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The Effect of Selective Logging on the Community of Chewing lice and Feather mites Associated with Forests Birds in Sabah, Malaysia

Ramón Soto Madrid
Master of Science in Ecology

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Ramón Soto Madrid

Abstract

Selective logging is degrading tropical rainforests worldwide at high rates altering its microclimate and structure. Hence, changes in the assemblages of some taxa have been recorded after selective logging. This is the first study assessing the effect of selective logging on the community composition, species richness and interaction networks of chewing lice and feather mites associated with birds. The current study was conducted in Sabah, North Borneo, which is part of the Sundaland biodiversity hotspot region. Surprisingly, significant differences were found just in the chewing louse-bird and feather mite-bird interactions networks. Chewing louse-bird interactions were more stable in primary than in logged as happened in the case of feather mites. This study revealed that changes in the interaction networks are possible even when the community composition, abundance and species richness persisted after logging. The consequences of logging on host and therefore parasite survival and the resulting consequences in the whole interaction network is an area that requires further research.

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1. Introduction

Tropical rainforests harbour a biodiversity and an ecological complexity much higher than any other terrestrial communities around the world (Laurance 1999). Approximately half of the global species richness exists here, although these areas occupy between 6-7 % of the earth's land surface (Dirzo & Raven 2003). However, less than 10 % of the worlds tropical rainforests are located within a strictly protected area (Gardner et al. 2009), and many rainforest regions are under heavy pressure due to agricultural expansion, forest fires, infrastructural development (roads and dams), exploitation of natural resources (food, timber, oil, gas, minerals) and other disturbances (Geist & Lambin 2001; Koh & Sodhi 2010). Rainforest deforestation and degradation may lead to the immigration of alien species, loss of keystone species, edge effects, dispersal limitation and reduction of population size and genetic diversity (Pimm & Askins 1995; Turner & Corlett 1996). Global problems, such as climate change and pollution may act in synergy to intensify these negative effects (Koh & Sodhi 2010).

Selective logging, a method of extracting timber targeting just a few tree species (Meijaard & Sheil 2007), is practiced in rainforests worldwide. Approximately 20 % of these forests were affected by selective logging between 2000 and 2005 (Asner et al. 2009). Selective logging alters the microclimate (Miller et al. 2007), forest structure (Uhl & Vieira 1989), increases vulnerability to fires and droughts (Nepstad et al. 1999), increases the intrusion of light (Edwards et al. 2014b) and create roads that facilitate access to hunters (Robinson et al. 1999). Selective logging changes community composition and abundance of species, like the occurrence of lianas and trees (Magrach et al. 2016), and promotes changes in species interactions, such as pollination and seed dispersal (Schleuning et al. 2011). Hence, selective logging may affect species, the pairwise interactions and the whole network of interactions (Magrach et al. 2016).

Still, selectively logged forest preserve a high percentage of primary forest species and these areas are thus valuable for conservation (Edwards et al. 2014a; Gibson et al. 2011; Putz et al. 2012; Wells et al. 2007a). In addition, many functions and services present in the primary forest are retained in logged forest (Edwards et al. 2014b). Nevertheless, we know little about how logging affects interactions between different species and groups of species, although species interactions are one of the main factors that shapes an ecosystem (McCann 2007). The study of such interaction network adds fundamental information on how species are related to one another and how human disturbance affects them (Morris 2010). Indeed, sometimes the study of these interactions is the only way to uncover negative effects after logging as demonstrated by observed changes in food-web structure (Tylianakis et al. 2007), changes to the feeding ecology of birds (Edwards et al. 2013) and reduction in the robustness of liana-tree interaction network (Magrach et al. 2016). This study aims to assess how selective logging affects chewing louse and feather mite communities, and their interactions with their avian hosts.

Chewing lice are permanent parasites of birds, meaning that they need to be on the host to go through all the stages of their life cycle. They are insects belonging to the order Phthiraptera, of which the suborders Amblycera and Ischnocera are present on birds. (Johnson & Clayton 2003). Chewing lice act as parasites and have negative effects on birds, for example, impacting flight performance (Barbosa et al. 2002; Vas et al. 2008), body condition (Potti & Merino 1995), and sexual selection (Kose & Møller 1999). Both suborders Amblycera and Ischnocera feed on their host´s feathers, and suborder Amblycera also feed on blood (Johnson & Clayton 2003). Species from both suborders are highly specialized to the different microhabitats provided by their host (Johnson & Clayton 2003). However, some species can be present in many different hosts (Price et al. 2003). Chewing louse transmission usually occurs due to physical contact between hosts, for example from parents to offspring or between copulating individuals (Hillgarth 1996; Johnson & Clayton 2003). However, phoresy of chewing lice has been observed - although this is a rare event and is more likely to happen in immobile species than more mobile ones (Bartlow et al. 2016).

The extent of the effect that feather mites can have on birds is still debated. Some studies portray feather mites as parasites (Harper 1999; Thompson et al. 1997), where they feed and inhabit living tissue (Mironov 2003), while others class them as commensals or mutualists, as their diet includes algae, fungi, and secretions produced by the oil gland (Blanco et al. 1997; Blanco et al. 2001; Mironov 2003; Proctor & Owens 2000; Proctor 2003). Feather mites go through all the life cycle stages on the host (Gaud & Atyeo 1996; Proctor 2003). They belong to two superfamilies: Analgoidea and Pterolichoidea of the suborder Astigmata (Dabert 2005; Norton et al. 2009). The majority of feather mites live on the bird plumage, though some species of the latter superfamily also live on and under the skin of birds, and in their nasal cavities (Proctor 2003). Feather mites are highly specialized to particular microhabitats on the body of their hosts (Dabert & Mironov 1999; Mironov 2003). Hence, transmission normally occurs between parents and offspring (Mestre et al. 2011) and rarely occurs between different host species (Dabert & Mironov 1999; Dabert 2005).

We know very little about how selective logging may affect the interactions of chewing lice and feather mites on birds. However, they have been mentioned as useful indicators of environmental stress, food web structure and biodiversity (Bush et al. 2013; Gómez & Nichols 2013; Marcogliese 2005). Previous research has mainly focused on the impact of forest size on these taxa (Bush et al. 2013), taxonomy and species specificity (Hellenthal & Price 2003; Mironov 2003) and assessing their effects on birds (Blanco et al. 1997). However, it is possible to make a number of predictions based on previous research. Since selective logging does not affect bird species richness in Bornean rainforests (Berry et al. 2010; Edwards et al. 2011), a decrease in chewing louse and feather mite species richness and abundance should not be expected. However, logging promotes an alteration of the bird community composition after the first logging rotation and a more substantial change after the second (Edwards et al. 2011). Thus, if chewing louse and feather mite bird host specificity is high, corresponding changes to their community composition would also be expected. In addition, logging opens up the canopy and alters forest microclimate. Changes in the chewing louse and feather mite communities may therefore also be anticipated due to the alteration in the humidity (Gaede & Knülle 1987; Johnson & Clayton 2003) and light exposure (Johnson & Clayton 2003; Mestre et al. 2011), to which these groups are sensitive.

