Impacts of land use on native pollinator diversity and survival in Sumatra, Indonesia

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1 Abstract

Biodiversity is an essential driver of ecosystem functions and biodiverse habitats can improve ecosystem processes as well as benefit species living in that ecosystem by providing them a higher variety of resources. Key pollinators are bees and their survival and health are crucial to sustain pollination services and therefore help to obtain a high biodiversity in an ecosystem. Using the stingless bee species *Tetragonula laeviceps*, native to Southeast Asia, we tested if more natural land use types and more natural habitats in the surrounding support colony health and growth and buffer negative effects. The study was conducted between August and November 2018 in Jambi Province, Sumatra, Indonesia in plots in secondary forest, jungle rubber, oil palm plantations and shrub. Our study proposes, that more natural habitats such as forest and rubber increase colony health and growth, whereas more natural landscapes in the surrounding benefit forest and shrub plots but can have negative or no effects in other land use types. Even if vegetation analysis in this study didn't show significant effects on colony performance, the importance of floral resources for bee colonies is well established and the missing significance is probably caused by insufficient vegetation data.

2 Introduction

It is well established that biodiversity is a crucial driver of ecosystem functions and that a larger number of species are essential to maintain the stability of ecosystem processes (Loreau et al., 2001). Especially when the environment is changing, the resilience of an ecosystem is increasing with an increasing number of species living in it. Individual species benefit from higher biodiversity, as a higher diversity of resources is available, and they can use different niches. Especially under changing conditions, species living in a high biodiversity environment are able to adapt to new niches (Brittain et al., 2013). Insects in particular have a very high diversity due to their ability to fly, which improves dispersal; a complete metamorphosis, which allows the larva to feed from different resources than the adult and reduces competition; sexual selection and competition which seems to be linked with diversity too (Mayhew, 2007).

Indonesia is one of the biodiversity hotspots of the world but also one with a serious loss of biodiversity, mainly driven by deforestation. Since the 1970s, forest cover in Sumatra has dropped from 93 % to 38 % (Miettinen et al., 2012). Rainforests have been cleared to exploit forest products like timber or to transform the land into agricultural plantations (Mudiyarso et al., 2002). Barnes et al. (2014) state that land transformation from forest to oil palm plantations had severe impacts on single species as well as on whole communities, with species richness and biomass most affected. In Jambi Province of Sumatra, where this study was conducted, around 400.000 people were resettled between 1967 to 2007 as part of the transmigration program to be able to transform forests to agricultural land. By 2014, roughly 590.000 ha of oil palm and 650.000 ha of rubber plantations were being cultivated (Drescher et al., 2016).

Within the highly biodiverse class of Insecta, the key pollinators of natural and agricultural environments throughout the world are bees. Their survival and health are crucial to sustain pollination services and therefore help to obtain a high biodiversity in an ecosystem. Especially wild pollinators (solitary bees) are able to still provide pollination services under extreme weather conditions when the service of honey bees declines, even if their niches differ under normal circumstances (Brittain et al., 2013).This is even more important considering that roughly one third of the human diet is an outcome of bee pollination (Cappellari et al., 2013). However, bee development and survival relies on the availability of sufficient floral resources and essential nutrients (Di Pasquale et al., 2013). The reception of an adequate amount of nutrients is guaranteed through food mixing. This effect has been observed in several generalist herbivores (Palminteri et al., 2016) and suggests that resources are required to fulfill many different functions, like toxin dilution and nutritional balance of essential micro- and macronutrients, allowing optimal performance in growth and survival (Pijl, 2013). Therefore, it is necessary for wild bees to have various floral resource species in an acceptable range. On the other hand, specific functions like high pollen protein content and strong antimicrobial activity of resin can be provided by only a few resources (Kaluza et al., 2017).

However, the transformation of tropical landscapes to monocultures leads to farther distances between flowering plants and pollinator habitats, thus a strong decrease in pollination service with increasing distance to natural habitats has been observed (Ricketts et al., 2008). Small cavity-nesting bees in particular require nearby forest structures as a source of nesting, mating and resting sites, as well as food resources (Kevan, 1999; Klein et al., 2008). Overall bee species abundance and richness are affected by forest structures, for example, increases when forest size and flower abundance increases within a 1000 m radius (Gutiérrez-Chacón et al., 2018). Even so, the effect changes for different guilds. Social bees seem to be positively related in richness and abundance with a larger forest within a 500 m to 1000 m radius, whereas solitary bee species seem to be only more abundant with a forest close by, and ground nesting bees did not show any effect related to forest proportion (Gutiérrez-Chacón et al., 2018). Hence it is very important to understand how land use and landscape composition may affect diversity and health of local pollinators.

Stingless bees (Meliponinae) have a pantropical distribution and can be found in Indonesia. Most of their characteristics resemble those of honeybees, whereas they differ in sting rudiment, appearance of virgin queens and nest structure (Heard, 2016). The appearance of the perennial hives is related to forest cover in the surrounding area but most species can adapt to urban environments if food and nesting resources are abundant (Aidar et al., 2013). They are known to pollinate around 90 crop species, of which nine are confirmed to rely solely on stingless bee pollination (Amano et al., 2000; Heard, 1999). Stingless bee species richness and abundance is closely related to forest cover but not plant species richness and abundance. However, the communities of stingless bees appears to be related to plant species richness (not floral resources) and only weakly to forest cover (Brosi, 2009). Whereas some South American species like *Melipona seminigra* and *Melipona grandis* seem to be unaffected by deforestation, other common species like *Melipona melanoventer* and *Melipona rufiventris* are relatively susceptible and occur only in areas which are at least bordered by forest (Brown and Albrecht, 2001). Nevertheless, most meliponin (stingless) bees depend on forests, which is why it is important to include or preserve at least small forest patches in agricultural systems to ensure bee richness and abundance (Brosi, 2009)

One of the stingless bee species found in Indonesia is *Tetragonula laeviceps* SMITH, 1857. This study will record the development and survival of hives as a function of plot land use and surrounding natural areas. It was conducted between August and November 2018 in Jambi Province (Sumatra, Indonesia). The study's goal is to identify the best habitat for the stingless bee species as well as to advice local farmers on where to keep hives in order to remain healthy hives and facilitate their growth. Therefore, we want to test in our first hypothesis if measures of *Tetragonula laeviceps* colony health and growth are higher in more natural (forest) land use types and with more surrounding natural habitat. In a second hypothesis we aim to find out if more natural land use types and more natural landscape compositions are additive, i.e. a more intensified land use either at the plot or landscape level may be compensated for at the other level. For that reason, the project will investigate which variables, plot land cover and the composition of the surrounding landscape, as well as environmental parameters, affect *Tetragonula laeviceps*. Landscape composition and plot land use type were selected prior to the field work with classified satellite images. We used colony structures as well as foraging activity and colony numbers to later statistically investigate colony health and growth. Furthermore, vegetation analyzes were carried out to look into possible floral resource intake.

3 Material and Methods

3.1 Study area

The study was conducted in Jambi Province of Sumatra, Indonesia. EFForTS (Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation System, a collaborated Research Centre 990 this study was embedded in) originally installed 112 plots in four land use types, composed of secondary forest, oil palm plantations, jungle rubber and shrub, for a bird landscape survey (Darras, unpublished). Shrub is a cleared land use type that has regrown and is now dominated by shrubby vegetation. Jungle rubber (in the following called rubber) and oil palm plots are plantations owned by smallholder farmers and forest plots are mainly used as reference sites. Forty of these plots, which are located in the Batang Hari regency between Harapan forest and Jambi City were used in this study (Figure 1). We installed three hives in each plot (120 hives in total), covering ten sites of each land use type. Sites were chosen to cover a similar gradient of natural habitat (forest and shrub) composition for all the land use groups while maximizing their extremes. This mainly means a trade-off between oil palm and forest or shrub.

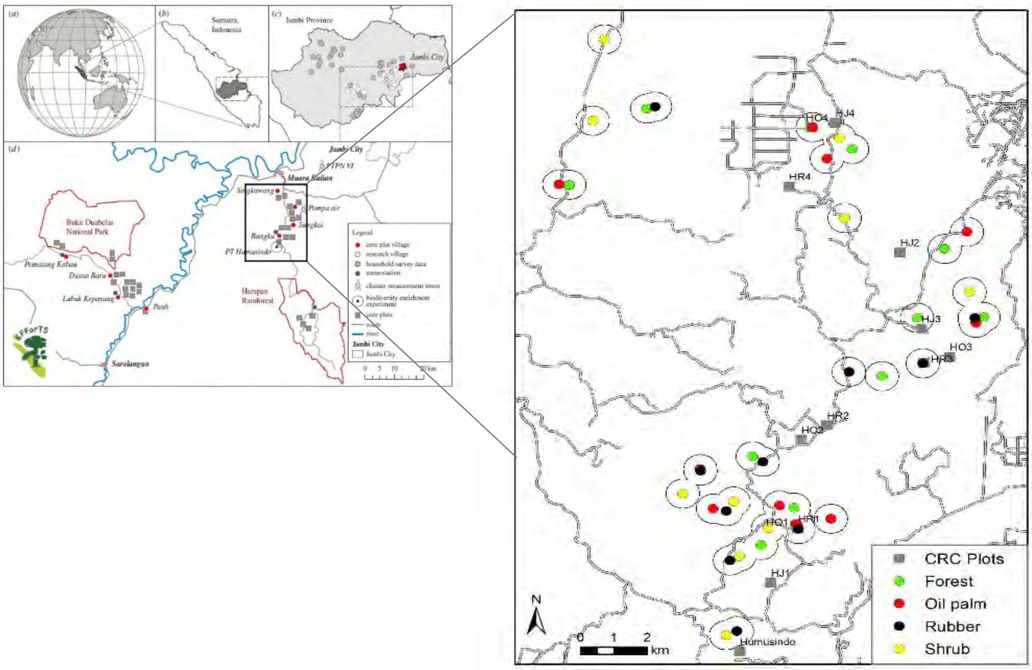

Figure 1: The location of our 40 study sites for this study in relation to villages that are part of the province-level household surveys and the landscapes Bukit Duabelas National Park and Harapan Rainforest, where the Collaborated Research Centre 990 core plot design has been implemented (modified from Drescher et al., 2016)

