitoid species richness. A similar explanation, known as the 'Resource Fragmentation Hypothesis' (Janzen, 1981; Janzen and Pond, 1975) has been brought forward as a possible reason for why species richness of parasitoids (especially Ichneumonidae) apparently does not increase in the tropics compared to temperate regions (Gauld, 1986; Janzen and Pond, 1975; Owen and Owen, 1974). The 'Resource Fragmentation Hypothesis' (Janzen, 1981; Janzen and Pond, 1975) explains this observation with lower individual density of host species resulting from higher species richness of host organisms. This would lead to tropical parasitoids having to be more adapt on locating individual hosts or more generalistic than their counterparts from temperate regions, subsequently reducing parasitoid species density (Janzen, 1981). As for lower species richness and diversity of parasitoid wasps in Harapan compared to Bukit Duabelas, there are arguments for both explanatory approaches. A survey of butterflies – possible host organisms for parasitoid wasps – found more species and a higher diversity in HF compared to BF (Hidayat, 2018). This might indicate a general higher diversity of host insects, leading to lower density of individual host species and subsequently to lower species richness and diversity of specialized parasitoid wasps. On the other hand, lower species richness in Harapan forest and Jungle Rubber has been found in ants (Drescher, personal communication), indicating that arthropod species richness might generally be lower in HF than in BF. This would strengthen the idea that lower species richness of parasitoids in HF is linked to lower host richness.

At the level of individual families, species richness of Scelionidae and Encyrtidae in Harapan Jungle Rubber (HJ) was higher than in HF. However, in Bukit Duabelas both families follow the general trend of decreasing species richness from forest over Jungle Rubber to monocultures. Given the aforementioned idea that HF might be more degraded than BF, these findings might indicate that in both families, forest species are particularly sensitive to disturbance. Additionally, inverse Simpson Diversity in Encyrtidae was higher in HJ and Harapan oil palm (HO) than in HF. Inverse Simpson Diversity Index depends on species richness and dominance of individual species. Hence, this observation might be caused by a higher proportion of rare species in HF compared to HO and HJ, accompanied with relatively low species richness of HF compared to HJ.

5.2 Community composition

I hypothesized that community composition of forest and Jungle Rubber would be similar, while oil palm and Jungle Rubber communities would be distinct from the other land-use systems. This hypothesis could be confirmed for the complete parasitoid community, as indicated by the Detrended Correspondence Analysis (DCA).

The findings for community structure presented in this master thesis are in line with observations of canopy ants from the exact same plots (Drescher et al. in prep.). These results can be interpreted as an indicator that community composition is altered in disturbed systems. Rembold et al. (2017), reported a high abundance and relatively high proportion of non-forest plants in oil palm and rubber monocultures for the EFForTS study area. Those plants are likely to introduce new herbivore host species and consequently non-forest parasitoid species. These 'alien' parasitoids might also explain the observation of Msp that were only found in monocultures. Additionally, plant species originating from forest might become more abundant after rainforest conversion. Parasitoids specializing on host organisms associated with these particular plant species might therefore be favored in monocultures. Following the previously outlined cascading effect from plant over herbivore insects to parasitoid wasps, the relative similarity of community composition in forest and Jungle Rubber can be interpreted as a result of similar plant species composition in these two habitats. A survey conducted in Jambi Jungle Rubber by Gouyon et al. (1993) revealed that all plant species except rubber originated from natural forest, and while Rembold et al. (2017) found a high abundance of non-forest plants in Jungle Rubber, most plant species did originate from natural forest. Given these findings, it seems likely that parasitoid fauna of forest is a main source for parasitoid communities in Jungle Rubber, which would explain why communities from these two systems map closely together in the DCA.

5.3 Species turnover

For the dissimilarity of species composition between sampling sites within the same land-use system, referred to as species turnover, I hypothesized that turnover rates would be highest in forest and lowest in monocultures. This hypothesis was rejected by findings that turnover rate in forest is either lowest or second lowest for the complete parasitoid community and at the family-level.

This finding seems counterintuitive, as higher species richness in forest compared to other land-use systems, together with undersampling as indicated by species accumulation curves would predict a higher difference in community assembly between forest plots. That being said, relatively low turnover rate in herbivore insects of lowland rainforest has been reported before (Novotny et al., 2007), which might explain the comparatively low species turnover of parasitoids in rainforest. A possible explanation for the high dissimilarity in parasitoid composition especially in oil palm systems might be the method of clearing. Forest and Jungle Rubber are often converted to monocultures using the slash-and burn method (Ketterings et al., 1999). Additionally, taller vegetation is often completely removed when monoculture plantations are replanted. It can be expected that intense clearing methods remove most of the previous canopy fauna, with chances of survival for faunal elements being random. This random survival, together with random colonization of external species might lead to a stochastic community assembly in oil palm monocultures, resulting in high turnover. In contrast, deterministic community assembly might be the predominant mechanism behind species composition in forest, meaning that forest parasitoid community composition would mostly be determined by vegetation and the associated arthropod fauna, rather than by random survival and colonization. While rubber monocultures are intensively managed, species turnover rate was comparatively low at the parasitoid community level. This observation is strongly influenced by the Encyrtidae, the only family in which turnover rate was lowest in rubber monocultures in both landscapes. A possible interpretation could be that despite management intensity, influence of deterministic factors in rubber monocultures on parasitoid community assembly is still high, especially for Encyrtidae. This could be linked to possible lower diversity of certain vegetation elements in rubber plantations compared to oil palm, limiting the number of possible parasitoid species to colonize rubber plantation. E.g. lower species richness, abundance and diversity of vascular epiphytes have been reported for rubber compared to oil palm monocultures (Böhnert et al., 2016). Despite its comparatively low management intensity (Gouyon et al., 1993), species turnover in Jungle Rubber is the highest of all land-use systems in Harapan and second highest in Bukit Duabelas for the parasitoid community. A possible cause for this observation might be different successional stages of vegetation within Jungle Rubber, with older patches developing increasingly towards mature forest (Gouyon et al., 1993). Subsequently, Jungle Rubber overall might have high spatial heterogeneity, resulting in its comparatively high species turnover rate.

Bukit Duabelas has an overall lower species turnover rate than in Harapan, as indicated by the GLM analysis. This was due to lower turnover in BF, BJ and BR than in HF, HJ and HR. While no intensive survey comparing both landscapes has been conducted to the best of my knowledge, this observation could indicate general higher disturbance in HF, HJ and HR compared to its Bukit Duabelas counterparts. This would also fall in line with the findings of significantly lower species richness and diversity in the Harapan landscape.

6 Summary and conclusion

Overall, my findings confirm patterns observed in other arthropod taxa: Abundance, species richness and inverse Simpson Diversity declined from rainforest to intensively managed monocultures. These observations are likely the result of a cascading trophic effect caused by overall higher plant biomass and diversity, followed by higher total abundance and species richness of host organisms. While community structure was more similar between forest and Jungle Rubber than between other land-use systems, overlap was relatively small, indicating that community composition of parasitoid wasps cannot adequately be replaced by any other of the three land-use systems. Species turnover between core plots within the same land-use system was comparatively low in forest land-use systems and in Bukit Duabelas. Differences in species turnover rate between land-use systems might be explained by different management intensity, varying diversity of accompanying vegetation and different spatial heterogeneity. The observation of generally higher species dissimilarity in Harapan might be a result of higher disturbance in forest, Jungle Rubber and rubber in this landscape.

The findings of this study indicate high conservation value for forest, especially in the Bukit Duabelas landscape, where parasitoid wasps showed highest abundance, species richness and diversity. When it comes to protection of parasitoids and their ecosystem functions, none of the other land-use systems can substitute forest. This is not only true for species richness in general, but also for community composition. That being said, Jungle Rubber comes closest to forest in regard of parasitoid abundance, species richness, diversity and community composition, indicating that Jungle Rubber itself has a high conservation value of its own when compared to monocultures. When it comes to conservation policies, the insights of this study lead to the conclusion that policy makers should intensify efforts to protect lowland rainforest, especially in the Bukit Duabelas area. Furthermore, conversion of Jungle Rubber to monoculture plantations should be prevented wherever possible. When new concessions for converting forest and Jungle Rubber to monocultures are granted, policy makers should ensure that patches of the precursor vegetation system are kept untouched. This may improve conservation value of plantations as well as important ecosystem functions provided by parasitoids. Adding to that, enrichment of plant diversity within the plantations, preferably with natural forest species, might lessen the damage to biodiversity and ecosystem functions.

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Appendix

Results for family-level analyses

Braconidae

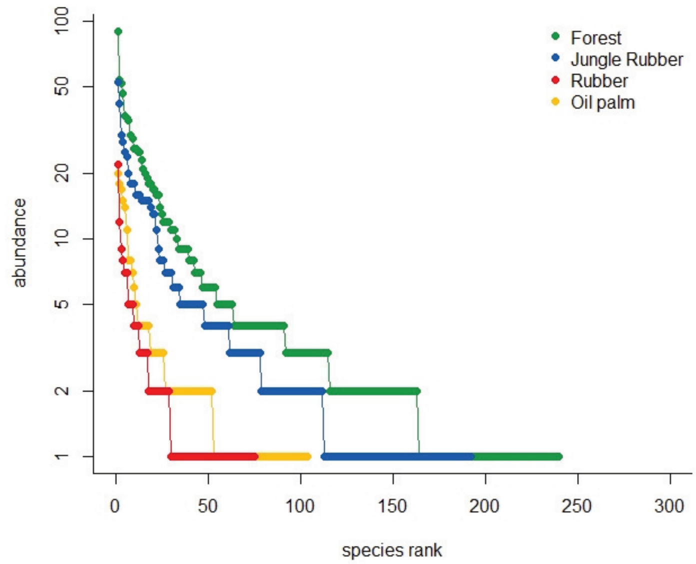

Figure A1. Rank-abundance curves for braconid wasps in four land-use systems. Abundance is shown as logarithm of abundance using base 10.

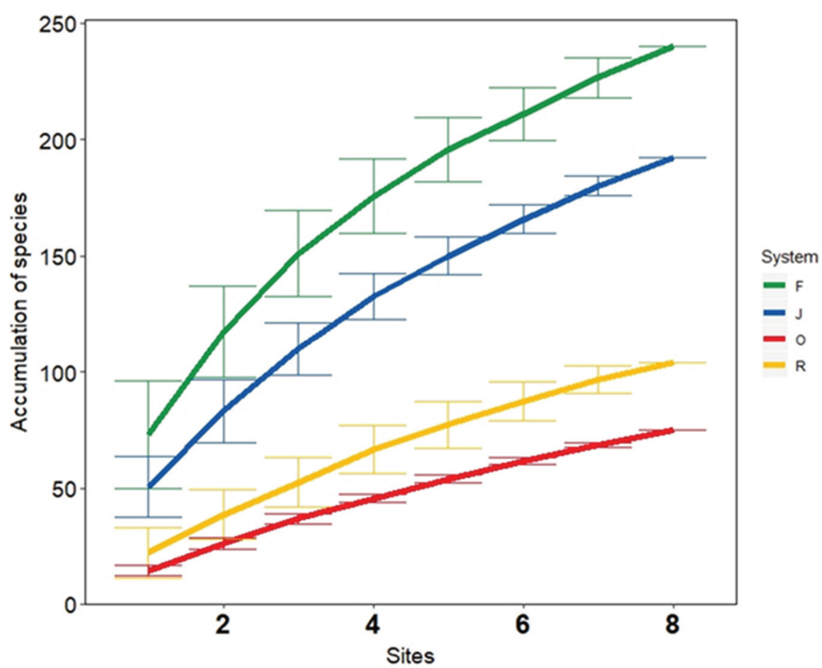

Figure A2. Species accumulation curves for braconid wasps in four land-use systems. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Error bars represent standard deviation.

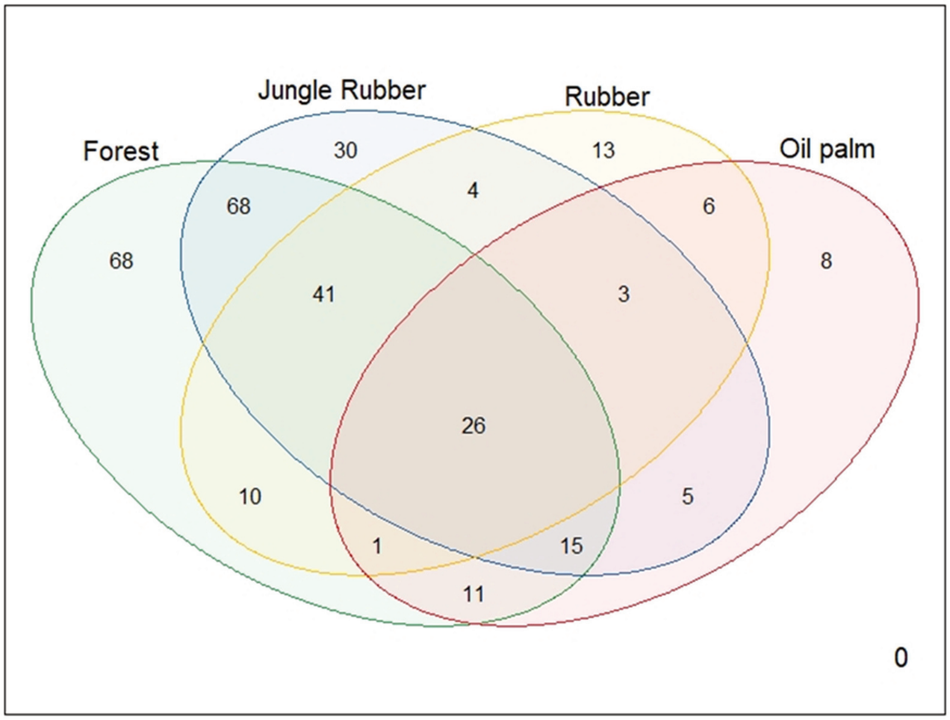

Figure A3. Venn diagram for braconid wasps in four different land-use systems. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated land-use systems.

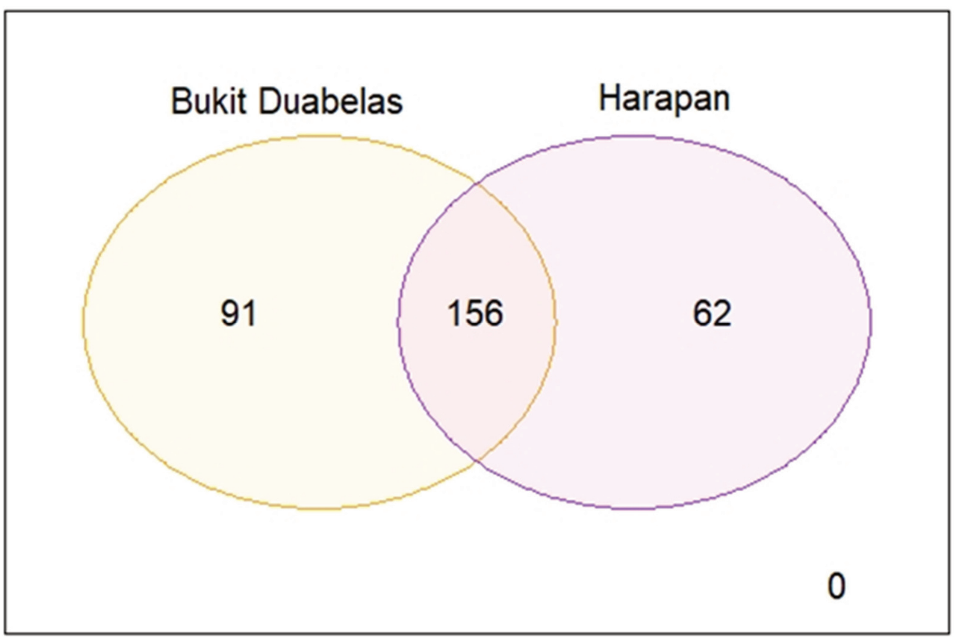

Figure A4. Venn diagram for braconid wasps in the two landscapes. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated landscapes.