The current study took place in Sabah, which is part of the Sundaland Biodiversity Hotspot (Myers et al. 2000). This region has one of the highest rates of tropical deforestation and degradation in the world (Achard et al. 2002), but also contains some well-preserved forest sites (Reynolds et al. 2011). It is therefore an ideal location in which to study the effect of selective logging on interactions networks. Specifically, the aim of this study is to address the above-mentioned predictions by investigating the effects of selective logging on chewing lice, feather mites and birds in terms of their: (i) community composition, (ii) species richness, (iii) abundance, and (iv) the chewing louse-bird and feather mite-bird interaction networks.

2. Materials and Methods

2.1 Study area and design

The fieldwork was carried out from June to August 2014 and 2015 within the Yayasan Sabah Forest Management Area (YSFMA) in Sabah, North East Borneo (4º 58´ N, 117º 4´ E). YSFMA covers approximately 10.000 km^2 representing one-third of the entire commercial logging in the region. YSFM also has three areas of pristine forest, Danum Valley Conservation Area (DVCA) (438 km^2), Maliau Basin (588 km^2) and Imbak Canyon (300 km^2). These areas are considered some of the best conservation spots in South East Asia (Reynolds et al. 2011). DVCA was chosen as primary forest and the Ulu Segama Forest Reserve that surrounds DVCA was chosen as logged forest in this study (Figure 1).

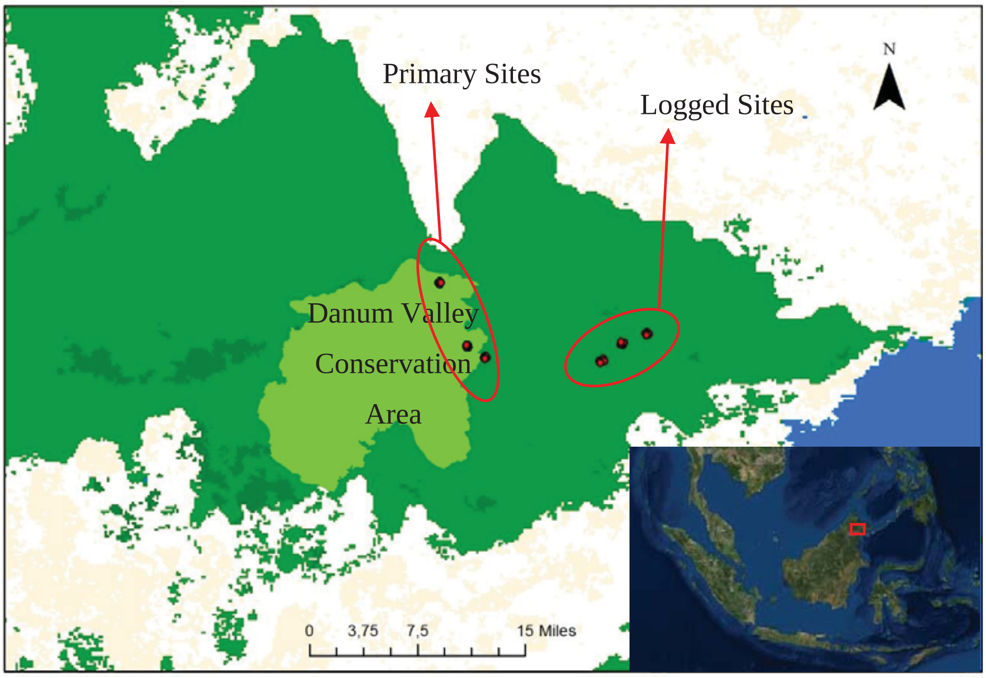

Figure 1. The location of the study in Sabah, Borneo. The red dots represent the sampling areas.

The Ulu Segama Forest Reserve has been selectively logged twice, the first time between 1970 and 1990, extracting trees over 60 cm in diameter at breast height (dbh), and the second time between 2000 and 2007, extracting trees over 40 cm dbh (Fisher et al. 2011).

In DVCA, precipitation events are more frequent during the months of May-June and October-November. Due to this tendency, the fieldwork was carried out in the months of June, July and August. The mean annual temperature is 26.9ºC and the average annual rainfall is 2669 mm (Walsh & Newbery 1999).

2.2 Mist-netting

Three plots in primary and three plots in selectively twice-logged forest were sampled, with each plot comprising of two transects. Transects within each plot were 250 m apart to obtain statistically independent data (Edwards et al. 2009; Hill & Hamer 2004; Whitman et al. 1998). At each transect, 15 mist nets (12 x 2.7 m; 25 mm size) were erected end-to-end in a straight line and opened from 06:00 to 12:00 for two consecutive days. The mist-netting was carried out by two teams of 2 or 3 people and team visits were alternated between the different transects. This allowed the collection of ectoparasites from different places within each plot of primary and selectively logged forest. Sampling was rotated among forest types to diminish temporal effects (Edwards et al. 2009).

Figure 2. Extraction of a Little spiderhunter, *Arachnotera longirostra*, from a mist-net. Photo: Paul Thuesen.

Each captured bird was ringed with an individually numbered ring, and data on gender, age, brood patch, body molt were collected. Measures of wing, tail, tarsus, and bill length and depth were also collected. All birds were identified to species level using field guides (Myers 2009; Phillipps 2014) and the nomenclature in this thesis follows the Clements Checklist of the world (Clements et al. 2015).

Figure 3. Black and red broadbill, *Cymbirhynchus macrorhynchos*, being processed. Photo: Ramón Soto Madrid.

2.3 Collection of ectoparasites

Dust-ruffling was used to collect ectoparasites from the birds. This technique is good for collecting permanent ectoparasites, such as chewing lice and feather mites, which stay on the body when the bird has been caught (Koop & Clayton 2013; Walther & Clayton 1997). Insecticide powder containing effective permethrin (Johnsons Pigeon Mite and Insect Powder) was applied to the bird feathers. Permethrin is a compound that targets the nervous system of insects causing their death (US EPA). With a paint brush, powder was applied to the legs, wings, belly, neck and back. On the head, the powder was applied very carefully to avoid contact with the eyes, which can cause irritation.

Subsequently, each bird was dust-ruffled for a standardised three minutes. It has been shown that three minutes is sufficient to remove most of the parasites in Common Swift, which has a similar size to the birds processed in this study (Walther & Clayton 1997). Processing the birds was done by securing the bird with hand while gently ruffling the feathers of the bird with the other over a white sheet of paper. Ectoparasites dislodged from the feathers thus fell onto the sheet of paper. A plastic sheet was laid beneath the sheet of paper to keep the paper clean and dry. Using another paintbrush, all the powder and particles visible to the naked eye were brushed from the sheet of paper into a 5 ml vial containing 2.5 ml of 95 % ethanol (Walther & Clayton 1997).

Subsequently, the sheet of paper and paintbrushes were cleaned meticulously or replaced by new ones to avoid cross-sample contamination of parasites.

Figure 4. Dust-ruffling a Black-crowned pitta, *Erythropitta ussheri*, to collect chewing lice and feather mites. Photo: Gail Stride.

2.4 Chewing louse identification

Chewing lice were identified at the University of Veterinary and Pharmaceutical Sciences in Brno, Czech Republic, under the supervision of Dr Oldřich Sychra.