3.2 Study species

Tetragonula laeviceps SMITH, 1857, also called *Trigona laeviceps*, is a widespread stingless bee species or species complex in Southeast Asia (Rasmussen and Michener, 2010) often used for meliponiculture (Nugitrangson et al., 2016). These bees are generalists, feeding mostly on the Fabaceae and Palmae families (Nurasiqin, 2016). Their natural habitat is in forests, where it builds its nests in cavities on the base or in higher parts of trees (Sakagami et al., 1983). However, the species is highly anthropophilous and can nest in pillars and eaves of wooden houses (Sakagami et al., 1983). Bees enter their nests through a two to five centimeter long entrance tube which is commonly guarded by four to five guards. Inner nest architecture is similar in natural and human built constructs, where storage pots for honey and pollen are clustered together with adjacent pots sharing the same cell wall. Usually storage pots are stuck to the box walls and the floor. Brood cells are separated from storage pots and built at the floor or the wall. Old brood cells are getting recycled. Resin is sampled in extra areas of the box and stored either on the walls in more or less thick layers or in a very thin layer along the top of the box (personal observation). Sakagami et al. (1983) state that worker stages can be tracked by the different color of each stage from an entirely whitish yellow at emergence to further darkening color to black with progressing age. Compared to other stingless bee species, colony sizes of *Tetragonula laeviceps* are slightly lower. The forager/worker ratio depends on the colony size but is slightly larger than in honeybees (30 % in *Apis melifera*, ca. 40 % in *Tetragonula laeviceps*). Most workers of stingless bee species have a life span of approximately 100 days, whereas queens can life a year or even more depending on the species (Heard, 2016). Exact lifespan data for *Tetragonula laeviceps* are not yet researched.

3.3 Survey Methods

Source of the stingless bee colonies was an apiary on a coffee plantation in Bengkulu from Dr. Rustama (University of Bengkulu, Sumatra). The stingless bees were kept in wooden boxes of 30x20x16 cm and were transported from the apiary to Humusindo field station by car and set up on 12.07.2018. Therefore, three hives were placed under one shelter with entrances facing East where possible.

The survey methods during the field work were divided into three main parts:

1) Foraging activity and number of workers were conducted to test the effects of environmental parameters and landscape conditions on bee activity and health.

2) Hive Structure was conducted to measure hive sizes and their change in time and

3) Vegetation surveys were conducted to test if species numbers and or floral resources have an impact on worker numbers.

3.3.1 Foraging activity and hive structure

We surveyed bee activity four times between August and November within a time range between 9 am and 11 am, when the bees are most active. We conducted these observations on rain-free days to standardize conditions of bee activity. Following the methods of Kaluza et al. (2016) the overall foraging activity of each hive was recorded by counting the returning foragers for five minutes. Using four counters (Hand Tally Counter), we recorded every bee leaving the hive, returning with no load, returning with pollen, and returning with resin. During every survey, each of the three hives in a plot were observed twice for five minutes by a different observer. Furthermore, daily weather conditions, temperature and humidity (Thermometer-Hygrometer AZ-HT-02, TFA), and light (Light meter LX-101AS, Lutron) were recorded at the end of each five-minute counting interval.

We also recorded the hive structure after each bee activity survey. Hive boxes were built with a transparent plastic window under their lids that allowed us to observe the hive structures when we removed the lid without disturbing the colony. We placed a 2x2 cm grid over the top of the window to estimate the volumes of the different structures of the hive, namely resin (R), brood cells (B), pollen- (P) and honeypots (H), which we drew on a datasheet. The volumes of the overall hive structure, brood cells, pollen- and honey pots and resin, were estimated in “hive volume units” (referred to as “Hvu” in the following text). This unit is defined as a grid cell (2x2 cm) multiplied by a height unit equal to 1/3 of the depth of the hive box (16 cm). This method was used to facilitate volume estimation in the field and allowed relative quantification of hive structure development but is not meant to be a precise estimate of the volume of each structure (data and pictures in soft copy).

Pictures from the structure were taken as a back up to be able to check the development of the hives afterwards. To reduce the reflections caused by the plastic foil covering the top of the hive box, we put a pillowcase over the hive and if necessary, we used a polarized card to further reduce reflections. Finally, the weight of the hive box was recorded using a portable electronic scale (WeiHeng).

At the end of November and beginning of December (end of study period), overall hive performance was assessed. All the remaining beehives (60) were put into a freezer for at least 12 hours to kill the bees. The colony size was determined by counting the bees in each hive and weighing them.

3.3.2 Vegetation survey

Flowering vegetation survey was conducted in August. We counted flower units in four 25 m^2 quadrats placed in the cardinal directions in 10 m distance of the hives. A flower unit was defined as a cluster of flowers within ca. 5 cm, the distance a bee could easily walk. Flower unit counting was limited to those within 5 m above the ground. To identify the flowering plants we used the field guide “Common wayside plants of Jambi Province (Sumatra, Indonesia) from Rembold et al. (2017b) and expert identification (Brambach, personal communication). Following the results of a species accumulation curve analysis, we conducted additional surveys in September to ensure sufficient sampling of species richness. Therefore, we resampled three shrub and oil palm plots each, five rubber plots, and eight forest plots by placing quadrats in the Northeast, Southeast, Southwest and Northwest positions. Moreover, we added six forest survey sites close to the hive plots to help better characterize the forest flowering vegetation community. In addition, a second survey was carried out in January 2019 to include species of both seasons (dry and rainy season).

3.4 Analytical Methods

Classified satellite imagery from 2015 was used to quantify the surrounding natural habitat of the hives. We assumed forest and shrub cover to be high value land covers for resource collection and added them to our statistical models. Forest and shrub cover together ranged from 38 % to 74 % of the total area within a 500 m radius around the hive plots.

All statistical analyzes were done with R Studio from R Core Team (2018). The R-package “lme4” (Bates et al., 2015) and “lmerTest” (Kuznetsova et al., 2017) were used to create linear models; “MASS” (Venables and Ripley, 2007) was used to create generalized linear mixed effect models (GLMMs) and the package “pscl” (Jackman, 2017) was used to calculate the pseudo R^2. We also used “vegan” (Oksanen et al., 2019) to evaluate vegetation analyzes.

Linear models were used to depict the relationship between hive structure and number of workers in November within the hives and the relationship of number of workers with temperature. Since pollen and honey pots are not always distinguishable, a sum of those was created per hive and are found with the name “sum.HP” in the associated model below. Midday temperature is the monthly mean of temperatures measured at 12:00 o’clock local time. Linear models were also used to test the effect of land cover, month and land use on the entire hive size (Hvu of Resin, Honey, Pollen and Brood of each hive

To model the number of workers in all months, we first used a negative binomial generalized linear mixed effect model to test which hive structures had a significant effect on the number of counted workers in November (Figure 2). The output of that model was then used to predict the worker numbers in the preceding months with the R function “predict”.

```
Nr.workers.res.br.weight$pred.workers<-predict(nb.mod1,Nr.workers.res.br.weight,type="response")
```

Figure 2: R function to predict the number of workers in all months based on brood and honey/pollen Hvu. Nr.workers.res.br.weight=table name with data used for statistical analysis, pred.workers=new column in table to fill with predicted number of workers, nb.mod1=model used to test the effect of brood and honey/pollen Hvu on the number of counted workers in November.

The pseudo R^2 was calculated to see the fit of the prediction model compared to the counted number of workers in November.

We used a generalized linear mixed effect model (family poisson) to test the effects of land use type, gradient of surrounding percent of forest plus shrub cover, the number of flower units and the number of expected species (chao index) on worker numbers. A similar model was used to test the effect of forest and shrub cover, land use type and worker numbers on outgoing foragers. Furthermore, we used a mixed effect binomial regression to test the effect of land use type on survival probability in November. Using a linear mixed effect model, we tested the effects of the interaction between forest-shrub cover, month and land use on differences in size from the initial hive size in August. In all mixed effects analyzes, site identity (plot ID) was treated as a random effect in order to partition variability due to inherent differences between sites that are not accounted for by the main explanatory, fixed effect variables.

4 Results

4.1 Bee survival and health

From 37 plots (111 hives) at the beginning of the study period in August, only 25 plots (one forest plot, four oil plots, two rubber plots and five shrub plots died or were destroyed) with 63 hives surviving at the end of the period in November. Three plots, F02, O04, and S02, were lost before the study started in August.