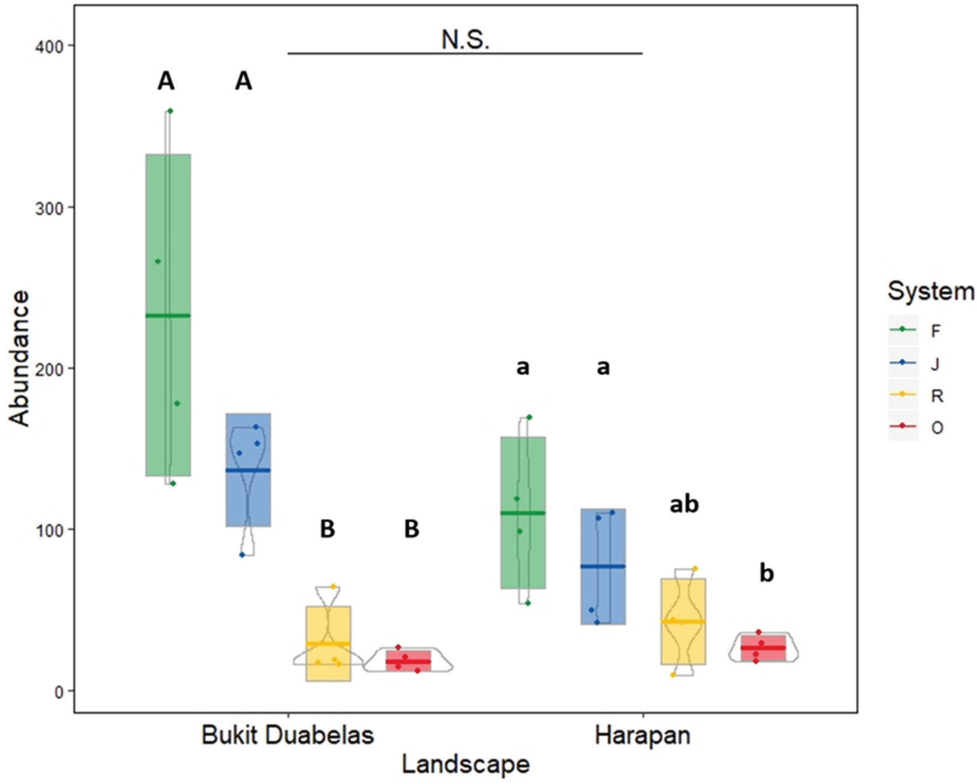

Figure A5. Pirate plots of braconid wasp abundance in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A1. Abundance of braconid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	171.37 ± 98.55	106.87 ± 46.25	171.37 ± 24.4	106.87 ± 7.97
Bukit Duabelas Landscape	232.75 ± 101.67	136.75 ± 35.78	29 ± 23.36	18 ± 6.32
Harapan Landscape	110 ± 47.75	77 ± 36.5	42.25 ± 26.94	26.25 ± 7.93

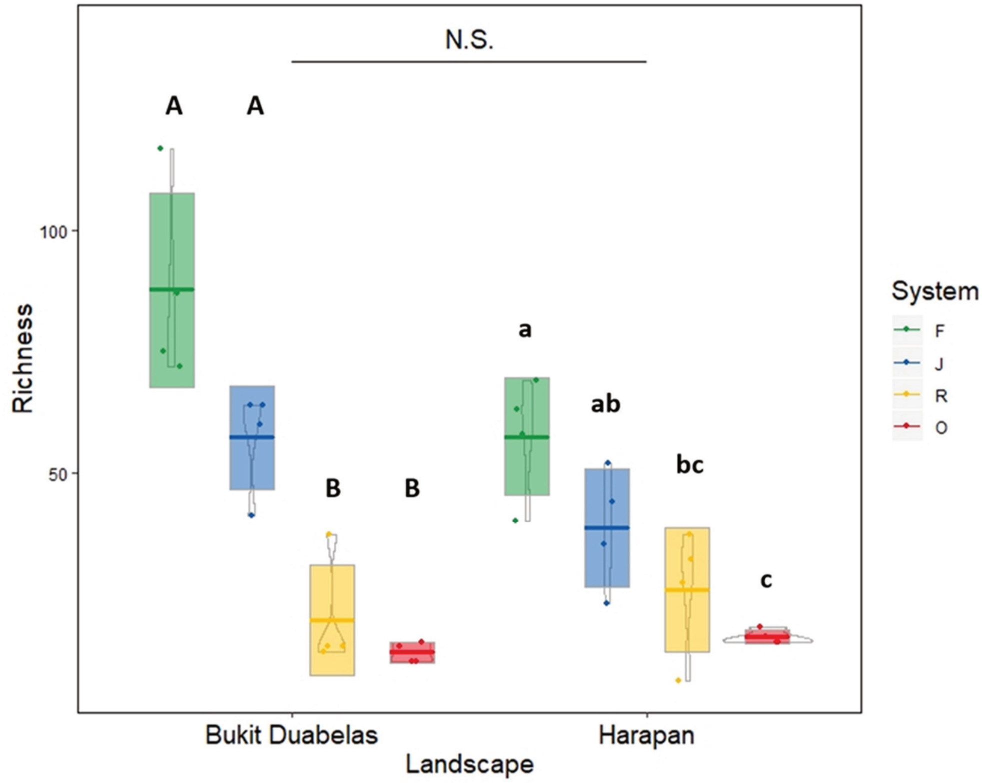

Figure A6. Pirate plots of braconid wasp species richness in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A2. Species richness of braconid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	72.62 ± 22.57	47.87 ± 14.78	22.62 ± 11.98	14.37 ± 2.38
Bukit Duabelas Landscape	87.75 ± 20.54	57.25 ± 10.99	19.5 ± 11.67	12.75 ± 2.06
Harapan Landscape	57.5 ± 12.5	38.5 ± 12.44	25.75 ± 13.14	16 ± 1.41

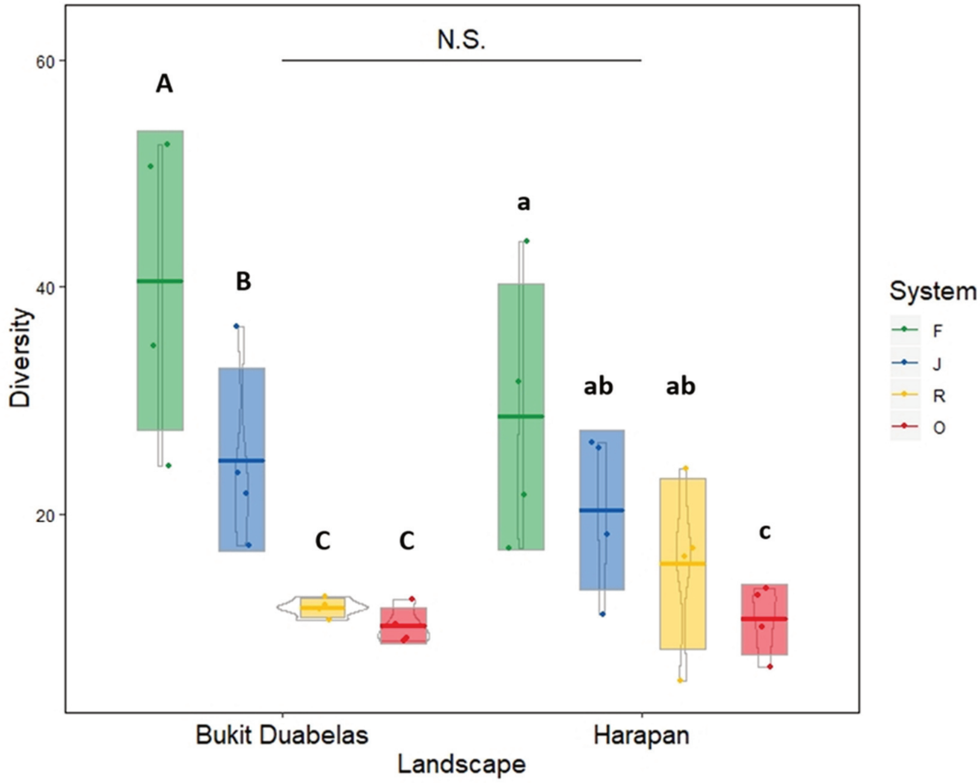

Figure A7. Pirate plots of braconid wasp inverse Simpson Diversity in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A3. Inverse Simpson Diversity of braconid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	34.59 ± 13.39	22.6 ± 7.54	13.72 ± 5.47	10.49 ± 2.35
Bukit Duabelas Landscape	40.56 ± 13.42	24.82 ± 8.26	11.78 ± 0.86	10.2 ± 1.64
Harapan Landscape	28.62 ± 11.97	20.38 ± 7.17	15.66 ± 7.68	10.78 ± 3.15

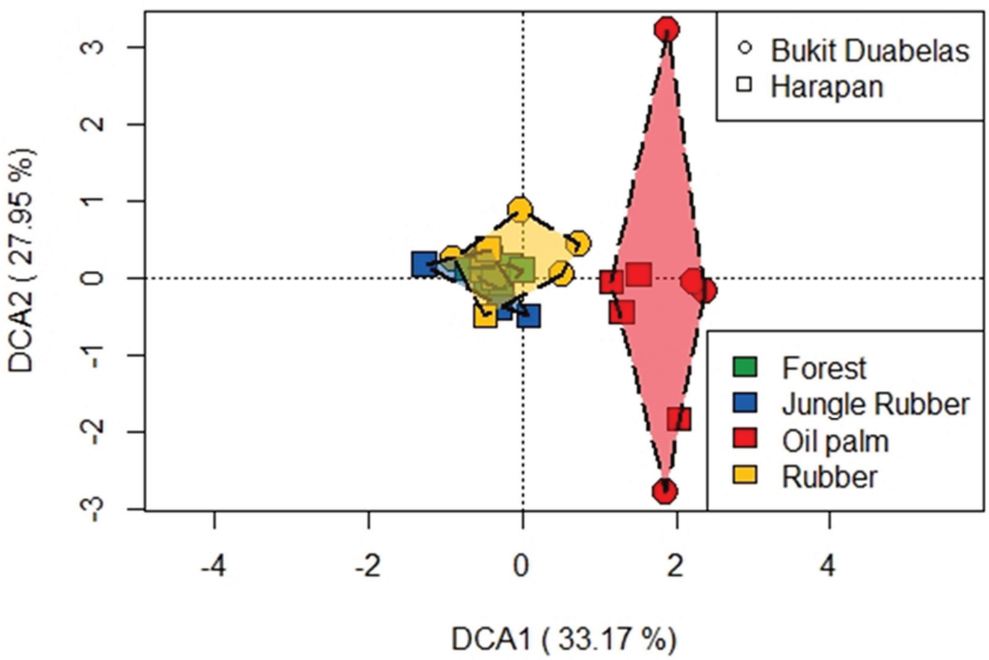

Figure A8. Detrended Correspondence Analysis for braconid wasps in four land-use systems based on a matrix of Hellinger-transformed data. Percentages on axes represent the proportion of total variation shown in the ordination.

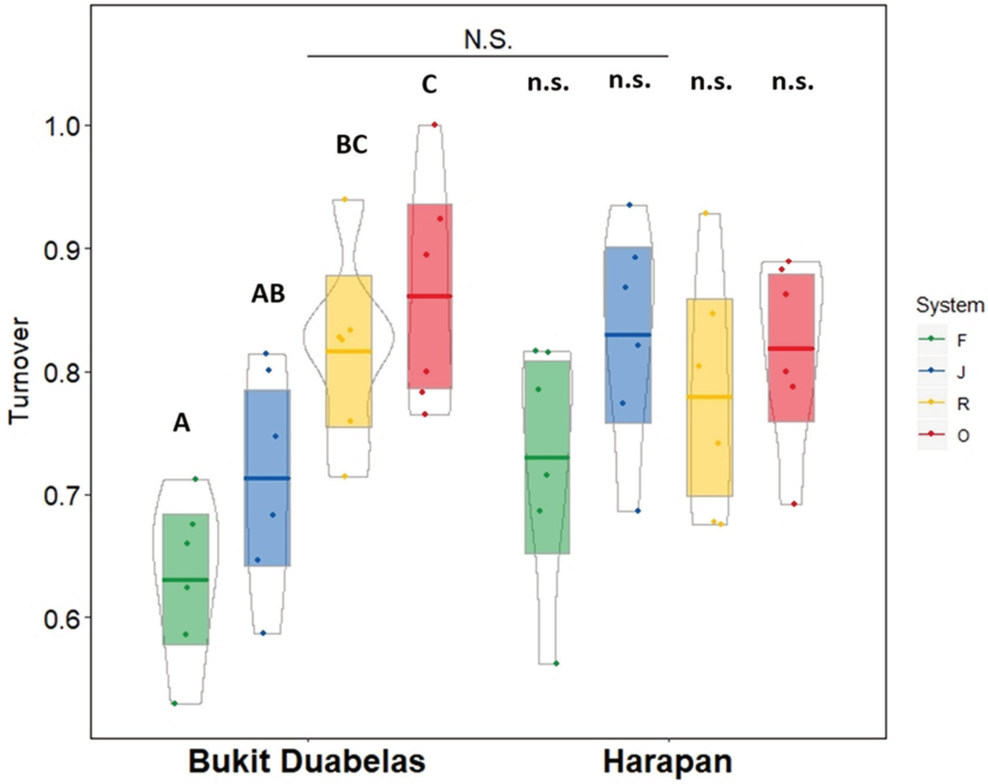

Figure A9. Pirate plots of braconid wasp species turnover rate in four land-use systems in two landscapes calculated as Bray-Curtis dissimilarity index. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant (p < 0.05) difference between landscapes. Capital letters indicate significant (p < 0.05) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant (p < 0.05) differences between land-use systems in Harapan.

Table A4. Species turnover rate of braconid wasps measured as Bray-Curtis dissimilarity index in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	0.7 ± 0.09	0.79 ± 0.08	0.82 ± 0.08	0.85 ± 0.07
Bukit Duabelas Landscape	0.63 ± 0.06	0.71 ± 0.08	0.81 ± 0.07	0.86 ± 0.09
Harapan Landscape	0.73 ± 0.09	0.82 ± 0.08	0.77 ± 0.09	0.81 ± 0.07

Ceraphronidae

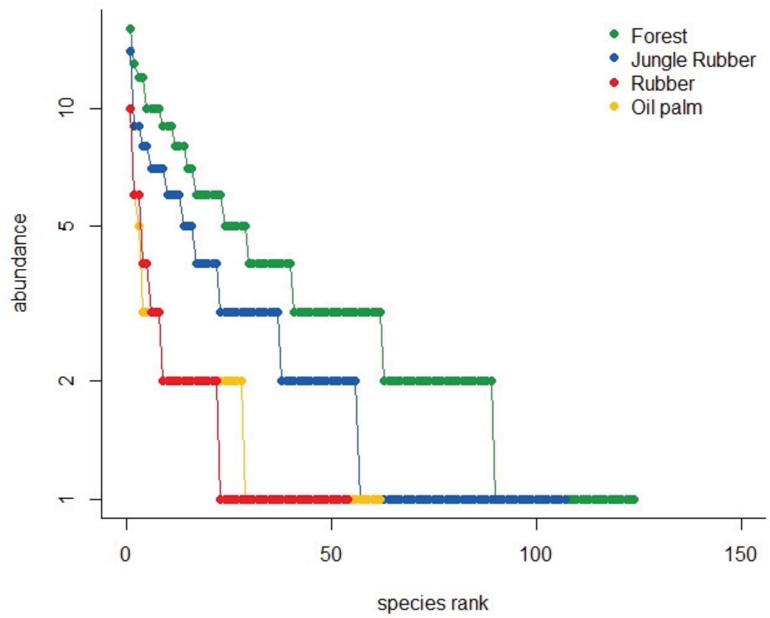

Figure A10. Rank-abundance curves for ceraphronid wasps in four land-use systems. Abundance is shown as logarithm of abundance using base 10.

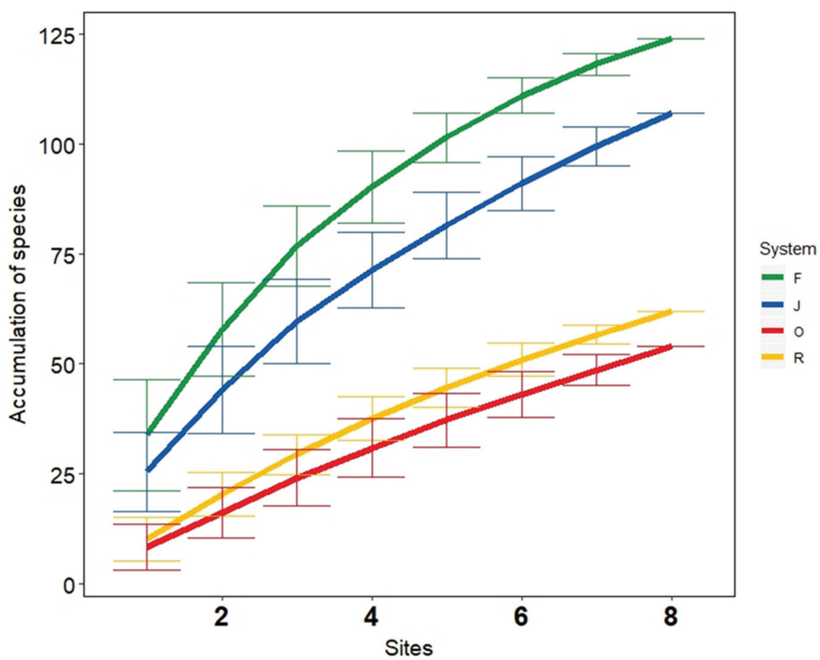

Figure A11. Species accumulation curves for ceraphronid wasps in four land-use systems. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Error bars represent standard deviation.

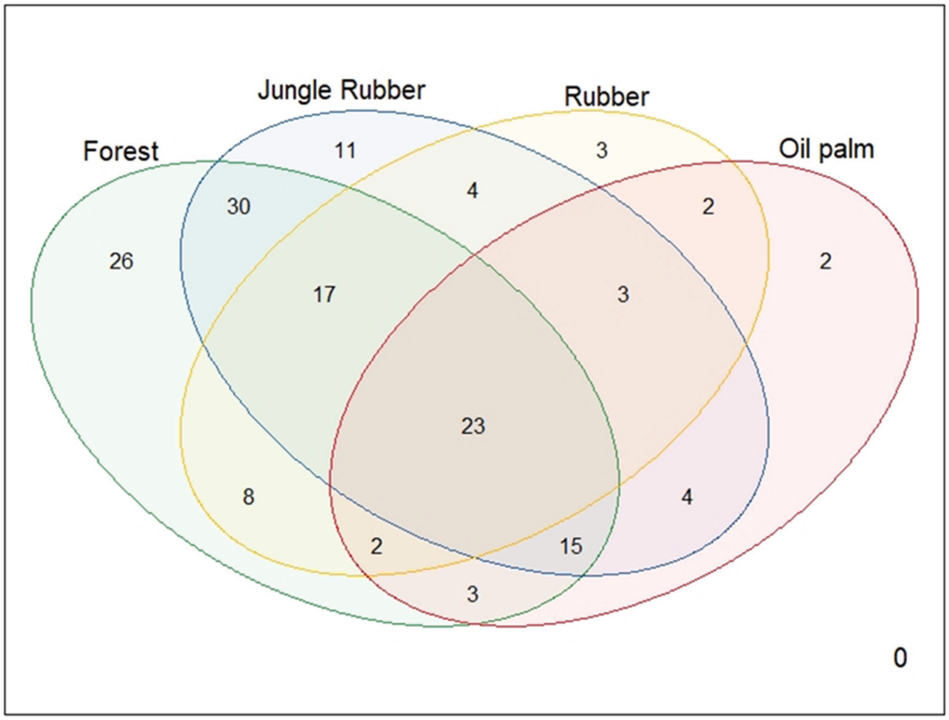

Figure A12. Venn diagram for ceraphronid wasps in four different land-use systems. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated land-use systems.