For identification, chewing lice samples were treated using the following protocol: 1) Select the chewing lice with a small pipette from the 5 ml vials into petri dishes with approximately 1 ml of 96 % ethanol. 2) Transfer the chewing lice from a petri dish containing 96 % ethanol into another containing potassium hydroxide (KOH). 3) Leave for 5 h to soften the chewing lice in preparation for dissection and to remove the food contained in their bodies. 4) Remove the KOH from the petri dish, add H_20 and leave for 30 min. 5) Remove the H_20, add 50 % ethanol and leave for 30 min. 6) Remove the 50 % ethanol, add 70 % ethanol and leave for 30 min. 7) Remove the 70 % ethanol, add 96 % ethanol and leave for 30 min. 8) Remove the 96 % ethanol, add clove oil and leave for 24 h. 9) Mount chewing lice on a glass slide using Canada balsam. 10) Heat of mounted specimens in an oven at +55ºC for 1-2 days (Palma 1978).

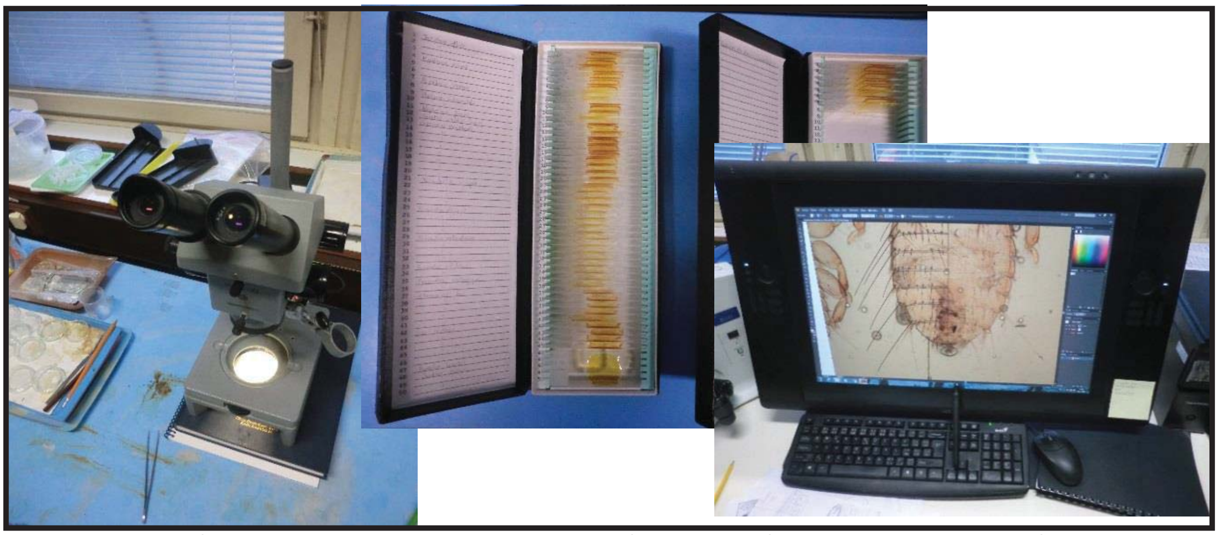

Figure 5. Some of the equipment and slides used in Brno for the identification and description of chewing lice. Photo: Ramón Soto Madrid.

Once the slides were mounted, the chewing lice were identified following taxonomic publications (Halajian et al. 2012; Hellenthal & Price 2003; Price et al. 2006).

Figure 6. Chewing louse. Photo: Marte Fandrem.

2.5 Feather mite identification

Feather mites were identified at the Zoological Institute of the Russian Academy of Sciences in St. Petersburg, Russia, under the supervision of Dr Sergei Mironov. For identification, feather mites samples were treated using the following protocol: 1) Select the feather mites with a small pipette from the 5 ml vials and place on a small watch glass with a small amount of 70 % ethanol. 2) Add some 10-15 % lactic acid (1-2 drops of 85 % lactic acid and 1-1.5 ml of distilled water). 3) Leave of feather mites in the same watch glass for at least 24 h at room temperature (~20 °C) to soften and make them more transparent. 4) Mounting of mites on a slide glass in Hoyer´s medium. 5) Heat of mounted specimens in an oven at +55ºC for 5-7 days.

Figure 7. Some of the equipment and slides used in Saint Petersburg for the identification and description of feather mites. Photo: Ramón Soto Madrid

Once we had the slides mounted, the feather mites were identified following taxonomic publications (Atyeo & Braasch 1966; Fain 1965; Gaud & Atyeo 1982; Gaud & Atyeo 1996; Mironov 2009; Mironov et al. 2005; Orwig 1967; Park & Atyeo 1971; Santana 1976).

Figure 8. Feather mite. Photo: Marte Fandrem.

2.6 Statistical analysis

Multi-dimensional scaling (MDS) plots were used to visualise differences in community composition of chewing lice, feather mites and birds in primary and selectively logged forest. Differences were tested using a permutational ANOVA, a method that describes the level of variation generated for different treatments or uncontrolled covarities and provided numeric information to explain the results.

The package "*iNEXT*" was used to create rarefaction curves for bird, mite and lice species richness. This package generates a prediction by doubling the number of individuals or presence for each taxon (Edwards et al. 2014a), and indicate if the sampling had an adequate effort. A General Linear Mixed Model (GLMM) was performed to evaluate whether there were changes in species richness and abundance for any of the sampled taxonomic groups between selectively logged and primary forests. Site was included as a random effect to account for non-independence of sites sampled repeatedly in time (two years). It was not possible to identify every feather mite individual due to time constraints and hence the number of sampled birds was included as an offset within the models.

Interaction networks were created using the package "*bipartite*" in R, which uses different variables to explain the patterns in the network and creates a visual representation of it. Quantitative bipartite networks were created, where links determine the frequency of interactions between host bird and parasite species. Four variables within the network were estimated: 1) links between species (links_sps) measures the number of links per species (Dormann et al. 2009); 2) weighted connectance measures the number of links per species, but weighted by the number of interactions (Dormann et al. 2009); 3) nestedness (NODF) means that generalists species interact more with the other guild and specialists interact only with a subset of the species interacting with the more generalist species (Burgos et al. 2009). Hence, a set of species that interact with others is contained in a bigger set, and those contained in a bigger one, and so on (Bascompte & Jordano 2007); and 4) evenness compares the abundance between the different species in the community: equal abundance has high value for evenness, bigger differences in abundance has low evenness (Smith & Wilson 1996). A GLMM was performed to evaluate whether logging affected any of the network metrics). Due to the small size of networks, data were pooled for the two sample years. All analyses were done in R version 3.3 (R CoreTeam 2014).

3. Results

3.1 Distribution of chewing lice and feather mites on birds

Bird abundance in logged forest during 2014 was higher than in 2015 and in primary forest sites. Numbers of birds dust-ruffled was similar between years. However, the number of bird species dust-ruffled was higher in 2015 (Table 1).

Chewing louse abundance was much higher during 2015 than in 2014. However, chewing louse species richness (the raw number of species) was similar between years and sites. Chewing lice prevalence (percentage of birds sampled with chewing lice or feather mites) was different in each site and period (Table 1).