The generalized mixed effect model with the family binomial predicted the mean survival probability (Figure 7 in appendix) for a hive in a forest or shrub plot to be very high (forest 99.9 %, rubber 99.6 %), and to be very low for an oil palm plot (18.7 %) and even lower for hives in shrub plots (1.1 %).

Temperatures (for complete temperature curves over the study period look into appendix Figure 8, Figure 9, Figure 10 and Figure 11) in shrub plots were highest (mean daily 26.8°C, mean midday temperature 33.5°C) followed by rubber (mean daily 26.8°C, mean midday temperature 32.7°C) and oil palm plantations (mean daily 26.6°C; mean midday temperature 32.4°C) and were lowest in forest plots (mean daily 25.8°C, mean midday temperature 30.2°C).

4.1.1 Land use and landcover

When testing the effect of land use type, gradient of surrounding percent of forest and shrub cover, number of flower units and number of expected species (chao index) on worker numbers with a generalized linear mixed effect model (family poisson), we found a significant interaction between forest and shrub cover and all land use types on the number of workers in November. However, the number of flowers and the expected number of flowering species (chao) did not have a significant effect. Worker numbers rose with an increasing percentage of forest-shrub cover in the 500 m radius ($p<0.001$) in forest plots. Interactions between increasing forest-shrub composition and rubber plots ($p<0.001$) and oil palm plots ($p<0.001$) leads to decreasing worker numbers in the former and almost no differences in the latter, whereas the number of workers in shrub plots increases slightly with an increasing forest-shrub cover (Figure 3, Table 1).

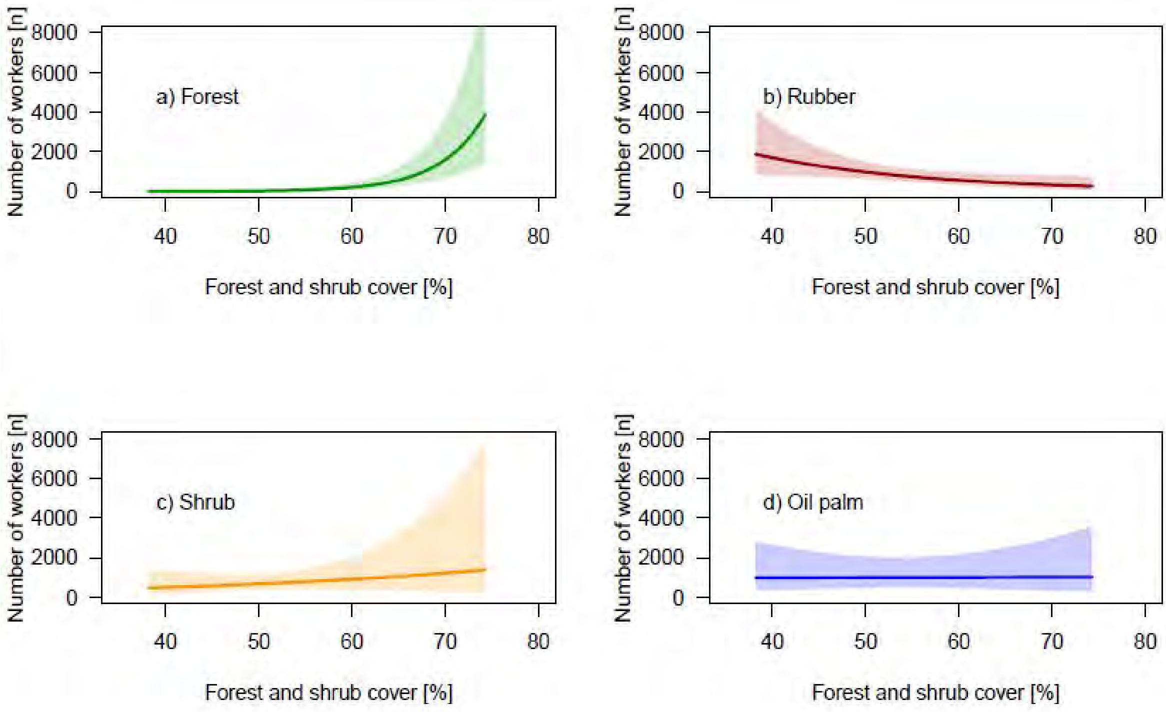

Figure 3: Effect of forest-shrub cover and land use type on worker numbers November. The line indicates the predicted number of workers per hive and the transparent color the upper and lower confidence intervals.

Table 1: Output of the GLMM, family: poisson, showing the effects of the interaction between land use type and forest-shrub cover (scaled in analysis) as well as the number of flowers (sum.flowers) per plot and the expected number of flowering species (chao index) as fixed effects on the number of workers in November with Plot as a random effect. Forest.Shrub = forest and shrub cover in the surrounding of the plot; land.use = land use type with Forest as baseline, O=Oilpalm, R=Rubber, S=Shrub.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	4,18	0,47	8,91	< 0.001
scale(Forest.Shrub)	2,02	0,29	6,91	< 0.001
land.useO	2,76	0,65	4,24	< 0.001
land.useR	2,50	0,48	5,24	< 0.001
land.useS	2,49	0,52	4,77	< 0.001
scale(sum.flowers)	0,05	0,50	0,09	0,925
scale(chao)	0,14	0,21	0,67	0,506
scale(Forest.Shrub):land.useO	-2,01	0,39	-5,20	< 0.001
scale(Forest.Shrub):land.useR	-2,56	0,37	-6,87	< 0.001
scale(Forest.Shrub):land.useS	-1,73	0,46	-3,72	< 0.001

4.1.2 Outgoing foragers

To test the effect of the number of outgoing foragers in November and the interaction between land use type and forest shrub cover on the number of outgoing foragers, we used a GLMM with the family poisson. Forest-shrub cover and the number of workers had a significant positive effect on the number of outgoing foragers as well as the interaction between forest-shrub and rubber had a significant negative effect on the number of foragers leaving the hive (Table 2). Numbers of outgoing foragers with increasing forest shrub cover increased in forest and oil palm plots whereas number decreased on rubber and slightly in shrub plots (Figure 4)

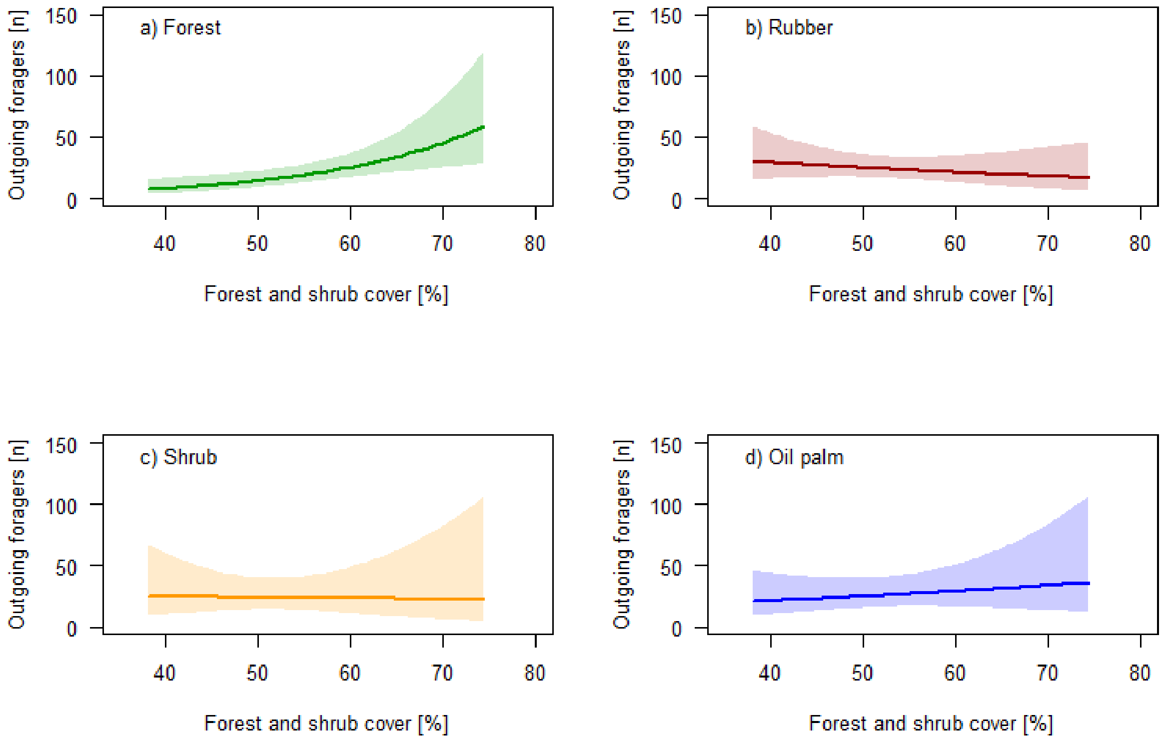

Figure 4: Effect of forest-shrub cover and land use type on leaving foragers in November. The line indicates the predicted number of workers per hive and the transparent color the upper and lower confidence intervals.