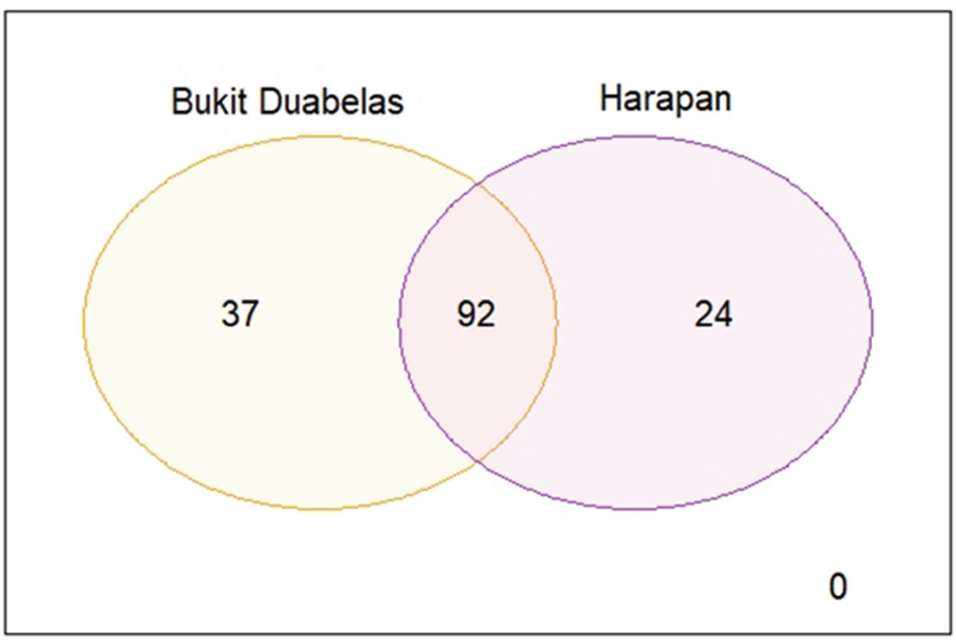

Figure A13. Venn diagram for ceraphronid wasps in the two landscapes. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated landscapes.

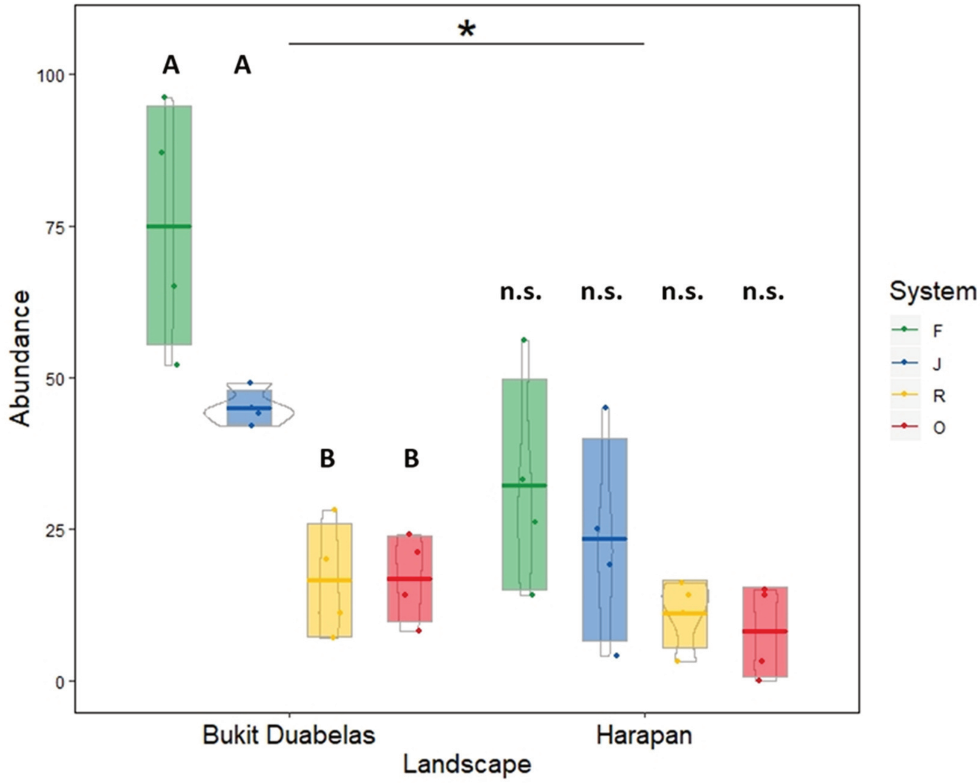

Figure A14. Pirate plots of ceraphronid wasp abundance in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant (p < 0.05) difference between landscapes. Capital letters indicate significant (p < 0.05) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant (p < 0.05) differences between land-use systems in Harapan.

Table A5. Abundance of ceraphronid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	53.62 ± 28.79	34.12 ± 16.19	13.75 ± 7.77	14.14 ± 7.15
Bukit Duabelas Landscape	75 ± 20.11	45 ± 2.94	16.5 ± 9.39	16.75 ± 7.18
Harapan Landscape	32.25 ± 17.67	23.25 ± 16.97	11 ± 5.71	10.66 ± 6.65

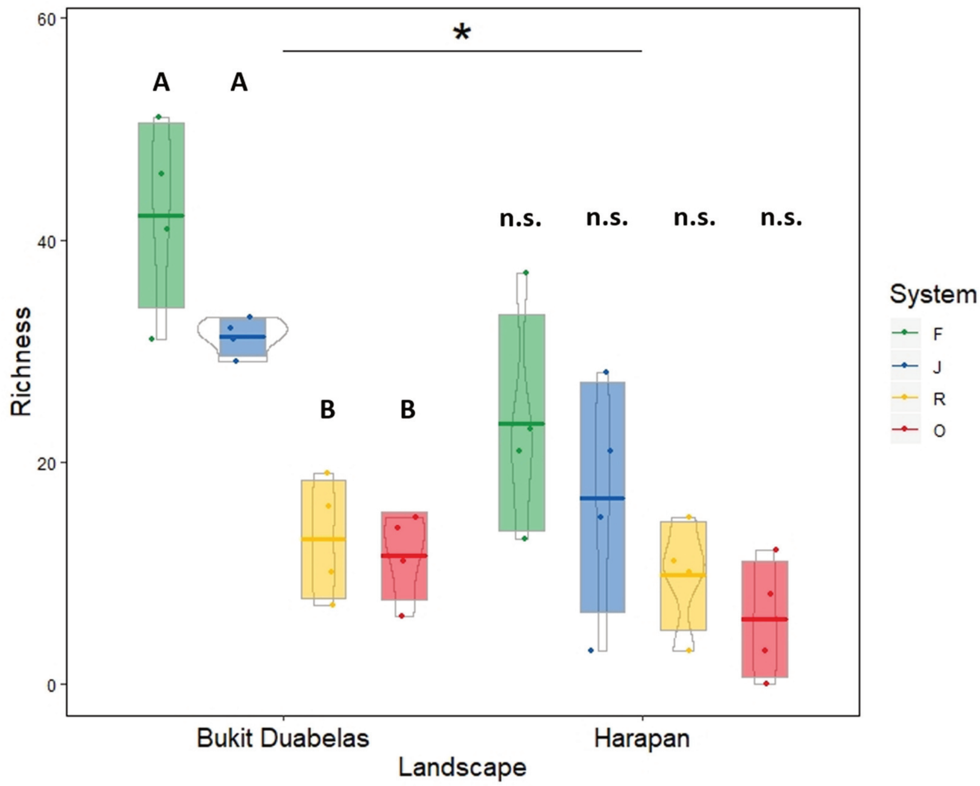

Figure A15. Pirate plots of ceraphronid wasp species richness in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant (p < 0.05) difference between landscapes. Capital letters indicate significant (p < 0.05) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant (p < 0.05) differences between land-use systems in Harapan.

Table A6. Species richness of ceraphronid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	32.87 ± 13.2	24 ± 10.46	11.37 ± 5.15	9.857 ± 4.37
Bukit Duabelas Landscape	42.25 ± 8.53	31.25 ± 1.7	13 ± 5.47	11.5 ± 4.04
Harapan Landscape	23.5 ± 9.98	16.75 ± 10.59	9.75 ± 4.99	7.66 ± 4.5

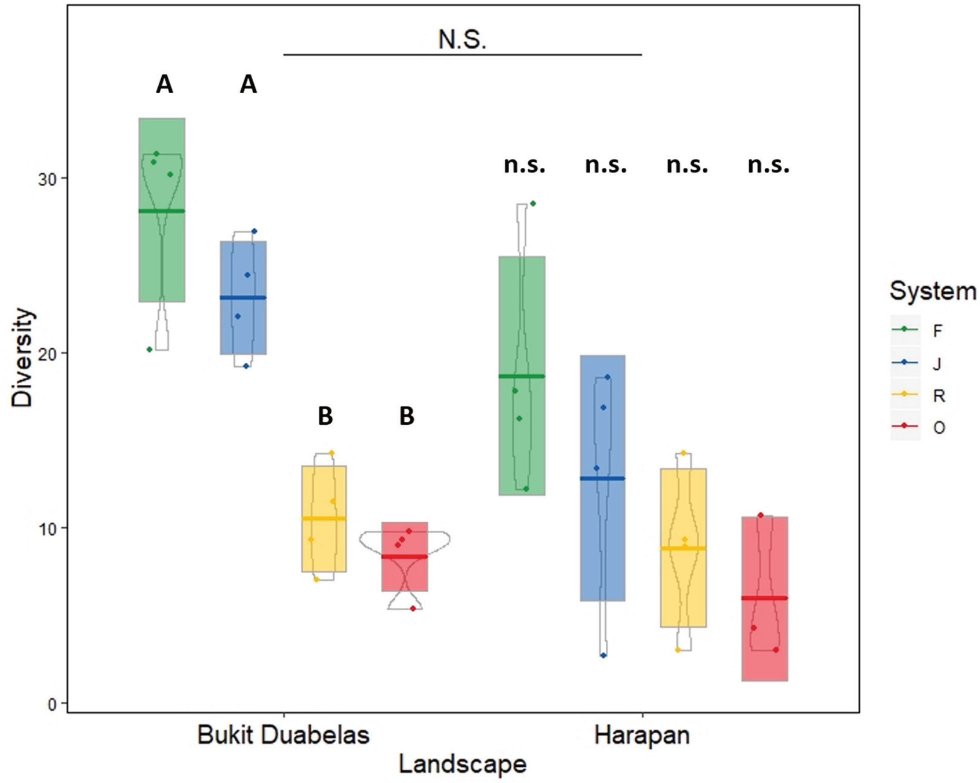

Figure A16. Pirate plots of ceraphronid wasp inverse Simpson Diversity in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A7. Inverse Simpson Diversity of ceraphronid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	23.41 ± 7.62	17.99 ± 7.51	9.69 ± 3.74	7.34 ± 3.06
Bukit Duabelas Landscape	28.13 ± 5.32	23.12 ± 3.29	10.53 ± 3.11	8.35 ± 2.04
Harapan Landscape	18.7 ± 6.94	12.87 ± 7.14	8.85 ± 4.59	5.99 ± 4.13

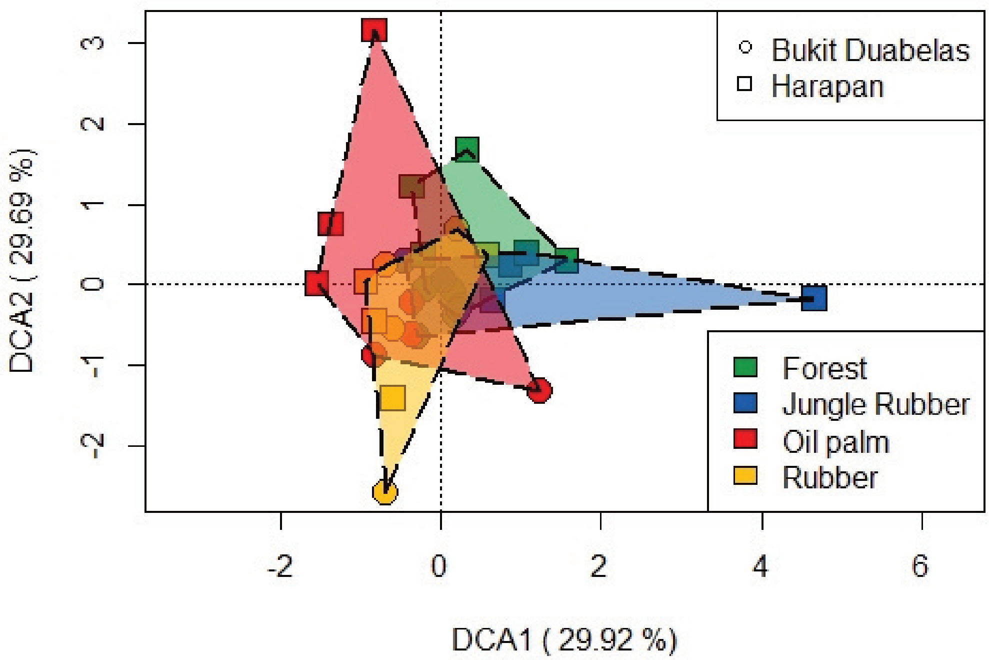

Figure A17. Detrended Correspondence Analysis for ceraphronid wasps in four land-use systems based on a matrix of Hellinger-transformed data. Percentages on axes represent the proportion of total variation shown in the ordination.

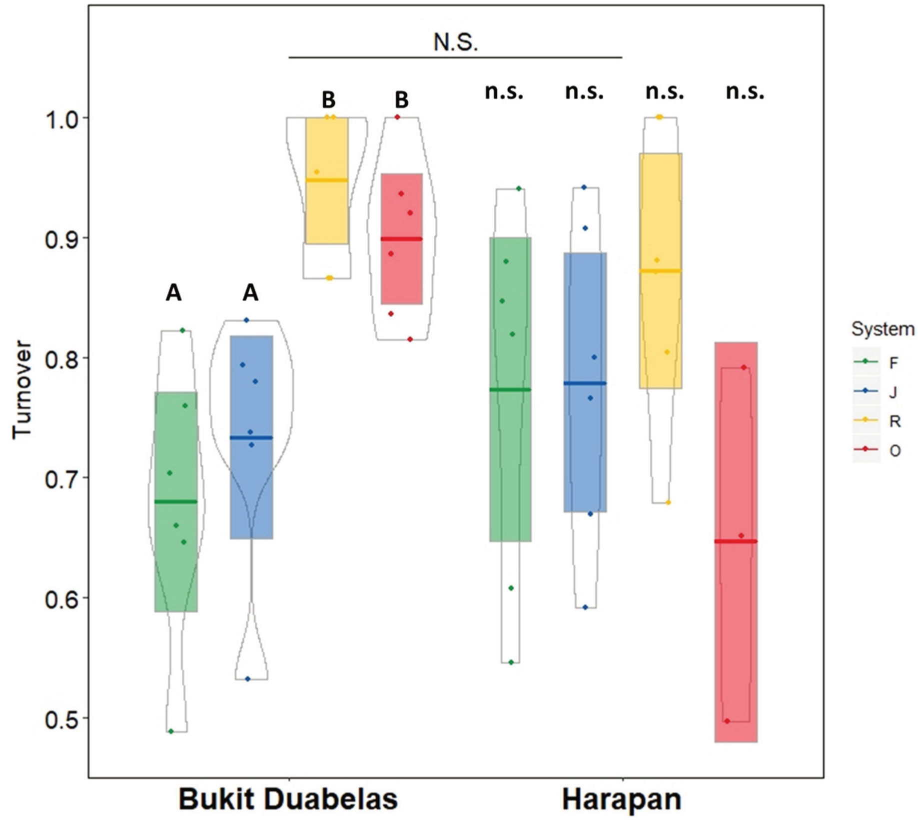

Figure A18. Pirate plots of ceraphronid wasp species turnover rate in four land-use systems in two landscapes calculated as Morisita-Horn dissimilarity index. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A8. Species turnover rate of ceraphronid wasps measured as Morisita-Horn dissimilarity index in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	0.79 ± 0.11	0.81 ± 0.12	0.88 ± 0.13	0.89 ± 0.13
Bukit Duabelas Landscape	0.68 ± 0.11	0.73 ± 0.1	0.94 ± 0.06	0.89 ± 0.06
Harapan Landscape	0.77 ± 0.15	0.77 ± 0.13	0.87 ± 0.12	0.64 ± 0.14

Encyrtidae

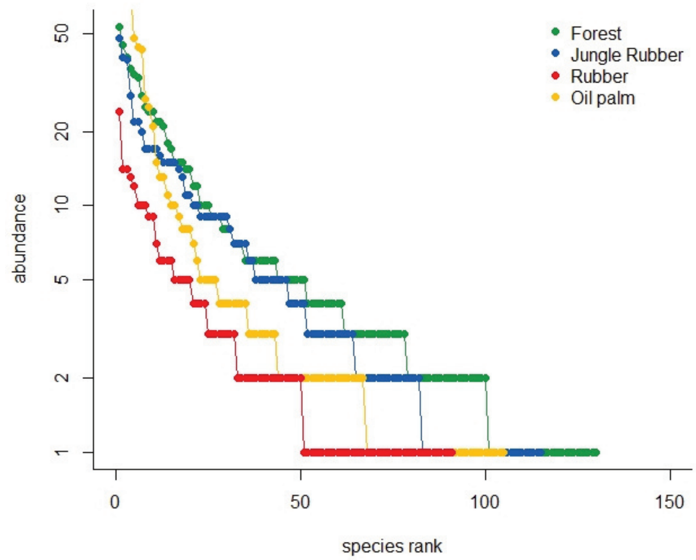

Figure A19. Rank-abundance curves for encyrtid wasps in four land-use systems. Abundance is shown as logarithm of abundance using base 10.