Feather mite abundance was higher in 2015 than in 2014. However, prevalence and species richness was similar during both years (Table 1).

Table 1. Birds, chewing lice and feather mites distribution. Total number found per year in brackets.

Year	Landscape type	Bird abundance	Birds dust-ruffled	Bird species dust-ruffled	Chewing louse abundance	Chewing louse prevalence	No. of chewing louse species	Feather mite abundance	Feather mite prevalence	No. of feather mite species
2014	Primary	691	106	25	17	10.4 %	5 (10)	1400	73 %	57 (78)
2014	Logged	1098	99	25	47	19.2 %	8 (10)	1121	71 %	58 (78)
2015	Primary	544	144	46	122	26.2 %	11 (14)	2564	76 %	57 (78)
2015	Logged	687	144	46	145	15.2 %	9 (14)	1745	68 %	58 (78)

3.2 Community composition

No significant changes in the bird (F = 0.95, p = 0.51), chewing louse (F =1.32, p = 0.24) and feather mite (F = 0.79, p = 0.74) community composition were found between logged and primary forest (Figure 9). However, there were significant differences in chewing louse (F = 4.65, p < 0.001) and feather mite (F = 0.18, p < 0.01) community composition between sampling years. No difference was found for birds (F = 1.2, p = 0.28).

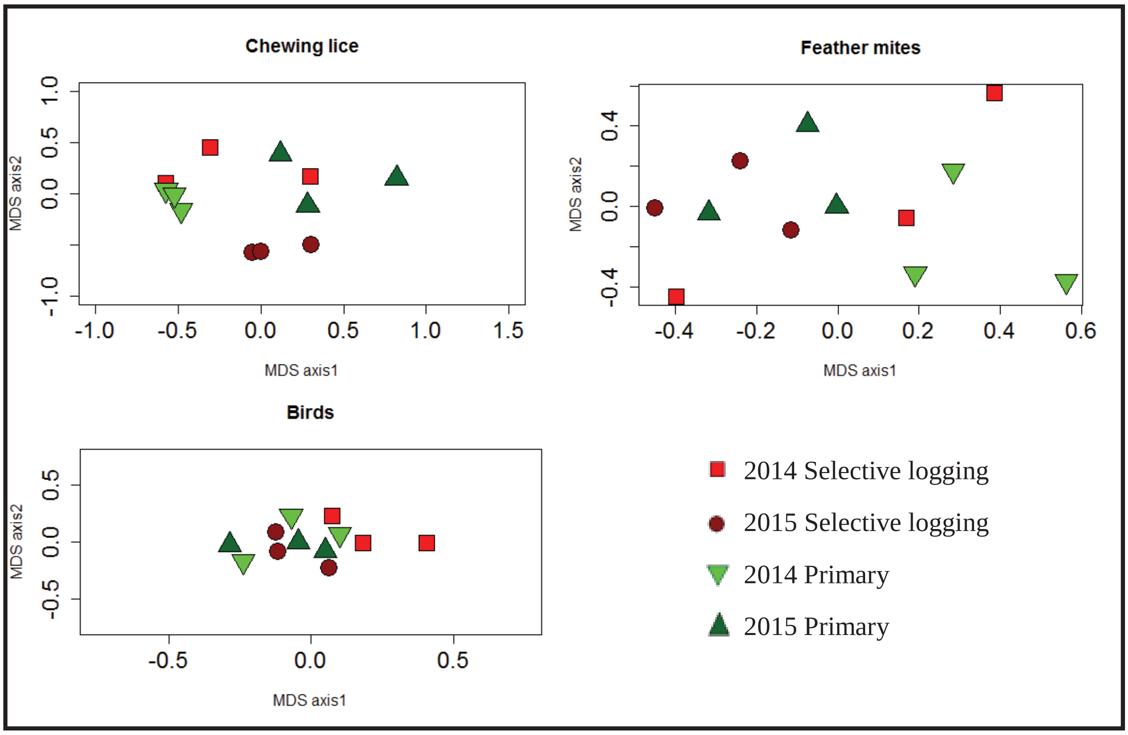

Figure 9. NMDS ordination of the chewing louse, feather mite and bird community in logged and primary forest during 2014 and 2015.

3.3 Species richness

The rarefaction curves (Figure 10) show that the sampling of chewing lice in selectively logged forest reached an asymptote. This was not the case in primary forest, although the slope was minimal. For birds, the curves are still increasing in both primary and selectively logged forest.

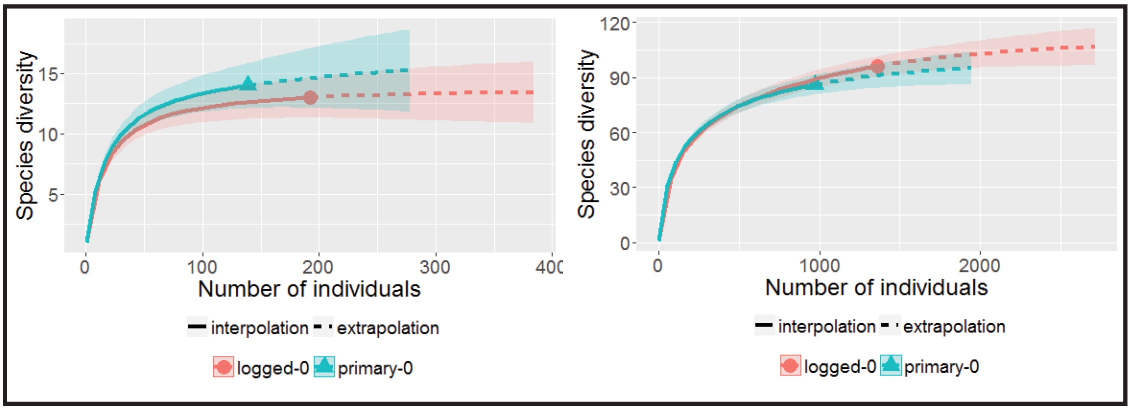

Figure 10. Rarefaction curves showing sampling effort of chewing lice (left) and birds (right).

Estimates of chewing louse species richness (Figure 11) show that there was no significant difference between primary and selectively logged forest (Estimate = -1.00, Std. error = 1.02, $p = 0.32$). However, there was a significant difference between sampling years (Estimate = 2.67, Std. error = 1.02, $p < 0.01$).

Estimates of feather mite species richness (Figure 11) show that there was no significant difference between primary and selectively logged forest (Estimate = -1.00, Std. error = 2.57, $p = 0.69$). However, there was a marginally significant difference between sampling years (Estimate = 4.00, Std. error = 2.43, $p < 0.1$).

Estimates of bird species richness (Figure 11) shows that there was no significant difference between primary and logged forest (Estimate = -7.67, Std. error = 4.88, $p = 0.11$). However, there was a highly significant difference between sampling years (Estimate = -12.00, Std. error = 3.33, $p < 0.001$). In addition, there was a significant interaction between forest and year, which shows that richness was greater in logged forest in 2014 and greater in primary in 2015 (Estimate = 12.00, Std. error = 4.71, $p < 0.05$).