Table 2: Output of a GLMM, family: poisson, showing the effect of the interaction between land use type and forest-shrub cover (scaled in analysis) as well as the number of workers on the outgoing foragers. Forest.Shrub = forest and shrub cover in the surrounding of the plot; land.use = land use type with Forest as baseline, O=Oilpalm, R=Rubber, S=Shrub.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	291.25	0.19	15.05	< 0.001
scale(Forest.Shrub)	0.57	0.18	3.14	0.002
land.useO	0.37	0.31	1.21	0.226
land.useR	0.23	0.27	0.85	0.396
land.useS	0.26	0.34	0.76	0.446
scale(Workers)	-0.20	0.02	-9.07	< 0.001
scale(Forest.Shrub):land.useO	-0.42	0.29	-1.44	0.150
scale(Forest.Shrub):land.useR	-0.73	0.28	-2.63	0.009
scale(Forest.Shrub):land.useS	-0.59	0.37	-1.62	0.106

4.1.3 Worker numbers

The number of workers in November were positively correlated with a greater volume of brood cells ($p< 0.001$) and Honey and Pollen pots ($p< 0.001$) in the negative binomial GLMM (Table 3). Therefore, we used the brood, honey, and pollen volumes to predict the number of workers in the other months. The pseudo R^2 explains 32 % from the predicted model compared to the baseline model.

Table 3: Output of a negative binomial GLMM showing the effect of brood and a combined honey and pollen volume (Hvu) on the number of workers to be able to later predict the number of workers in the other months. Hvu.br = Hvu of brood cells, sum.HP = sum of Honey and Pollen Hvu.

	Estimate	**St. Error**	**z value**	**Pr(>|z|)**
Intercept	5.81	0.21	27.60	<0.001
Hvu.br	0.02	0.01	4.09	<0.001
sum.HP	0.02	0.01	2.61	0.01

Worker numbers declined rapidly in all four land use types from the start of the experiment until October and increased again in November. Mean worker numbers per month and land use type were highest in forest plots (mn. 1120.40, sd. 897.64), followed by rubber (mn. 984.07, sd. 713.58), oil palm (mn. 957.72, sd. 601.82) and shrub (mn. 841.39, sd. 359,96) plots in August. Lowest worker numbers can be observed in October where oil palm (mn. 744.15, sd. 404.72), rubber (mn. 736.97, sd. 280.04) and shrub (mn. 733.72, sd. 330.37) plots have similar quantities and forest plots (mn. 831.68, sd. 404.99) has the highest numbers. Nevertheless, differences are not significant. In November the worker numbers rose higher than the starting numbers in August. While forest plots still had the highest numbers of all land use types (mn. 1151.56, sd. 1186.50), rubber (mn. 1025.80, sd. 537.54) changed from the second position to the last. Oil palm (mn. 1115.73, sd. 619.12) and shrub (mn. 1072.19, sd. 663.80) seize the places two and three (Figure 5, for predicted worker numbers per hive see Figure 12 in the appendix).

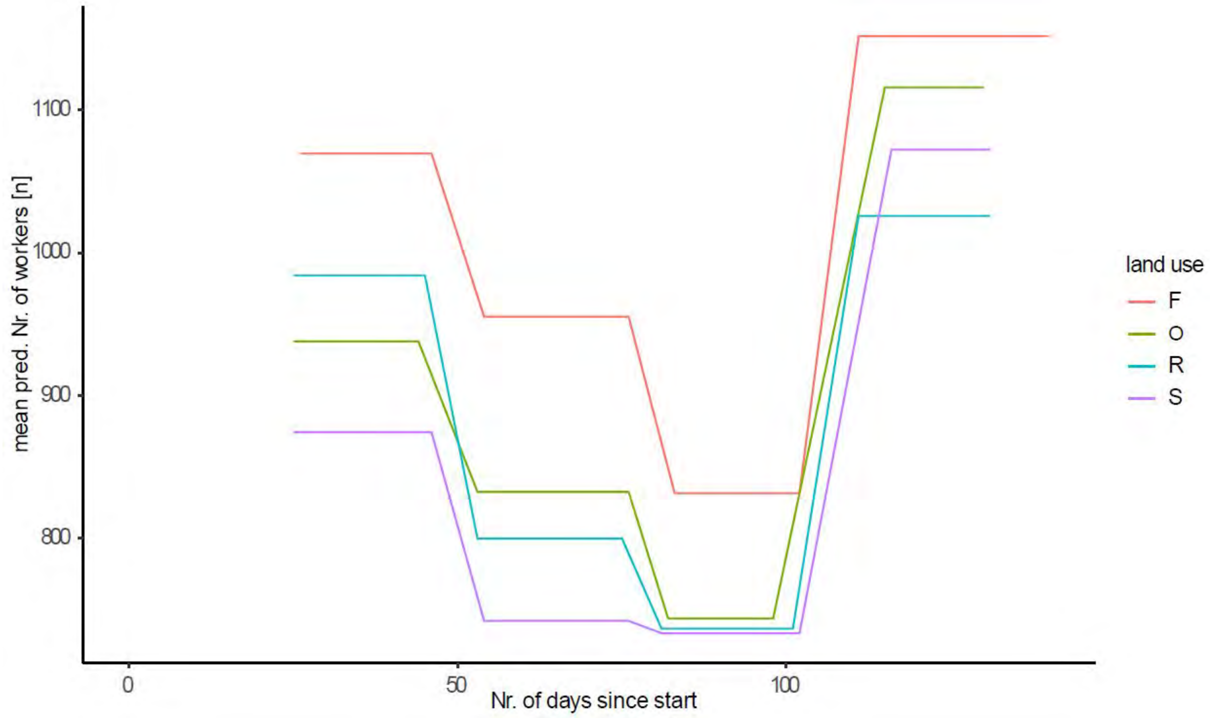

Figure 5: Predicted number of workers in different land use types. Day 0 marks the set up (13.07.2018), start of the experiment was the beginning of August and it ended end of November. The lines indicate mean worker numbers per hive in different months predicted by a model.

4.1.4 Hive size

Hive size changes were calculated with a linear mixed effect model by subtracting the August volume from subsequent months. We tested the interaction between forest-shrub cover, land use type and months (Figure 6). October is significantly different from August ($p<0.001$). The change in Hvu with increasing forest-shrub cover within 500 m was significantly negative in November for oil palm plots ($p<0.001$) and marginally positive in October in rubber plots ($p<0.1$) as well as marginally positive in November on shrub plots (Table 5 in the appendix). In forest and shrub plots, surrounding forest-shrub cover mediated the decrease in hive size in September and October from their starting size, whereas hive sizes on oil palm plantations decreased in all months with increasing forest shrub cover. Rubber plots are mostly unaffected by an increasing forest-shrub cover.