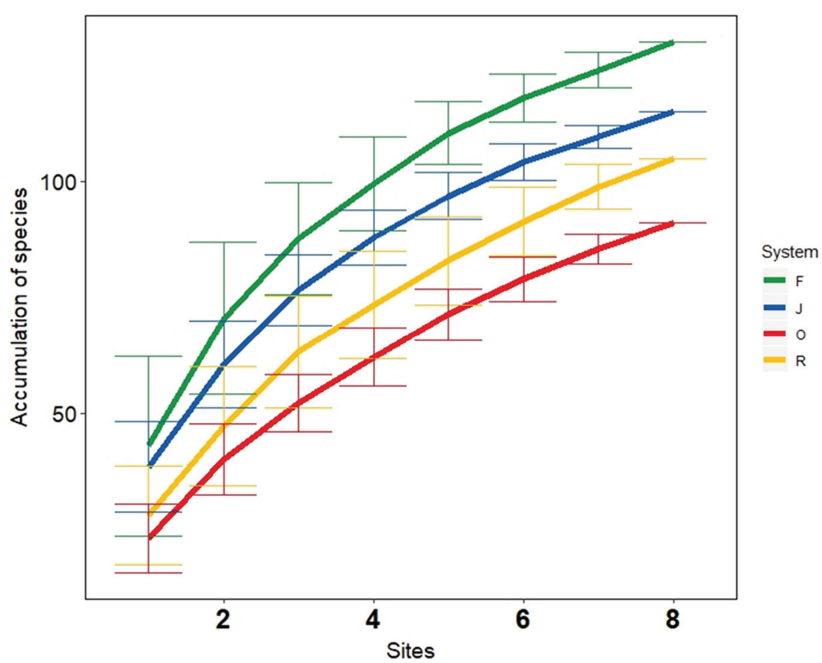

Figure A20. Species accumulation curves for encyrtid wasps in four land-use systems. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Error bars represent standard deviation.

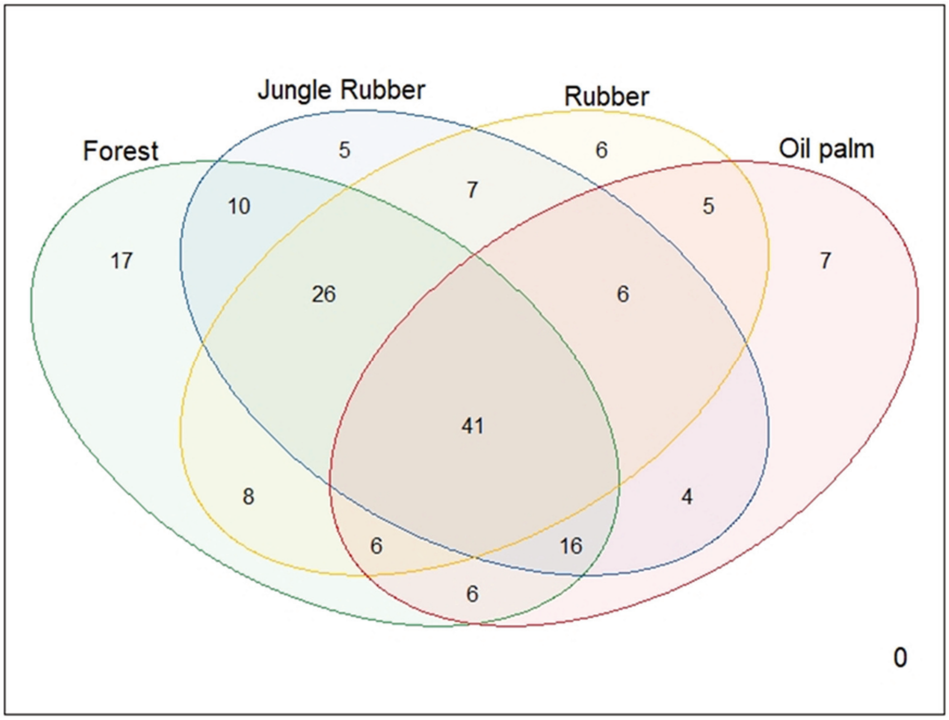

Figure A21. Venn diagram for encyrtid wasps in four different land-use systems. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated land-use systems.

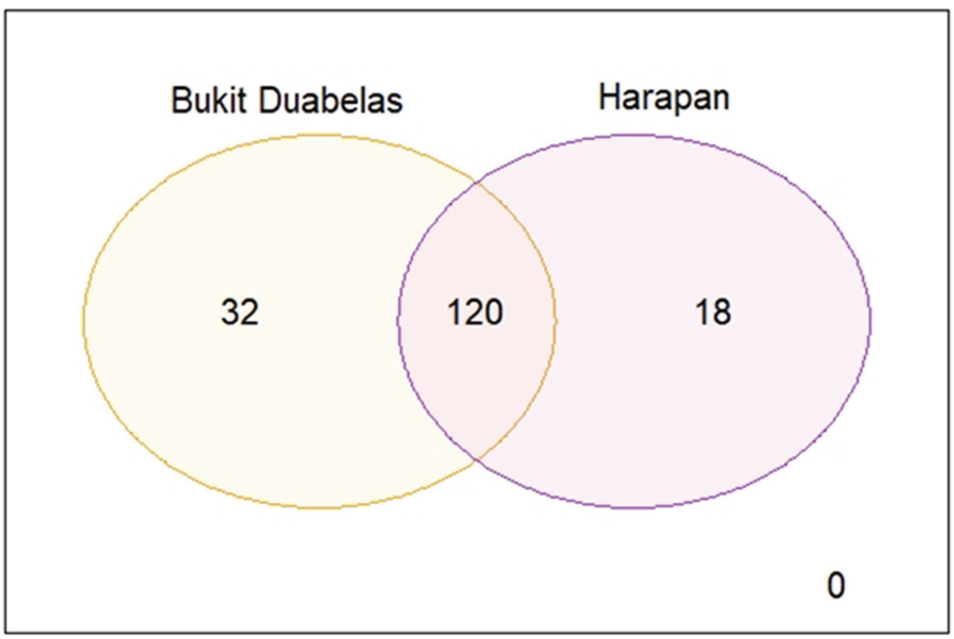

Figure A22. Venn diagram for encyrtid wasps in the two landscapes. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated landscapes.

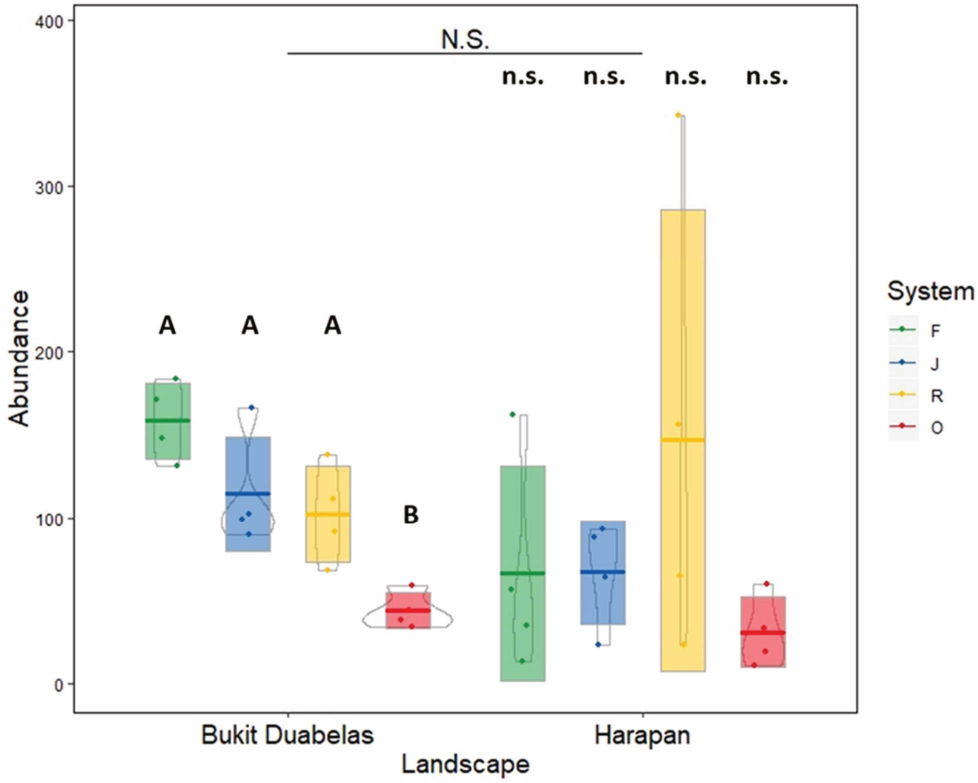

Figure A23. Pirate plots of encyrtid wasp abundance in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant (p < 0.05) difference between landscapes. Capital letters indicate significant (p < 0.05) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant (p < 0.05) differences between land-use systems in Harapan.

Table A9. Abundance of encyrtid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	**Jungle Rubber**	**Rubber**	**Oil palm**
Overall	112.5 ± 67.27	90.62 ± 39.95	124.37 ± 98.02	37.25 ± 17.26
Bukit Duabelas Landscape	158.5 ± 23.61	114.25 ± 34.87	102 ± 29.74	43.75 ± 10.96
Harapan Landscape	66.5 ± 66.04	67 ± 31.94	146.75 ± 142.12	30.75 ± 21.51

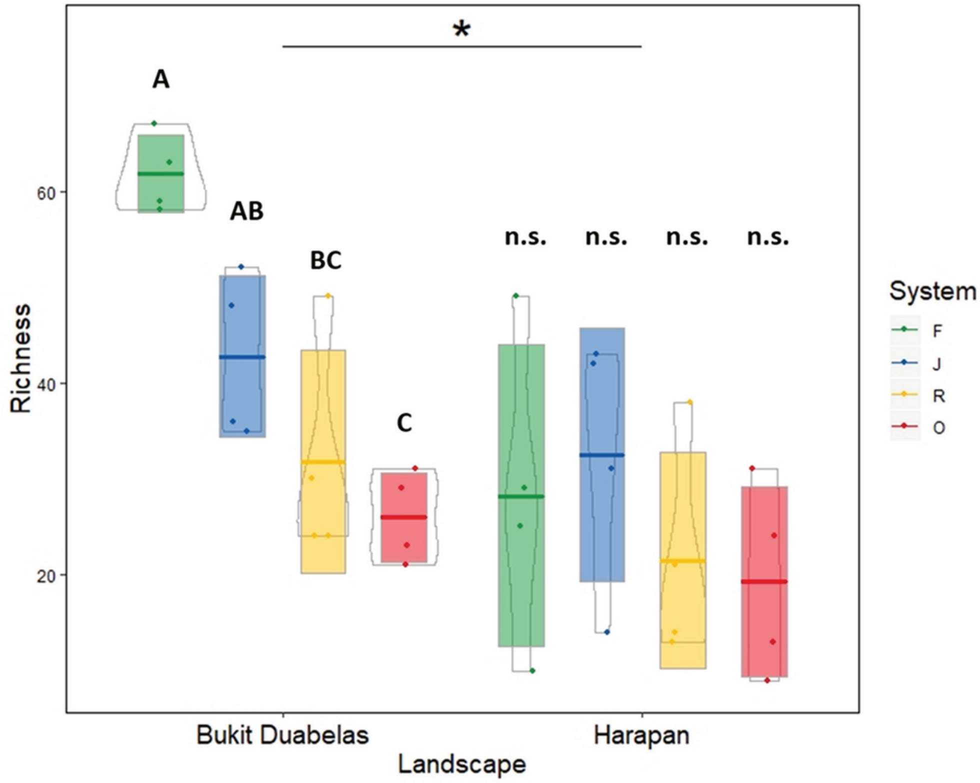

Figure A24. Pirate plots of encyrtid wasp species richness in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A10. Species richness of encyrtid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	45 ± 20.94	37.62 ± 11.79	26.62 ± 12.14	22.62 ± 8.14
Bukit Duabelas Landscape	61.75 ± 4.11	42.75 ± 8.53	31.75 ± 11.84	26 ± 4.76
Harapan Landscape	28.25 ± 16.07	32.5 ± 13.47	21.5 ± 11.56	19.25 ± 10.07

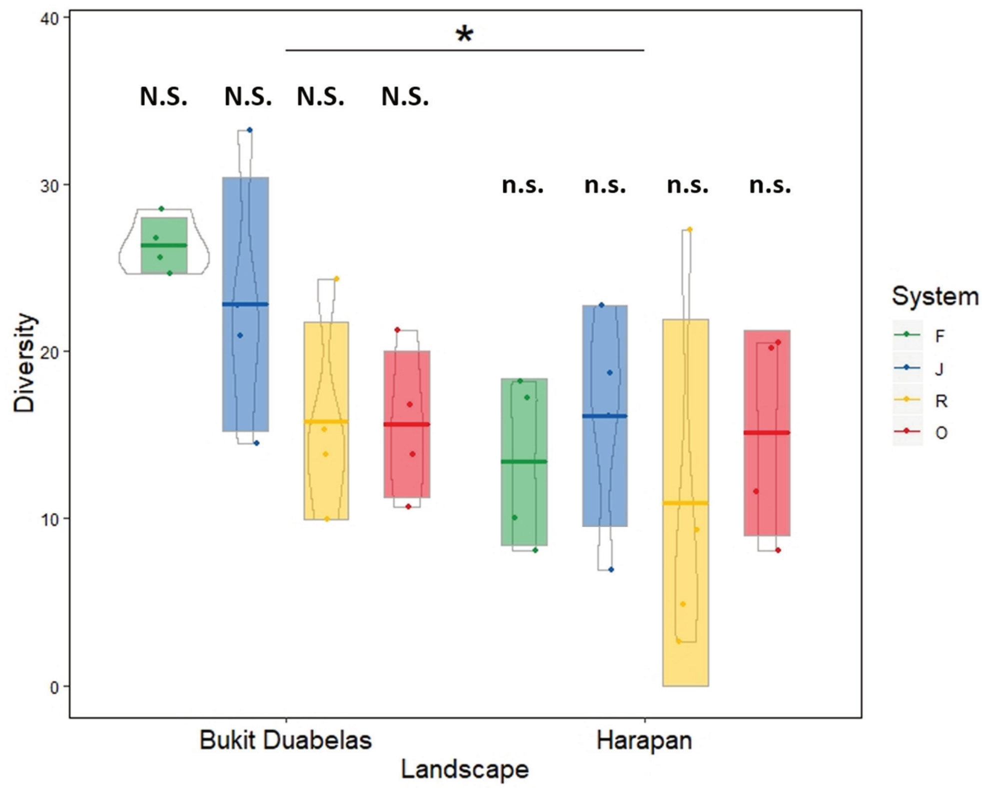

Figure A25. Pirate plots of encyrtid wasp inverse Simpson Diversity in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A11. Inverse Simpson Diversity of encyrtid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	19.88 ± 7.77	19.47 ± 7.63	13.41 ± 8.73	15.38 ± 5.04
Bukit Duabelas Landscape	26.38 ± 1.68	22.83 ± 7.78	15.85 ± 6.05	15.64 ± 4.48
Harapan Landscape	13.39 ± 5.1	16.11 ± 6.74	10.97 ± 11.2	15.12 ± 6.25

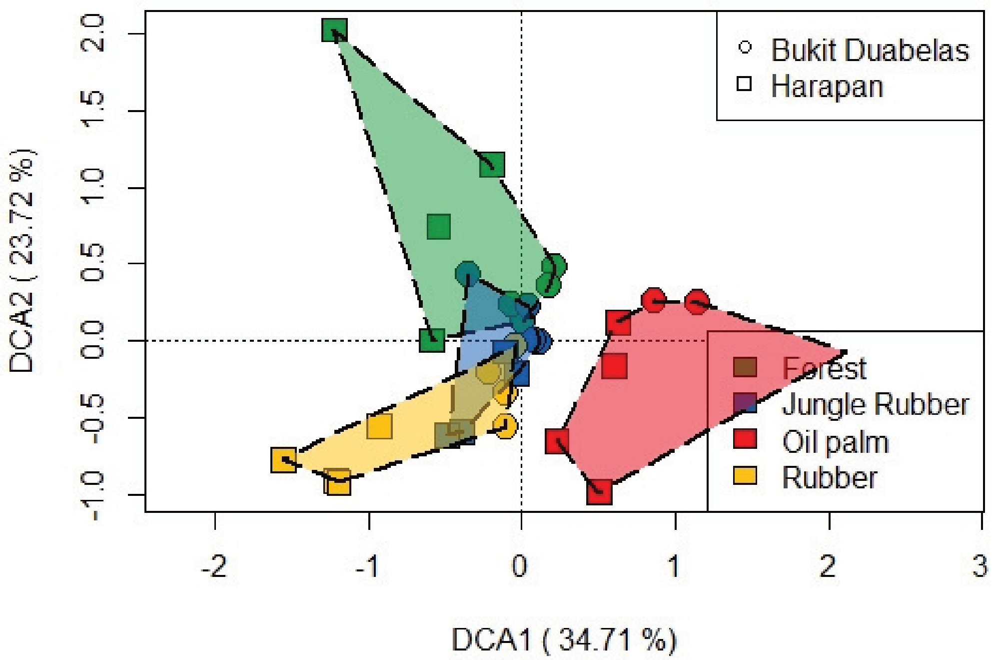

Figure A26. Detrended Correspondence Analysis for encyrtid wasps in four land-use systems based on a matrix of Hellinger-transformed data. Percentages on axes represent the proportion of total variation shown in the ordination.