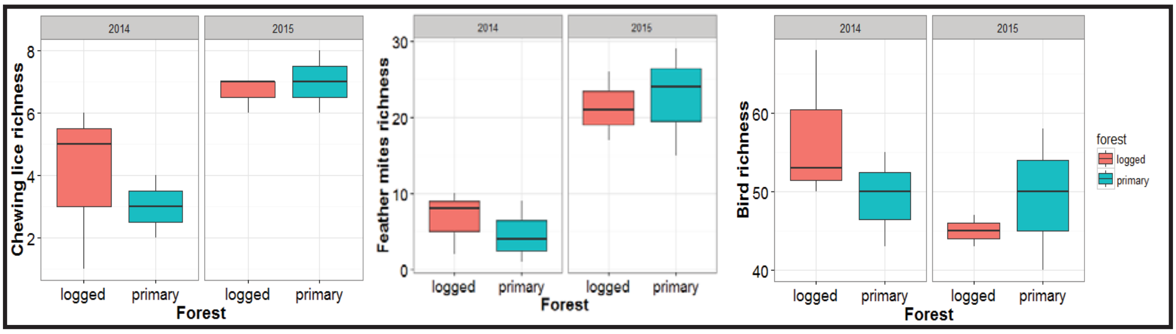

Figure 11. Chewing louse, feather mite and bird species richness in logged and primary forests.

3.4 Abundance

Estimates of chewing lice abundance (Figure 12) show that there was no significant difference between primary and logged forest (Estimate = -10.30, Std. error = 8.93, p = 0.247). However, a significant difference was found between sampling years (Estimate = 32.33, Std. error = 6.10, $p < 0.001$).

Estimates of feather mites abundance (Figure 12) show that there was no significant difference between primary and logged forest (Estimate = 93.00, Std. error = 159, p = 0.55), or between sampling years (Estimate = 208.00, Std. error = 159, p = 0.19).

Estimates of bird abundance (Figure 12) show that there was no significant difference between primary and logged forest (Estimate = -135.66, Std. error = 73.25, p = 0.13), or between sampling years (Estimate = -137.00, Std. error = 65.30, p = 0.10).

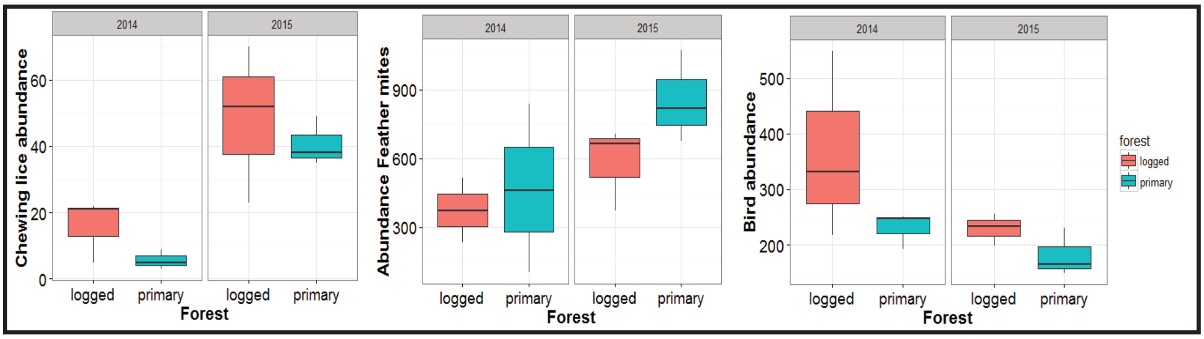

Figure 12. Chewing louse, feather mite and bird abundance in logged and primary forests.

3.5 Structure of the interaction networks

In total, 31 chewing louse-bird host associations were observed for both sample years combined; eleven were previously known associations and twenty were new. Moreover, eleven bird species were recorded to have lice for the first time, and four species of chewing louse new to science were discovered. Of the 78 species of feather mites collected, 51 are also new to science.

3.5.1 Chewing louse-bird network

The *P*-values from the four variables chosen to build the interaction network differed significantly between primary and unlogged forest: links between species and weighted connectance was higher in primary than in logged forest. Nestedness was higher in logged, which means that the number of specialists was lower in logged forests. Evenness was lower in logged, which means that some species were more dominant in logged forests (Table 2, Figure 13).

In selectively logged forest (Figure 14) there were 16 louse-host interactions. On 15 bird species, 13 species of chewing lice were found and two of them were present on more than one host. Two birds had more than one chewing louse species, both hosting two different species.

In primary forest (Figure 15) there were 25 louse-host interactions. On 20 bird species, 14 species of chewing lice were found and seven of these were found on more than one host. Five birds had more than one chewing louse species, all of them hosting two different species.

Table 2. Variables used to build the chewing louse-bird interaction network.

Variables	Estimate	Std. Error	z value	Pr(>|z|)
links_sps	0.02972	0.00209	14.2	<2e-16 ***
NODF	-0.9743	0.0282	-34.5	<2e-16 ***
weigh_connectance	0.002226	0.000727	3.06	0.0022 **
int_evenness	0.016979	0.001320	12.9	<2e-16 ***