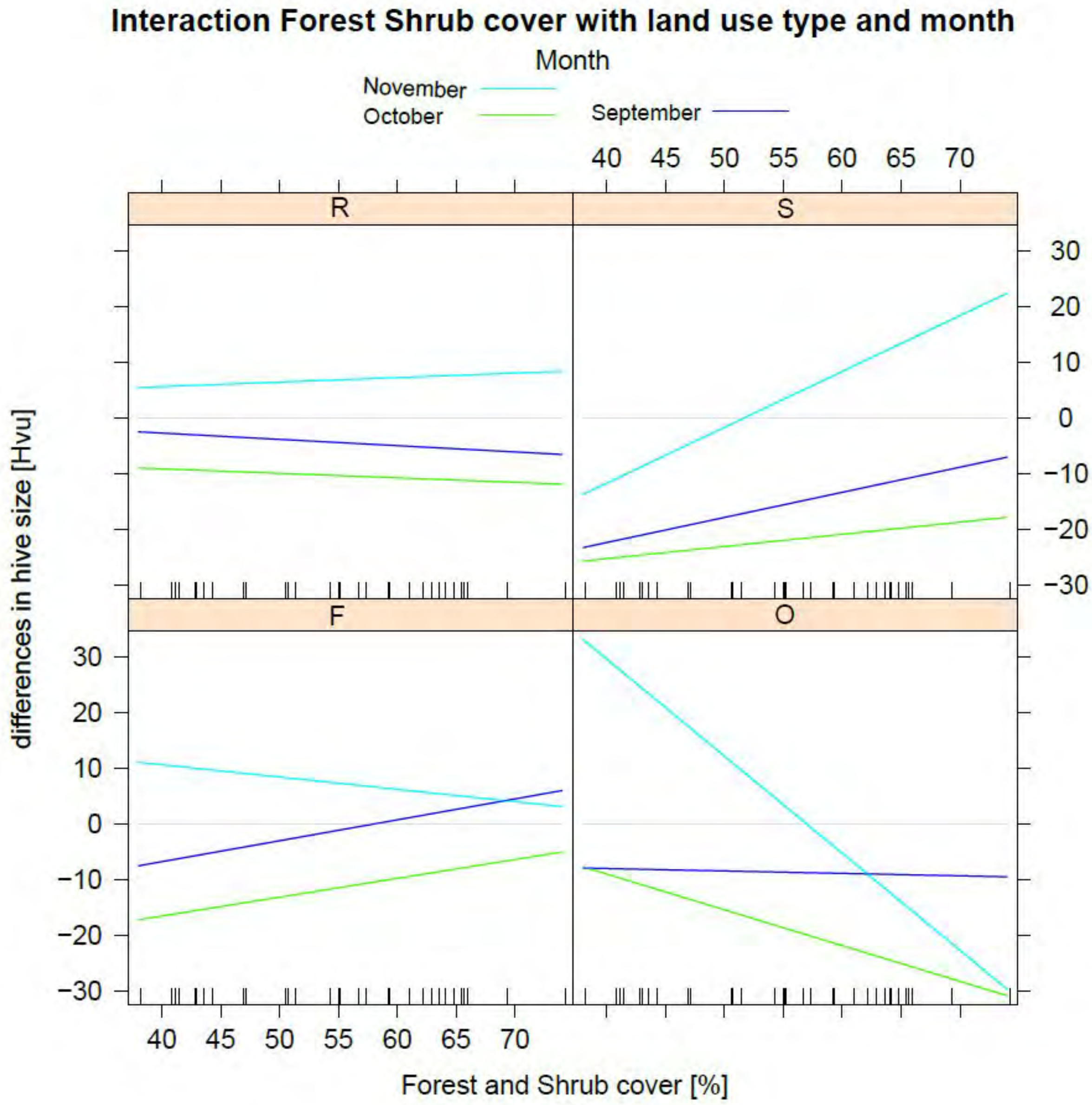

Figure 6: Differences in hive sizes in different land use types and months based on percentage of forest-shrub cover. F=Forest, R=Rubber,S=Shrub, O=Oil palm, Hvu= hive volume unit.

4.2 Vegetation

The vegetation cover was conducted twice, once at the beginning of the study period in August and one after in January (species list Table 6 in appendix). Both surveys were used to calculate the mean Shannon index per land use type as well the mean evenness (Table 4). Forest has the lowest number of species (4) and a low evenness (0.51), which means the species are irregularly distributed. Rubber and shrub plots have a maximum number of seven species but a slightly different mean (3.08 rubber and 4.0 shrub). Oil palm plots has the highest number of species (max. 8) and also the highest mean number of species (5 over all plots) with a more evenly distribution than the other land use types (evenness: 0.66). Species accumulatio curves can be seen in the appendix (Figure 13). Forest plots have a mean number of flower units (the distance a bee can easily walk) of 201.8, followed by rubber with 212.8, oil palm with 222.9 and has the highest numbers on shrub plots with 229.8 flower units.

Table 4: Vegetation data from August/September and January showing the maximum number of species found on the different land use types, the mean number of species, Shannon-Index and the mean evenness.

	Max. Nr. of species	**mean nr. of species & sd**	**Mean shannon-index & sd**	**Mean evenness**
Forest	4	2.19 ± 0.9	0.40 ± 0.33	0.51
Oil	8	5.00 ± 1.75	1.06 ± 0.45	0.66
Rubber	7	3.08 ± 1.51	0.64 ± 0.32	0.57
Shrub	7	4.00 ± 1.95	0.91 ± 0.47	0.65

5 Discussion

5.1 Bee survival and health

Unsurprisingly the predicted survival probability in forest plots was very high (Figure 7). The natural habitat of the stingless bee provides everything they need: food sources, nesting, resting and mating sites (Kevan, 1999; Matheson, 1996). The same applies for the rubber plots. Most of the rubber plantations which were used for this study were so-called jungle rubber and had similar structures as a secondary forest. Jungle rubber is a transformed land use system which is able to sustain more constant microclimatic conditions ((Meijide et al., 2018) compared to oil palm and rubber plantations. The almost negligible difference we found between forest and rubber plots could be caused by monkey induced losses or unfavorable microclimate in some plots. However, the predicted survival probability of oil palm and shrub plots was very low or almost not existing. We expect environmental factors to be most likely the main source of the high mortality rate. Temperatures in shrub plots were in mean one degree higher than in forest plots (mean daily temperature forest: 25.8°C, shrub: 26.8°C) and the mean midday temperature at 12 o´clock (forest: 30.2°C, shrub: 33.5°C) was 3.2°C higher in shrub plots than in the natural habitat. The few hives in shrub plots which survived, belonged almost exclusively to three plots. Those plots had in common, that vegetation cover in the surrounding was higher than in other shrub plots and microclimatic conditions therefore better (Plots S11, S23 and S26, see appendix Figure 9). Also, temperatures in oil palm plots were in mean almost one degree higher than in forest plots and the mean midday temperature was 2.2°C higher (mean 26.6°C; mean midday 32.4°C). However, since we also found higher temperatures in rubber plots than in forest plots (mean 26.8°C, mean midday 32.7°C), which are still paired with a high survival probability, temperature is unlikely the only explanation. As Grundel et al. (2010) and Di Pasquale et al. (2013) state, plant diversity plays a significant role in bee richness (Grundel et al., 2010) and floral resources are necessary for bee health (Di Pasquale et al., 2013). Plant species richness and abundance of floral resources may play a bigger role in rubber plots leading to a better survival probability than in shrub or oil palm plots. Pesticides, which have a strong negative impact according to Kevan (1999), were found in some oil palm plantations and in a shrub plot (personal observation) and could have lowered the survival probability further. In addition, some hives were also destroyed by the common parasite *Aethina tumida* (small hive beetle) or were invaded by ants.

5.1.1 Land use and landcover

Number of workers increased in forest plots with an increasing forest-shrub cover. We found higher overall worker numbers in forest plots with a high percentage of forest-shrub cover in the surrounding (Figure 3). Bee fitness is higher and population growth is faster in habitats with a high floral diversity (Kaluza et al., 2018). An increasing percentage of forest-shrub cover also increases the diversity of flowering plant species and individuals flowering at the same time. Increasing shrubby vegetation in the surrounding, which is added to the forest cover, can increase this effect. This is very important in tropical forests, where individuals of the same species are often far apart and resources hard to find. Plus, in this study only plots in secondary forests were used, which are less diverse than primary forests in terms of beta diversity (Margono et al., 2014). Shrub plots show a similar effect of increasing number of workers with an increasing percentage of forest-shrub cover, even though not as strong as in forest plots. A possible explanation why shrub is not affected as strongly by an increasing forest-shrub cover, could be because it already has a relatively high amount of species (max. 7, mn. 4.0) itself compared to forest (max. 4, mn. 2.19).

Most jungle rubber plots resemble a secondary forest in terms of age and structure (Böhnert et al., 2016). However, in contrary to forest plots, Rubber plots show a negative effect on worker numbers with an increasing forest-shrub cover. This effect could be because of a relatively high resource abundance in rubber plots compared to forest plots. In forests, flowers are often clustered together, for example on a flowering tree. However, individuals of the same species are often far from each other and neighboring trees might not bloom at the same time. If more forest and shrub cover surround the plot, foraging bees have to travel longer distances to find their resources and therefor have a higher mortality probability but can maximize resource diversity intake in the more diverse habitat (Kaluza et al., 2017). Hives on rubber plots might therefore have the advantage of high resource diversity without long distance travelling and its disadvantages. However, oil palm plots in this study are not affected by an increasing forest-shrub cover. We found that oil palm plantations contain the highest number of flowering species (max. 8, mn. 5) which might dominate a possible effect of increasing forest-shrub cover. Furthermore, in oil palm plantations, bees have the constant food resource of oil palm flowers in close distance.

5.1.2 Outgoing foragers

We found that forest-shrub cover had a significant effect on the outgoing foragers as well as the interaction between forest-shrub cover and rubber, which had a negative effect (Figure 4).

The number of outgoing foragers in forest plots increases with an increasing percentage of forest-shrub cover, whereas the number of outgoing foragers in rubber plots decreases with an increasing percentage of forest-shrub cover. This pattern is similar to the response we got from the number of workers in forest and rubber plots with increasing forest-shrub cover. It appears to be logic that with an increasing number of workers the number of bees reaching an adequate age to become foragers is rising as well. However, the pattern is dissolving in oil palm and shrub plots. Hence, we must be careful when only considering the effect of worker numbers. According to Kaluza et al. (2017) plant species richness and resource abundance must be taken into account rather than land use type and landscapes to explain foraging behavior.

5.1.3 Worker numbers

A heavy decrease in worker numbers was registered until October (Figure 5). In a similar study conducted by Kaluza et al. (2016) the hives of the study species *Tetragonula carbonaria* were left undisturbed for at least three months before the start of the experiments. Due to limited information of the previous situation on how the bees were kept and how often they got disturbed, the strong decline in worker numbers could have been a result of disturbances prior to the set up. Moreover, the transport itself and the set up took a full day which could have been very stressful for the bees as well and therefore affected the colony performance. Furthermore, the time the bees need to get adjusted to a new environment needs to be taken into account as well. We observed the strongest decline in rubber plots. Forest plots, on the other hand, seem to buffer the negative effects of relocation, since the decrease in in worker numbers was the least among the land use types. Another possible explanation for the heavy decrease in worker numbers might be an oscillation rhythm between brood volume and worker numbers. When there is a high amount of worker numbers, the brood volume is low, because a lot of workers hatched recently. Since there are now more workers building up brood cells, the brood volume is rising with an increasing number of workers. Nevertheless, worker numbers are based on the brood cell and the sum of pollen and honey Hvu, which is not the real volume. Even if the model used to predict the number of workers has a good fit (pseudo R^2=32%), the lag in the oscillatory relationship could lead to an error, which we could not detect because we only counted worker numbers once. Henceforth, more research is needed to verify if oscillation is visible in a longer study period.