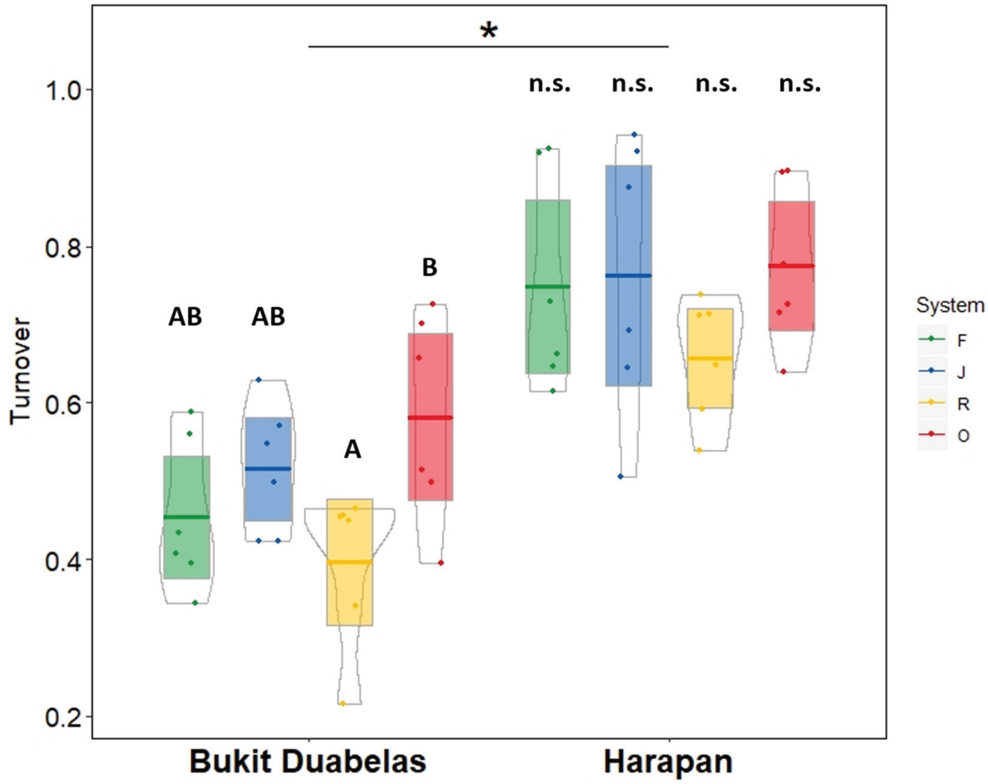

Figure A27. Pirate plots of encyrtid wasp species turnover rate in four land-use systems in two landscapes calculated as Morisita-Horn dissimilarity index. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant (p < 0.05) difference between landscapes. Capital letters indicate significant (p < 0.05) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant (p < 0.05) differences between land-use systems in Harapan.

Table A12. Species turnover rate of encyrtid wasps measured as Morisita-Horn dissimilarity index in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	0.7 ± 0.16	0.7 ± 0.15	0.62 ± 0.15	0.71 ± 0.14
Bukit Duabelas Landscape	0.45 ± 0.09	0.51 ± 0.08	0.39 ± 0.1	0.58 ± 0.13
Harapan Landscape	0.74 ± 0.13	0.76 ± 0.17	0.65 ± 0.07	0.77 ± 0.1

Eulophidae

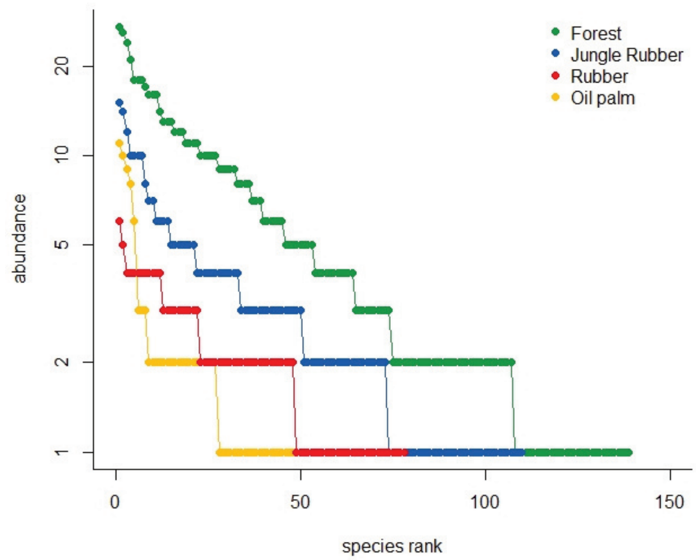

Figure A28. Rank-abundance curves for eulophid wasps in four land-use systems. Abundance is shown as logarithm of abundance using base 10.

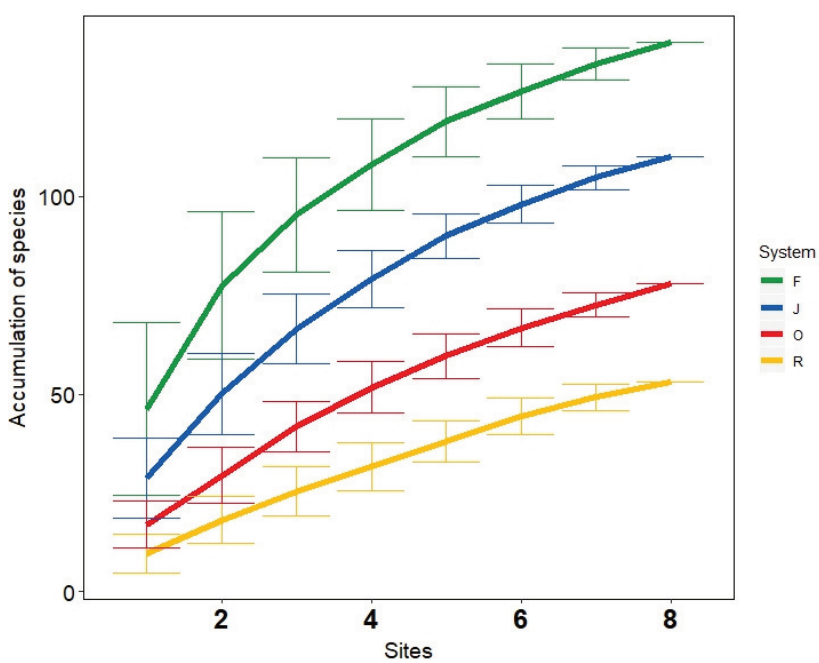

Figure A29. Species accumulation curves for eulophid wasps in four land-use systems. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Error bars represent standard deviation.

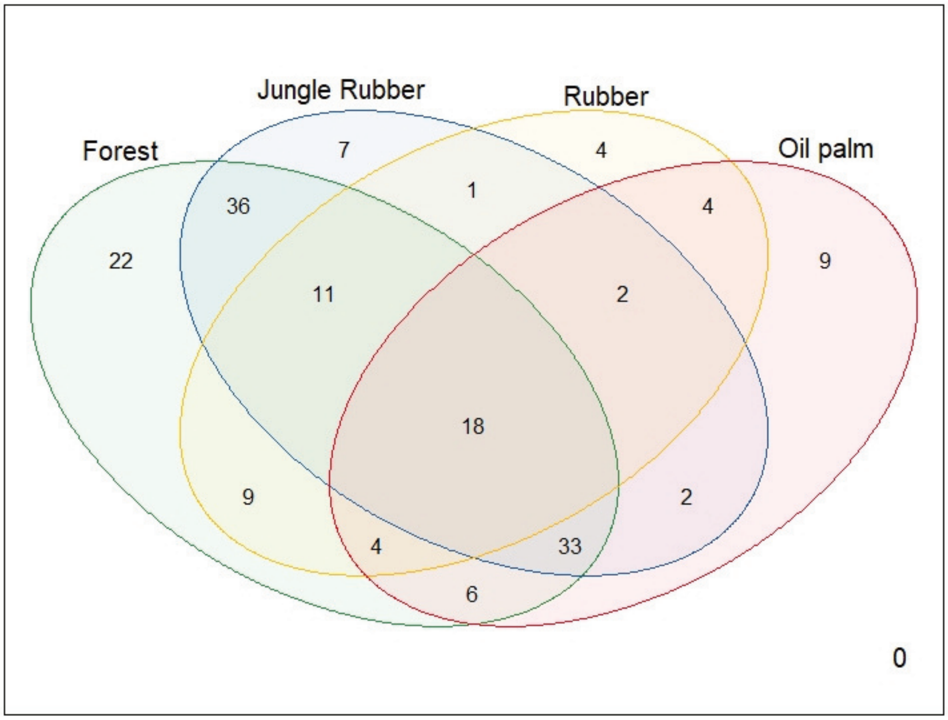

Figure A30. Venn diagram for eulophid wasps in four different land-use systems. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated land-use systems.

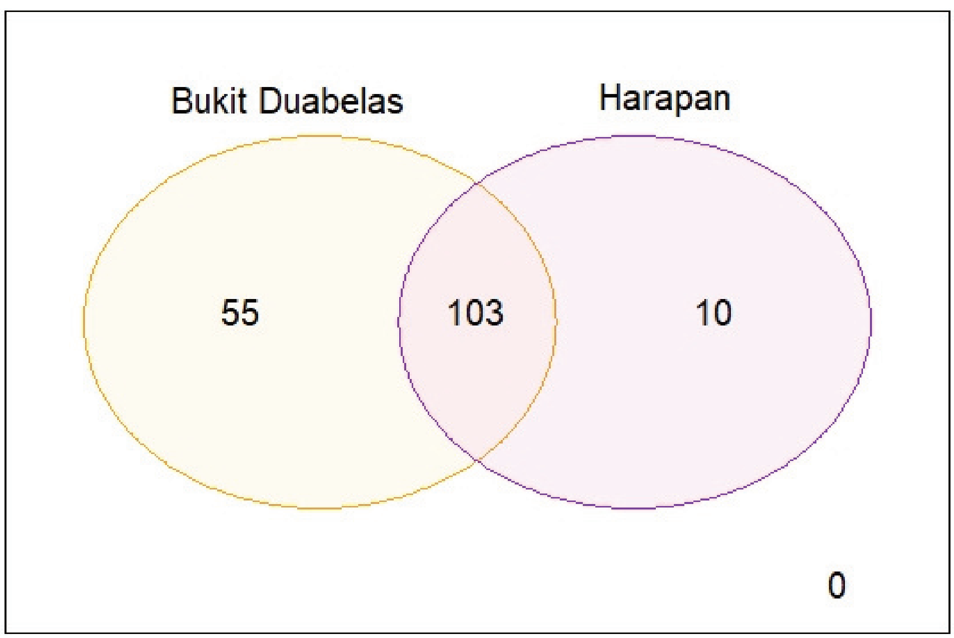

Figure A31. Venn diagram for eulophid wasps in the two landscapes. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated landscapes.

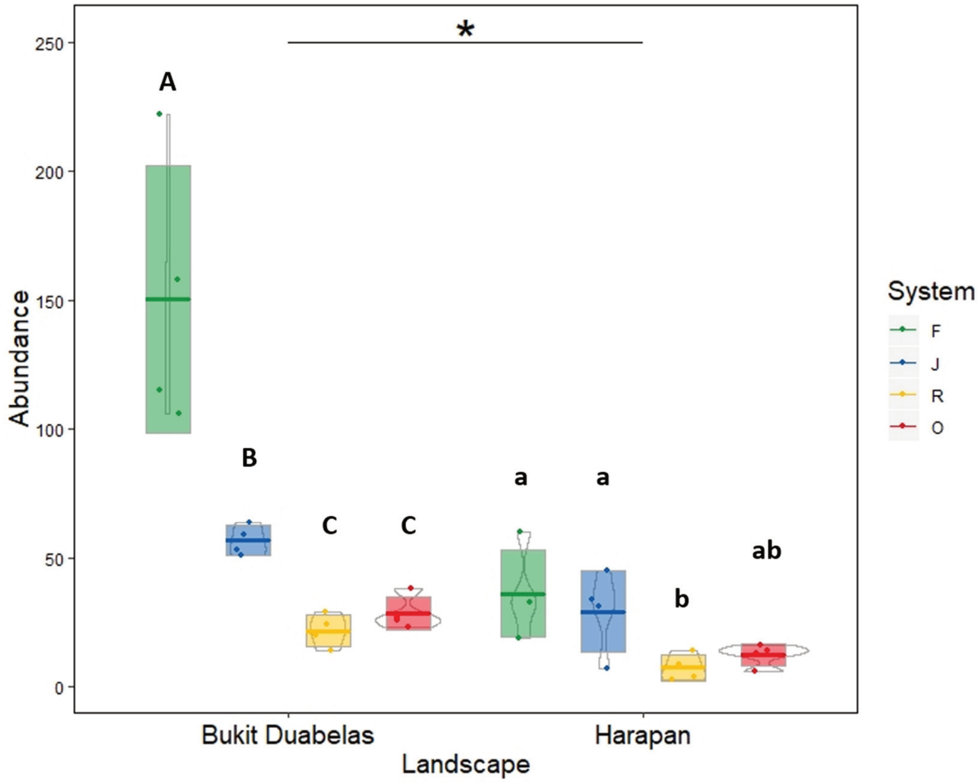

Figure A32. Pirate plots of eulophid wasp abundance in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A13. Abundance of eulophid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	93.25 ± 70.99	43 ± 18.46	14.62 ± 9.28	20.37 ± 10.09
Bukit Duabelas Landscape	150.25 ± 52.94	56.75 ± 5.9	21.75 ± 6.34	28.5 ± 6.55
Harapan Landscape	36.25 ± 17.15	29.25 ± 16	7.5 ± 5.06	12.25 ± 4.34

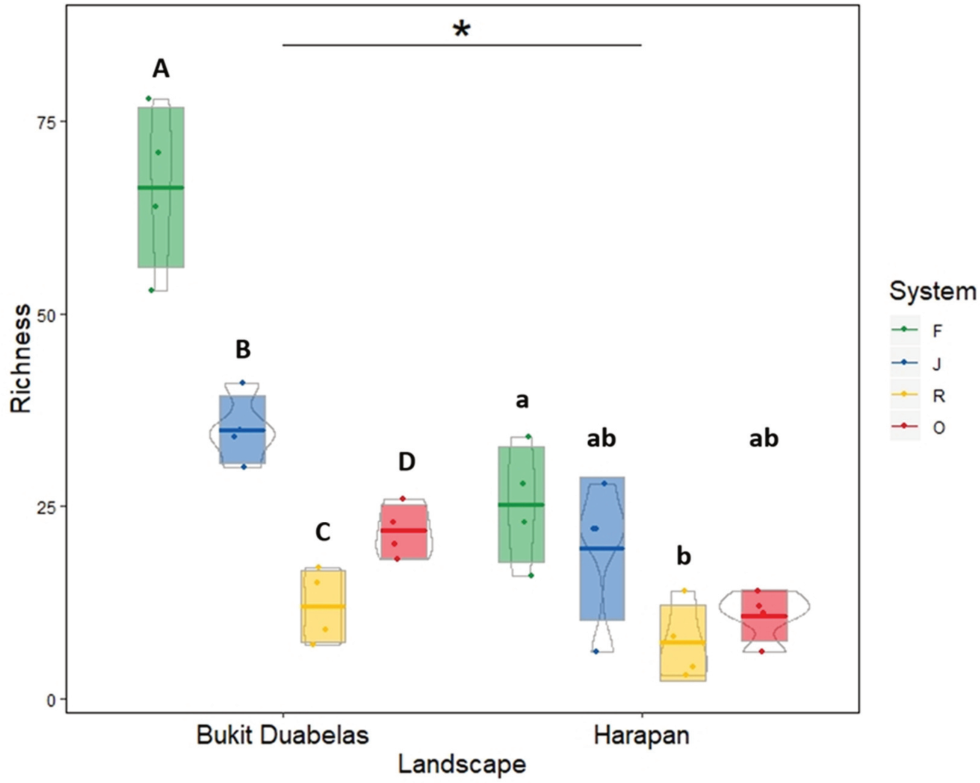

Figure A33. Pirate plots of eulophid wasp species richness in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A14. Species richness of eulophid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	45.87 ± 23.66	27.25 ± 10.75	9.62 ± 5.18	16.25 ± 6.69
Bukit Duabelas Landscape	66.5 ± 10.66	35 ± 4.54	12 ± 4.76	21.75 ± 3.5
Harapan Landscape	25.25 ± 7.63	19.5 ± 9.43	7.25 ± 4.99	10.75 ± 3.4

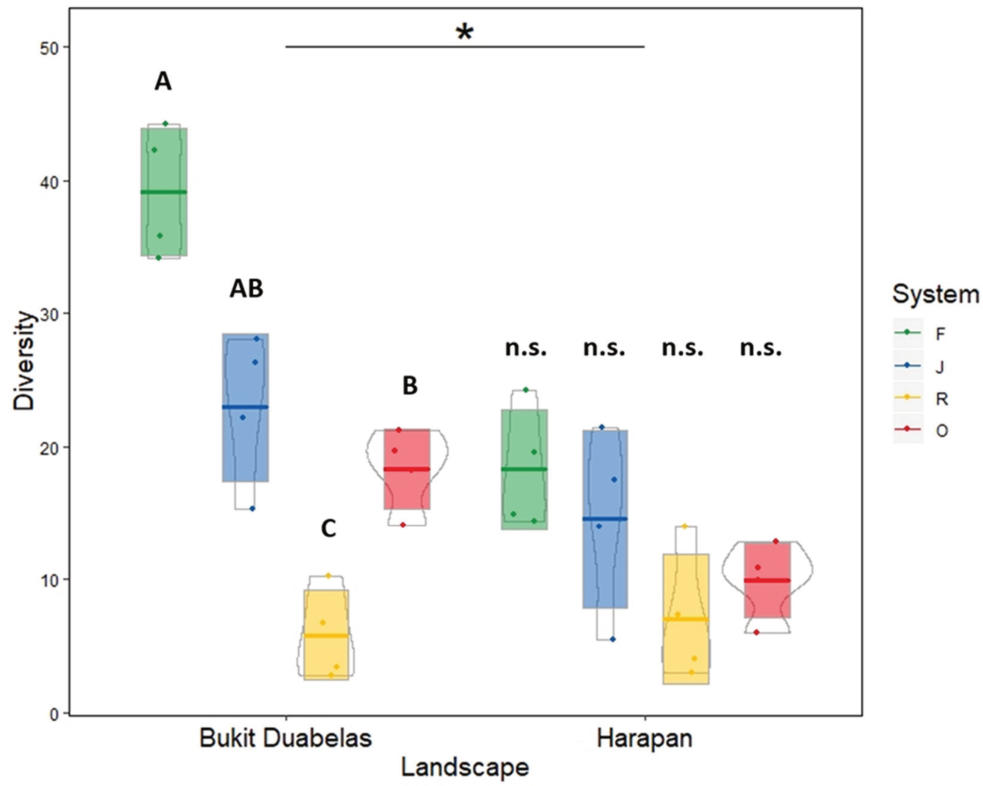

Figure A34. Pirate plots of eulophid wasp inverse Simpson Diversity in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A15. Inverse Simpson Diversity of eulophid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	28.7 ± 11.97	18.75 ± 7.31	6.45 ± 4.01	14.11 ± 5.26
Bukit Duabelas Landscape	39.13 ± 4.86	22.94 ± 5.65	5.81 ± 3.44	18.31 ± 3.07
Harapan Landscape	18.28 ± 4.57	14.57 ± 6.8	7.09 ± 4.96	9.9 ± 2.86