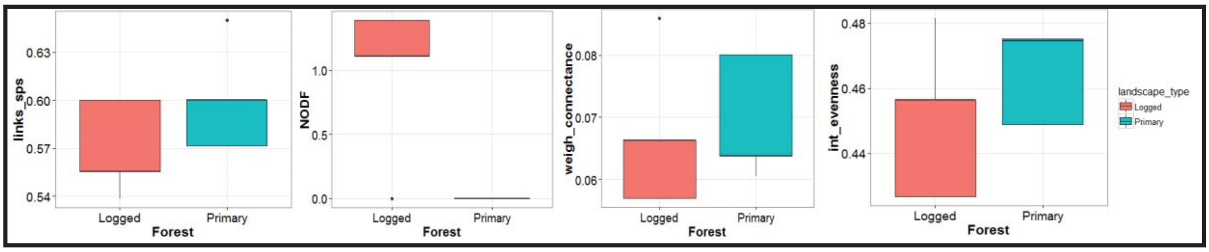

Figure 13. Variables used to build the chewing louse-bird network

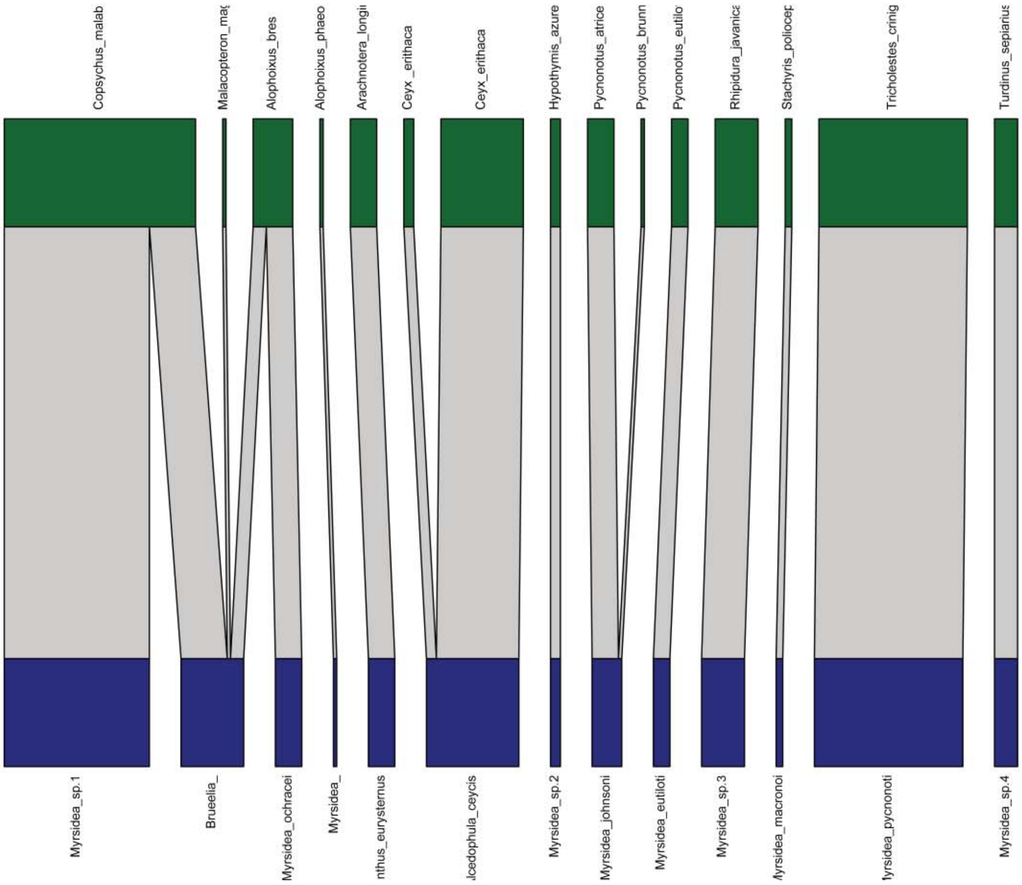

Figure 14. Chewing lice-bird network in selectively logged forest.

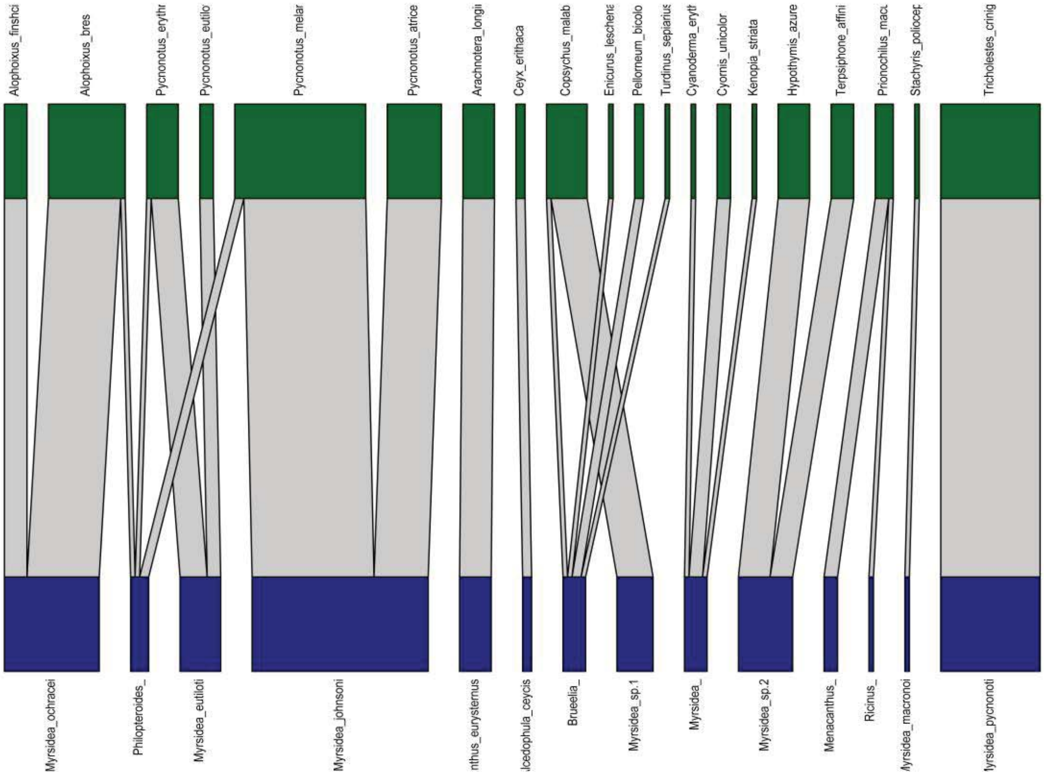

Figure 15. Chewing lice-bird network in primary forest.

3.5.2 Feather mite-bird network

Two *P*-values from the four variables chosen to build the interaction network differed significantly between primary and unlogged forest: weighted connectance was higher in primary forests. Evenness was lower in logged forests, which means that some species were more dominant in logged forests. However, links between species and nestedness did not differ between primary and logged forests (Table 3, Figure 16).

In selectively logged forest (Figure 17) there were 85 mite-host interactions. On 38 bird species, 60 species of feather mites were found, and 11 species were found on more than one host. 26 birds had more than one feather mite specie, hosting a maximum of five.

In primary forest (Figure 18), there were 78 mite-host interactions. On 38 species of birds, 59 species of feather mites were found, and 11 species were found on more than one host. 24 birds had more than one feather mite species, hosting a maximum of four.

Table 3. Variables used to build the feather mite-bird interaction network.

Variables	Estimate	Std. Error	z value	Pr(>|z|)
links_sps	0.01140	0.00793	1.44	0.15
NODF	-0.00612	0.03055	-0.2	0.84
weigh_connectance	0.003643	0.000955	3.81	0.00014 ***
int_evenness	0.00448	0.00172	2.61	0.009 **

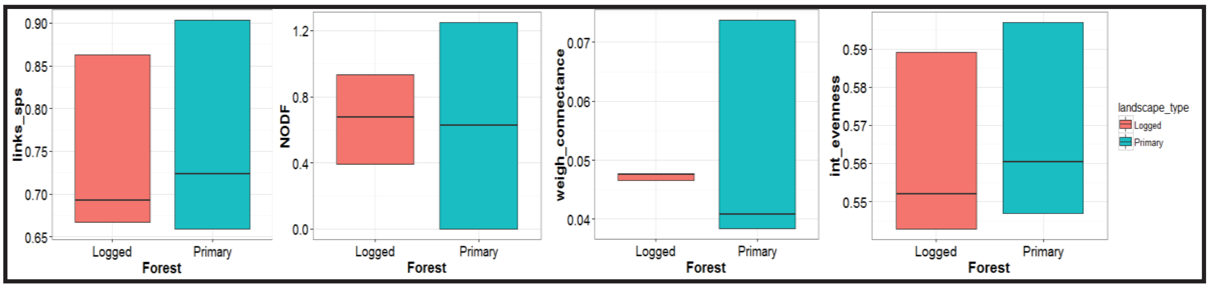

Figure 16. Variables used to build the feather mite-bird network.