5.1.4 Hive size

We found a significant negative change in Hvu with increasing forest shrub cover in November for oil palm plots and a marginally positive change on rubber plots in October and marginally positive on shrub plots in November (Figure 6). As described above environmental factors like microclimatic conditions, plant diversity and floral resources influence worker numbers and therefore hive sizes. More natural environments like forest and rubber are likely to have a buffering effect on strong hive size changes. Especially in rubber, where floral resources are high and in favorable reaching distance, hive size differences with increasing forest-shrub cover and in different months, are low. Hive sizes on forest plots increased with an increasing forest-shrub cover probably due to higher floral resources which are not directly in the surrounding of the hive. For shrub plots, increasing forest-shrub cover positively changed the hive sizes in all months. More forest in the surrounding could help finding better microclimatic conditions than on the very hot shrub plots and therefore increases the survival probability of individuals and hives. This effect supports the importance of favorable microclimatic conditions for the health and performance of the hives. Oil palm plots have a high amount of floral resources and as an increasing forest-shrub cover might buffer negative effects of the relocation in the first months, floral resources predominate in November where worker numbers are generally strong.

5.2 Vegetation

Vegetation analysis were conducted twice during the study period on four plots (25 m^2 each) located 10 m from the hives in each cardinal direction. On forest plots, the surveyed area was limited to a height of five meters, which might have reduced the number of flowering plants and flower units we could count. In contrast to our expectations, forest had the lowest number of species (mean 2.14) within the four land use types. However, Rembold et al. (2017a) found the highest levels of alpha, beta and gamma diversity of plant species in forests in the Jambi Province compared to rubber and oil palm plantations. Inadequate plot size and the inability to count flowers in heights more than 5°m might have been leading to a lack of sufficient vegetation data in our study, especially in forests (Figure 13). Oil palm plantations in contrast, were distinguished by their high number of herbaceous weeds in Rembold et al. (2017a) study, which confirms the high amount of flowering species (mean 5) we found in this study. Rembold et al. (2017a) also found an increasing number of alien species with an increasing land use intensity, which peaks in oil palm plantations with 25 % of the species and 62 % of the individuals belonging to non-indigenous species. This goes in accordance with our study where alien plants like *Ageratum conyzoides*, *Asystasia gangetica*, *Clidemia hirta* and *Hyptis capitata* provided the highest amount of flower units on oil palm plots.

6 Conclusion

Changes in ecosystems have a strong effect on their functions, on single species as well as on whole communities. Especially the effect on bees as key pollinators is very important to understand. Sumatra, as home of the study species *Tetragonula laeviceps*, experienced an explosive oil palm and rubber plantation expansion in the last decades, which is responsible for 6.02 million hectares of forest loss between 2000 and 2012 (Morgano et al 2014).

This study´s goal was to identify suitable habitats out of four main land use types (secondary forest, jungle rubber, oil palm plantations and shrub) in the Jambi Province in Sumatra, to keep the stingless bee species. In accordance to our first hypothesis, we found that *Tetragonula laeviceps* health and growth is higher in more natural habitats. General survival probabilities of hives were highest in more natural habitats like forest and rubber plots. Moreover, worker numbers at the end of the study period were also highest in forests. However, when testing an expected positive effect of more surrounding natural habitat on number of workers and foraging activity, we got more diverse results. For example, higher amounts of forest-shrub cover in the surrounding of rubber plots had a negative effect on outgoing foragers and worker numbers, but a positive effect in forest and shrub plots. These results suggest, that surrounding natural habitats are only one factor to explain colony growth and activity. It is therefore important to also take floral resources, species numbers and microclimatic conditions into account. Oil palm plantations, for example, had the second highest amount of worker numbers at the end of the study period, which might be the result of buffering effects from the high amount of floral resources and number of flowering species. However, it is crucial to mention, that most of the flowering species in oil palm plantation are alien species and their appearance likely an effect of previous land use changes.

In our second hypothesis we tried to find out, if more natural land use types and more natural surrounding habitats are additive and may compensate for negative effects on the other level. Our study suggests, that more forest-shrub in the surrounding benefits forest and shrub plots but can have negative or no effects in other land use types. Floral resources and microclimatic conditions are not only important on the direct site but also in the surrounding to buffer negative effects.

Under given circumstances, jungle rubber plots seem to be favorable sites for local farmers to keep stingless bees beside forests. Rubber plots showed a relatively high amount of floral resources and similar structures as the natural habitat forest. This resulted in lower hive size changes during the study period than in other land use types and might buffer negative effects of higher temperatures and disturbances during set up and hive transportation at the beginning of the study. Keeping stingless bees such as *Tetragonula laeviceps* could give local farmers an extra income and simultaneously helps to support pollination services in a changing ecosystem.

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9 Appendix

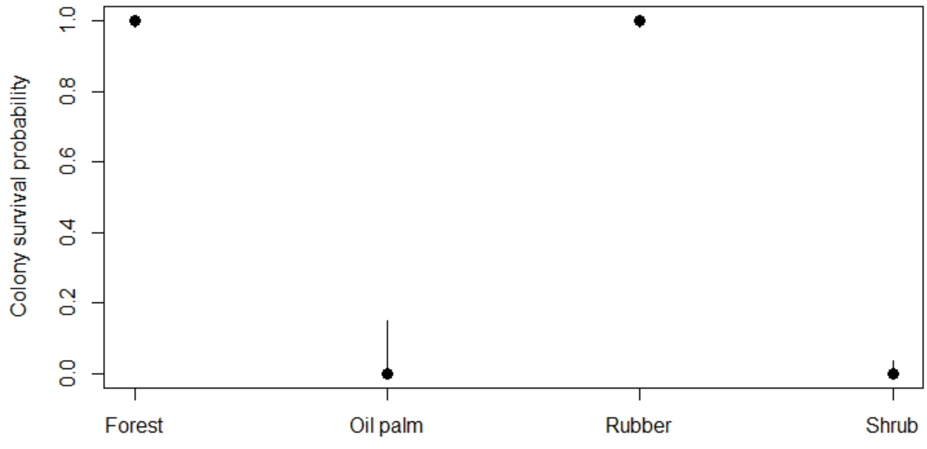

Figure 7: Predicted survival probability of each land use type in November. The prediction model was a generalized mixed effect model with family binomial.

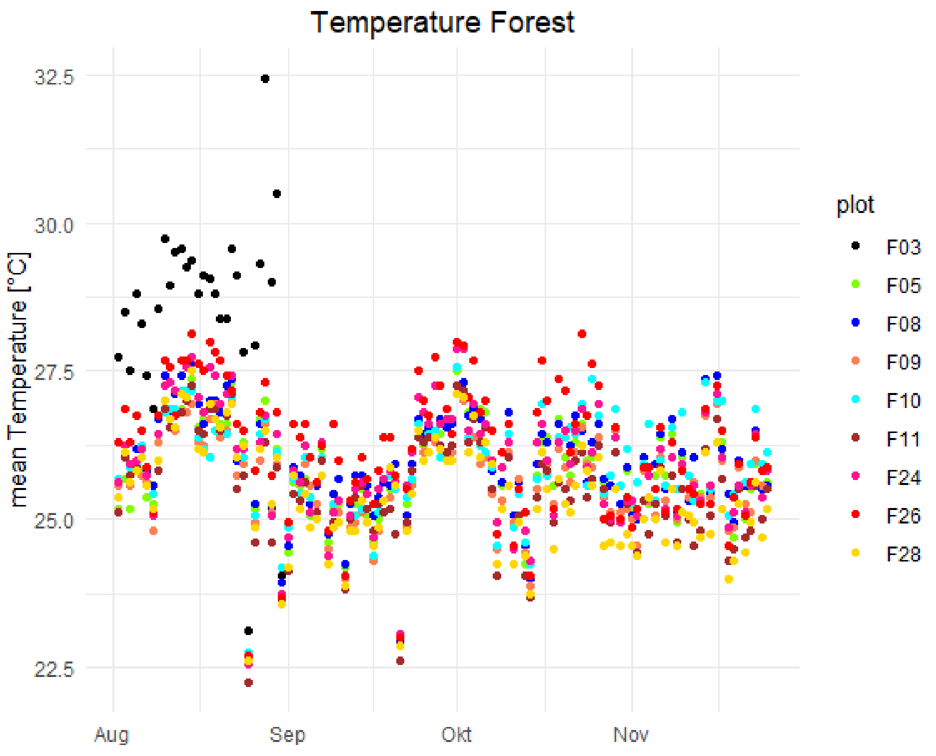

Figure 8: Mean daily temperatures for each forest plot over the whole study period.

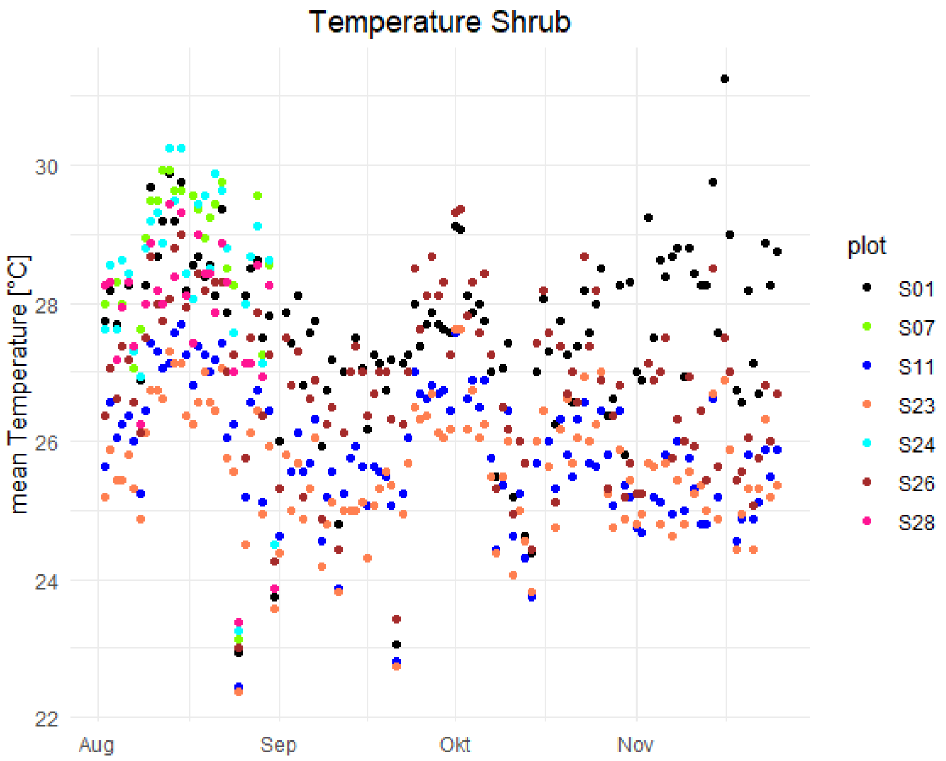

Figure 9: Mean daily temperatures for each shrub plot over the whole study period.

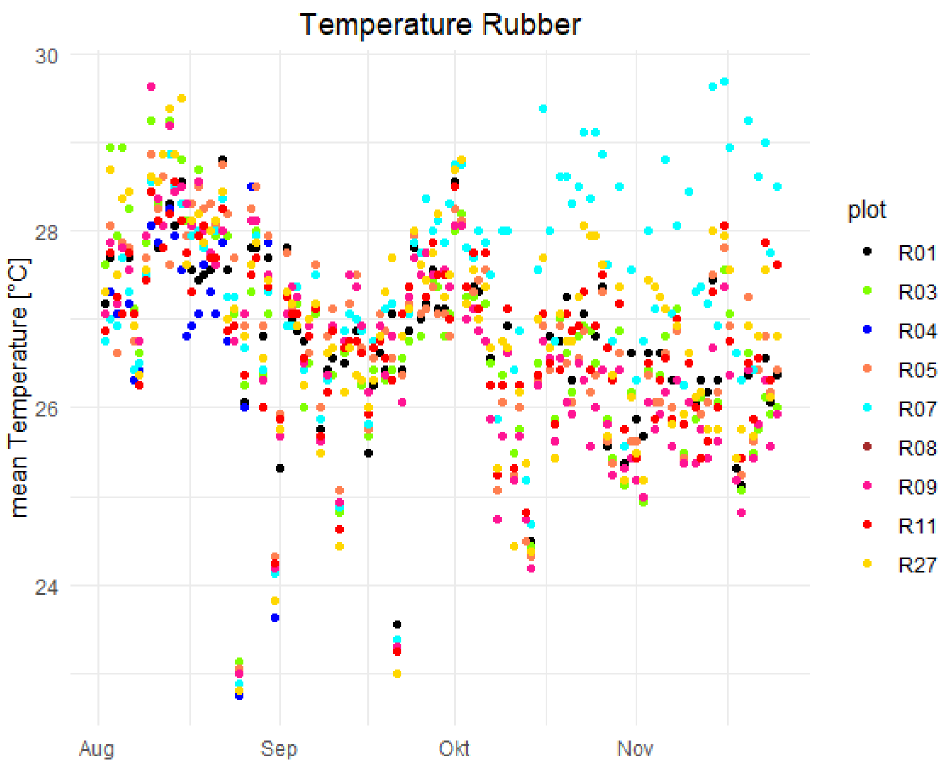

Figure 10: Mean daily temperatures for each rubber plot over the whole study period.

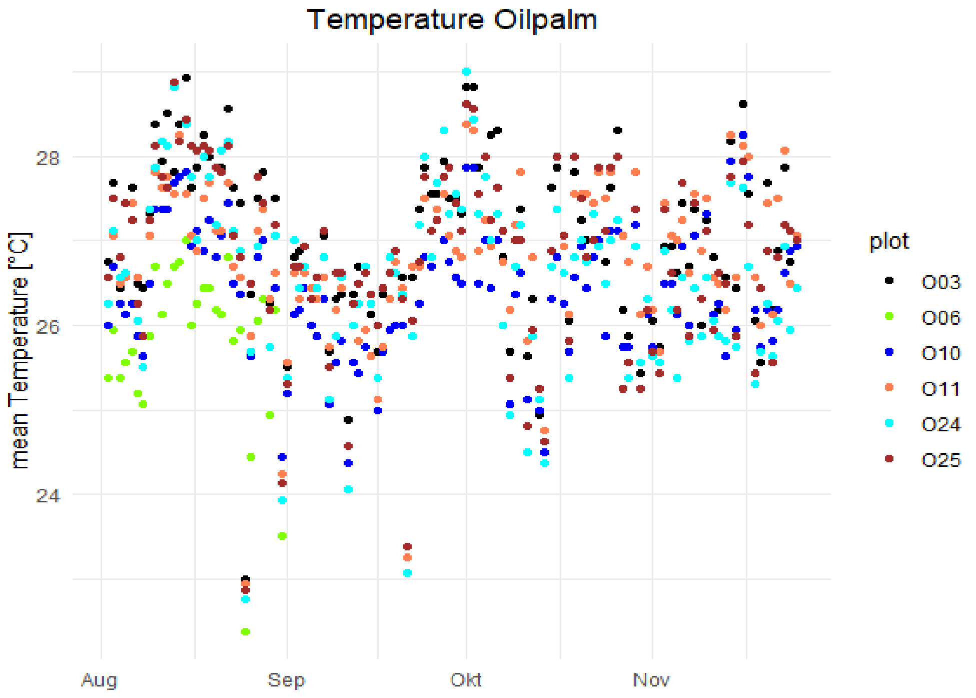

Figure 11: Mean daily temperatures for each oil palm plot over the whole study period.

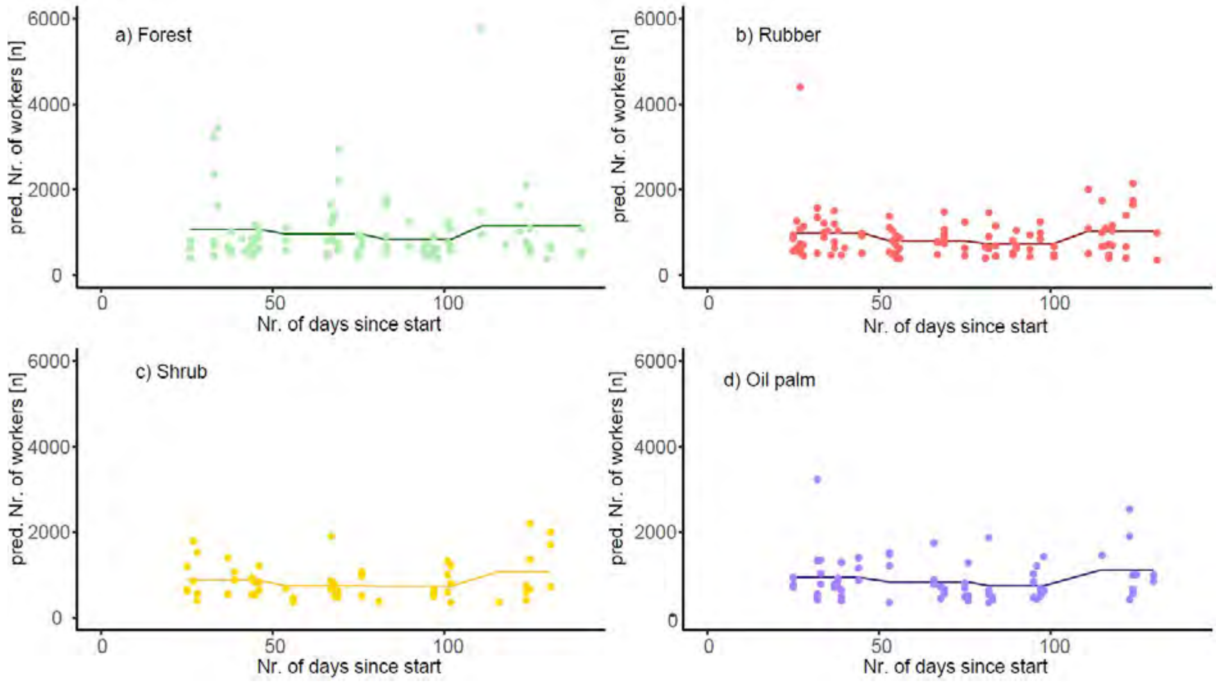

Figure 12: Predicted number of workers from the start of the experiment in August until the end of November on different land use types. Points mark the predicted worker number per hive whereas the lines mark the mean number of workers per month.

Table 5: Output of an LMM to test the effect of the interaction between forest-shrub landcover, land use and month on the absolute increase of the hive size. The August Hvu of all hives has been set to zero and the change to the next month measured. Difference from August to September, August to October and August to November. O=Oil palm, R=Rubber, S=Shrub.

	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	-8,09	14,65	25,37	-0,55	0,59
Forest.Shrub	0,12	0,25	25,32	0,49	0,63
Month.Nov	11,21	12,98	606,52	0,86	0,39
Month.Oct	35,64	12,63	604,63	2,82	<0,001
Month.Sept	9,88	12,24	601,36	0,81	0,42
land.useO	35,50	20,96	27,57	1,69	0,10
land.useR	7,66	21,32	26,11	0,36	0,72
land.useS	-23,45	24,03	32,25	0,98	0,34
Forest.Shrub:Month.Nov	-0,16	0,22	607,52	-0,71	0,48
Forest.Shrub:Month.Oct	-0,47	0,21	605,08	-2,18	0,03
Forest.Shrub:Month.Sept	-0,02	0,21	601,51	-0,12	0,91
Forest.Shrub:land.useO	-0,73	0,37	29,20	-1,95	0,06
Forest.Shrub:land.useR	-0,15	0,38	26,74	-0,40	0,69
Forest.Shrub:land.useS	0,29	0,43	34,20	0,69	0,50
Month.Nov:land.useO	60,49	19,96	618,24	3,03	<0,001
Month.Oct:land.useO	8,78	19,13	612,20	0,46	0,65
Month.Sept:land.useO	-3,08	18,28	603,35	-0,17	0,87
Month.Nov:land.useR	-11,33	18,89	615,18	-0,60	0,55
Month.Oct:land.useR	-32,38	18,50	606,06	-1,75	0,08
Month.Sept:land.useR	-4,19	182,23	601,42	-0,23	0,82
Month.Nov:land.useS	-44,52	23,58	621,30	-1,89	0,06
Month.Oct:land.useS	-24,36	22,99	617,78	-1,06	0,29
Month.Sept:land.useS	-25,77	23,25	606,60	-1,11	0,27
Forest.Shrub:Month.Nov:land.useO	-1,15	0,37	621,86	-3,09	<0,001
Forest.Shrub:Month.Oct:land.useO	-0,06	0,35	615,18	-0,17	0,86
Forest.Shrub:Month.Sept:land.useO	0,04	0,34	604,26	0,11	0,92
Forest.Shrub:Month.Nov:land.useR	0,22	0,34	619,56	0,64	0,52
Forest.Shrub:Month.Oct:land.useR	0,60	0,33	607,91	1,81	0,07
Forest.Shrub:Month.Sept:land.useR	0,02	0,33	601,73	0,06	0,95
Forest.Shrub:Month.Nov:land.useS	0,78	0,43	614,97	1,79	0,07
Forest.Shrub:Month.Oct:land.useS	0,63	0,42	617,75	1,51	0,13
Forest.Shrub:Month.Sept:land.useS	0,40	0,43	607,66	0,95	0,34

Table 6: Species list and their appearance in the land use types.

Species	**Forest**	**Rubber**	**Oil palm**	**Shrub**
Ageratum conyzoides	x	x	x	x
Asystasia gangetica	x	x	x	x
Centrosema pubescens		x		
Chassalia curviflora	x			
Chromoalena odorata				x
Cleome rutidosperma			x	
Clibadium surinamense	x	x	x	x
Clidemia hirta	x	x	x	x
Cratoxylum cf. formosum				x
Croton hirtus			x	

Species	**Forest**	**Rubber**	**Oil palm**	**Shrub**
Cyanthillum cinereum			x	
Derris sp.	x			
Globba pendula	x			
Gonocaryum gracile	x			
Hevea brasiliensis		x		
Hibiscus macrophyllum				x
Hyptis capitata		x	x	x
Ixora cf. grandiflora	x			
Lantana camara		x	x	x
Lasianthus reticulatus	x			
Lindernia diffusa			x	
Maesa ramentacea				x
Melastoma malabathricum	x	x	x	x
Mikania micrantha	x		x	x
Mussaenda frondosa				x
Oxalis barrelieri			x	
Passiflora foetida				x
Polygala paniculata			x	
Rolandra fructicosa			x	
Saraca indica			x	x
Solanum jamacense		x		x
Spermacoce alata			x	x
Spermacoce cf. ocymifolia		x	x	x
Stachytarpheta indica			x	x
Synedrella nodiflora			x	
Tabernaemontana pauciflora		x		
Unidentified arboreal sp. 1	x			
Unidentified arboreal sp. 2	x			
Unidentified aroberal sp. 3	x			
Unidentified Asteraceae sp. 1				x
Unidentified Celastracea sp. 1	x			
Unidentified Malvaceae sp. 1	x			
Unidentified Meliaceae sp. 1	x			
Unidentified Salicaceae sp.1	x			
Unidentified sp. 1		x		
Unidentified sp. 2			x	
Urena lobata		x		
Urophyllum cf. arboreum	x			x

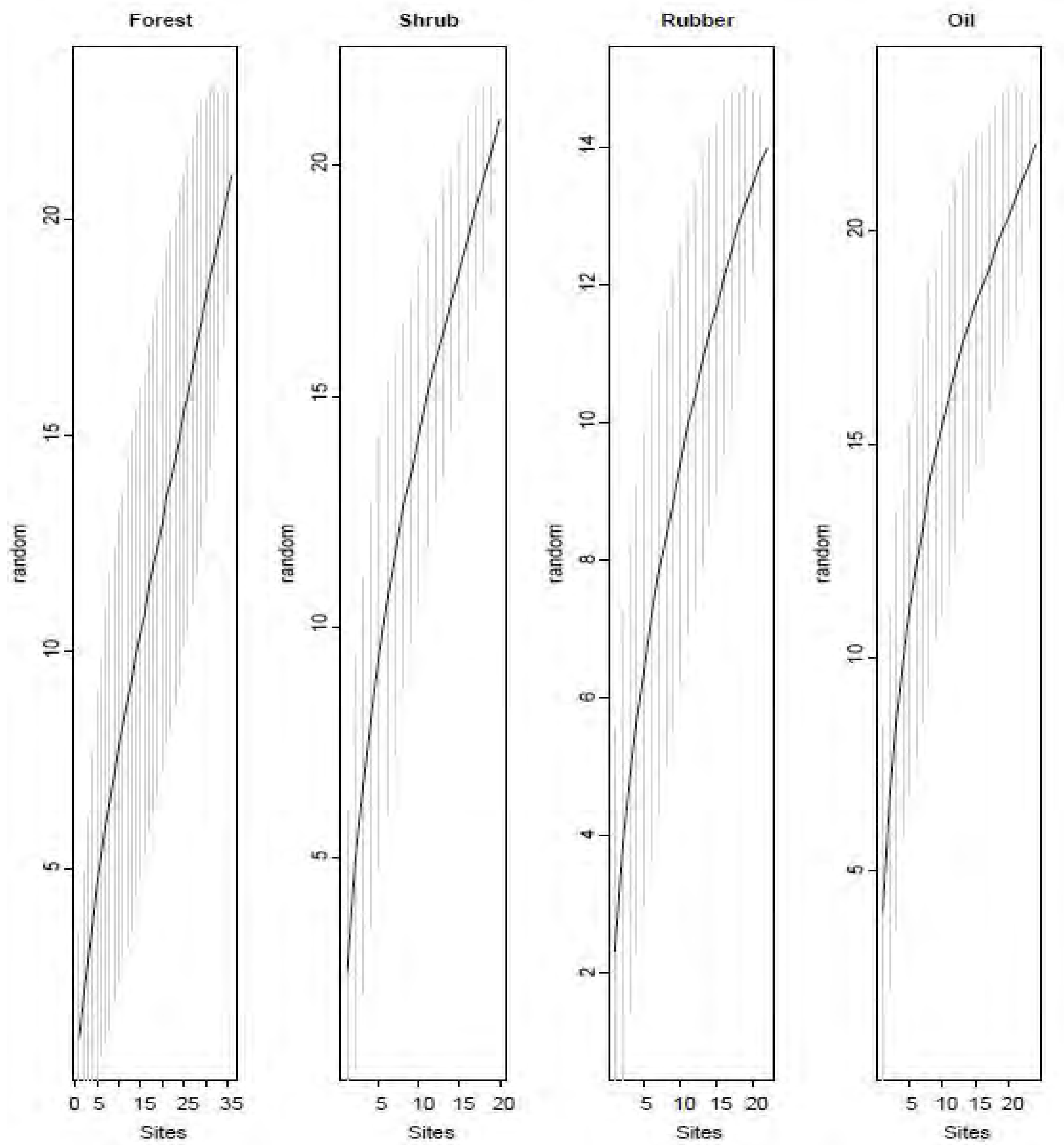

Figure 13: Species accumulation curves of vegetation data in different land use types. Vegetation surveys in August and January were used for this graph. X-Axis indicates the number of plots sampled per land use type, Y-Axis indicates number of species.