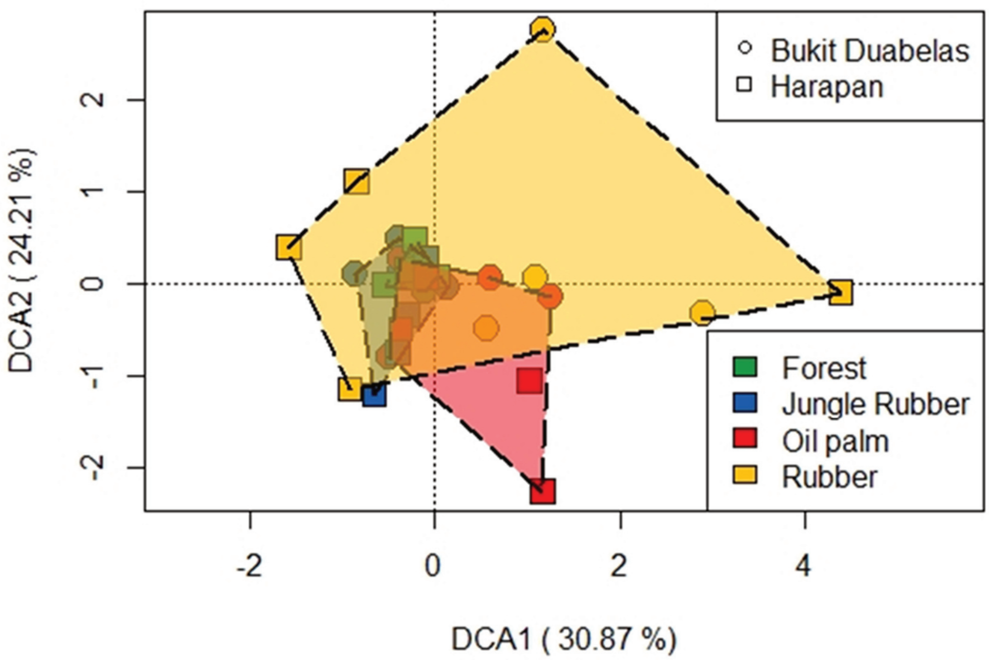

Figure A35. Detrended Correspondence Analysis for eulophid wasps in four land-use systems based on a matrix of Hellinger-transformed data. Percentages on axes represent the proportion of total variation shown in the ordination.

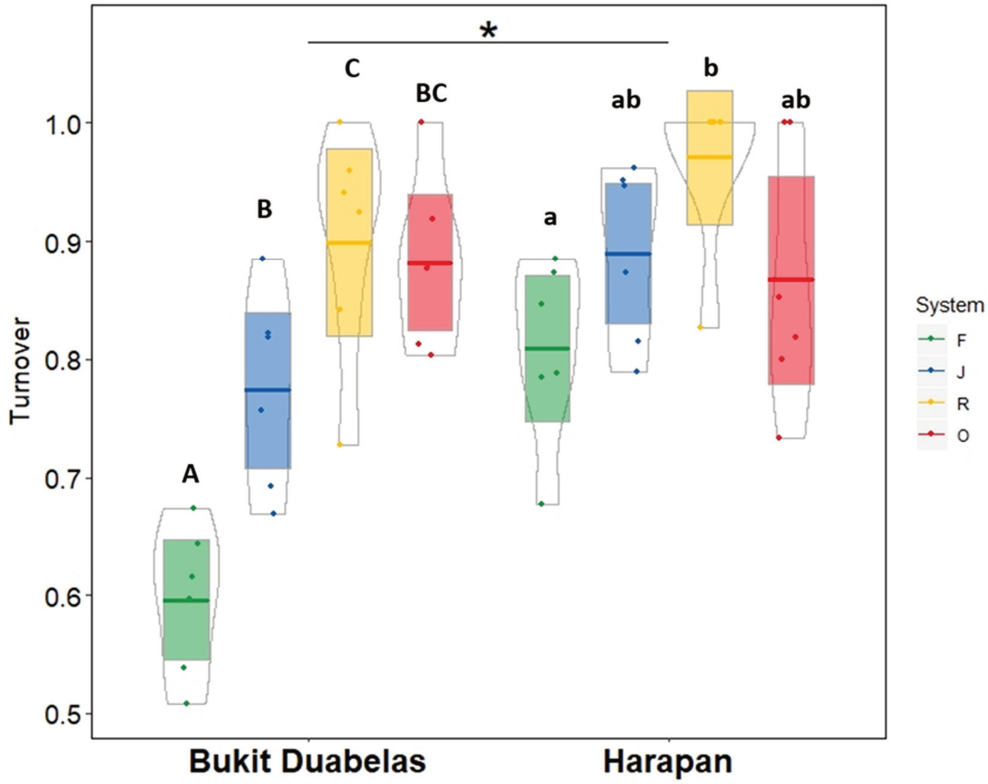

Figure A36. Pirate plots of eulophid wasp species turnover rate in four land-use systems in two landscapes calculated as Bray-Curtis dissimilarity index. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A16. Species turnover rate of eulophid wasps measured as Bray-Curtis dissimilarity index in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	0.75 ± 0.1	0.84 ± 0.1	0.94 ± 0.08	0.87 ± 0.07
Bukit Duabelas Landscape	0.59 ± 0.06	0.77 ± 0.08	0.89 ± 0.09	0.88 ± 0.07
Harapan Landscape	0.8 ± 0.07	0.88 ± 0.07	0.97 ± 0.07	0.86 ± 0.1

Platygastridae

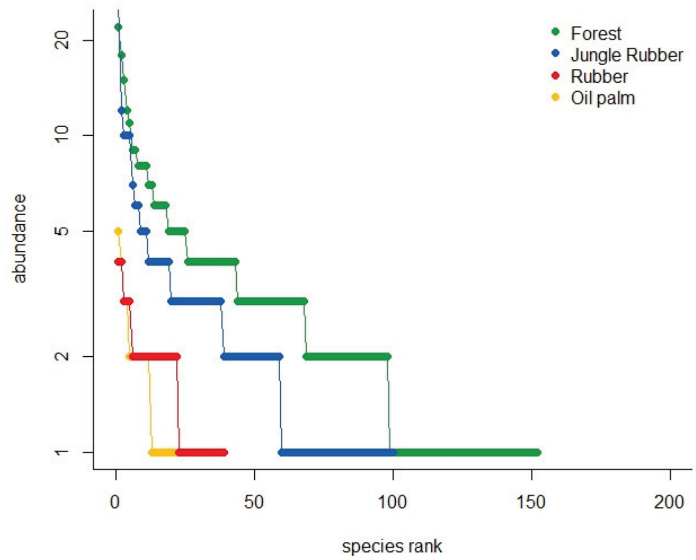

Figure A37. Rank-abundance curves for platygastrid wasps in four land-use systems. Abundance is shown as logarithm of abundance using base 10.

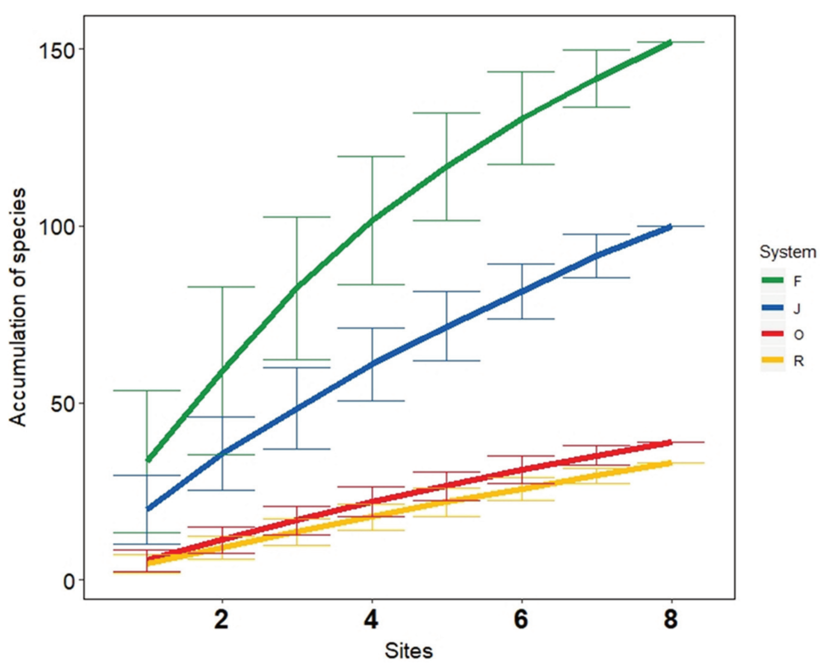

Figure A38. Species accumulation curves for platygastrid wasps in four land-use systems. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Error bars represent standard deviation.

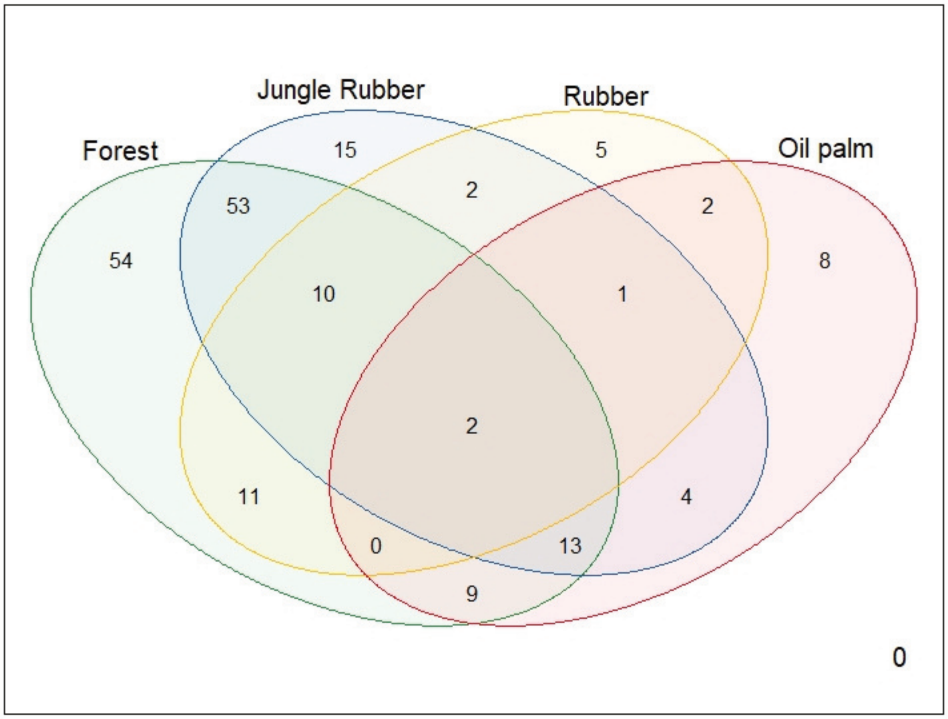

Figure A39. Venn diagram for platygastrid wasps in four different land-use systems. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated land-use systems.

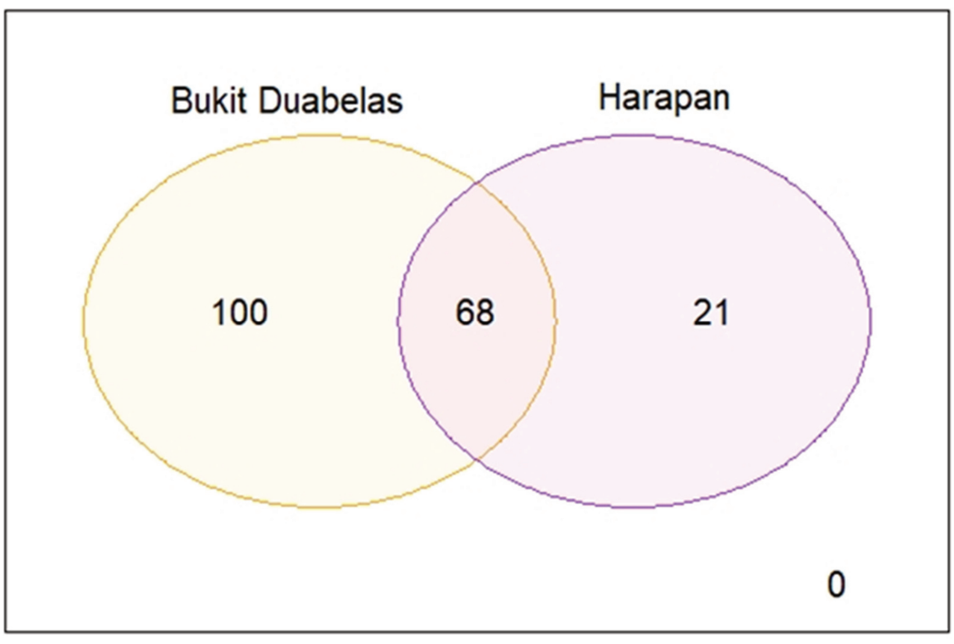

Figure A40. Venn diagram for platygastrid wasps in the two landscapes. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated landscapes.

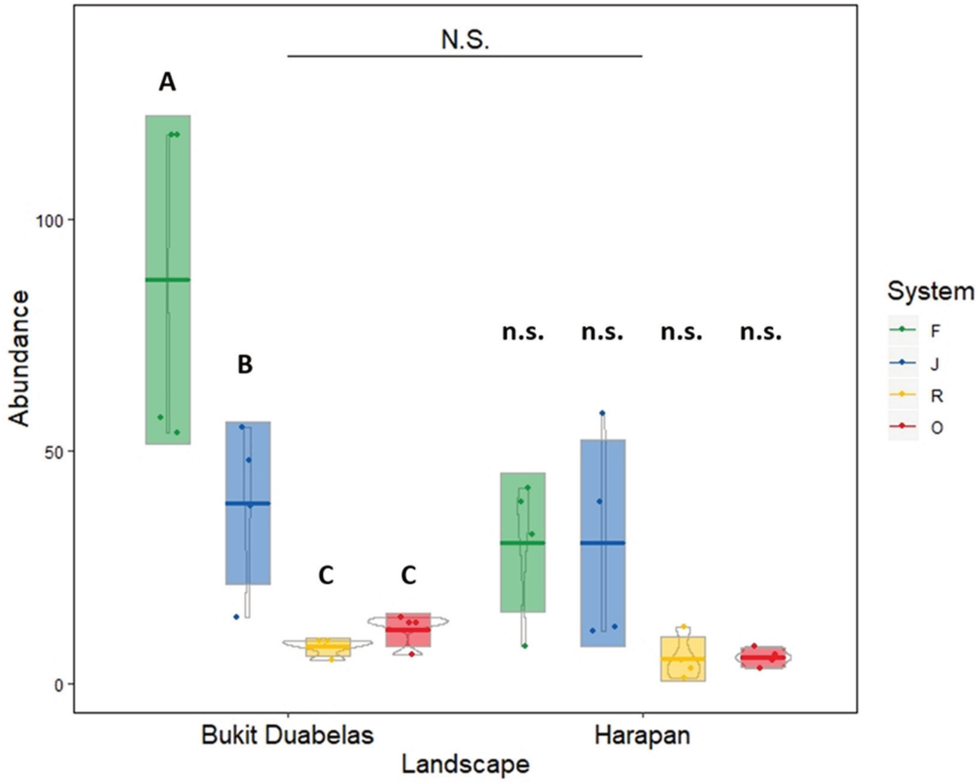

Figure A41. Pirate plots of platygastrid wasp abundance in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A17. Abundance of platygastrid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	58.5 ± 39.65	34.37 ± 19.51	6.5 ± 3.62	8.5 ± 4.24
Bukit Duabelas Landscape	86.75 ± 36.1	38.75 ± 17.91	7.75 ± 1.89	11.5 ± 3.69
Harapan Landscape	30.25 ± 15.41	30 ± 22.73	5.25 ± 4.78	5.5 ± 2.08

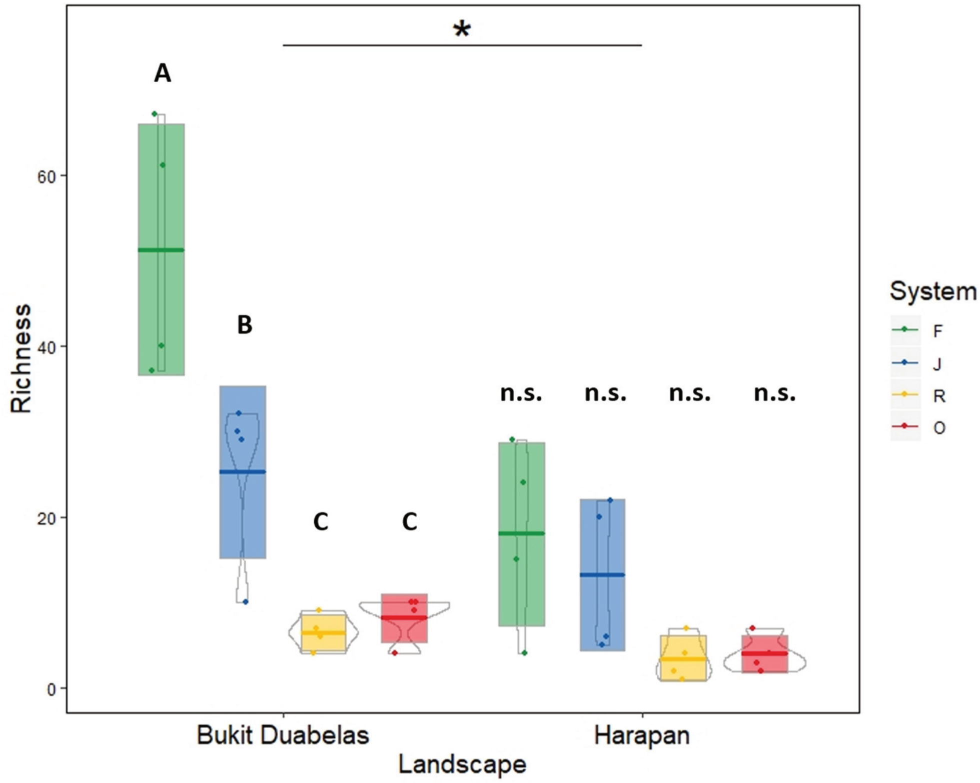

Figure A42. Pirate plots of platygastrid wasp species richness in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A18. Species richness of platygastrid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	34.62 ± 21.53	19.25 ± 10.99	5 ± 2.72	6.12 ± 3.27
Bukit Duabelas Landscape	51.25 ± 14.97	25.25 ± 10.24	6.5 ± 2.08	8.25 ± 2.87
Harapan Landscape	18 ± 10.98	13.25 ± 8.99	3.5 ± 2.64	4 ± 2.16

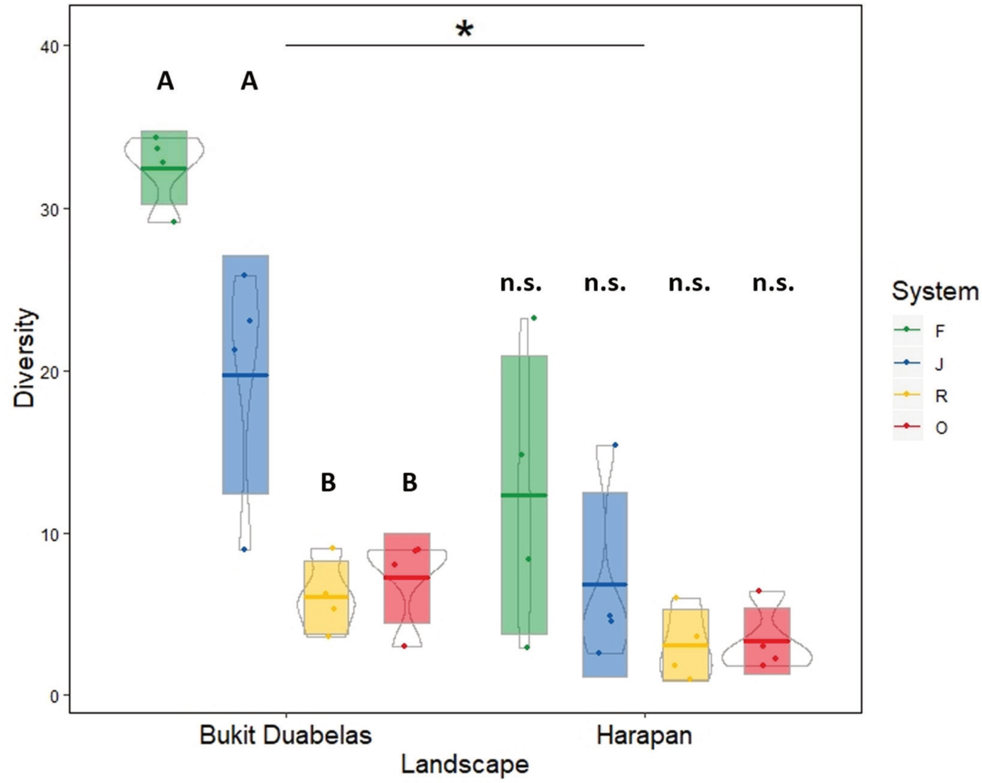

Figure A43. Pirate plots of platygastrid wasp inverse Simpson Diversity in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant (p < 0.05) difference between landscapes. Capital letters indicate significant (p < 0.05) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant (p < 0.05) differences between land-use systems in Harapan.

Table A19. Inverse Simpson Diversity of platygastrid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	**Jungle Rubber**	**Rubber**	**Oil palm**
Overall	22.39 ± 12.28	13.29 ± 9.27	4.56 ± 2.6	5.29 ± 3.08
Bukit Duabelas Landscape	32.47 ± 2.29	19.75 ± 7.47	6.03 ± 2.26	7.21 ± 2.83
Harapan Landscape	12.32 ± 8.72	6.83 ± 5.77	3.09 ± 2.21	3.36 ± 2.08

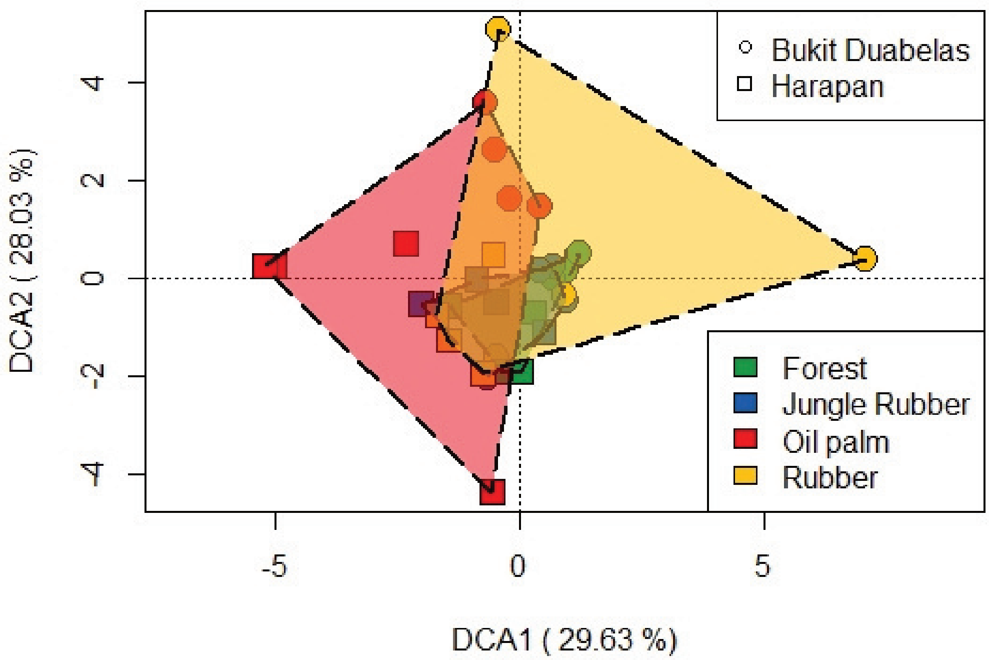

Figure A44. Detrended Correspondence Analysis for platygastrid wasps in four land-use systems based on a matrix of Hellinger-transformed data. Percentages on axes represent the proportion of total variation shown in the ordination.

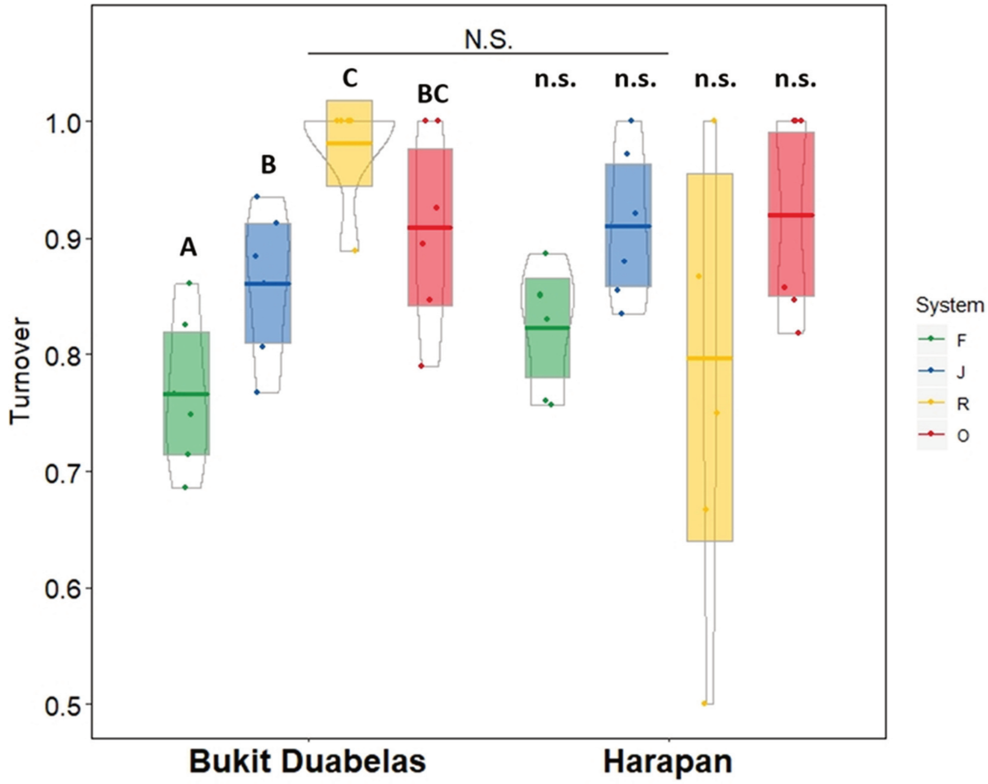

Figure A45. Pirate plots of platygastrid wasp species turnover rate in four land-use systems in two landscapes calculated as Bray-Curtis dissimilarity index. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A20. Species turnover rate of platygastrid wasps measured as Bray-Curtis dissimilarity index in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	0.85 ± 0.08	0.89 ± 0.05	0.92 ± 0.12	0.95 ± 0.07
Bukit Duabelas Landscape	0.76 ± 0.06	0.86 ± 0.06	0.98 ± 0.04	0.9 ± 0.08
Harapan Landscape	0.82 ± 0.05	0.91 ± 0.06	0.79 ± 0.19	0.92 ± 0.08

Scelionidae

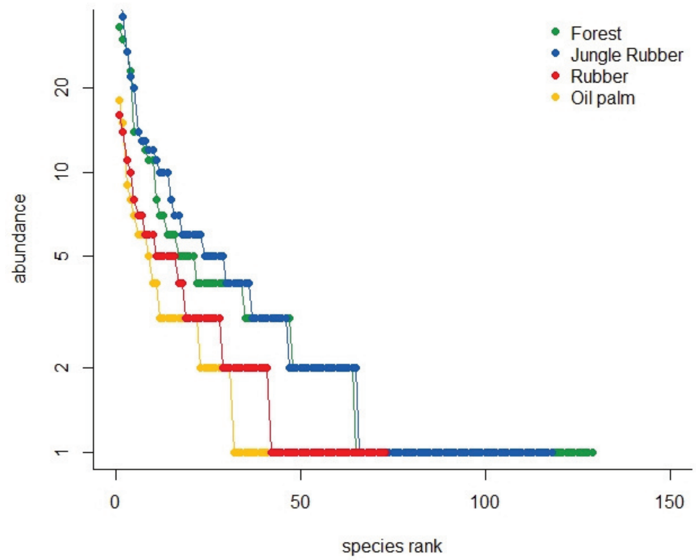

Figure A46. Rank-abundance curves for scelionid wasps in four land-use systems. Abundance is shown as logarithm of abundance using base 10.

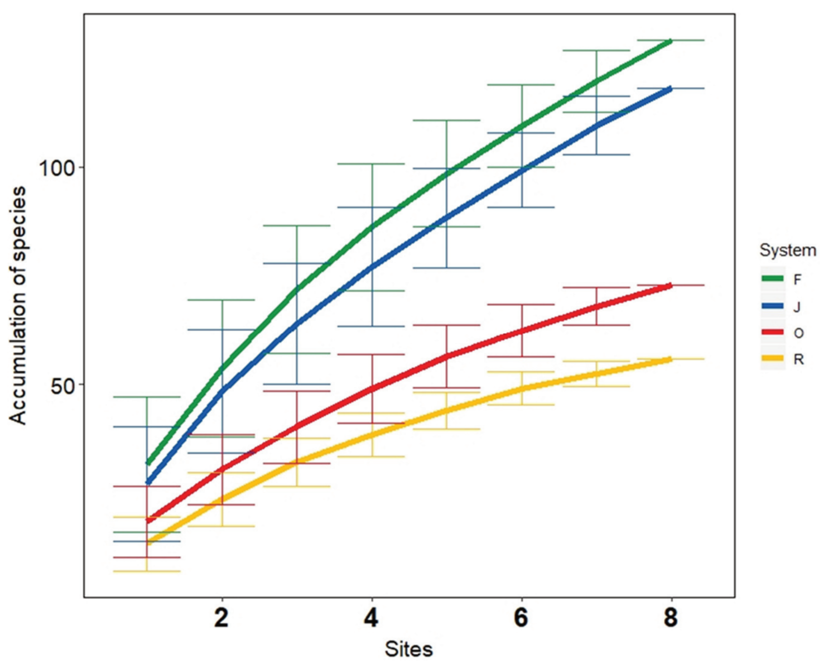

Figure A47. Species accumulation curves for scelionid wasps in four land-use systems. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Error bars represent standard deviation.

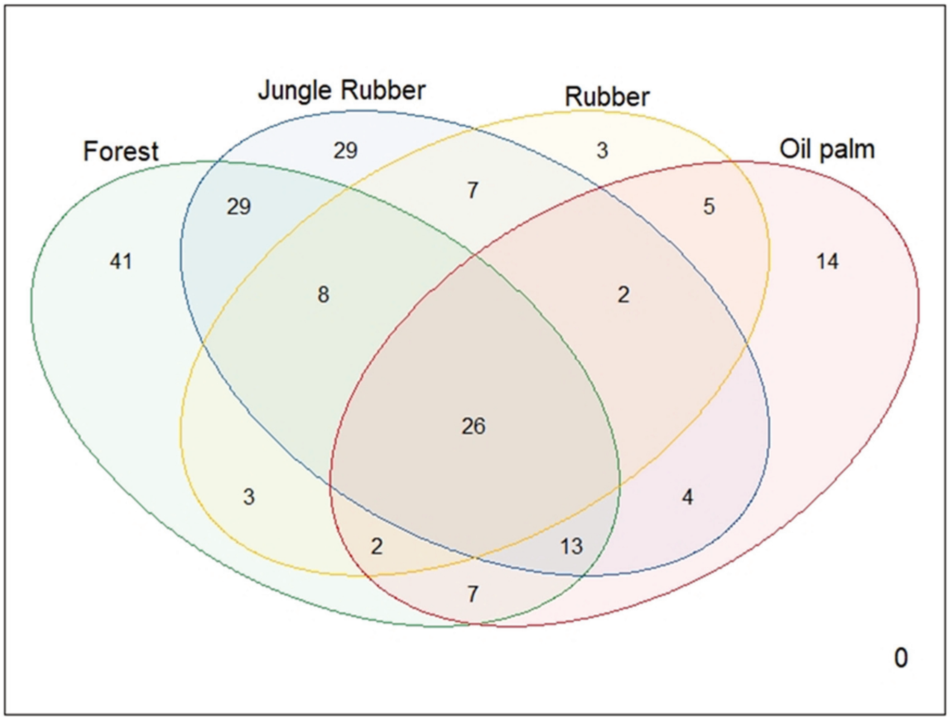

Figure A48. Venn diagram for scelionid wasps in four different land-use systems. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated land-use systems.

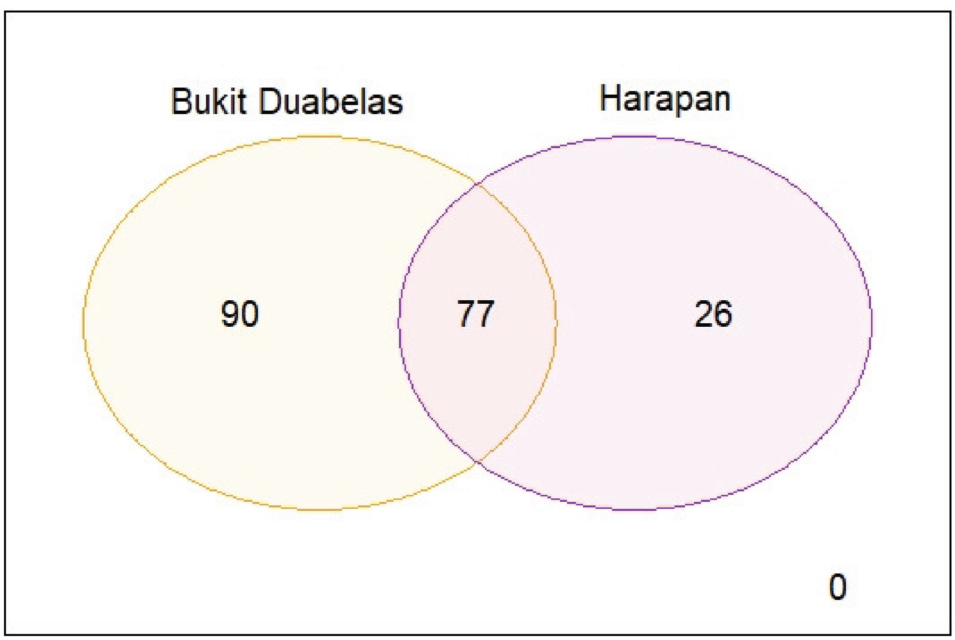

Figure A49. Venn diagram for scelionid wasps in the two landscapes. Numbers represent counts of Morphospecies. Zero at bottom right indicates no Morphospecies were found outside the investigated landscapes.

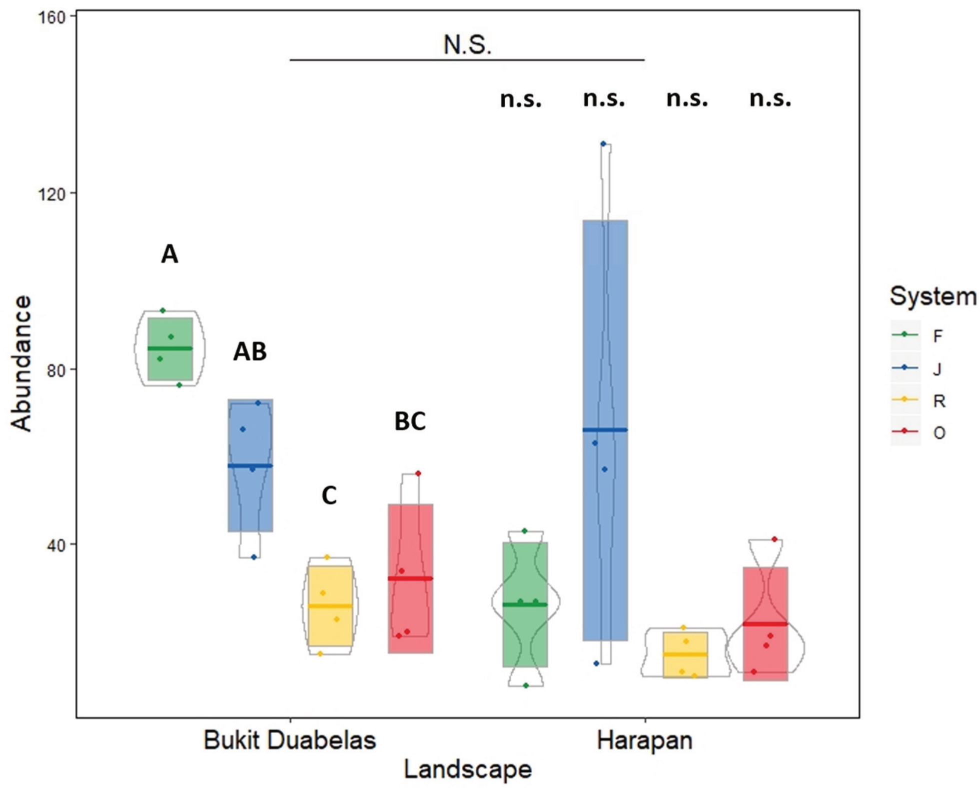

Figure A50. Pirate plots of scelionid wasp abundance in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant (p < 0.05) difference between landscapes. Capital letters indicate significant (p < 0.05) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant (p < 0.05) differences between land-use systems in Harapan.

Table A21. Abundance of scelionid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	55.37 ± 32.85	62 ± 33.7	20.5 ± 9.16	27.12 ± 15.2
Bukit Duabelas Landscape	84.5 ± 7.23	58 ± 15.29	26 ± 9.3	32.25 ± 17.25
Harapan Landscape	26.25 ± 14.31	66 ± 48.73	15 ± 5.35	22 ± 13.11

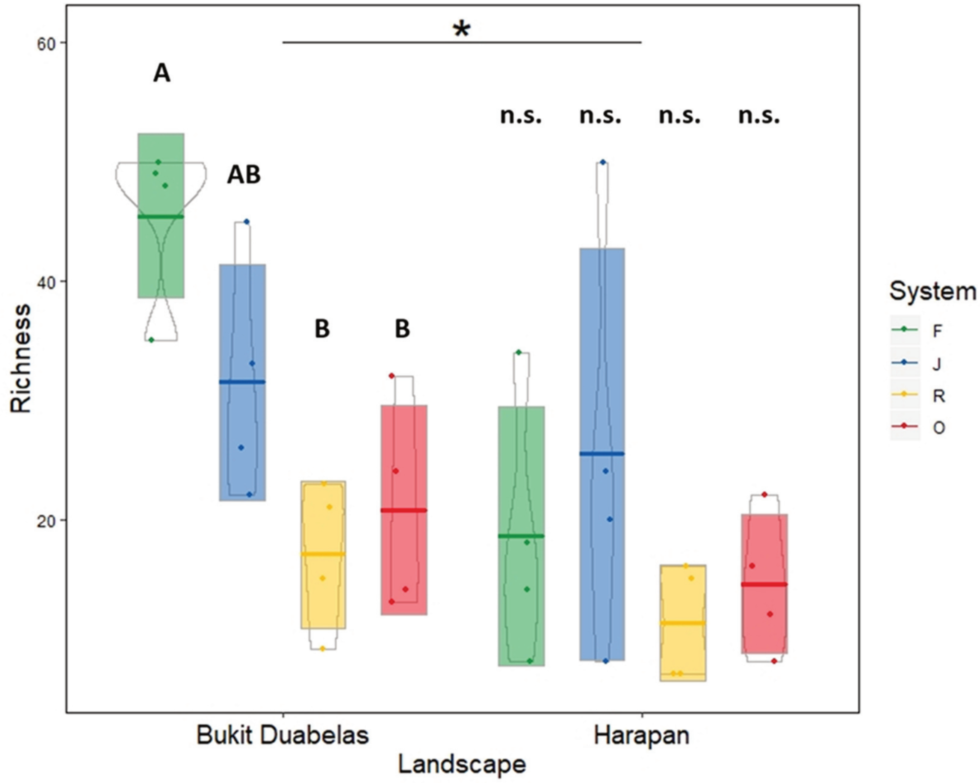

Figure A51. Pirate plots of scelionid wasp species richness in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A22. Species richness of scelionid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	32 ± 16.8	28.5 ± 13.71	14.12 ± 6.08	17.62 ± 7.81
Bukit Duabelas Landscape	45.5 ± 7.04	31.5 ± 10.08	17 ± 6.32	20.75 ± 8.99
Harapan Landscape	18.5 ± 11.12	25.5 ± 17.69	11.25 ± 4.92	14.5 ± 5.97

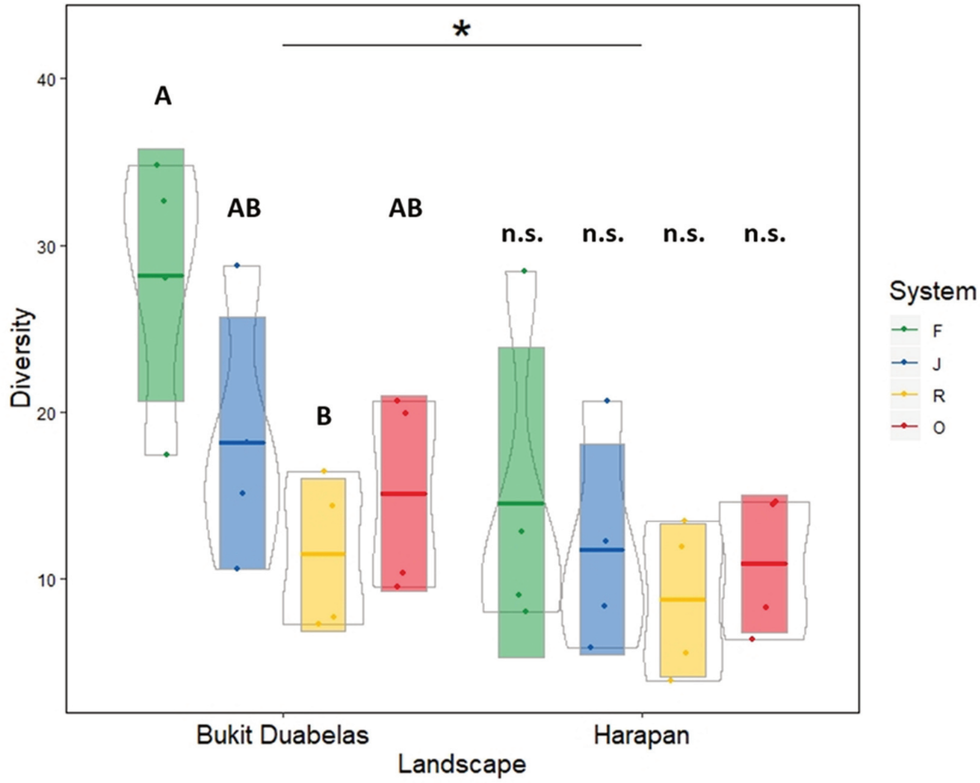

Figure A52. Pirate plots of scelionid wasp inverse Simpson Diversity in four land-use systems in two landscapes. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant ($p < 0.05$) difference between landscapes. Capital letters indicate significant ($p < 0.05$) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant ($p < 0.05$) differences between land-use systems in Harapan.

Table A23. Inverse Simpson Diversity of scelionid wasps in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	21.39 ± 10.83	14.97 ± 7.43	10.08 ± 4.58	13.01 ± 5.3
Bukit Duabelas Landscape	28.23 ± 7.7	18.16 ± 7.73	11.45 ± 4.69	15.1 ± 5.99
Harapan Landscape	14.55 ± 9.48	11.77 ± 6.48	8.71 ± 4.7	10.92 ± 4.23

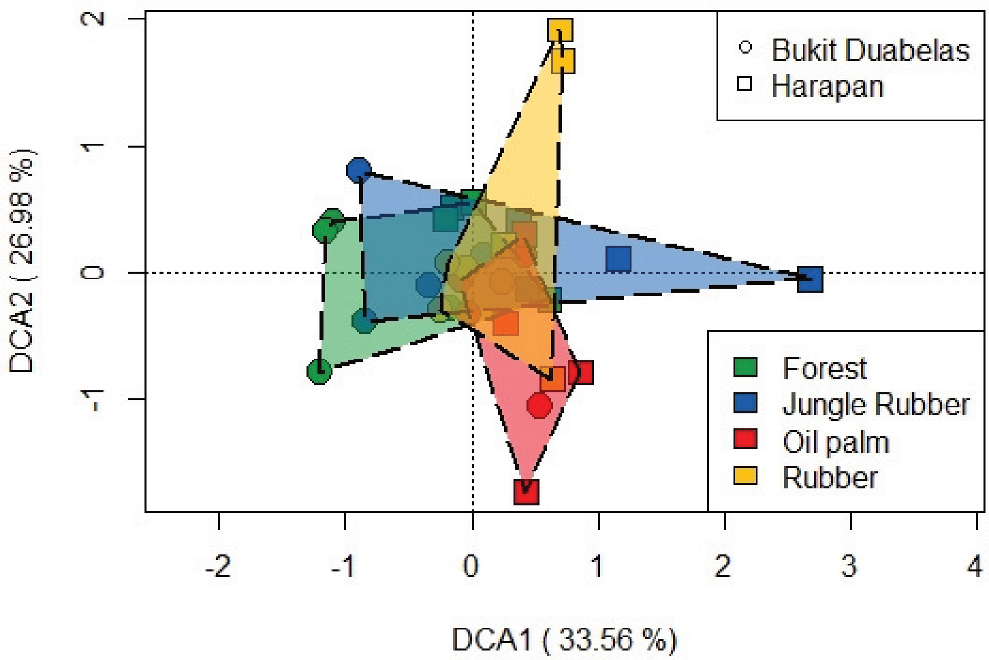

Figure A53. Detrended Correspondence Analysis for scelionid wasps in four land-use systems based on a matrix of Hellinger-transformed data. Percentages on axes represent the proportion of total variation shown in the ordination.

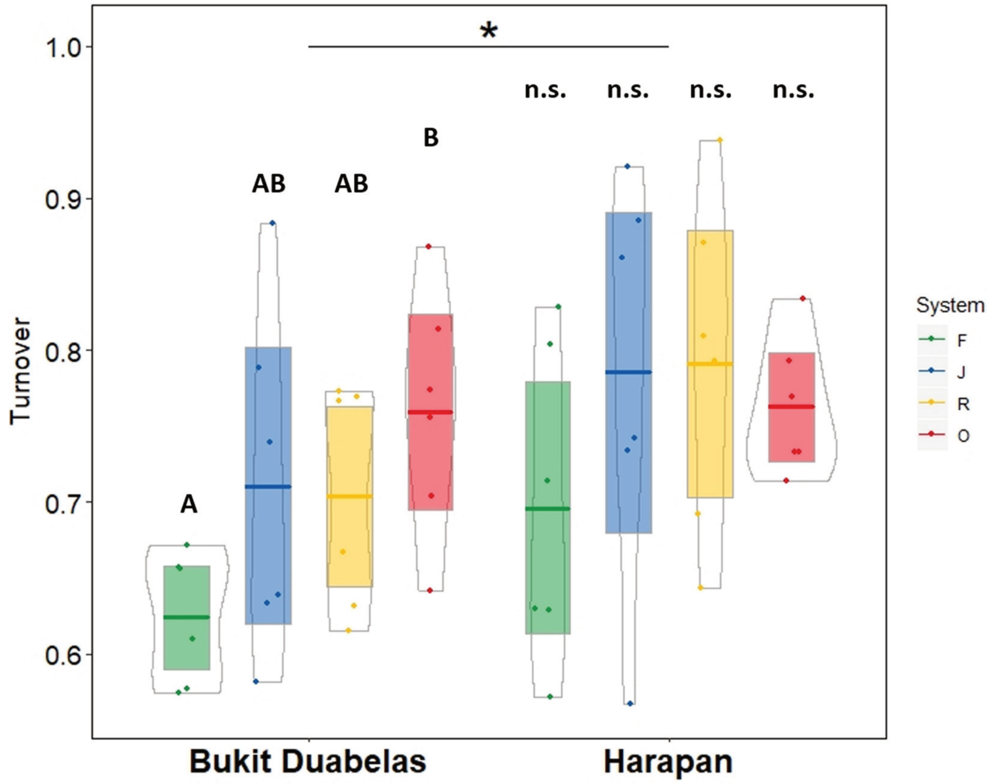

Figure A54. Pirate plots of scelionid wasp species turnover rate in four land-use systems in two landscapes calculated as Bray-Curtis dissimilarity index. Points = data points, horizontal line = mean, box = 95% confidence interval, lines = smoothed density of data. System-legend: F = Forest, J = Jungle Rubber, R = Rubber, O = Oil palm. Horizontal bar indicates significant (p < 0.05) difference between landscapes. Capital letters indicate significant (p < 0.05) differences between land-use systems in Bukit Duabelas, lower case letters indicate significant (p < 0.05) differences between land-use systems in Harapan.

Table A24. Species turnover rate of scelionid wasps measured as Bray-Curtis dissimilarity index in four land use systems, both in total and individually for both landscapes (Mean ± SD).

	Forest	Jungle Rubber	Rubber	Oil palm
Overall	0.71 ± 0.1	0.76 ± 0.09	0.77 ± 0.1	0.77 ± 0.06
Bukit Duabelas Landscape	0.62 ± 0.04	0.71 ± 0.11	0.7 ± 0.07	0.75 ± 0.08
Harapan Landscape	0.69 ± 0.1	0.78 ± 0.13	0.79 ± 0.1	0.76 ± 0.04

Molecular experiments with pooled DNA

Methods

Since previous experiments with individual-based PCR products failed, I opted to work with pooled DNA on plot-level. Following this approach, 10 µl of individual DNA were pooled together on plot level. 5 µl of pooled DNA template from each plot were used for first-step PCR. This PCR was performed using the Phusion High-Fidelity DNA Polymerase PCR kit (Thermo Fischer Scientific), with the program described in *Material and Methods*. Product from pooled PCRs was purified using the DNA Purification Mini Spin Column Kit (Genaxxon Bioscience) according to the manufacturers protocol. To ensure maximal concentration, all four replicates per plot were pooled together for purification and eluted in a final volume of 50 µl H_2O. Concentration of purified products was measured as described in *Material and Methods*. For plots that did not yield a minimum concentration of 10 ng/µl, PCR was repeated with template that had been concentrated by reducing its volume by 80% and with template that had been diluted 1:1 and 1:2.

Table A25. Mastermix for first-step PCR per 5 µl of DNA template.

Reagent	Amount (µl)
H_2O	25.5
5x Phusion HF Buffer	10
dNTP Mix	1
Primer forward	4
Primer reverse	4
Phusion DNA Polymerase (2U/µl)	0.5

Results and Outlook

The first trial resulted in only 50% of products having a minimum concentration of 10 ng/µl. Increasing the concentration by reducing its original volume by 80% did not result in any PCR product. 1:1 dilutions of template yielded products in all previously failed plots except BR2, and dilution of 1:2 resulted in the same outcome. This indicates that template concentration of several samples was probably too high and impeded the PCR, reinforcing the notion that standardization of template DNA concentration would have been a meaningful optimization of the experiments. Overall, the experiments resulted in products with sufficient concentration in 22 out of 24 samples (Tab. A26). Samples from plot BR2 never showed any signs of PCR success, and in plot BR1, the highest concentration achieved was 3.167 ng/µl. Product from all plots but BR2 were pooled equimolarly on level of land use system per landscape, with product from BR1 having been concentrated via volume-reduction. Subsequently, six samples containing pooled PCR product of up to 200 individuals were send to the department of Microbiology for MiSeq-sequencing.

Table A26. Final concentration of PCR-Products from pooled template (ng/ µl).

BF1	BF2	BF3	BF4	BO2	BO3	BO4	BO5	BR1	BR2	BR3	BR4
20.96	24.75	23.81	17.25	12.5	28.33	20.82	21.97	3.16	0.35	25.3	32.1
HF1	**HF2**	**HF3**	**HF4**	**HO1**	**HO2**	**HO3**	**HO4**	**HR1**	**HR2**	**HR3**	**HR4**
17.91	10	22.18	32.11	22.44	12.45	33.24	11.04	17.75	20.96	25.81	42.5

Due to the loss of time that occurred while conducting the (failed) individual-based experiment, bioinformatic processing of raw data into an Operational Taxonomic Unit (OUT)-table and statistical evaluation of that table could not be performed in time to make it into this manuscript. However, this experiment will be carried on. I expect the results of this 'metabarcoding' experiment to confirm the findings of the abundance-based Morphospecies dataset, meaning that statistical analysis will reveal a decline in molecular OTU diversity from forest to monocultures. If this expectation turns out to be true, 'metabarcoding' of pooled DNA samples will indeed prove to be a straightforward, cost- and time efficient alternative to morphological identification of species when it comes to investigate general biodiversity patterns in individual-rich samples.

Statement of Authorship

I confirm that the work presented in this thesis has been performed and interpreted solely by myself.

Except where specific reference is made in the main text of the thesis, this thesis contains no material extracted in whole or in part from a thesis, dissertation or research paper presented by me for another degree or diploma. No other persons work (published or unpublished) has been used without due acknowledgement in the main text of the thesis. This thesis has not been submitted for the award of any other degree or diploma in any other tertiary institution.

I confirm that the printed copies do not differ from the electronic ones.

Göttingen, January 22, 2019

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