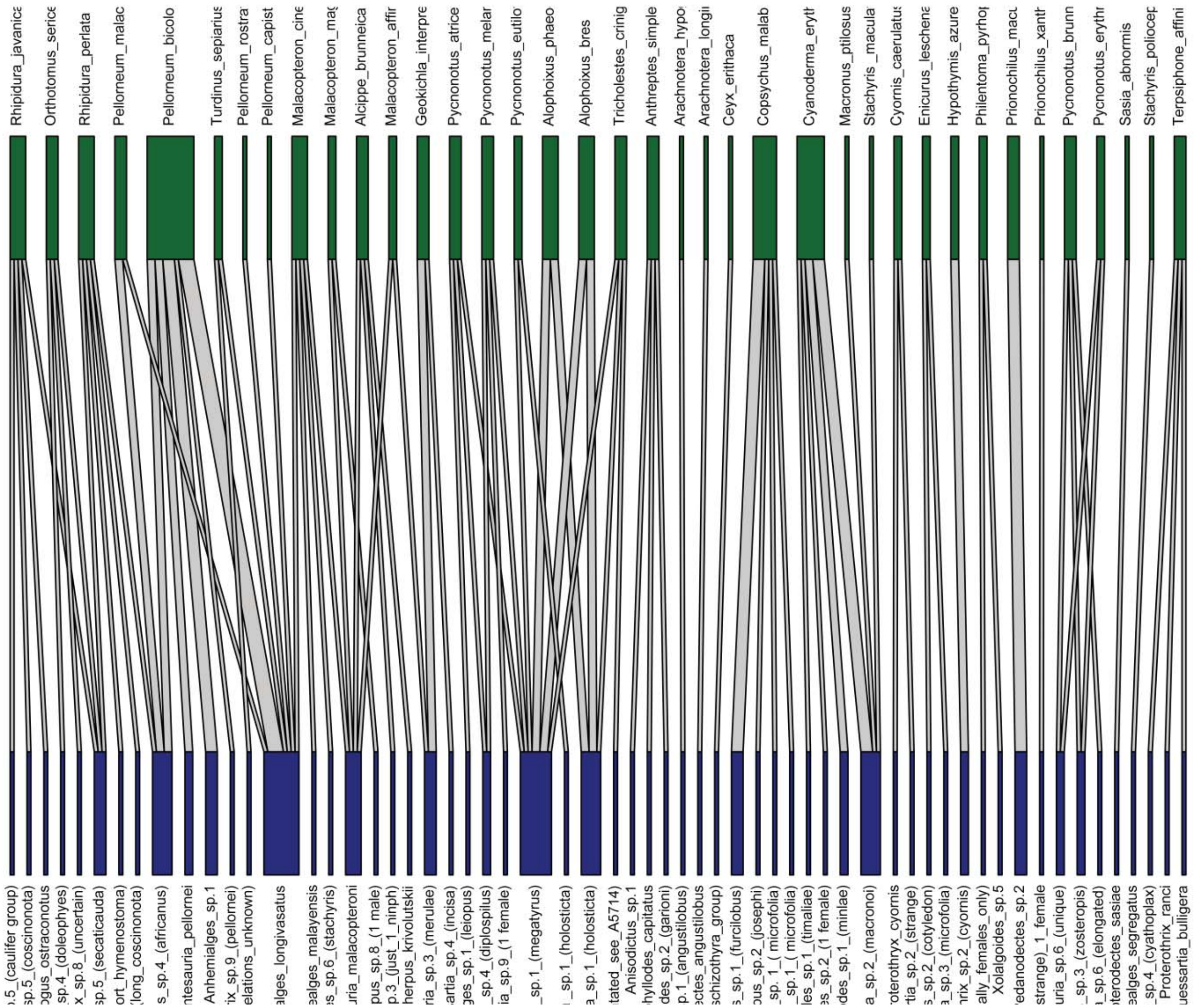

Figure 17. Feather mite-bird interaction network in selectively logged forest.

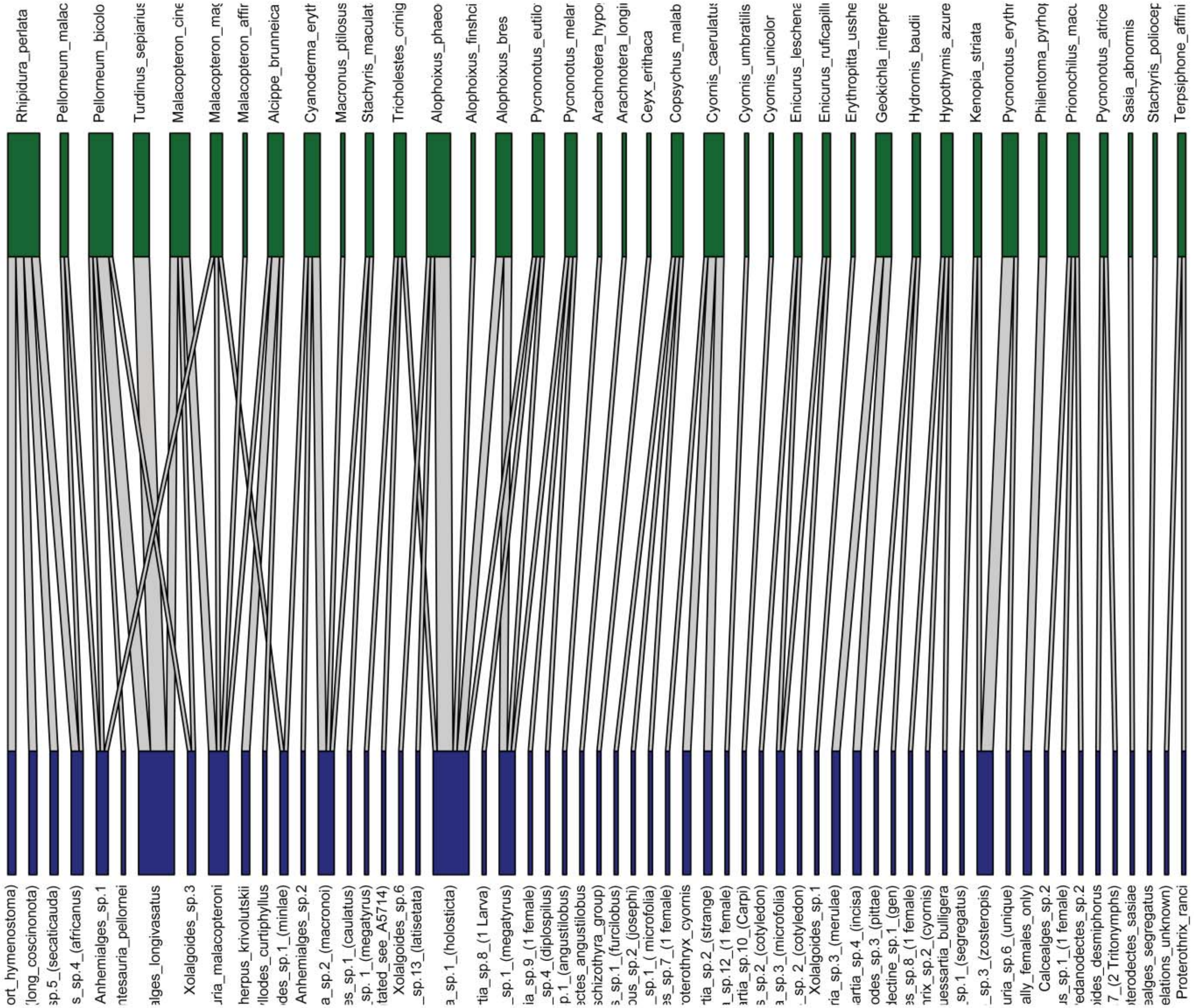

Figure 18. Feather mite-bird interaction network in primary forest.

4. Discussion

To my knowledge, this is the first study assessing the effect of selective logging on the community composition, species richness and interaction networks of chewing lice and feather mites associated with birds. As a result of this research, 20 new louse-host associations have been discovered and 11 bird species had chewing lice recorded for the first time. In addition, four new species of chewing louse and 51 new species of feather mites have been discovered. Feather mites in Borneo are very poorly studied, which is probably why the current study has found so many species new to science. However, the four new species of chewing louse discovered in this study and 16 new species found by Hellenthal & Price (2003) in South East Asia, suggests that we still have a lot to learn about this group as well.

4.1 Distribution of chewing lice and feather mites on birds

The prevalence of chewing lice in this study between forests sites was inconsistent, finding with higher prevalence in selectively logged forest (19.2 %) than primary (10.4 %) in 2014 and finding the opposite in 2015, selectively logged had lower prevalence (15.2%) than primary forest (26.2 %). These results are in agreement with previous studies, which also reported varying levels of prevalence. A study in China recorded 44.6 % prevalence on birds (Bush et al. 2013); 40% for non-passeriformes and 27% for Passeriformes in Senegal (Najer et al. 2012); 47% for Turdidae in Costa Rica (Kounek et al. 2013); 19% for passeriformes in Vietnam (Najer et al. 2014); 12% for Passeriformes in South Africa (Sychra et al. 2014); in Brazil 66.7 % for non-Passeriformes and 57.8 % for Passeriformes (Enout et al. 2012). This may correspond with different people collecting the chewing lice, or with differences in abiotic and biotic conditions.

Feather mite prevalence in this study was similar to a study in Brazil, which found a feather mite prevalence of 50 % in non-Passeriformes and 75.6 % in Passeriformes (Enout et al. 2012).

In general, prevalence of chewing lice is lower than of feather mites. This may be because the former are true parasites and the latter are rather commensals. Grooming may therefore be more effective on chewing lice than feather mites.

4.2 Community composition

The community composition of birds in this study did not differ significantly between primary and selectively logged forest (Figure 7). These results are different from previous studies that found significant differences in community composition of birds, scavenging mammals, leaf-litter ants and dung beetles (Edwards et al. 2014a) and in birds and dung beetles (Edwards et al. 2011), but are in agreement with a previous study that found no differences in the community composition of beetles, flies, springtails, true bugs, bees, wasps and ants between primary and logged areas (Edwards et al. 2014a).

The community composition of chewing lice and feather mites between primary and logged forest did not reveal significant differences (Figure 7). This trend may be driven by the similar bird community composition between logged and primary forest. Chewing lice and feather mites are highly host specific and host species heterogeneity is related to parasite heterogeneity (Hechinger & Lafferty 2005; Poulin 2014), which could be why this study did find differences in chewing louse and feather mite communities between forest types. However, this study found significant differences in chewing louse and feather mite community composition between sampling years (Figure 7), but not in bird community compositions. This suggests that the community composition of chewing lice and feather mites may be driven by abiotic and biotic factors as much as by bird species composition.

4.3 Species richness

This study found no significant differences in species richness (Figure 11) of chewing lice, feather mites and birds between primary and selectively logged forest. These results are in agreement with previous studies. Edwards at al. (2014a) found a similar bird species richness and richness of several other taxa between primary and logged forest. Edwards et al. (2011) also documented a similar trend for birds, whereas a small decline in dung beetles species richness was observed.

Earlier studies have found a positive correlation between host and parasite species richness (Johnson et al. 2016; Poulin 2014). Since bird (host) species richness was similar across logged and primary forest, this is probably why chewing louse and feather mite species richness also was similar across forest types (Figure 11). However, external factors may also influence ectoparasite species richness. For example, Bush et al. (2013) show that ectoparasite species richness decreases with decreasing forest area, finding that birds in smaller forest areas had fewer ectoparasites species and lower ectoparasite prevalence. In fact, some ectoparasite species went extinct even though the host persisted (Bush et al. 2013).

The selectively logged forest in my study remains connected to a much bigger forest area. The importance of connectivity in the maintenance of chewing louse and feather mite associations with birds is evident from other taxa. Johnson et al. (2016) found that connection between communities increases the relationship between hosts and parasites. However, different responses have been observed for different species even within the same taxonomic group. Wells et al. (2007b) found that certain mammal species had a higher species richness and prevalence of parasites in logged forest than in primary forest, while Yet, other mammal species in the sample had an opposite trend (Wells et al. 2007b). This suggests that the specific host and parasite life histories are important in these comparisons (Wells et al. 2007b) and further work is clearly needed to better understand the dynamics of parasite-host interactions in tropical forests.

4.4 Abundance

Chewing louse and feather mite abundance did not differ between primary and selectively logged forest. A previous study has related host abundance with the abundance of parasites (Hechinger & Lafferty 2005). This is supported by the current study, as no significant differences in bird abundance between primary and selectively logged forest were found. This suggests that a higher abundance of a certain host in an area may influence its ectoparasite health due to higher resource availability and increase in transmission (Bush et al. 2013; Johnson et al. 2016). Hence, ectoparasites may be good indicators of the status of the host populations (Bush et al. 2013).

4.4 Structure of the interaction network

Chewing louse-bird interaction network showed higher weighted connectance, links between species and evenness but lower nestedness in primary than in logged forest. Hence, the stability of the interaction network in chewing lice was higher in primary forest than in logged. Feather mite-bird interaction network showed higher weighted connectance in primary forests. Nestedness did not differed between forest types. Therefore, the stability of the interaction in primary was also higher than in logged forest.

In conclusion, this study found no significant differences between primary and selectively logged forest in the abundance, species richness and community composition of chewing lice, feather mites and birds. Surprisingly, differences in the interaction network in these taxa were present between forests types. The consequences of logging on host and therefore parasite survival, and the resulting consequences in the whole interaction network is an area that requires further research.

This research adds evidence in the existing literature of the high conservation value of selectively logged forest and its importance for biodiversity, despite differences in interactions networks were found in this study. We need to demonstrate the high biodiversity value of logged forest in order to protect it against conversion to oil palm plantations or other land uses with a much reduced conservation value. Future research on this topic should collect samples from a wider range of logging intensities and from isolated forest fragments of different sizes and compare them to selectively logged and primary forest. Furthermore, the collection of temperature, humidity, light and other environmental variables would be very useful in building up a clearer picture of the microclimatic changes generates by logging which would help us to understand the responses of chewing lice and feather mites that we have seen.

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Norges miljø- og biovitenskapelig universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway