Assessment of functional bird biodiversity along a restoration gradient in the tropical cloud forests of Northwest Ecuador

Nele Devriendt

Promotor: Prof. Dr. Luc Lens

Copromotor: Prof. Dr. Eduardo de la Peña

Mentor: Dr. Debbie Eraly

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1. Introduction

Forests perform an indispensable role in numerous ecosystem services, important for the health of the planet and all species living within. Besides providing habitats for animals, forests also regulate the global climate and air quality, prevent soil erosion, support nutrient cycles, offer cyclone protection and provide energy and timber (Alamgir et al. 2016). However, these important ecosystems are being lost worldwide at a high rate. Since 2016, a yearly average of 28 million hectares have been cut down worldwide (TheWorldCounts 2020). Main causes for deforestation are timber extraction for fuel, manufacturing or construction and land-clearing for agricultural use or cattle breeding (Rueda et al. 2019). The current level of deforestation could lead to species extinction rates of 18% to 40% by 2100, depending on protection actions of biodiverse habitats in the near future (Knoke et al. 2020). The health of forests is largely supported by its biodiversity, through irreplaceable vegetation-animal interactions, such as top-down control on herbivorous insects, pollination and seed dispersal (Bregman et al. 2016, Gardner et al. 2019). The loss of biodiversity is expected to have large consequences for forest functioning (Gardner et al. 2019).

Reforestation is of large importance to re-establish forest's ecological communities and functions. For many projects the desired endpoint is the restoration of species diversity, as a higher biodiversity is both linked to more resistant and resilient communities and to a higher ecosystem functioning (Falk 2006, Mori et al. 2013). A high biodiversity provides ecological insurance for ecosystem functioning under changing environments, as there is a high probability that the function performed by a lost species can be taken over by a redundant species (Matias et al. 2013, Ulanowicz 2018). It is also crucial to consider biotic interactions among organisms in a community, as these interactions may determine restoration outcomes (Falk 2006). Particularly with respect to ecosystem function, the properties of a diverse community can be larger than predicted by the sum of its parts, through interspecific facilitation (Cardinale et al. 2002).

Much effort is needed in the restoration of tropical forests, as these provide the largest flow of multiple ecosystem services among terrestrial ecosystems, such as CO_2 fixation, water supply, flood control and soil maintenance (Alamgir et al. 2016, Shimamoto et al. 2018). This important ecosystem is largely threatened, with in the last decade an average loss of 3.7 million hectares of primary forest per year (Butler 2019). Tropical forest areas have been converted into agricultural lands and pastures for e.g. cattle ranching, soybean farming and oil palm plantations (Shimamoto et al. 2018). The consequences of land-cover change for the health and stability of tropical forest ecosystems, and their ability to recover, are still largely unclear (Bregman et al. 2016). In recent years, reforestation efforts in tropical areas have increased, focusing on the recovery of the structure, function and biodiversity of degraded ecosystems (FAO 2018, Shimamoto et al. 2018).

As part of the Tropical Andes, the Andean cloud forests of Ecuador belong to one of the world's hotspots of biodiversity (Dislich et al. 2009). Ecuador has an official National Protected Areas Network covering about 20% of the country, but still efforts are insufficient for the conservation of the country's rich biodiversity. The northern cloud forests are rapidly declining due to large-scale timber extraction, and the oil and mining industry are leading to severe water pollution and habitat destruction. New roads are continuously being opened in fragile areas, triggering further colonisation and consequent habitat degradation (Freile et al. 2010). The loss and degradation of the cloud forests lead to a reduction of species richness and an increase in biological homogenization, which has on their turn large impacts on ecosystem services (Bregman et al. 2016). Ecuador is one of the ornithologically richest countries worldwide. Especially the Ecuadorian cloud forests harbour a high amount of bird species, i.e. roughly 800 species (Freile et al. 2010). Rapid land cover change for agriculture is a major threat for up to 15% of the bird species in Ecuador and most Ecuadorian endemic species are on the brink of extinction because of habitat alteration (Cresswell et al. 1999).

Birds contribute to different services, directly beneficial to human. Provisioning services are provided by birds as they are part of the human diet, and feathers can be used for insulation, bedding and ornamentation (Whelan et al. 2015). Birds also provide some cultural services through e.g. photography, art and bird watching (Whelan et al. 2008). Bird watching is popular in Ecuador, resulting in direct economic benefits and indirect benefits through numerous citizen science programs involving bird watchers. A great number of bird species also has a supporting or regulating role in an ecosystem, including scavenging carcasses, nutrient cycling, seed dispersal, seed predation, pollination, ecosystem engineering and pest control (Whelan et al. 2008). These could either be directly beneficial to human (e.g. birds can regulate a pest species on crops, scavenging carcasses reduces human diseases, etc.), or indirectly beneficial through their underlying ecosystem functions (Whelan et al. 2015).

In this study, the focus was on different functional groups, critical to the long-term resilience of forests threatened by anthropogenic change (Bregman et al. 2016). Seed dispersal by frugivorous birds is crucial to plant distribution and recruitment, knowing that more than 80% of tropical woody plants produce vertebrate-dispersed seeds (Gardner et al. 2019). These plant species rely on frugivores for their seed dispersal, as they consume fleshy fruits and release the seeds elsewhere. Frugivores tend to be highly vulnerable to deforestation, so it is likely that these birds are easily lost from disturbed forest systems (De Coster et al. 2015). This loss can alter the vegetation and impede regeneration of disturbed areas (Bregman et al. 2016). Seed dispersal by birds is key to the speed and diversity of the succession in reforested areas (Carlo and Morales 2016). Rates of forest regeneration are also influenced by the presence of insectivorous birds. They regulate top-down control of herbivory by forest insects. Without insectivores, there would be an increase in leaf damage, and hence increased seedling mortality and reduced plant growth (Bregman et al. 2016). The come-back of birds in reforested areas is thus crucial for the restoration of degraded forest ecosystems.

A large-scale reforestation project in Northern Ecuador started in 2011, with the main target to increase carbon sequestration. This project is coordinated by the Flemish non-profit organization BOS+ Tropen and the local conservation organization Mindo Cloudforest Foundation (MCF). The Belgian company Telenet and the coffee company Roastery 7 from the US are the main investors of the project, aiming to neutralize their carbon emissions. The project is located on the land of private landowners and currently covers more than 400 ha, spread over seven separated strata. These strata differ in altitude, environmental conditions and species composition. In addition to carbon sequestration, enhancing biodiversity is also of great importance in the project. Therefore, there is an underpinned selection of native tree species before planting in each stratum (Thierens 2017). Other project goals are providing employment opportunities and consequently helping to reduce poverty in rural communities, and improving ecosystem services such as erosion prevention and water availability (Krohnke 2012). From the beginning of the project, scientific research and monitoring in both the reforested areas and natural forests have been done, focusing on the recovery of the vegetation (Strubbe 2013, Bruneel 2016, Thierens 2017). However, the restoration of the physical habitat will not automatically lead to the restoration of communities and ecosystem functions (Falk 2006). An assessment of how fauna is responding to the restoration efforts, focusing on their functional diversity, had not yet been conducted.

The main objective of this study was to examine to what extent reforested areas were recovering in terms of

i) general bird biodiversity and species composition

ii) presence of forest and indicator bird species with high sensitivity to disturbance

iii) ecosystem functioning performed by birds

Monitoring of biodiversity and community composition within the framework of reforestation projects gives essential information to confirm whether sites are developing on-track and to signal if further management intervention is needed (Catterall et al. 2012). Recent studies have found that birds tend to respond well to reforestation, which mostly results in a similar bird richness in reforested areas as in reference forests (Santos et al. 2016). However, the bird species composition is usually different (Santos et al. 2016). Therefore, it is important to investigate both changes in diversity and composition of species and functional units, as the effect of degradation on ecosystem functioning may be intertwined with both (De Coster et al. 2015). The return of typical forest and indicator species to reforested areas indicates a good recovery from a previously degraded situation. These groups include species of special conservation concern, as they are sensitive to degradation and therefore diminishing in their abundance due the large-scale loss of suitable habitat. Ecosystem functions performed by birds play an important role in the full recovery of reforested areas. Hence it is interesting to investigate to what extent these functions have been restored already, by examining the species richness and composition of different functional groups. It could be expected that the more species present belonging to a certain functional group, the higher the performance of their ecosystem functions (Bregman et al. 2016). The bird species that contribute to a certain ecosystem function could be totally different along the restoration gradient, going from more generalist species in pastures towards specialists in natural forests. Therefore, the species composition of each functional group in the reforested areas would give an indication which groups and to what extent they are recovering towards the reference forest state. An experiment on the direct performance of top-down control by insectivores has been done, using dummy caterpillars. It would be expected that the more insectivorous species present in a certain location, the higher the top-down control is. A deviation of this expectation would indicate that other factors strongly influence the performance of this ecosystem function (Habel and Ulrich 2020).

Most studies only focus on the recovery of the vegetation, but the restoration of the physical habitat is not automatically followed by its ecological restoration (Falk 2006). Therefore, this study deviates from the vegetation-centric approach to restoration, focusing on the recovery of bird species richness and composition (Falk 2006, Cross et al. 2020). This study gives insights in how bird species communities and their ecosystem functions are recovering after a decade of reforesting previously degraded pasture in Northwest Ecuador, provides general tools how to investigate the response of fauna and emphasizes the importance of monitoring to improve restoration trajectories.

2. Objectives

The main objective of this study was to examine to what extent reforested areas are recovering towards a qualitative forest, focusing on three different aspects.

The first aspect considered was the restoration of bird diversity on a local and regional scale, as well as the differentiation in species composition among habitats along the restoration gradient.

Second, the return of typical forest and indicator bird species that are sensitive to degradation has been examined. This would indicate that reforested areas provide good habitat for these species, therefore it can be assumed that these areas are recovering well.

Third, the restoration of ecosystem functions has been investigated, focusing on different functional groups. It can be assumed that the more species are present belonging to a certain functional group, the higher the performance of its ecosystem function. Therefore, the number of species per functional group was counted and compared between different habitats, as well as the species composition within each functional group. An experiment was conducted to see whether top-down control differs along the habitats and whether there is a correlation between the number of predominant insectivores and the performance of top-down control.

3. Materials and methods

3.1 Study area

In the North-western Ecuadorian Andes, a large-scale reforestation program has been implemented by BOS+ and the Mindo Cloudforest Foundation (MCF), which started in 2011. The reforested areas are located in 4 provinces: Pichincha, Imbabura, Carchi and Esmeraldas. For the scope of this study, only areas within the province Pichincha have been investigated. The reforested areas were classified into different strata, related to their altitude. In this study, the focus was on strata 1, 2 and 3, ranging from high altitudes in stratum 1 to low levels in stratum 3 (Table 1). In each of the 3 strata, there is an area which has been reforested between 2012 and 2014, an intact natural forest and a deforested area (pasture) which are all comparable in terms of altitude and abiotic conditions. Each comparison between the three habitats was conducted within a single stratum, as the species pool occurring at low altitudes may be completely different from the species pool at higher altitudes, independent of the habitat type. In the second stratum, two different reforested areas were included, so a total of 10 different locations has been monitored.

	Natural forest	Reforested area(s)	Pastures
Stratum 1	Puyucunapi (1890-1968m)	Santa Rosa (2047-2160m)	Pasture Santa Rosa (2149-2265m)
Stratum 2	Milpe (973-1109m)	Piedras Negras (1518-1551m) La Yumbada (1753-1881m)	Pasture Milpe (1080-1147m)
Stratum 3	Silanche (383-412m)	Suamox (326-383m)	Pasture Silanche (394-418m)

Table 1. Names and elevation of the natural forest, reforested area(s) and pasture within each of the 3 strata. The names are the same used in the project description of BOS+ Tropen and Mindo Cloud Forest Foundation. The minimum and maximum elevation was measured with GPS during the field work.

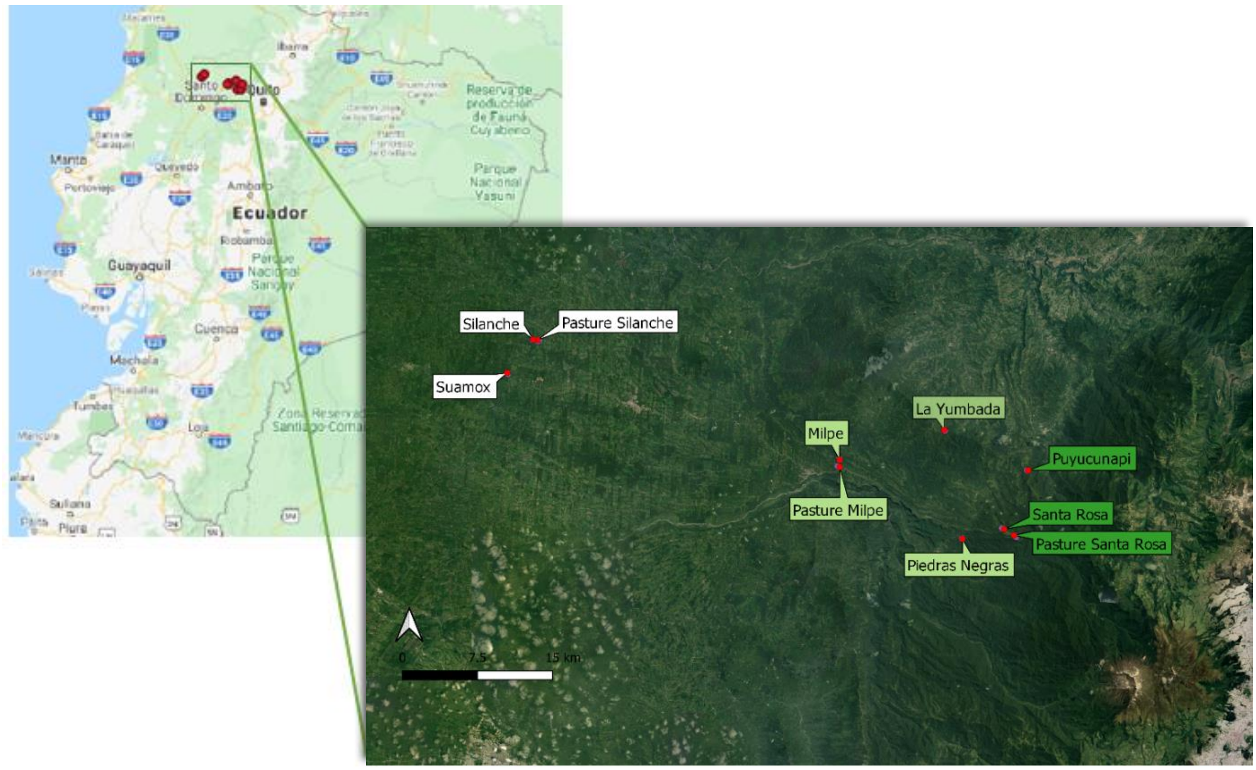


Figure 1. Location on map of reforested areas, natural forests and pastures of stratum 1, 2 and 3. Stratum 1 is indicated in dark green, stratum 2 in light green and stratum 3 in white.

3.2 Point counts

In each of the 10 locations, 6 plots of 5x5m were chosen and delineated with ribbon. These plots were situated at least 60m apart from each other and were representative for the habitat of the location. The coordinates of each plot were measured by GPS. All point counts happened between 24 July 2019 and 24 August 2019. In the morning of two consecutive days, point counts were conducted for 20 minutes per plot within one of the locations. These point counts were done auditory, by using a recording app on a smartphone. All point counts took place between 7h and 11h30 am, the first day starting at plot 1 and ending at plot 6, the second day the other way around. This was done to reduce the effect of time on the presence of birds. The recordings were afterwards analysed by an independent and experienced recognizer of local bird vocalizations. All bird species heard on the recordings were listed per plot per day, excluding birds that flew over and those that were heard outside the range of 30m around the centre of the plot. Based on the species list, a comparison between reforested plots, natural forest plots and pasture plots within a stratum has been conducted, focusing on bird species diversity, presence of true forest and indicator species and ecosystem functioning.

3.2.1 Bird species diversity

First of all, the research question whether reforested areas are recovering in terms of bird biodiversity has been approached. This was done by comparing the alpha, beta and gamma diversity between the reforested area, natural forest and pasture within each stratum. The alpha diversity was measured as the total number of species recorded per plot per day. Only the presence or absence of a certain bird species in each plot was listed, but not the abundances of the species, as this was impossible to determine based on the recordings. A Generalized Linear Mixed Model (GLMM) was performed per stratum with the independent variable being the alpha diversity, only one fixed factor being the habitat (either reforested, pasture or natural forest) and random factors being the plot and day of observation. GLMM analyses were done in RStudio using the packages lme4, lmerTest and lsmeans. The gamma diversity can be seen as the regional species diversity. This was measured as the total number of species that was recorded in either a reforested area, natural forest or pasture within a single stratum. Also, the total number of observations per location was determined, being the sum of the alpha diversities of the plots belonging to one location. By comparing the gamma diversity and the total number of observations, the proportion of species that were found back in more than one plot could be derived. The beta diversity was defined as the differentiation in species composition among habitats, which were in this study natural forest, reforested area and pasture. This beta diversity was calculated based on the Jaccard similarity index, by the formula $c/(S1+S2-c)$, with S1 the number of species recorded in the first habitat, S2 the number of species recorded in the second habitat and c the number of species common to both habitats. The Jaccard similarity index gives a value between 0 and 1: the closer this index to 1, the more the species compositions of both habitats resemble each other.

3.2.2 Forest and indicator species

Secondly, the focus was on the recovery of the number and composition of typical forest and indicator bird species in the reforested areas. From the total species list obtained by analysing the recordings, true forest species were selected based on the habitat description by the Cornell Lab of Ornithology –

Birds of the World (TheCornellLabOfOrnithology 2020). In case a species only prefers forested areas, and avoids parks, gardens, pastures, urban areas, etc., the species is considered to be a true forest species. From those forest species, a selection of indicator species has been made. These forest species are sensitive to degradation and destruction of their environment. The International Union for Conservation of Nature (IUCN) provides information about the habitat and ecology of every bird species on earth (IUCN 2020). Suitable habitats for a certain bird species were listed according to a classification scheme. Indicator species are only allowed to have class “1. Forest”, whereas other forest species may also have class “14. Artificial/Terrestrial” listed as suitable habitat. Especially subclass “14.6. Artificial/Terrestrial - Subtropical/Tropical Heavily Degraded Former Forest”, makes clear that the species is not sensitive to degradation. These selections were made to investigate whether the number of bird species and species composition, focusing on true forest and indicator species, is restoring in reforested areas. The number of forest and indicator species present per plot was calculated and compared using a GLMM, with as fixed factor the habitat (reforested, natural or pasture) and as random factors the plot and day of observation. The species composition, after selecting forest and indicator species, has been compared between each of the three habitats within a single stratum using a non-metric multidimensional scaling (NMDS). NMDS analyses were performed in RStudio using the packages Vegan and Adonis. A Permanova test indicates whether there is a significant clustering of the three habitats or not. A post-hoc analysis was performed by executing a pairwise Adonis test.

3.2.3 Ecosystem functioning

Thirdly, research has been done about how well ecosystem functions performed by birds are restoring in reforested plots. Therefore, the total species list obtained after recording has been split up into seven functional groups, based on the predominant diet of the species: predominantly frugivorous birds, predominantly insectivorous birds, frugivores-insectivores, predominantly granivorous birds, predominantly vertebrate-eaters, predominant nectarivores and omnivores (Table 2). Species were assigned to one of the groups based on the information found on the Cornell Lab of Ornithology (TheCornellLabOfOrnithology 2020).

Name	Explanation
Predominantly frugivorous	Birds feeding mainly on fruits
Predominantly insectivorous	Birds feeding mainly on insects and spiders
Frugivores-insectivores	Adult birds feeding equally much on fruits and insects
Predominantly granivorous	Birds mainly feeding on seeds
Predominantly vertebrate-eaters	Birds mainly feeding on small invertebrates
Predominantly nectarivorous	Birds mainly feeding on nectar
Omnivores	Birds with a mixed diet, consisting of more than only insects and fruits, without a clear preference

Table 2. Functional groups with the abbreviated name and full explanation.

Per plot, the number of species belonging to each of the functional groups was counted. By using a GLMM, this number has been compared between the three habitats. Similar as for the forest and indicator species analyses, the fixed factor is habitat and random factors are the plot and day of observation. This gives an indication how well certain ecosystem functions could be performed in each of the habitats. The species composition of each functional group within reforested, natural forest and pasture plots of one single stratum has been compared, using a NMDS analysis. The outcome of a Permanova test indicates whether there is a significant clustering between at least two of the three habitats. A post-hoc analysis has been done using a pairwise Adonis test, to make a comparison between each habitat. This gives a clearer view on how well certain ecosystem functions are restoring in reforested areas. A species composition in a reforested area that is already quite similar to the reference forest would indicate a restoration trend of that specific functional group.

3.3 Caterpillar experiment

Analysing the number and composition of predominantly insectivorous bird species, gives a first insight in how well the top-down control is restoring in reforested areas. However, this does not measure the actual performance of this important ecosystem function by insectivores. To investigate whether top-down control performed by insectivorous birds is actually restoring in reforested plots, an experiment was set up with dummy caterpillars. The methodology of this experiment is based on a previously conducted study concerning top-down control (Roslin et al. 2017). Insectivorous birds attempt to eat the dummy caterpillars but release them once they find out these are fake, eventually leaving a beak mark. The more dummy caterpillars have beak marks within a plot, the higher the top-down control, and thus the better the ecosystem function has restored when comparing with the reference forest.

Before starting the actual experiment, a try-out was conducted to pick the best size (small 4cm or large 6cm), shape (curved or straight) and colour (dark or light green) for the caterpillars. For each of the combinations, 16 caterpillars were placed. Bite marks were counted after 24h and there was a clear preference for the small (4cm), curved, light green caterpillars. For the further experiment, this is the type of caterpillars used in each plot. The dummy caterpillars were made from organic, odourless plasticine, so it would not do any harm when eaten accidentally. These caterpillars mimic the prevalent Lepidopteran larvae.

The same 5x5m plots as for the point counts were used for the caterpillar experiment. In each of the 6 plots per habitat (reforested, natural forest or pasture), 20 dummy caterpillars were fixed on branches and leaves with iron wire (Figure 2). 10 of those were placed at ground level and 10 at 1.5m height. This was done to prevent excluding either ground species or species that prefer feeding higher. The caterpillars were placed at least 1m apart from each other. After 24h, the caterpillars were gathered again and the number of beak marks per plot was counted. As not only birds were able to bite the dummy caterpillars, also ant and rodent bites were scored (Figure 3).

Figure 2. A caterpillar was placed on a leave at 1.5m height with iron wire. The pink ribbon indicates the edge of the plot.

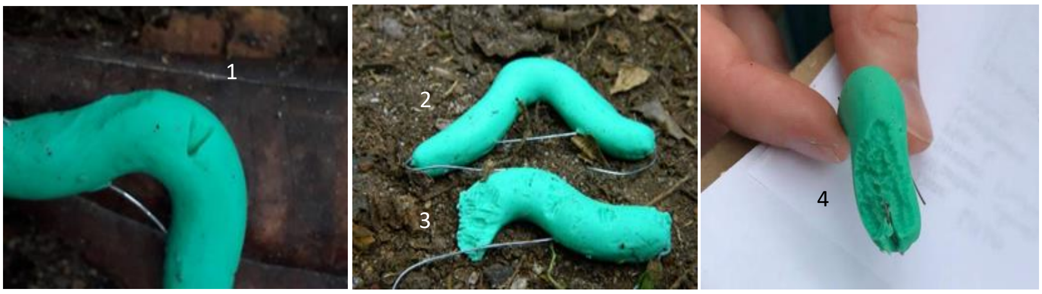


Figure 3. The possible outcomes: (1) bird bite, (2) not bitten, (3) ant bites, (4) rodent bites.

To make a correct comparison of the number of caterpillars bitten by birds between the reforested, natural forest and pasture plots within a stratum, a GLMM has been conducted. There is a binary response, as a caterpillar can be either bitten (1) or not bitten (0) by a bird. This outcome can be dependent of the habitat (reforested, natural forest or pasture), the height (ground level or 1.5m) and the diversity of predominantly insectivorous birds present in the plot, which has been extracted from the recording data. Habitat, height and diversity of insectivores are thus the three fixed factors investigated in the analysis. Random effects are the individual caterpillar ID (ranging from 1 to 20) within each plot, and each plot (ranging from 1 to 6) nested within a certain habitat.

The number of beak marks in a certain plot could have been dependent on a lot of factors. Therefore, a multiple correlation analysis in Rstudio was conducted to investigate which factors may have had an influence on the outcome. Factors included in the correlation analysis are the diversity of insectivores, tree density, weather (rain, temperature and insolation), distance to the closest forest, distance to the closest pasture and the presence of ants. The number of insectivores present in the plot was based on the recording data. Information about the tree density was extracted from datasets obtained by thesis students from the faculty of bioengineering in Ghent, which have been doing vegetation studies for several years in the cloud forests. Additional information was given by researcher Eva Tamargo, who has been investigating the growth and survival of seedlings and mature trees in the reforested areas in Northern Ecuador. Weather data for each plot were obtained from a NASA research project (POWERProjectTeam 2020), based on the coordinates measured by GPS. The distances from the plot to the closest forest and pasture were measured in QGIS. The presence of ants was based on the number of caterpillars that showed ant bites in the plot.

4. Results

4.1 Point counts

A total of 217 bird species were recorded over all the different plots during the study period. The entire bird species list, with specification of the functional and sensitivity group, is added in the appendix.

4.1.1 Bird species diversity

The alpha diversity was compared between each of the habitats within a stratum using a GLMM. In stratum 1 (Figure 4.a), the alpha diversity in the pasture was significantly higher than in the natural forest Puyucunapi and in the reforested area Santa Rosa. There was no significant difference in the number of species recorded in the natural forest compared to the reforested area (mean alpha diversity±SE: Santa Rosa (R)=7.03±1.12, pasture Santa Rosa (P)=13.74±1.09, Puyucunapi (N)=9.21±1.11; χ^2_2=23.824, p<0.0001; Tukey comparisons: R-P, *p*<0.0001; R-N, *p*=0.19; P-N, *p*=0.01). In the second stratum (Figure 4.b), there was a significant higher alpha diversity in each of the two reforested areas (La Yumbada and Piedras Negras) than in the natural forest Milpe, but no difference between the reforested areas mutually. There was a significant higher alpha diversity in the pasture compared to the natural forest Milpe (mean alpha diversity±SE: La Yumbada (R1)=12.94±1.10, Piedras Negras (R2)=13.46±1.09, pasture Milpe (P)=16.78±1.09, Milpe (N)=7.32±1.12; χ^2_3=35.19, p<0.0001; Tukey comparisons: R1-R2, *p*=0.99; R1-P, *p*=0.13; R1-N, *p*=0.0006; R2-P, *p*=0.25; R2-N, *p*=0.0002; P-N, *p*<0.0001). In stratum 3 (Figure 4.c), there was a significant higher alpha diversity in the pasture compared to the reforested area Suamox. There was also a significant higher alpha diversity in the natural forest Silanche than in the reforested area Suamox (mean alpha diversity±SE: Suamox (R)=9.58±1.10, pasture Silanche (P)=17.29±1.07, Silanche (N)=13.74±1.08; χ^2_2=25.573, p<0.0001; Tukey comparisons: R-P, *p*<0.0001; R-N, *p*=0.008; P-N, *p*=0.08). In each of the three strata, the alpha diversity was thus remarkably highest in the pastures.

The gamma diversity shows a similar result, with the highest total number of species in the pasture within each of the three strata (Figure 5). In stratum 2, the lowest number of species was found in the natural forest Milpe. In both reforested areas, La Yumbada and Piedras Negras, the amount of recorded species was higher. Piedras Negras had a considerably higher number of species compared to La Yumbada. In the first and third stratum, the number of species heard in the natural forest was higher than in the reforested area. The total number of observations follows the same trend as the gamma diversity, but there was clearly a high proportion of double counts in each of the pastures. In the pasture of the first stratum, 73% of the species observed, have been recorded in at least two different plots. This was remarkably higher than in the reforested area Santa Rosa (64%) and the natural forest Puyucunapi (65%). In the second stratum, this proportion was higher in the reforested area La Yumbada (72%) compared to the pasture (67%), the reforested area Piedras Negras (66%) and the natural forest in Milpe (65%). The proportion of double counts in the pasture of stratum 3 was 66%, which is higher than in the reforested area Suamox (60%) and the natural forest Silanche (62%).

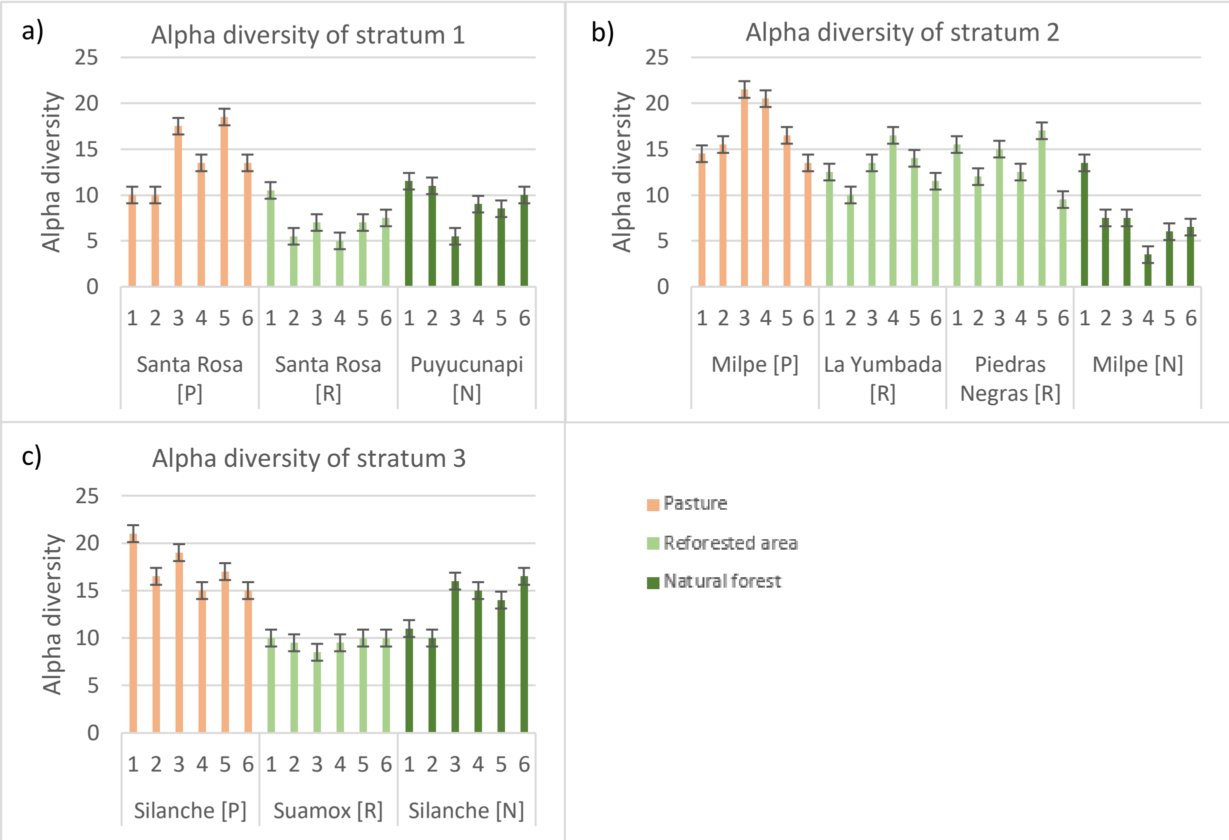


Figure 4. Mean alpha diversity per plot and its standard error, for each habitat within a) stratum 1, b) stratum 2 and c) stratum 3. The orange bars represent the alpha diversity in pasture plots, the light green in reforested area plots and the dark green in natural forest plots. Next to the name of each area, an abbreviation of the situation is given (P: pasture, R: reforested, N: natural forest).

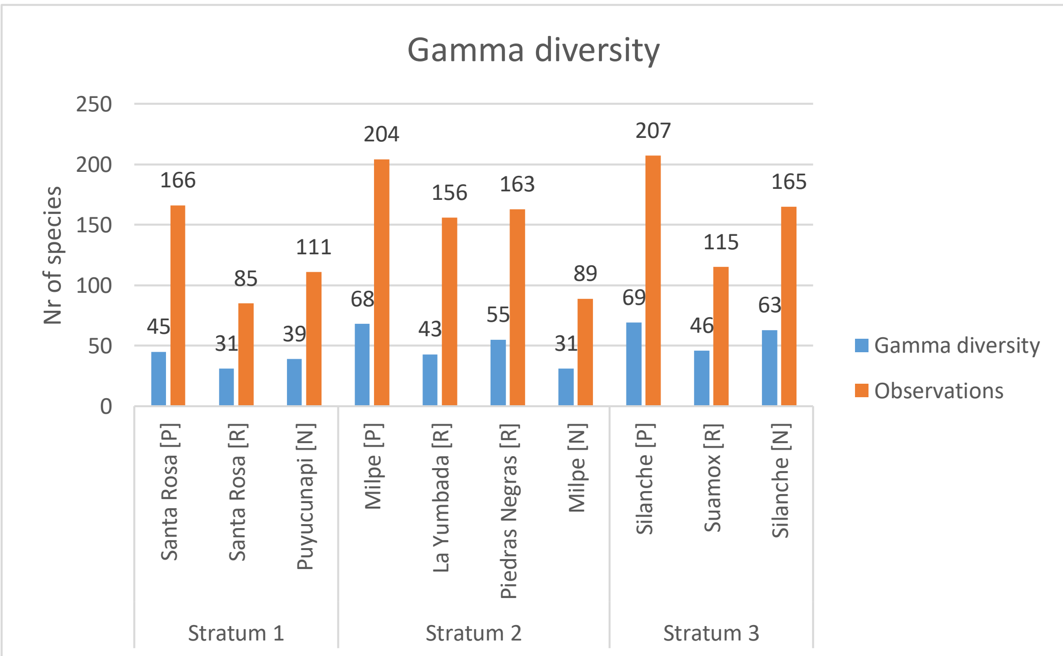


Figure 5. The gamma diversity and number of bird observations for each location (R: reforested, P: pasture and N: natural forest). The gamma diversity can be seen as the total number of species observed in a certain area. The number of observations includes species that were counted more than once in different plots within a location.

In Table 3, the beta diversities for each of the three strata according to the Jaccard similarity index is visualised. The darker the colour in the grid, the lower the beta diversity, thus the more similar the species composition between the corresponding areas.

In the first stratum, the species composition was almost equally similar between the reforested area Santa Rosa and both the pasture and the natural forest Puyucunapi. Between the pasture and natural forest in stratum 1, there was a clearly lower similarity. In the second stratum, there was a high differentiation among the reforested area La Yumbada and both the pasture and natural forest in Milpe. The Jaccard similarity index was clearly higher when comparing both reforested areas. The reforested area Piedras Negras was more similar in its species composition to the pasture than to the natural forest in Milpe. The species composition was quite different between the pasture and natural forest in Milpe. In the third stratum, the highest similarity has been found between the reforested area Suamox and the natural forest Silanche. There was a high Jaccard similarity index as well when comparing this reforested area with the pasture in Silanche. The species occurring in this pasture are still quite similar as in the natural forest Silanche.

		Santa Rosa (P)	Puyucunapi (N)
Stratum 1	Santa Rosa (R)	0.31 (18|40)	0.32 (17|36)
	Santa Rosa (P)		0.25 (17|50)

		Piedras Negras (R)	Milpe (P)	Milpe (N)
Stratum 2	La Yumbada (R)	0.31 (23|52)	0.12 (12|87)	0.14 (9|56)
	Piedras Negras (R)		0.27 (26|71)	0.19 (14|58)
	Milpe (P)			0.24 (19|61)

		Silanche (P)	Silanche (N)
Stratum 3	Suamox (R)	0.30 (27|62)	0.37 (29|51)
	Silanche (P)		0.28 (29|75)

Table 3. Beta diversity values based on the Jaccard similarity index. The closer the value to 1, the darker the grid, and the more similar the species composition between the two habitats. The habitat type of each area is marked between brackets, with R for reforested area, P for pasture and N for natural forest. Next to the Jaccard similarity index, between the brackets, the first number gives the amount of species that both habitats had in common and the second number is the amount of dissimilar species.

4.1.2 Forest and indicator species

A total of 91 forest and 56 indicator species out of the 217 bird species were selected. Using a GLMM, the number of forest and indicator species recorded in each of the three habitats (reforested area, natural forest and pasture) has been compared within each stratum. In the first stratum, no significant differences in the number of forest species between the three habitats were found (mean number of forest species±SE: Santa Rosa (R)=4.57±1.14, pasture Santa Rosa (P)=6.69±1.12, Puyucunapi (N)=5.10±1.14; χ^2_2=5.166, p=0.08; Tukey comparisons: R-P, p=0.08; R-N, p=0.84; P-N, p=0.25). The number of indicator species heard in the pasture was significantly higher than in both the natural forest Puyucunapi and the reforested area Santa Rosa (mean number of indicator species±SD: Santa Rosa (R)=2.50±1.20, pasture Santa Rosa (P)=4.58±1.14, Puyucunapi (N)=2.67±1.19; χ^2_2=9.628, p=0.008; Tukey comparisons: R-P, p=0.02; R-N, p=0.97; P-N, p=0.04). In stratum 2, the reforested areas La Yumbada and Piedras Negras had a significant higher number of forest species compared to the natural

forest in Milpe. La Yumbada also had a significant higher number of forest species than the pasture (mean number of forest species±SE: La Yumbada (R1)=8.00±1.11, Piedras Negras (R2)=6.69±1.12, pasture Milpe (P)=4.44±1.15, Milpe (N)=3.94±1.16; χ^2_3=22.358, p<0.0001; Tukey comparisons: R1-R2, *p*=0.62; R1-P, *p*=0.003; R1-N, *p*=0.0004; R2-P, *p*=0.09; R2-N, *p*=0.02; P-N, *p*=0.93). There was a significant higher number of indicator species in the reforested area La Yumbada compared to the natural forest in Milpe (mean number of indicator species±SE: La Yumbada (R1)=5.26±1.13, Piedras Negras (R2)=3.32±1.17, pasture Milpe (P)=3.60±1.16, Milpe (N)=2.92±1.18; χ^2_3=9.805, p=0.02; Tukey comparisons: R1-R2, *p*=0.11; R1-P, *p*=0.22; R1-N, *p*=0.03; R2-P, *p*=0.99; R2-N, *p*=0.94; P-N, *p*=0.80). In stratum 3, a significant higher number of forest and indicator species was heard in the natural forest Silanche, compared to both the pasture and reforested area Suamox (mean number of forest species±SE: Suamox (R)=2.75±1.19, pasture Silanche (P)=2.08±1.22, Silanche (N)=6.59±1.12; χ^2_2=34.049, p<0.0001; Tukey comparisons: R-P, *p*=0.55; R-N, *p*=0.0001; P-N, *p*<0.0001; mean number of indicator species±SE: Suamox (R)=1.25±1.29, pasture Silanche (P)=0.92±1.35, Silanche (N)=4.25±1.15; χ^2_2=32.228, p<0.0001; Tukey comparisons: R-P, *p*=0.71; R-N, *p*=0.0001; P-N, *p*<0.0001).
To investigate to what degree the species composition of forest and indicator species resembled each other in each of the three habitats, NMDS analyses were performed. First, an NMDS was done over the three different strata, without any selection of species (Figure 6). The three strata differed significantly in their species composition, indicating the importance of comparing the different habitats per stratum (Permanova test: $F_{2,118}$=25.96, *p*=0.0005).

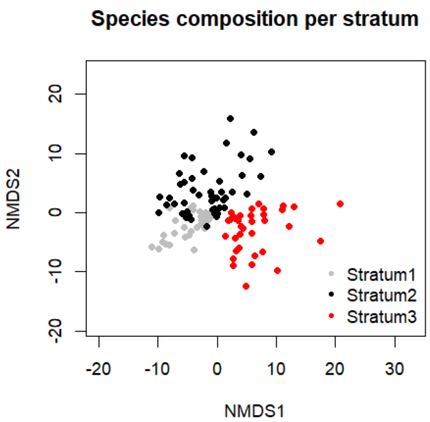


Figure 6. The result of an NMDS analysis for all species per stratum. The three strata differ significantly in their species composition.

In stratum 1, there was a significant difference in species composition between the three habitats when considering all species (All species S1 - Permanova test: $F_{1,34}$=3.39, *p*=0.01). After the selection of forest and indicator species, these differences stayed significant (Forest species S1 - Permanova test: $F_{1,34}$=3.30, *p*=0.008, pairwise comparisons: Figure 7.a; Indicator species S1 - Permanova test: $F_{1,33}$=2.70, *p*=0.03, pairwise comparisons: Figure 7.b). In stratum 2, without any selection, there was a significant difference in the species composition between the reforested area La Yumbada, the reforested area Piedras Negras, the pasture and the natural forest in Milpe (All species S2 - Permanova test: $F_{1,46}$=9.40, *p*=0.0005). These differences were still significant after selecting forest species (Forest species S2 - Permanova test: $F_{1,46}$=15.19, *p*=0.0005, pairwise comparisons: Figure 7.c). The species composition of indicator species was significantly different between all the habitats, except between the reforested area Piedras Negras and the pasture in Milpe (Indicator species S2 - Permanova test: $F_{1,46}$=18.27, *p*=0.0005, pairwise comparisons: Figure 7.d). In stratum 3, the species composition was different between the reforested area Suamox, the pasture and the natural forest Silanche, when taking into account all species and only forest species (All species S3 - Permanova test: $F_{1,34}$=2.57, *p*=0.008; Forest species S3 - Permanova test: $F_{1,33}$=4.15, *p*=0.0005, pairwise comparisons: Figure 7.e). When selecting for indicator species, the difference in species composition between the reforested area Suamox and the pasture was not significant (Indicator species S3 - Permanova test: $F_{1,29}$=3.90, *p*=0.002, pairwise comparisons: Figure 7.f).

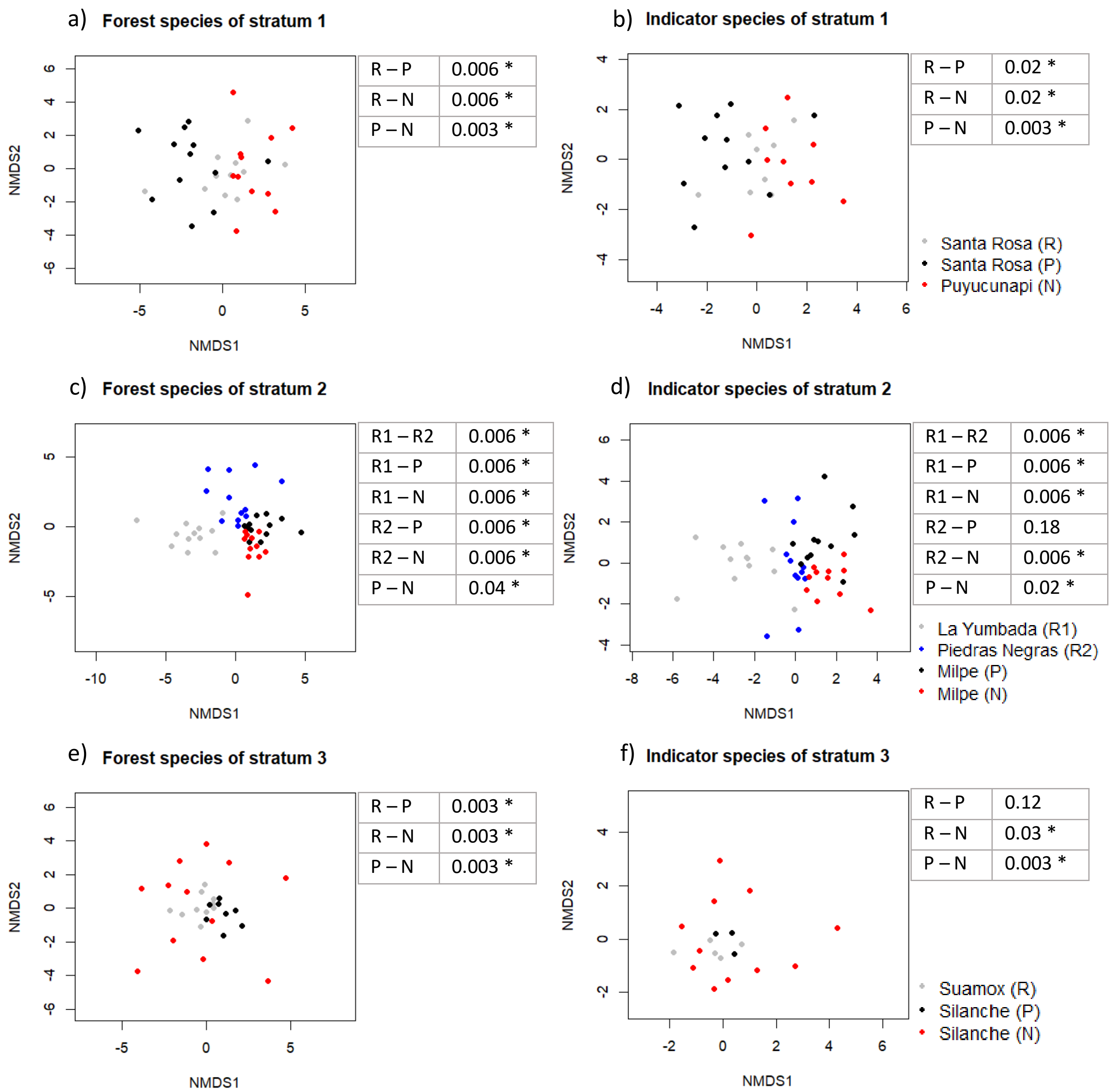


Figure 7. The result of the NMDS after selection of forest and indicator species for each stratum: a) forest species of stratum 1, b) indicator species of stratum 1, c) forest species of stratum 2, d) indicator species of stratum 2, e) forest species of stratum 3, f) indicator species of stratum 3. The p-value for each pairwise comparison between the reforested area (R), pasture (P) and natural forest (N) is given in the tables.

4.1.3 Ecosystem functioning

A total of 7 functional groups were determined based on the bird's predominant diet. In figure 8, the number of species (out of the total of 217 species) belonging to each of the functional groups is visualised.

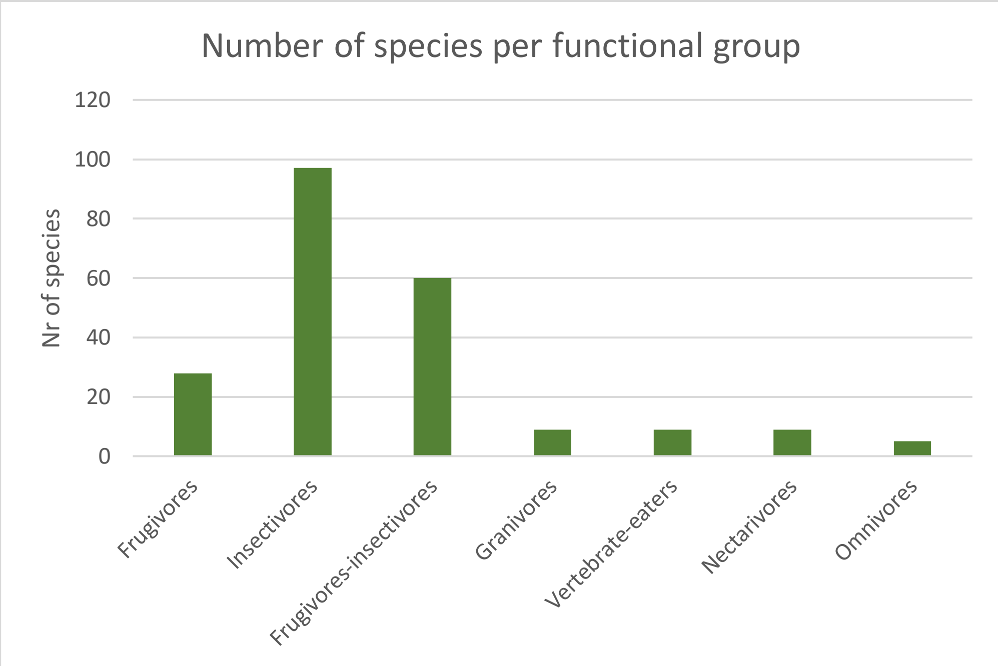


Figure 8. The number of species observed that belong to each of the functional groups: predominant frugivores, predominant insectivores, frugivores-insectivores, predominant granivores, predominant vertebrate-eaters, predominant nectarivores and omnivores.

For each of the three strata, an analysis has been performed on each of the seven functional groups. However, in some cases too few observations of a certain functional group made it impossible to perform valuable analyses. In the following section, the results for each functional group are given for the three strata separately.

Stratum 1

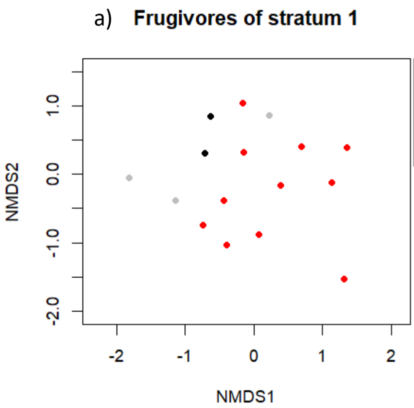
In stratum 1, the number of **predominantly frugivorous species** was significantly higher in the natural forest Puyucunapi compared to the pasture (mean number of frugivores±SE: Santa Rosa (R)= 0.75±1.40, pasture Santa Rosa (P)=0.42±1.56, Puyucunapi (N)=1.67±1.25; χ^2_2=9.49, p=0.009; Tukey comparisons: R-P, *p*=0.54; R-N, *p*=0.11; P-N, *p*=0.02). There was no significant difference in the species composition of predominant frugivores between the three habitats (Frugivores S1 - Permanova test: $F_{1,21}$=2.73, *p*=0.05, pairwise comparisons: Figure 9.a). The number of **predominantly insectivorous species** was significantly higher in the pasture than in both the natural forest Puyucunapi and the reforested area Santa Rosa (mean number of insectivores±SE: Santa Rosa (R)= 3.94±1.16, pasture Santa Rosa (P)=6.69±1.12, Puyucunapi (N)=3.42±1.17; χ^2_2=15.27, p=0.0005; Tukey comparisons: R-P, *p*=0.01; R-N, *p*=0.80; P-N, *p*=0.002). Concerning the predominant insectivores, there was a significant difference in the species composition between each of the three habitats (Insectivores S1 - Permanova test: $F_{1,34}$=2.72, *p*=0.03, pairwise comparisons: Figure 9.b). The number of **frugivorous-insectivorous species** was significantly higher in the pasture than in the reforested area Santa Rosa (mean number of frugivores-insectivores±SE: Santa Rosa (R)=1.83±1.24, pasture Santa Rosa (P)=4.92±1.14, Puyucunapi (N)=3.00±1.18; χ^2_2=16.87, p=0.0002; Tukey comparisons: R-P, *p*=0.0002; R-N, *p*=0.16; P-N, *p*=0.05). When looking at the species composition of frugivores-insectivores, there was a significant difference between the three habitats (Frugivores-insectivores S1 - Permanova test: $F_{1,33}$=3.25, *p*=0.02, pairwise comparisons: Figure 9.c). Concerning the **predominantly granivorous birds** and the **vertebrate-eaters** too little data was available to perform valuable analyses. No significant differences were found between the three habitats in their number of **predominantly nectarivorous species** (mean number of nectarivores±SE: Santa Rosa (R)=0.08±2.72, pasture Santa Rosa (P)=0.67±1.42, Puyucunapi (N)=0.83±1.37; χ^2_2=4.82, p=0.09; Tukey comparisons: R-P, *p*=0.12; R-N, *p*=0.07; P-N, *p*=0.89). There was a significant difference in the species composition of predominant nectarivores between the pasture and natural forest Puyucunapi (Nectarivores S1 - Permanova test: $F_{1,13}$ =9.86, *p*=0.002, pairwise comparisons: Figure 9.d). Concerning the **omnivores** as well, it was impossible to conduct valuable analyses because of too little observations.

Stratum 2

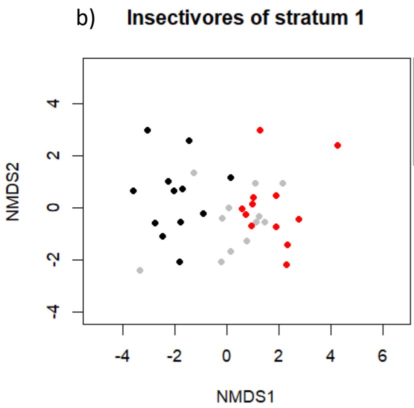
In stratum 2, there was a significant higher number of **predominantly frugivorous species** in the reforested area Piedras Negras compared to the reforested area La Yumbada and the natural forest in Milpe (mean number of frugivores±SE: La Yumbada (R1)=0.64±1.47, Piedras Negras (R2)=2.49±1.24, pasture Milpe (P)=1.68±1.29, Milpe (N)=0.87±1.40; χ^2_3=14.76, p=0.002; Tukey comparisons: R1-R2, *p*=0.006; R1-P, *p*=0.12; R1-N, *p*=0.91; R2-P, *p*=0.58; R2-N, *p*=0.03; P-N, *p*=0.35). The species composition of predominant frugivores differed significantly between the reforested area La Yumbada and the pasture (Frugivores S2 - Permanova test: $F_{1,28}$=7.18, *p*=0.001, pairwise comparisons: Figure 10.a). When looking at the **predominant insectivores**, the number of species was significantly lower in the natural forest in Milpe compared to the pasture and the reforested area Piedras Negras (mean number of insectivores±SE: La Yumbada (R1)=5.42±1.13, Piedras Negras (R2)=6.69±1.12, pasture Milpe (P)=7.61±1.11, Milpe (N)=3.60±1.16; χ^2_3=17.98, p=0.0004; Tukey comparisons: R1-R2, *p*=0.60; R1-P, *p*=0.16; R1-N, *p*=0.15; R2-P, *p*=0.84; R2-N, *p*=0.006; P-N, *p*=0.0003). For the predominant insectivores, all the habitats differed significantly in their species composition (Insectivores S2 - Permanova test: $F_{1,46}$=8.39, *p*=0.0005, pairwise comparisons: Figure 10.b). There was a significant lower number of **frugivorous-insectivorous species** in the natural forest in Milpe, compared to the reforested area La Yumbada, the reforested area Piedras Negras and the pasture (mean number of frugivores-insectivores±SE: La Yumbada (R1)=5.88±1.14, Piedras Negras (R2)=3.97±1.17, pasture Milpe (P)=5.21±1.15, Milpe (N)=1.99±1.23; χ^2_3=21.43, p<0.0001; Tukey comparisons: R1-R2, *p*=0.20; R1-P, *p*=0.92; R1-N, *p*=0.0001; R2-P, *p*=0.54; R2-N, *p*=0.04; P-N, *p*=0.0006). All the habitats differed significantly in their species composition of frugivores-insectivores (Frugivores-insectivores S2 - Permanova test: $F_{1,45}$=15.60, *p*=0.0005, pairwise comparisons: Figure 10.c). Concerning **predominant granivores** and **vertebrate-eaters**, it was impossible to conduct valuable analyses because of too little observations. No significant differences in the number of **predominant nectarivores** were found between the three habitats (mean number of nectarivores±SE: La Yumbada (R1)=0.58±1.46, Piedras Negras (R2)=0.08±2.72, pasture Milpe (P)=0.75±1.40, Milpe (N)=0.50±1.50; χ^2_3=4.48, p=0.21; Tukey comparisons: R1-R2, *p*=0.26; R1-P, *p*=0.96; R1-N, *p*=0.99; R2-P, *p*=0.16; R2-N, *p*=0.35; P-N, *p*=0.87). The species composition of these predominant nectarivores was significantly different between the reforested area La Yumbada and both the pasture and natural forest in Milpe, as well as between the pasture and the natural forest in Milpe (Nectarivores S2 - Permanova test: $F_{1,18}$=8.02, *p*=0.0005, pairwise comparisons: Figure 10.d). There were too few observations of **omnivores** in the second stratum, so no valuable analyses could be made.

Stratum 3

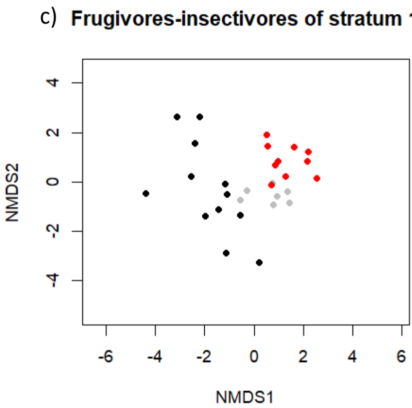
In stratum 3, the number of **predominantly frugivorous species** was not significantly different between the three habitats (mean number of frugivores±SE: Suamox (R)=1.33±1.28, pasture Silanche (P)=2.58±1.20, Silanche (N)=2.75±1.19; χ^2_2=6.22, p=0.04; Tukey comparisons: R-P, *p*=0.08; R-N, *p*=0.05; P-N, *p*=0.97). A significant difference in the species composition of predominant frugivores was found between the natural forest Silanche and both the pasture and reforested area Suamox (Frugivores S3 - Permanova test: $F_{1,31}$=4.03, *p*=0.005, pairwise comparisons: Figure 11.a). The pasture in Silanche contained a significantly higher number of **predominantly insectivorous species** than the reforested area Suamox (mean number of insectivores±SE: Suamox (R)= 3.42±1.17, pasture Silanche (P)=7.03±1.12, Silanche (N)=4.90±1.14; χ^2_2=14.73, p=0.0006; Tukey comparisons: R-P, *p*=0.0005; R-N, *p*=0.17; P-N, *p*=0.09). There was a significant difference in the species composition of predominant insectivores between each of the three habitats (Insectivores S3 - Permanova test: $F_{1,34}$=1.74, *p*=0.12, pairwise comparisons: Figure 11.b). The number of **frugivorous-insectivorous species** was not significantly different between the three habitats (mean number of frugivores-insectivores±SE: Suamox (R)=4.44±1.15, pasture Silanche (P)=6.36±1.12, Silanche (N)=4.26±1.15; χ^2_2=6.36, p=0.04; Tukey comparisons: R-P, *p*=0.11; R-N, *p*=0.98; P-N, *p*=0.07). All the three habitats were significantly different in their species composition of frugivores-insectivores (Frugivores-insectivores S3 - Permanova test: $F_{1,34}$=3.65, *p*=0.001, pairwise comparisons: Figure 11.c). There was no significant difference in the number of **predominantly granivorous species** between the three habitats (mean number of granivores±SE: Suamox (R)=0.14±2.16, pasture Silanche (P)=0.72±1.56, Silanche (N)=0.43±1.69; χ^2_2=4.03, p=0.13; Tukey comparisons: R-P, *p*=0.12; R-N, *p*=0.41; P-N, *p*=0.64). In the species composition of predominant granivores as well no significant differences were found (Granivores S3 - Permanova test: $F_{1,10}$=1.31, *p*=0.31, pairwise comparisons: Figure 11.d). The number of **predominant vertebrate-eaters** was not significantly different between the three habitats (mean number of vertebrate-eaters±SE: Suamox (R)=0.08±2.72, pasture Silanche (P)=0.25±1.78, Silanche (N)=0.75±1.40; χ^2_2=6.13, p=0.05; Tukey comparisons: R-P, *p*=0.61; R-N, *p*=0.09; P-N, *p*=0.23). There was as well no significant difference in the species composition between the habitats (Vertebrate-eaters S3 - Permanova test: $F_{1,9}$=0.15, *p*=0.95, pairwise comparisons: Figure 11.e). No significant differences were found in the number and the species composition of **predominant nectarivores** between the three habitats (mean number of nectarivores±SE: Suamox (R)=0.17±2.03, pasture Silanche (P)=0.17±2.03, Silanche (N)=0.42±1.56; χ^2_2=1.87, p=0.39; Tukey comparisons: R-P, *p*=1.00; R-N, *p*=0.52; P-N, *p*=0.52; Nectarivores S3 - Permanova test: $F_{1,7}$=2.13, *p*=0.15, pairwise comparisons: Figure 11.f). There were too few observations of **omnivores**, so no valuable comparisons could be made for this functional group.



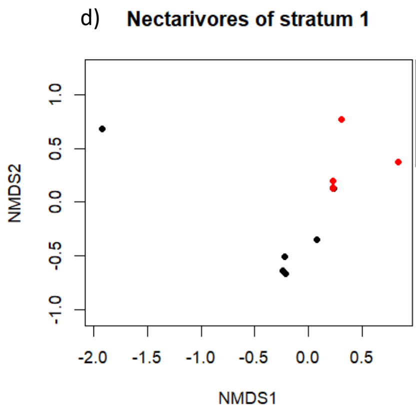
R – P	0.14
R – N	0.39
P – N	0.23



R – P	0.003*
R – N	0.03*
P – N	0.003*



R – P	0.003*
R – N	0.003*
P – N	0.003*



R – P	1.00
R – N	0.36
P – N	0.01*

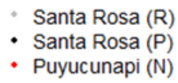
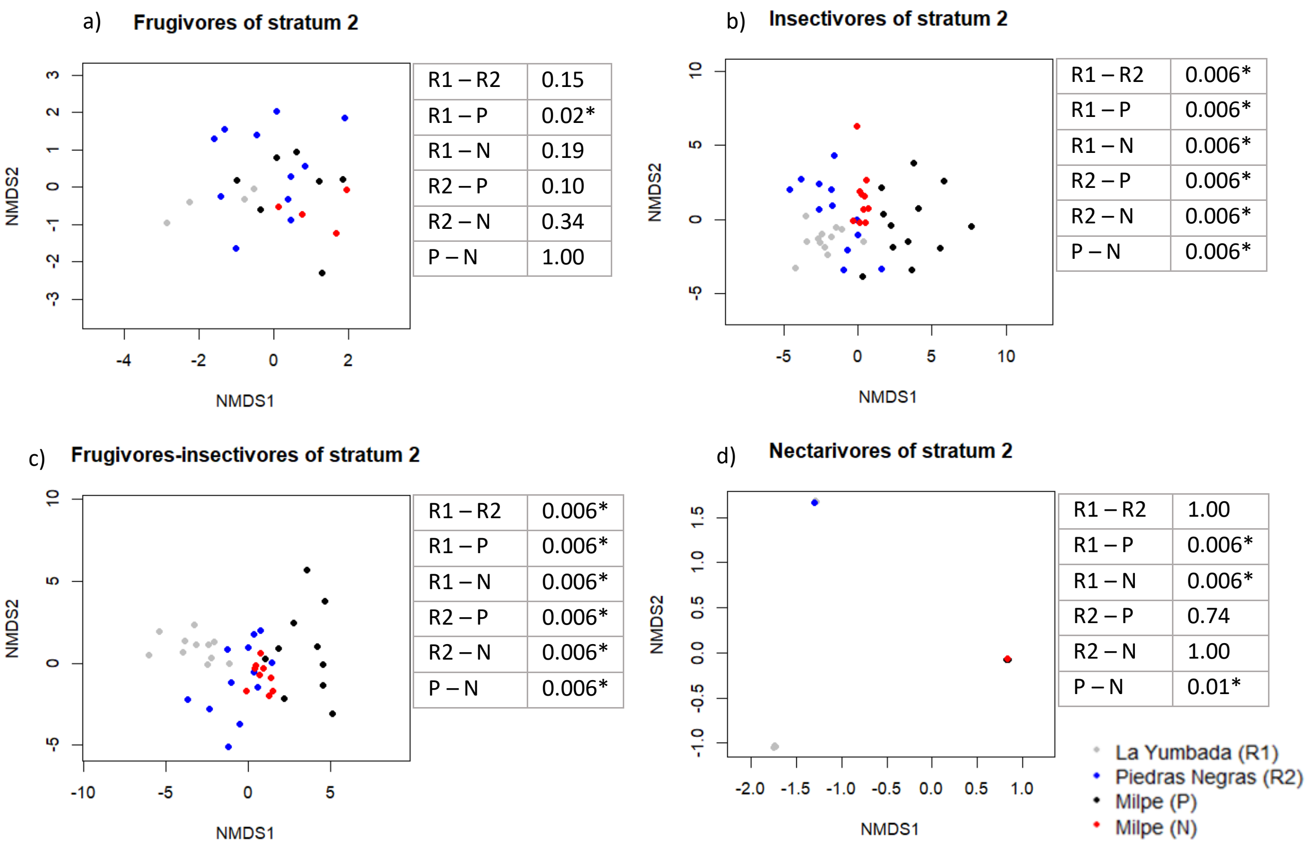


Figure 9. Results of NMDS analyses for 4 different functional groups of stratum 1 i.e. a) predominant frugivores, b) predominant insectivores, c) frugivores-insectivores and d) predominant nectarivores. Each time the species composition is compared between the three habitats: reforested area Santa Rosa (R), pasture (P) and natural forest Puyucunapi (N).



a)

R1 – R2	0.15
R1 – P	0.02*
R1 – N	0.19
R2 – P	0.10
R2 – N	0.34
P – N	1.00

b)

R1 – R2	0.006*
R1 – P	0.006*
R1 – N	0.006*
R2 – P	0.006*
R2 – N	0.006*
P – N	0.006*

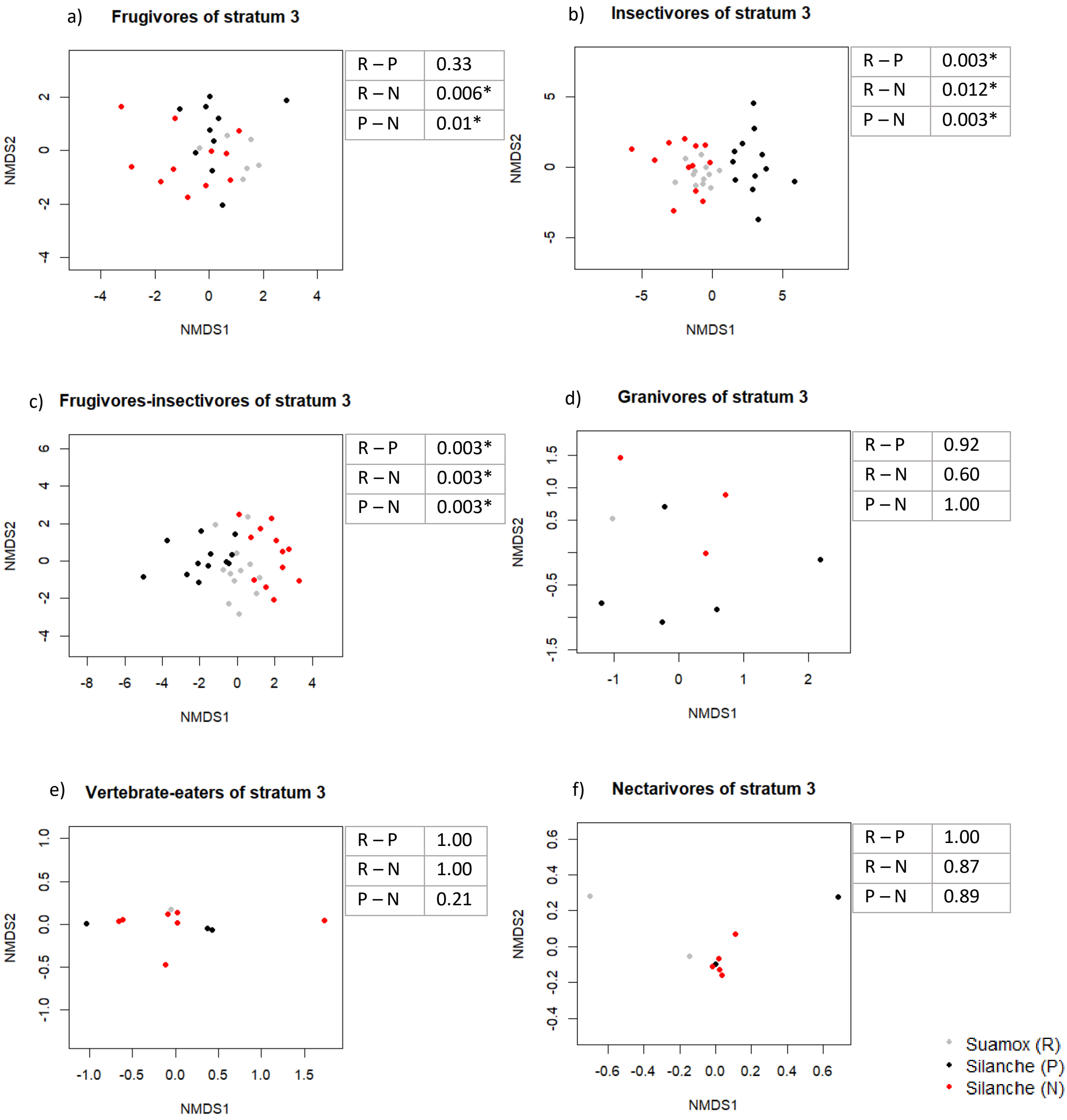
c)

R1 – R2	0.006*
R1 – P	0.006*
R1 – N	0.006*
R2 – P	0.006*
R2 – N	0.006*
P – N	0.006*

d)

R1 – R2	1.00
R1 – P	0.006*
R1 – N	0.006*
R2 – P	0.74
R2 – N	1.00
P – N	0.01*

Figure 10. Results of NMDS analyses for 4 different functional groups of stratum 2 i.e. a) predominant frugivores, b) predominant insectivores, c) frugivores-insectivores and d) predominant nectarivores. Each time the species composition is compared between the habitats: reforested areas La Yumbada (R1) and Piedras Negras (R2), pasture (P) and natural forest Milpe (N).



a)

R – P	0.33
R – N	0.006*
P – N	0.01*

b)

R – P	0.003*
R – N	0.012*
P – N	0.003*

c)

R – P	0.003*
R – N	0.003*
P – N	0.003*

d)

R – P	0.92
R – N	0.60
P – N	1.00

e)

R – P	1.00
R – N	1.00
P – N	0.21

f)

R – P	1.00
R – N	0.87
P – N	0.89

Figure 11. Results of NMDS analyses for 6 different functional groups of stratum 3 i.e. a) predominant frugivores, b) predominant insectivores, c) frugivores-insectivores, d) predominant granivores, e) predominant vertebrate-eaters and f) predominant nectarivores. Each time the species composition is compared between the three habitats: reforested area Suamox (R), pasture (P) and natural forest Silanche (N).

4.2 Caterpillar experiment

In stratum 1, there were no significant effects of the habitat (N. natural forest, P. pasture and R. reforested), height (low (L) and high (H)) and the presence of predominant insectivores on the number of caterpillars bitten by birds (mean number of bird bites±SE: N. Puyucunapi (L) = 1.00±0.63, N. Puyucunapi (H) = 0.33±0.21, P. Santa Rosa (L) = 0.00±0.00, P. Santa Rosa (H) = 0.33±0.21, R. Santa Rosa (L) = 1.33±0.56, R. Santa Rosa (H) =0.33±0.21; Figure 12.a). In the second stratum, a significant effect of the habitat was found on the number of bird bites (χ^2_2=9.10, p=0.01). There was a significantly higher amount of bird bites in the reforested area Piedras Negras at low level compared to the natural forest in Milpe at high level (p=0.02) and low level (p=0.02) and the reforested area La Yumbada at low level (p=0.03) (mean number of bird bites±SE: N. Milpe (L) = 0.50±0.34, N. Milpe (H) = 0.50±0.34, P. Milpe (L) = 0.50±0.22, P. Milpe (H) = 0.17±0.17, R. La Yumbada (L) = 0.50±0.22, R. La Yumbada (H) = 1.50±0.22, R. Piedras Negras (L) = 3.17±0.60, R. Piedras Negras (H) = 2.00±0.45; Figure 12.b) . In stratum 3, no significant differences were found in the number of bird bites due to the situation, height and predominant insectivores present (mean number of bird bites±SE: N. Silanche (L) = 0.00±0.00, N. Silanche (H) = 0.33±0.21, P. Silanche (L) = 0.00±0.00, P. Silanche (H) = 0.50±0.22, R. Suamox (L) = 0.17±0.17, R. Suamox (H) =0.17±0.17; Figure 12.c).

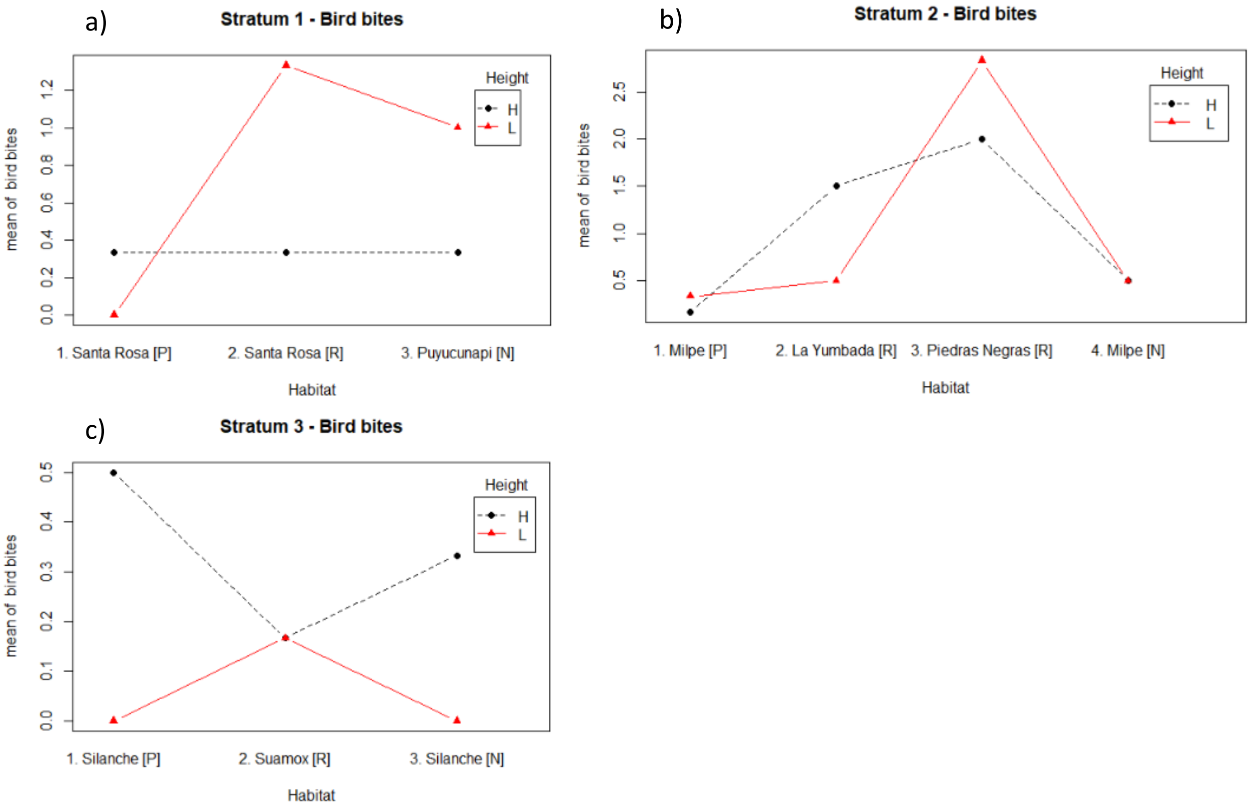


Figure 12. The average number of caterpillars bitten by birds for each of the three habitats (R: reforested, P: pasture and N: natural forest) at low (L) and high level (H), for a) stratum 1, b) stratum 2 and c) stratum 3.

The correlation analyses revealed which factors could have affected either positively or negatively the number of caterpillars bitten in each plot (Table 4). There was no strong correlation with the number of predominant insectivores present. Both the distance to the closest forest and to the closest pasture seemed to positively affect the number of bitten caterpillars. The stem density as well had a positive effect on the number of bird bites. Rain correlated positively with the number of bird bites, whereas the temperature and the insolation showed a negative correlation with the caterpillars bitten by birds. The presence of ants showed a negative correlation with the number of bird bites.

Factors	Correlation
Predominant insectivores	0.138
Distance to closest forest	0.325
Distance to closest pasture	0.374
Stem density	0.324
Rain	0.266
Temperature	-0.479
Insolation	-0.188
Ants	-0.339

Table 4. Different factors with either a positive or negative correlation with the number of bitten caterpillars. Factors included in the analysis are: the number of predominantly insectivorous species, the distance from a plot to the closest forest and to the closest pasture, the stem density, the amount of rain, the temperature, the insolation and the abundance of ants.

5. Discussion

The first objective was to examine bird biodiversity on a local and regional scale. The alpha diversity was in each of the strata higher in the pasture compared to the reforested area and the natural forest. When comparing reforested areas with natural forests, each stratum showed a different outcome. The gamma diversity followed a similar trend as the alpha diversity. According to the beta diversity, the species compositions in the reforested areas were recovering on different paces. The second objective was to examine the return of forest and indicator species. Each stratum showed a different trend in the number and composition of these valuable species along the restoration gradient. The third objective was to examine the recovery of ecosystem functioning by birds. Predominantly frugivorous species had most difficulties to recover in the reforested areas. Only in stratum 1, there was already a tendency towards restoration of this functional group. Concerning the predominant insectivores and frugivores-insectivores, the three strata showed a different trend in their restoration trajectory. The results of the caterpillar experiment showed no clear trend in the number of attacks by birds along the restoration gradient. Neither a clear correlation was found between the number of predominant insectivores and the performance of top-down control. Each reforested area in this study responded differently to restoration efforts, which points out the importance of investigating each area independently and being cautious in generalising outcomes.

5.1 Bird species diversity

In each of the strata, the alpha diversity was highest in the pastures. As this habitat was most impacted by human inference and thus the most degraded environment of all three, this seemed like an overrepresentation of bird species observed in the pastures. This could be due to spillover effects, as most pastures were adjacent to forests, leading to a mixture of grassland and forest species in the pastures (Barros et al. 2019). There were some trees scattered over the pastures, so this could as well have attracted bird species. Most species that were recorded in the pastures were predominantly insectivorous, so the overrepresentation could be linked to a high abundance of insects in the pastures. Another possibility is that for an unknown reason the recordings in the pastures were clearer compared to the forest ecosystems, but this is rather unlikely. More species were found in the pastures, but this does not necessarily mean that the species composition over all pastures was more heterogeneous and valuable. Many studies have found proof for the homogenization of fauna due to land-use change (Vellend et al. 2007, Devictor et al. 2008, Liang et al. 2019). Areas which are affected by human-induced conversion of land usually have similar bird species compositions. This means that the overall bird species richness in pastures could be lower than in forest habitats on a regional level. As in this study only one pasture was considered in each stratum, comparisons between different pastures in the same region could not be made. The gamma diversity already showed some tendency towards this homogenization, as a large proportion of the observations were similar in the different plots within a pasture. This could be subject to further research, by including several pastures, natural forests and reforested areas within a single stratum. Unlike the outcome of this study, on a larger scale the highest biodiversity could be found in qualitative forests, with more resistant and resilient communities and a higher ecosystem functioning.

The total number of observations was lower than expected in the natural forest of stratum 2 (Milpe). Some plots within this habitat were located close to a river, so bird vocalizations may have been masked by the sound of the water. The observations from this natural forest thus could not be used as optimal reference material. The beta diversity gave an indication of the similarity in species composition between different habitats within a single stratum. In each stratum, a low similarity was found between the natural forest and pasture, which is as expected because these two habitats are largely different. The higher similarity in the species composition between the reforested area and both the pasture and natural forest in stratum 1 and 3, is an indication that the reforested situation was somewhere in between the high-qualitative natural forest and the degraded pasture state. This means that the species composition in the reforested area consisted of a mixture of species preferring pastures and species preferring natural forests. In the second stratum, the two reforested areas La Yumbada and Piedras Negras were similar in their species composition. This is an indication that some species were attracted to both reforested areas, which were not present in the natural forest and pasture. The species composition of La Yumbada was almost equally different from the pasture as from the natural forest in Milpe, indicating that recovery is happening. In Piedras Negras, the recovery of the species composition was happening slower, as there was still a remarkably larger resemblance with the pasture than with the natural forest. The low similarities in species composition between the reforested areas and both the natural forest and pasture indicated that only a small proportion of the species present in the reforested areas consisted of a mixture of forest and pasture species. A large proportion thus consisted of species that seemed to prefer the semi-disturbed state found in the reforested areas (e.g. Beryl-spangled Tanager and Tricolored Brushfinch). Many of these species had a similar ecology, mostly generalists that typically occur in clearings with scattered trees, tall secondary growth and forest borders (TheCornellLabOfOrnithology 2020). Some of the species that only occurred in both reforested areas were typically species that occurred on a slightly higher altitude (e.g. Tricolored Brushfinch and Montane Woodcreeper). As the reforested plots of stratum 2 were located at least 300m higher than the other habitats, it is likely that the main differences in the species compositions can be attributed to this difference in altitude (Table 1).

5.2 Forest and indicator species

In other studies, evidence has been found that habitat loss results in a rise in generalist bird species (De Coster et al. 2015). During the first decade after the start of a reforestation project, in general there is an increase in rainforest-associated species and a decrease in open-country species (Catterall et al. 2012). However, in this study each stratum had another trend in the number and composition of forest and indicator species along the restoration gradient. In the first stratum, the pasture contained the largest amount of forest and indicator species, compared to both forest habitats. This overrepresentation of valuable species was most likely because of the close distance to forested habitats, which was below 100 meters for each pasture plot. The number of forest and indicator species was similar between the natural forest and reforested area in stratum 1, indicating that recovery of valuable species is happening. The species composition of forest and indicator species was different in each habitat of the first stratum. It makes sense that the species composition of those valuable species was different comparing the pasture and natural forest, as these habitats are different. The species found in both the pasture and natural forest, might be forest and indicator species that are able to spend some time in a pasture (e.g. Grey-breasted Wood-Wren), while others never tend to leave the close forest (e.g. Green-and-black Fruiteater). In the reforested area, a mixture of valuable species was found, consisting of forest and indicator species that were also found in the pasture and/or natural forest Puyucunapi, and only a small amount of unique ones (e.g. Speckle-faced

Parrot). As the total number of observations was quite low, these dissimilarities in species composition could be attributed to a high degree of coincidence of recording certain valuable species.

In the second stratum, both reforested areas contained a higher number of forest species compared to the pasture and natural forest, which indicates a good restoration of those bird groups. Again, the low number of these species in the natural forest Milpe could be attributed to the disruptive sound of the river. The number of indicator species was remarkably lower in the reforested area Piedras Negras than in the reforested area La Yumbada. Also, the species composition of indicator species found in the reforested area Piedras Negras was comparable to the pasture, indicating a slower recovery in Piedras Negras.

In the third stratum, the reforested area Suamox contained a similar number of forest and indicator species as the pasture, remarkably less than in the natural forest Silanche. The species composition of indicator species was similar between the reforested area Suamox and the pasture. These are clear indications that Suamox was not recovering on-track in its number and composition of valuable species. Further intervention in this area to increase their presence could be considered. It is important to note that the reforested areas were only implemented recently (since 2012-2014), and that bird composition changes over time (Bregman et al. 2016, Santos et al. 2016). It would therefore be interesting to monitor the different locations over a longer time span to evaluate whether other forest and indicator species will be able to return to reforested areas.

5.3 Ecosystem functioning

By classifying species into functional groups, the assumption was made that every species within such a group has an exact same performance and that every species can compensate for the loss of another species. Classification was based on chosen ecosystem functions, so it does not mean species redundancy with respect to other ecosystem functions. Moreover, a species can be redundant under certain environmental conditions, but not under all conditions (Falk 2006). Results obtained from a particular environment focusing on a certain ecosystem function can thus not be extrapolated to other regions and functions. From the scope of ecosystem functioning, functional classification is more informative than taxonomic classification, though functional and taxonomic diversity are closely related to one another (Falk 2006). It would be expected that most species losses have little impact on a certain ecosystem function, as many species are likely to be redundant. On the other hand, when the change in biodiversity includes a non-redundant species, the change in ecosystem functioning may be consequential (Falk 2006). An advantage of classifying species into functional groups is that the functions that deviate from the reference forest can be easily highlighted. Therefore, restoration actions may be focusing on those under-represented groups or on groups that provide key ecological functions (Rolo et al. 2017). From a conservation point of view, it does matter which species are actually performing certain ecosystem functions in recovering habitats, as it is pursued to regain sensitive species of special conservation concern. Therefore, a closer look on the species composition per functional group clarifies more how well each reforested area is recovering.

5.3.1 Predominantly frugivorous and granivorous species

Frugivores are essential for seed dispersal among forest patches, therefore improving the regeneration of previously degraded land (Bregman et al. 2016). Frugivores tend to be sensitive to degradation, mostly because of the removal of fruiting trees (Bregman et al. 2016, Rolo et al. 2017). Granivorous species on the other hand, which attribute to seed predation, appear mostly in pastures (Carlo and Morales 2016).

In the first stratum, the sensitivity of frugivores to degradation was clear. The species richness of predominant frugivores was relatively high in the natural forest but declined to almost zero in the pasture and in the reforested area Santa Rosa. The species composition was similar between all three habitats. A similar subset of predominantly frugivorous species was present in the pasture and reforested area Santa Rosa, mainly consisting of species that were not highly sensitive to degradation (e.g. Golden-headed Quetzal). Some sensitive species have been recorded in both the reforested area and the natural forest (e.g. Toucan Barbet and Plumbeous Pigeon). This indicates that the reforested area Santa Rosa yet provided habitat for the slow returning, sensitive frugivores, but the natural forest Puyucunapi harboured clearly more of those species. Also, the number of individuals belonging to those valuable species populations may be much lower in the reforested areas compared to the natural forest, which was not investigated in this study.

In the second stratum, a different trend was found, with the lowest species richness of predominant frugivores in the natural forest in Milpe. This could be due to the masking noise of the river in the neighbourhood. The reforested area Piedras Negras seemed to have a relative high number of predominant frugivores, but the absolute species richness was still low. In the reforested area La Yumbada almost no predominant frugivores were observed. The species composition of the predominant frugivores in the reforested area Piedras Negras, the pasture and natural forest of Milpe were similar, largely determined by the presence of two toucan species (Chocó Toucan and Yellow-throated Toucan) in each of these locations. These are good performers of large-scale seed dispersal and typical inhabitants of the Chocó region, but not highly sensitive to degradation (TheCornellLabOfOrnithology 2020). Therefore, in a next step towards the reference state, management actions could focus on the return of these species in the reforested area La Yumbada to improve the seed dispersal among forest patches and thus the further recovery of the previously degraded state. Once the vegetation carrying fruits and berries has recovered better, the management focus could move towards more sensitive frugivorous species. In the reforested area Piedras Negras, these toucan species were already present, and also some sensitive forest species have been observed (e.g. Blue-fronted Parrotlet). This indicates that Piedras Negras provided a valuable habitat for predominant frugivores, although the population sizes of these sensitive species may be still small. Further investigation could therefore determine the need for further intervention by monitoring the population sizes of these sensitive species.

In the third stratum, a similarly low amount of predominantly frugivorous species was found in the reforested area Suamox, the pasture and the natural forest of Silanche. The species composition of predominant frugivores was similar between the pasture and the reforested area Suamox, mostly due to the presence of non-sensitive species in both areas e.g. Bronze-winged Parrot (TheCornellLabOfOrnithology 2020). In the natural forest of Silanche, some sensitive and valuable predominant frugivores were found e.g. Dusky Pigeon (TheCornellLabOfOrnithology 2020). The reforested area Suamox needs some more improvement of the environment before these sensitive species may be coming back. Only a small number of predominantly granivorous species has been recorded in each of the three habitats, so no significant differences in the species composition could be found.

In general, a low amount of predominantly frugivorous species has been observed in all the different locations, which indicates that there is possibly a large chance effect. The different plots were not selected based on the presence of certain vegetation parameters like fruiting trees, so it could be that there was a slightly higher frugivorous species richness wherever a fruiting tree was closer. This could be the case in each of the three habitats, as some fruiting trees or bushes were still present in the pastures or at least at the edge of a nearby forest, and fruiting trees have been replanted in the reforested areas. The results thus possibly do not show an effect of degradation, but rather an effect of the proximity of fruiting trees. On the other hand, the species compositions do give clear indications of the effect of degradation, with non-sensitive species present in each of the habitats, and sensitive species mostly occurring in natural forests and in some cases already present in the reforested areas. The ecosystem function of seed dispersal was thus almost equally performed in some of the habitats, but by a different set of predominantly frugivorous species. This result confirms the mechanism of functional redundancy, which means that species can compensate for the loss of another species performing the same function.

5.3.2 Predominantly insectivorous species

In the first stratum, a higher amount of predominant insectivores was observed in the pasture, with a significant different species composition compared to the natural forest Puyucunapi and the reforested area Santa Rosa. This was largely due to the high abundance in the pasture of species avoiding forest interior, like Black-crested warbler and Squirrel cuckoo, although some sensitive species have been found in pastures as well e.g. Capped Conebill (TheCornellLabOfOrnithology 2020). The species compositions of predominant insectivores found in the reforested area Santa Rosa and the natural forest Puyucunapi were slightly more similar, largely determined by species that are not sensitive to degradation occurring in both habitats e.g. Three-striped Warbler and Yellow-breasted Antpitta. Although, these two habitats were still significantly different in their species composition, as only a few sensitive species that occurred in the natural forest had as well been recorded in the reforested area (Grey-breasted Woodwren and White-tailed Tyrannulet), indicating that still some management actions should be taken to increase the habitat quality of this reforested area.

In stratum 2, the low number of predominant insectivores in the natural forest Milpe could be attributed to the river noise. An almost equal number of predominant insectivores was recorded in the reforested areas La Yumbada and Piedras Negras and in the pasture in Milpe, indicating that there was an equal performance of top-down control. The species compositions of predominant insectivores observed in all four areas were significantly different from each other. This implicates again redundancy, as the same performance of top-down control in the pasture and both reforested areas was fulfilled by different species. The different species composition in the two reforested areas of stratum 2 could be attributed to the difference in their restoration trajectory. More sensitive predominantly insectivorous species were recorded in the reforested area La Yumbada (a total of 8 species e.g. Flavescent Flycatcher), compared to the reforested area Piedras Negras (a total of 6 species e.g. Red-faced Spinetail). Moreover, most sensitive species that occurred in Piedras Negras were also recorded in at least one of the pasture plots (5 out of 6 species). There was thus an equal performance of top-down control in both reforested areas, but the presence of some unique valuable insectivorous species indicates a better restoration trajectory in La Yumbada compared to Piedras Negras.

In the third stratum, no significant higher number of predominantly insectivorous species was found in the natural forest Silanche compared to the reforested area Suamox. This indicates that the performance of top-down control was similar in both habitats. The species composition of predominantly insectivorous birds was significantly different in each of the three habitats, going from many non-sensitive species in the pasture (e.g. Tropical Parula), over a mixture of a couple of sensitive and mostly non-sensitive species in the reforested area and eventually a relative high prevalence of sensitive species in the natural forest (e.g. Tawny-faced Gnatwren). Further investment should be done to increase the habitat quality of the reforested area Suamox to regain more sensitive predominantly insectivores.

The high number of insectivores in the pastures of each stratum may be due to a high abundance of insects. No research has been done on the insect biodiversity in the different areas, but it would be an interesting complement to investigate the biotic interactions between insectivorous birds and their prey along a restoration gradient.

5.3.3 Frugivores-insectivores

Species with equivalently insects and fruits in their diet contribute to the performance of both top-down control and seed dispersal. Only a small proportion of these species are sensitive to degradation, as they can easily shift to another food source when one has been lost. The high occurrence of this functional group in pastures may be attributed to the supply of different food sources, as a high abundance of insects and some fruiting trees were likely to be present. In the second stratum, the number of frugivores-insectivores was equally high in the two reforested areas La Yumbada and Piedras Negras compared to the pasture, indicating that in these habitats as well a mixture of both food sources was present that attracted this functional group. In all the strata, the species composition of the frugivores-insectivores was significantly different in each of the three habitats. This could not be attributed to the presence or absence of sensitive species, as these occurred in each habitat. Some species, that actually prefer high qualitative forest, may tend to temporarily search for food in less qualitative habitats that still provide enough food sources. Therefore, the differences in species composition may be largely attributed to coincidence of observing certain species during the point counts, as not recording a certain species does not necessarily mean the absence of that species in the habitat. As this functional group is likely to respond easily to reforestation actions, further management should primarily be focused on the return of more sensitive groups and to a lower degree on this one.

5.3.4 Predominantly nectarivorous species

Nectarivorous birds, mostly consisting of small hummingbirds, are important in the pollination of flowering plants. The conservation of native vegetation cover plays a key role in the maintenance of hummingbird pollination services in tropical forest ecosystems (Tinoco et al. 2018). However, most nectarivorous species can survive for some time in gardens and pastures if enough flowers are present. Therefore, in each stratum, there was no significant difference in the number of predominantly nectarivorous species recorded in the different habitats. In the first stratum, a significant difference was found in the species composition between the pasture and the natural forest Puyucunapi. This was mainly due to the presence of the Lesser Violetear in almost every plot of the natural forest, and in only one pasture plot. As in the reforested area Santa Rosa only one species has been observed (i.e. Speckled Hummingbird), comparisons in the species compositions with this habitat were not valuable. In the second stratum, the species composition of predominant nectarivores was significantly different in the reforested area La Yumbada compared to both the pasture and natural forest in Milpe, as well as between the pasture and natural forest in Milpe. These differences were mainly determined by the presence or absence of only two predominantly nectarivorous species i.e. White-whiskered Hermit and Bananaquit. The Bananaquit is known for its good ability to adjust to human environments, therefore largely present in the pasture in Milpe, and absent in forest plots. The White-whiskered Hermit on the other hand occurs mainly in natural forest ecosystems, and to a lesser degree in degraded habitats. This nectarivore was not recorded in both reforested areas of stratum 2, most likely because of their higher altitude, as this species mostly occurs below 1200m above sea level (TheCornellLabOfOrnithology 2020). In stratum 3, no significant differences in the species composition between the different habitats could be found, as only 3 predominantly nectarivorous species were recorded.

The calls of hummingbirds are mostly quite soft, so only species that were close enough to the recorder could be identified based on the recordings. There is thus a high probability that many more hummingbirds were present in a certain habitat, which could not be recorded.

5.4 Caterpillar experiment

To investigate whether top-down control by birds on insects differs between the habitats, an experiment with dummy caterpillars was conducted. The number of caterpillars bitten per plot was a useful proxy for the performance of this ecosystem function.

In stratum 1 and 3, the performance of top-down control by birds was not significantly different between the three habitats, either at low or at high level, and was not affected significantly by the presence of insectivores. The total number of predominant insectivores was highest in the pastures of both strata, but this does not seem to influence the number of caterpillars bitten. In the second stratum, the performance of top-down control was highest in the reforested area Piedras Negras. Again, there was no significant effect of the presence of insectivores on the performance of the top-down control.

Previous studies have found that the caterpillar attack rates increase along the restoration gradient, in the following order: pasture < reforested area < natural forest. This outcome is linked to the plant diversity and habitat heterogeneity of each habitat (Roels et al. 2018). Other studies have found the opposite outcome, with the highest number of beak marks in pastures and the lowest number in tropical forest, which was directly attributed to the high abundance of insectivorous birds in degraded areas (Posa et al. 2007, Roels et al. 2018). As in this study only the number of bird species is considered and not the abundance of each species, it was not possible to investigate this direct association. In this study, no clear trend was found in the number of caterpillar attacks along the restoration gradient. This could be attributed to the equalizing effects of on the one hand the decrease in the number of insectivorous birds and on the other hand the increase of habitat quality along the restoration gradient. The number of bitten caterpillars may be misleadingly low in the natural forest, as the activity of birds is concentrated in the canopy and not at levels of 0 to 1,5m (Roels et al. 2018).

No clear correlation was found between the number of predominantly insectivorous birds and the performance of top-down control. Other factors may have had an influence on the number of beak marks on the dummy caterpillars. The distance to the closest forest was positively correlated to the performance of top-down control, indicating that predation by insectivorous birds decreased with native forest proximity, which is contradictory to what was found in previous studies (Roels et al. 2018). The same result was found for the distance to the closest pasture, meaning there was a higher number of caterpillars bitten in plots that were further away from pastures. The stem density had a positive effect on the performance of top-down control, because trees provide habitat for both insectivorous birds and their prey. Other studies as well indicated that structural heterogeneity of vegetation led to an increase of the predation pressure from insectivorous birds (Roels et al. 2018). The influence of weather conditions on the number of bird bites was contradictory to literature. Rain seemed to positively affect the amount of caterpillars bitten, whereas other studies have found evidence that less bird species were observed during a rainy day (Flynn et al. 2009). It has never been raining 24 hours a day during the presence of caterpillars in a certain habitat. As birds pause their search for food during rainy weather, it could be that after a rainstorm birds are hungrier and less selective in their food. Therefore, they may tend to try the dummy caterpillars more rapidly compared to less hungry, more choosy individuals. Rain does not seem to wash out beak marks from the plasticine surface, which was remarked in other studies with the same methodology (Howe et al. 2009). Temperature had a negative effect on the number of caterpillars bitten by birds. All average temperatures (over 24h) measured during the experiment were between 15 and 25°C. Within this temperature range, it can be expected that the activity of birds was quite similar. Therefore, the negative effect of temperature on the performance of top-down control could be explained by coincidence: some more beak marks were accidentally present in plots during colder weather. A slightly negative correlation was found between the number of bitten caterpillars and the insolation. As previous studies found little evidence that cloud cover had an effect on the activity of birds, this outcome may as well be attributed to coincidence (Flynn et al. 2009). The presence of ants had a remarkably negative effect on the number of bird bites. Ants left bite marks on dummy caterpillars, which could have masked the bird bites that were previously present. It is also possible that insectivorous birds were more predating on ants than on the caterpillars, in case both insects were likely to be consumed by the same bird species, thereby resulting in less beak marks. The combination of each of these factors may have resulted in the eventual number of caterpillars bitten by birds in each plot.

5.5 Suggestions for further research

It is suggested to perform a larger scale research on this topic, during a longer time span and over more plots within each habitat. This would reduce the effect of coincidence factors and would give a clearer view on how areas are actually recovering over time (Bregman et al. 2016, Santos et al. 2016). It would be interesting to investigate the recovery of reforested areas over different trophic levels within the same time span, as all are connected to each other in the restoration trajectory. Correlations between e.g. the regrowth of the vegetation, the return of insect species and the recovery of bird populations could point out where future management should best be focused on to regain a qualitative forest ecosystem. The functional approach of evaluating the restoration of bird communities could be applied on other faunal groups as well, as has already been done in other studies on e.g. mammals (Arevalo-Sandi et al. 2018, Derhe et al. 2018) and invertebrates (Paillex et al. 2013, Derhe et al. 2016, Cajaiba et al. 2020). These other faunal groups provide several ecosystem services, important in the maintenance and recovery of forest ecosystems.

In this study, the desired endpoint was to strive for a full-ecosystem recovery, but it has been suggested in literature that it could be more cost-efficient and realistic to manage towards a heterogeneous landscape containing different successional stages. This would enhance the landscape connectivity, rather than solely focusing on the full restoration of forest ecosystems (Alvarez-Yepiz 2020). The reforested areas considered in this study could already provide an improved connectivity between forest patches, even without having reached the natural forest state yet. This possible restoration in connectivity could be topic for further research.

6. Conclusion

In this study, results have made clear that each reforested area responds differently to restoration efforts. Therefore, most conclusions could only be made for each of the reforested areas separately (Table 5).

Concerning general species diversity, the reforested areas Santa Rosa and Suamox were recovering towards a forest state, but on a slow pace. The diversity in La Yumbada and Piedras Negras seemed to be restored already better, but no good comparison with the reference forest could be made due to the masking river sound on some recordings. The species composition was restoring well in Suamox, as there was a high resemblance with its reference natural forest Silanche. In Santa Rosa and La Yumbada, recovery was happening but slowly. In Piedras Negras, the species composition still resembled more a pasture state, so recovery was not yet happening as wanted. Indications have been found for spillover effects from nearby forests to each of the pastures, leading to an overrepresentation of bird species. The diversity on a regional scale showed a tendency towards homogenization in degraded ecosystems.

The come-back of forest and indicator species in Suamox was going slow, indicating that some change in management may be needed to improve the habitat quality of this reforested area. In Santa Rosa, the recovery of these valuable groups seemed to go well, when comparing the number and species composition between this reforested area and its reference forest Puyucunapi. In both reforested areas of the second stratum, the recovery of forest species was going as intended, but there was clearly a lower presence of indicator species in Piedras Negras compared to La Yumbada.

In all the reforested areas, predominant frugivores experienced difficulties to recover. Mostly in La Yumbada, this functional group was highly under-represented, largely determined by the absence of some important toucan species. Concerning the predominant insectivores, the number of individuals has been largely restored in reforested areas, although the species composition was not as in the reference forest state. In Santa Rosa, Piedras Negras and Suamox, there was an increase in the presence of sensitive insectivores along the restoration gradient, indicating that recovery is happening, but slowly. In the second stratum, La Yumbada harboured already a high number of sensitive insectivores, indicating that recovery of this functional group is going well. The high presence of predominant insectivores in pastures indicates that this functional group in general is not that sensitive to degradation, although the clear increase in sensitive insectivorous species along the restoration gradient points out the relevance of the recovery of forest ecosystems for maintaining this functional group. The reforested areas of stratum 2 seemed to provide good habitat for frugivores-insectivores. In the other strata, there was clearly a higher presence of this functional group in the pastures, indicating that this group in general is not that sensitive to degradation, if enough food sources can be found. Concerning the predominant granivores, vertebrate-eaters, nectarivores and omnivores, there were not enough observations for each of these functional groups to derive clear conclusions.

The performance of top-down control on insects showed no clear trends along the restoration gradient in each of the strata. Neither a correlation between the number of predominantly insectivorous bird species and the performance of top-down control was found. Most likely this outcome is linked to many environmental factors e.g. rain and habitat heterogeneity, which differed in each habitat. The presence of ants seemed to have a negative effect on the presence of beak marks, either because they masked the bird bites, either because insectivores tend to eat the ants instead of the caterpillars.

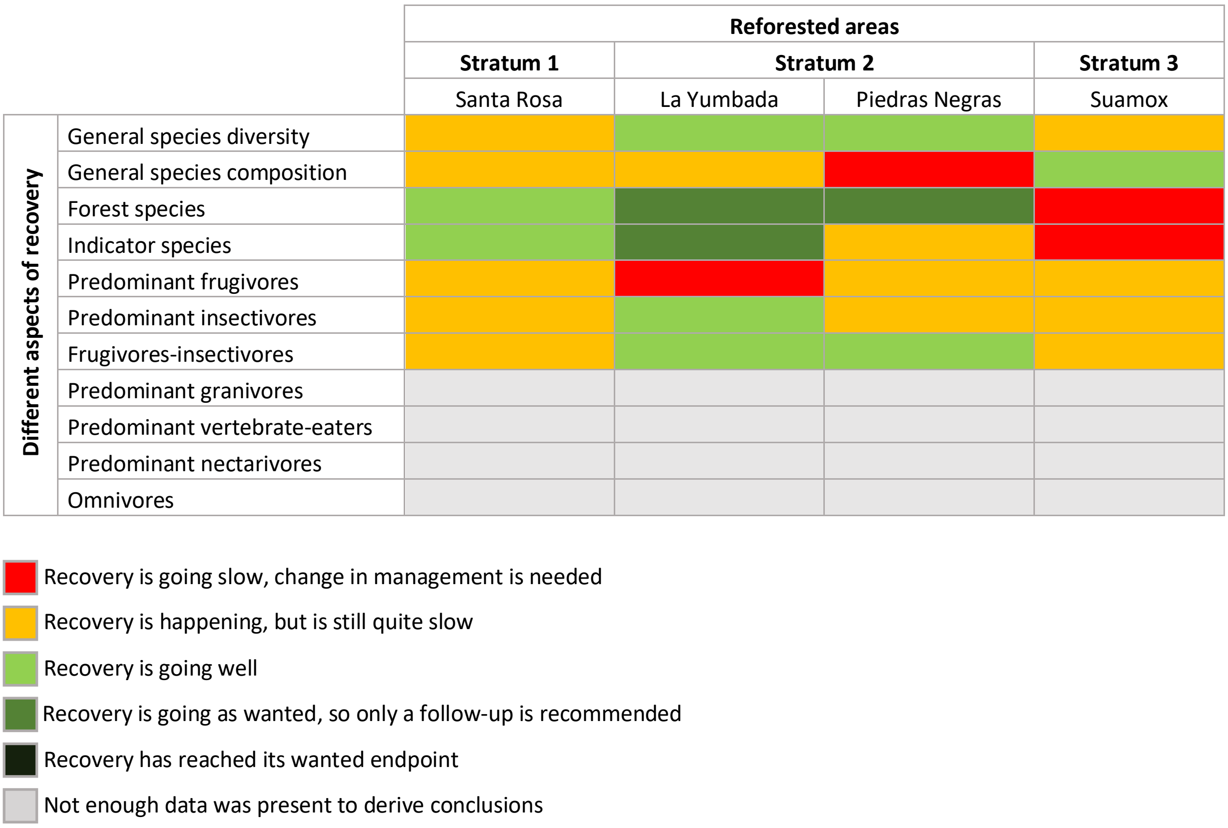


Table 5. A schematic overview on how well the different reforested areas (Santa Rosa, La Yumbada, Piedras Negras and Suamox) are recovering, focusing on different aspects: general species diversity and composition, forest and indicator species, functional groups i.e. predominant frugivores, predominant insectivores and frugivores-insectivores. The colours indicate how well recovery is going according to the legend. The grey grids indicate that not enough data was present to derive clear conclusions.

Further management should best be focused on the groups that do not recover as intended in specific areas. Certainly frugivorous birds deserve attention in future restoration actions, as this functional group has difficulties to recover well and is key to the further restoration of reforested areas.

It is recommended to investigate the restoration of reforested areas on different trophic levels in future research. Also, the research must be done over a longer time span concerning more plots per habitat. This would give clearer indications of how areas are recovering and where further management should be focusing on.

7. Summary

Forests provide many ecosystem services that are crucial for the health of the planet and all species living within. Birds play an important role supporting these ecosystem services by performing different ecosystem functions, including seed dispersal, top-down control on insects and pollination. These ecosystem functions are beneficial for the restoration of formerly degraded landscapes towards forest ecosystems. In the cloud forests of Northwest Ecuador, a large-scale reforestation project is being conducted, focusing on the restoration of degraded pastures to become highly qualitative forests again. In this study, an assessment has been performed to investigate to what extent these reforested areas are recovering.

As higher levels of biodiversity enhance the ability of a community to maintain higher levels of ecosystem functioning, the biodiversity has been investigated on a local (alpha diversity) and a regional scale (gamma diversity) as well as the differentiation in species composition among habitats (beta diversity). The return of typical forest and indicator species, sensitive to degradation, to reforested areas indicates a good recovery from a previously degraded situation. Therefore, it has been examined to what degree forest and indicator species have returned to reforested areas. As different ecosystem functions performed by birds enhance the recovery towards qualitative forests, the restoration of these ecosystem functions has been investigated.

Three strata, which differed in altitude, were selected in the province of Pichincha. In each of the three strata there was a degraded pasture, a reforested area and a natural forest, which represent a restoration gradient. Point counts were done in six different plots per habitat by recording bird vocalizations. The presence of bird species was analyzed using these recordings. Functional groups were determined based on the main diet of the bird species. Afterwards, comparisons have been done between the three habitats, focusing on bird biodiversity and species composition firstly, secondly on forest and indicator species and thirdly on different functional groups. To examine the correlation between the number of insectivorous species and the performance of top-down control by insectivores, an experiment with dummy caterpillars was performed. These were distributed in each of the plots and the proportion of bird-bitten caterpillars was compared between each of the habitats and linked with the number of insectivorous birds present.

The first objective was to examine biodiversity. On a local scale, in each of the three strata, the highest alpha diversity was found in pastures. This indicates a possible overrepresentation of species in pastures probably because of spillover effects. Comparing natural forests with reforested areas, different outcomes concerning alpha diversity were found in the three strata. In stratum 1 and stratum 3, there is a higher biodiversity in the natural forest compared to the reforested area, which is an indication that the reforested area has not reached its endpoint yet. Concerning the gamma diversity on a regional scale, a tendency towards homogenization of bird species in pastures was found. Based on the beta diversity, recovery of the species composition in reforested areas differs between the strata. Recovery in species composition is going best in Suamox (stratum 3) and least optimal in Piedras Negras (stratum 2). The second objective was to examine the return of forest and indicator species. Each stratum showed another trend in the number and composition of forest and indicator species along the restoration gradient. The third objective was to quantify the performance of ecosystem functions in each habitat. Concerning predominantly frugivorous birds, a trend towards recovery of the number and species composition was found in stratum 1. Little difference was found in stratum 2 concerning the predominant frugivores between the different habitats, except that toucan species were absent in one reforested area (La Yumbada). Further restoration management should here focus on retrieving these valuable species. In stratum 3, there was no tendency towards recovery of predominant frugivores in the reforested area. Concerning predominantly insectivorous birds, suboptimal recovery was found in stratum 1, indicating the need of management for this functional group. In stratum 2, a higher number of predominant insectivores, sensitive to degradation, was found in the reforested area La Yumbada compared to the other reforested area Piedras Negras. In stratum 3, the number of sensitive insectivores increases along the restoration gradient. The number of counted predominant nectarivores in all strata was low, so no strong conclusions could be made. No consistent trend was found in the number of caterpillar attacks by birds along the different habitats. Neither a clear correlation was found between the number of predominantly insectivorous species and the performance of top-down control. A negative correlation was found between the abundance of ants and the number of bitten caterpillars, indicating a masking effect due to the presence of ants. These outcomes point out whether reforested areas are recovering on-track and where further intervention is needed.

8. Samenvatting

Bossen voorzien in verschillende ecosysteemfuncties die cruciaal zijn voor de gezondheid van de planeet en alle soorten hiervan afhankelijk. Vogels spelen een belangrijke rol in het ondersteunen van deze ecosysteemdiensten via verschillende ecosysteemfuncties, zoals zaaddispersie, top-down controle op insecten en pollinatie. Deze ecosysteem functies zijn voordelig voor het herstel van gedegradeerde landschappen naar bosecosystemen. In de nevelwouden van noordwest Ecuador is een grootschalig herbebossingsproject aan de gang, waarbij de focus ligt op het herstel van gedegradeerde graslanden naar kwalitatieve bossen. In deze studie werd een onderzoek uitgevoerd om na te gaan in welke mate deze herbeboste gebieden aan het herstellen zijn.

Een hogere biodiversiteit is gelinkt aan een hogere uitvoering van ecosysteemfuncties. Daarom werd de biodiversiteit onderzocht op een lokale (alpha diversiteit) en regionale schaal (gamma diversiteit), alsook de differentiatie in soortensamenstelling langsheen de restoratiegradiënt. De terugkeer van typische bos- en indicatorsoorten, gevoelig aan degradatie, naar herbeboste gebieden wijst op een goed herstel van een voormalig gedegradeerd landschap. Daarom werd onderzocht in welke mate deze bos- en indicatorsoorten teruggekeerd zijn naar herbeboste gebieden. Aangezien verschillende ecosysteemfuncties, uitgevoerd door vogels, het herstel naar kwalitatief bos bevorderen, werd onderzocht in welke mate deze functies aan het herstellen zijn in elk van de herbeboste gebieden.

Er werden drie strata geselecteerd in de provincie Pichincha, verschillend in hun hoogteligging. In elk van deze strata bevond zich een gedegradeerd grasland, een herbebost gebied en een natuurlijk bos, wat een restoratiegradiënt voorstelt. Punttellingen werden uitgevoerd in zes verschillende plots per habitat, door vogelgeluiden op te nemen. De aanwezigheid van vogelsoorten werd op basis van deze opnames geanalyseerd. Functionele groepen werden bepaald volgens het hoofddieet van de vogelsoorten. Hierna werden vergelijkingen gemaakt tussen de drie habitats, ten eerste gefocust op vogelbiodiversiteit en soortensamenstelling, ten tweede op de terugkeer van bos- en indicatorsoorten en ten derde op verschillende functionele groepen. Om de correlatie na te gaan tussen het aantal insectivore vogelsoorten en de top-down controle door deze functionele groep, werd een experiment opgezet met plasticine rupsen. Deze werden verdeeld over de verschillende plots en de proportie gebeten rupsen werd vergeleken tussen de verschillende habitats. Ook werd dit gelinkt aan het aantal insectivore vogels aanwezig in elk habitat.

De eerste doelstelling was het nagaan van de biodiversiteit. Op een lokale schaal werd in elk van de drie strata de hoogste alpha diversiteit gevonden in de graslanden. Dit wijst op een mogelijke overrepresentatie van vogelsoorten in deze graslanden, vermoedelijk omwille van spillover effecten. Bij de vergelijking tussen natuurlijke bossen en herbeboste gebieden werden verschillende uitkomsten gevonden voor de alpha diversiteit in elk stratum. In stratum 1 en stratum 3 werd een hogere biodiversiteit gevonden in het natuurlijk bos. Dit is een indicatie dat het herbebost gebied nog niet zijn gewenste eindstadium van restoratie heeft bereikt. Op een regionale schaal werd voor de gamma diversiteit een tendens naar homogenisatie van vogelsoorten gevonden in graslanden. Op basis van de beta diversiteit verschilde de mate van herstel in soortensamenstelling in herbeboste gebieden tussen de drie strata. Het herstel in soortensamenstelling verloopt het meest optimaal in Suamox (stratum 3) en het minst optimaal in Piedras Negras (stratum 2). De tweede doelstelling was het evalueren van de terugkeer van bos- en indicatorsoorten. Elk stratum vertoonde een andere trend in het aantal en de samenstelling van deze waardevolle soorten langsheen de restoratiegradiënt. De derde doelstelling was het kwantificeren van ecosysteemfuncties in de verschillende habitats. In stratum 1, werd er een zekere mate van herstel in het aantal en de soortensamenstelling van voornamelijk frugivore vogelsoorten gevonden. In het tweede stratum werd weinig verschil gevonden tussen de habitats voor voornamelijk frugivore vogelsoorten, behalve dat toekansoorten afwezig waren in een van de herbeboste gebieden (La Yumbada). Restoratiemanagement zou hier kunnen focussen op de terugkeer van deze nuttige soorten. In het derde stratum werd geen trend gevonden richting herstel van voornamelijk frugivore vogelsoorten in het herbebost gebied. Voor voornamelijk insectivore vogels werd er een suboptimaal herstel gevonden in stratum 1, wat wijst op de nood aan management specifiek voor deze functionele groep. In stratum 2 werd een hoger aantal voornamelijk insectivore vogelsoorten, gevoelig aan degradatie, gevonden in het herbebost gebied La Yumbada in vergelijking met het andere herbeboste gebied Piedras Negras. In stratum 3, nam het aantal gevoelige insectivoren toe langsheen de restoratiegradiënt. Het aantal voornamelijk nectarivoren was in elk van de strata laag, waardoor voor deze groep geen sterke conclusies konden genomen worden. Er werd geen consistente trend gevonden in het aantal vogelbeten langsheen de verschillende habitats. Alsook werd geen duidelijke correlatie gevonden tussen het aantal voornamelijk insectivore vogels en de top-down controle op insecten. Wel werd een negatieve correlatie gevonden tussen de abundantie van mieren en het aantal vogelbeten, wat wijst op een maskerend effect door de aanwezigheid van mieren. Deze uitkomsten tonen aan in welke herbeboste gebieden het herstel al dan niet zoals gewenst verloopt en waar verdere tussenkomsten in management nodig zijn.

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11. Appendix

This species list was obtained by analyzing the recordings in each habitat. Assigning species to a functional and sensitivity group was based on the information found on the website of the Cornell Lab of Ornithology (TheCornellLabOfOrnithology 2020) and the IUCN (IUCN 2020)

				Stratum 1			***Stratum 2***				***Stratum 3***		
Common species name	**Scientific species name**	**Functional group**	**Sensitivity group**	**SR**	**PSR**	**PU**	**LY**	**PN**	**PMI**	**MI**	**SU**	**PSI**	**SI**
Black-winged Saltator	*Saltator atripennis*	Predominantly frugivorous	Forest					x				x	
Blue-fronted Parrotlet	*Touit dilectissimus*	Predominantly frugivorous	Indicator					x					
Bronze-winged Parrot	*Pionus chalcopterus*	Predominantly frugivorous	/						x	x	x	x	x
Brown-capped Tyrannulet	*Ornithion brunneicapillus*	Predominantly frugivorous	/										x
Buff-throated Saltator	*Saltator maximus*	Predominantly frugivorous	/									x	
Chocó Toucan	*Ramphastos brevis*	Predominantly frugivorous	/					x	x	x		x	x
Collared Aracari	*Pteroglossus torquatus*	Predominantly frugivorous	/					x	x	x		x	
Crested Guan	*Penelope purpurascens*	Predominantly frugivorous	Indicator						x				
Crimson-rumped Toucanet	*Aulacorhynchus haematopygus*	Predominantly frugivorous	/			x		x				x	
Dusky Pigeon	*Patagioenas goodsoni*	Predominantly frugivorous	Indicator										x
Glossy-black Thrush	*Turdus serranus*	Predominantly frugivorous	/	x	x		x						
Golden-headed Quetzal	*Pharomachrus auriceps*	Predominantly frugivorous	Forest	x		x	x	x		x			
Golden-rumped Euphonia	*Euphonia cyanocephala*	Predominantly frugivorous	/			x							
Green-and-black Fruiteater	*Pipreola riefferii*	Predominantly frugivorous	Indicator			x	x						
Maroon-tailed Parakeet	*Pyrrhura melanura*	Predominantly frugivorous	Forest				x			x		x	x
Orange-crowned Euphonia	*Euphonia saturata*	Predominantly frugivorous	/								x		x
Orange-fronted Barbet	*Capito squamatus*	Predominantly frugivorous	/								x		x
Pale-eyed Thrush	*Turdus leucops*	Predominantly frugivorous	Indicator			x		x					
Pallid Dove	*Leptotila pallida*	Predominantly frugivorous	Forest								x		
Plate-billed Mountain-Toucan	*Andigena laminirostris*	Predominantly frugivorous	Indicator	x	x								
Plumbeous Pigeon	*Patagioenas plumbea*	Predominantly frugivorous	Indicator		x	x	x	x					
Red-headed Barbet	*Eubucco bourcierii*	Predominantly frugivorous	Forest										x

Ruddy Pigeon	*Patagioenas subvinacea*	Predominantly frugivorous	Indicator					x	x		x	x	x
Speckle-faced Parrot	*Pionus tumultuosus*	Predominantly frugivorous	Indicator	x									
Thick-billed Euphonia	*Euphonia laniirostris*	Predominantly frugivorous	/						x				
Toucan Barbet	*Semnornis ramphastinus*	Predominantly frugivorous	/	x		x							
Wattled Guan	*Aburria aburri*	Predominantly frugivorous	Forest					x					
Yellow-throated Toucan	*Ramphastos ambiguus*	Predominantly frugivorous	/					x	x	x	x	x	x
Ashy-headed Tyrannulet	*Phyllomyias cinereiceps*	Predominantly insectivorous	Indicator					x					
Azara's Spinetail	*Synallaxis azarae*	Predominantly insectivorous	/	x	x								
Barred Puffbird	*Nystalus radiatus*	Predominantly insectivorous	/					x					x
Bay Wren	*Cantorchilus nigricapillus*	Predominantly insectivorous	/								x	x	x
Bicolored Antbird	*Gymnopithys bicolor*	Predominantly insectivorous	Indicator							x			
Black-capped Pygmy-Tyrant	*Myiornis atricapillus*	Predominantly insectivorous	/								x		x
Black-cheeked Woodpecker	*Melanerpes pucherani*	Predominantly insectivorous	/								x	x	x
Black-crested Warbler	*Myiothlypis nigrocristata*	Predominantly insectivorous	/		x								
Black-crowned Antshrike	*Thamnophilus atrinucha*	Predominantly insectivorous	Forest								x		x
Black-headed Tody-Flycatcher	*Todirostrum nigriceps*	Predominantly insectivorous	/								x		x
Black-streaked Puffbird	*Malacoptila fulvogularis*	Predominantly insectivorous	Indicator										x
Black-striped Woodcreeper	*Xiphorhynchus lachrymosus*	Predominantly insectivorous	Forest										x
Brown-capped Vireo	*Vireo leucophrys*	Predominantly insectivorous	/	x	x	x	x	x		x			
Buff-fronted Foliage-gleaner	*Philydor rufum*	Predominantly insectivorous	Indicator					x	x	x			
Buff-rumped Warbler	*Myiothlypis fulvicauda*	Predominantly insectivorous	/						x		x	x	
Capped Conebill	*Conirostrum albifrons*	Predominantly insectivorous	Indicator		x								
Checker-throated Antwren	*Epinecrophylla fulviventris*	Predominantly insectivorous	Indicator									x	x
Chestnut-backed Antbird	*Poliocrania exsul*	Predominantly insectivorous	Indicator						x		x		x
Chestnut-crowned Antpitta	*Grallaria ruficapilla*	Predominantly insectivorous	/	x	x								
Chivi Vireo	*Vireo chivi*	Predominantly insectivorous	/						x		x	x	x
Cinnamon Becard	*Pachyramphus cinnamomeus*	Predominantly insectivorous	/						x				
Common Tody-Flycatcher	*Todirostrum cinereum*	Predominantly insectivorous	/								x	x	
Coopmans's Elaenia	*Elaenia brachyptera*	Predominantly insectivorous	/						x				

Crimson-bellied Woodpecker	*Campephilus haematogaster*	Predominantly insectivorous	Indicator										x
Crimson-mantled Woodpecker	*Colaptes rivolii*	Predominantly insectivorous	/		x	x							
Dot-winged Antwren	*Microrhopias quixensis*	Predominantly insectivorous	/										x
Dusky Antbird	*Cercomacroides tyrannina*	Predominantly insectivorous	/									x	
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	Predominantly insectivorous	/			x		x	x				
Esmeraldas Antbird	*Sipia nigricauda*	Predominantly insectivorous	Indicator							x			
Flavescent Flycatcher	*Myiophobus flavicans*	Predominantly insectivorous	Indicator				x						
Golden-bellied Warbler	*Myiothlypis chrysogaster*	Predominantly insectivorous	Indicator						x	x			
Gray-breasted Martin	*Progne chalybea*	Predominantly insectivorous	/										
Gray-breasted Wood-Wren	*Henicorhina leucophrys*	Predominantly insectivorous	Indicator	x	x	x	x	x	x	x			x
Gray-rumped Swift	*Chaetura cinereiventris*	Predominantly insectivorous	Forest									x	x
Guayaquil Woodpecker	*Campephilus gayaquilensis*	Predominantly insectivorous	/								x		x
House Wren	*Troglodytes aedon*	Predominantly insectivorous	/						x		x	x	
Lesser Greenlet	*Pachysylvia decurtata*	Predominantly insectivorous	Forest						x		x	x	
Lineated Foliage-gleaner	*Syndactyla subalaris*	Predominantly insectivorous	/				x	x	x	x			
Lineated Woodpecker	*Dryocopus lineatus*	Predominantly insectivorous	/									x	
Little Tinamou	*Crypturellus soui*	Predominantly insectivorous	/								x	x	x
Long-tailed Tyrant	*Colonia colonus*	Predominantly insectivorous	/									x	
Marble-faced Bristle-Tyrant	*Phylloscartes ophthalmicus*	Predominantly insectivorous	Indicator				x						
Montane Woodcreeper	*Lepidocolaptes lacrymiger*	Predominantly insectivorous	/	x	x	x	x	x					
Mountain Wren	*Troglodytes solstitialis*	Predominantly insectivorous	Indicator			x							
Nariño Tapaculo	*Scytalopus vicinior*	Predominantly insectivorous	Indicator		x	x				x			
Ocellated Tapaculo	*Acropternis orthonyx*	Predominantly insectivorous	Indicator		x								
Olivaceous Piculet	*Picumnus olivaceus*	Predominantly insectivorous	/								x	x	
Olive-crowned Yellowthroat	*Geothlypis semiflava*	Predominantly insectivorous	/						x				
Ornate Flycatcher	*Myiotriccus ornatus*	Predominantly insectivorous	/			x	x	x	x	x		x	
Pacific Antwren	*Myrmotherula pacifica*	Predominantly insectivorous	/									x	
Pale-legged Hornero	*Furnarius leucopus*	Predominantly insectivorous	/						x			x	
Pearled Treerunner	*Margarornis squamiger*	Predominantly insectivorous	Indicator		x		x						

Plain-brown Woodcreeper	*Dendrocincla fuliginosa*	Predominantly insectivorous	Forest					x					
Powerful Woodpecker	*Campephilus pollens*	Predominantly insectivorous	Indicator			x							
Red-billed Scythebill	*Campylorhamphus trochilirostris*	Predominantly insectivorous	/										
Red-faced Spinetail	*Cranioleuca erythrops*	Predominantly insectivorous	Indicator					x	x				
Rufous-breasted Antthrush	*Formicarius rufipectus*	Predominantly insectivorous	/					x					
Rufous-crowned Tody-Flycatcher	*Poecilotriccus ruficeps*	Predominantly insectivorous	/		x								
Rufous-tailed Jacamar	*Galbula ruficauda*	Predominantly insectivorous	/									x	x
Rufous-winged Tyrannulet	*Mecocerculus calopterus*	Predominantly insectivorous	/						x				
Russet-crowned Warbler	*Myiothlypis coronata*	Predominantly insectivorous	Indicator	x	x		x						
Scale-crested Pygmy-Tyrant	*Lophotriccus pileatus*	Predominantly insectivorous	Forest					x	x		x	x	x
Scaly-breasted Wren	*Microcerculus marginatus*	Predominantly insectivorous	Indicator						x				x
Scaly-throated Foliage-gleaner	*Anabacerthia variegaticeps*	Predominantly insectivorous	Indicator				x	x	x				
Scarlet-backed Woodpecker	*Dryobates callonotus*	Predominantly insectivorous	/								x		
Scarlet-Rumped Cacique	*Cacicus uropygialis*	Predominantly insectivorous	Forest						x			x	x
Scrub Blackbird	*Dives warczewiczi*	Predominantly insectivorous	/						x				
Slate-throated Redstart	*Myioborus miniatus*	Predominantly insectivorous	/	x	x		x	x	x				
Slaty Antwren	*Myrmotherula schisticolor*	Predominantly insectivorous	Indicator				x	x	x				
Slaty Spinetail	*Synallaxis brachyura*	Predominantly insectivorous	/					x				x	
Slaty-backed Chat-Tyrant	*Ochthoeca cinnamomeiventris*	Predominantly insectivorous	Forest	x									
Slaty-capped Shrike-Vireo	*Vireolanius leucotis*	Predominantly insectivorous	Indicator							x		x	
Smoke-colored Pewee	*Contopus fumigatus*	Predominantly insectivorous	Forest	x	x	x		x					
Smoky-brown Woodpecker	*Dryobates fumigatus*	Predominantly insectivorous	/					x				x	
Social Flycatcher	*Myiozetetes similis*	Predominantly insectivorous	/									x	
Southern Rough-winged Swallow	*Stelgidopteryx ruficollis*	Predominantly insectivorous	/						x			x	
Spillman's Tapaculo	*Scytalopus spillmanni*	Predominantly insectivorous	Indicator	x	x	x							
Spotted Barbtail	*Premnoplex brunnescens*	Predominantly insectivorous	Indicator			x				x			
Spotted Woodcreeper	*Xiphorhynchus erythropygius*	Predominantly insectivorous	Forest					x	x	x			x
Squirrel Cuckoo	*Piaya cayana*	Predominantly insectivorous	/		x				x			x	

Streak-capped Treehunter	*Thripadectes virgaticeps*	Predominantly insectivorous	Forest		x	x	x						
Streak-headed Antbird	*Drymophila striaticeps*	Predominantly insectivorous	/		x								
Streak-headed Woodcreeper	*Lepidocolaptes souleyetii*	Predominantly insectivorous	/									x	
Striped Treehunter	*Thripadectes holostictus*	Predominantly insectivorous	Forest			x			x				
Tawny-faced Gnatwren	*Microbates cinereiventris*	Predominantly insectivorous	Forest						x		x		x
Three-striped Warbler	*Basileuterus tristriatus*	Predominantly insectivorous	Forest	x		x	x	x	x	x			
Tropical Gnatcatcher	*Polioptila plumbea*	Predominantly insectivorous	/									x	
Tropical Kingbird	*Tyrannus melancholicus*	Predominantly insectivorous	/						x			x	
Tropical Parula	*Setophaga pitiayumi*	Predominantly insectivorous	/			x	x	x	x			x	
Turquoise Jay	*Cyanolyca turcosa*	Predominantly insectivorous	Forest	x									
Tyrannine Woodcreeper	*Dendrocincla tyrannina*	Predominantly insectivorous	Forest	x		x		x					
Uniform Antshrike	*Thamnophilus unicolor*	Predominantly insectivorous	Forest				x	x					
White-collared Swift	*Streptoprocne zonaris*	Predominantly insectivorous	/	x									
White-flanked Antwren	*Myrmotherula axillaris*	Predominantly insectivorous	Forest										x
White-tailed Tyrannulet	*Mecocerculus poecilocercus*	Predominantly insectivorous	Indicator	x	x	x	x						
Yellow-breasted Antpitta	*Grallaria flavotincta*	Predominantly insectivorous	/	x		x							
Zeledon’s Antbird	*Hafferia zeledoni*	Predominantly insectivorous	Forest						x	x			
Andean Solitaire	*Myadestes ralloides*	Frugivores-insectivores	Forest	x	x	x	x	x		x			
Barred Becard	*Pachyramphus versicolor*	Frugivores-insectivores	Forest		x								
Bay-headed Tanager	*Tangara gyrola*	Frugivores-insectivores	/						x				
Beryl-spangled Tanager	*Tangara nigroviridis*	Frugivores-insectivores	Forest	x	x		x	x					
Black-and-white Becard	*Pachyramphus albogriseus*	Frugivores-insectivores	Indicator					x					
Black-capped Tanager	*Stilpnia heinei*	Frugivores-insectivores	/		x	x	x						
Blue-capped Tanager	*Thraupis cyanocephala*	Frugivores-insectivores	/		x								
Blue-gray Tanager	*Thraupis episcopus*	Frugivores-insectivores	/					x	x		x	x	x
Blue-necked Tanager	*Stilpnia cyanicollis*	Frugivores-insectivores	/						x			x	
Blue-tailed Trogon	*Trogon comptus*	Frugivores-insectivores	Indicator							x			x
Blue-winged Mountain-Tanager	*Anisognathus somptuosus*	Frugivores-insectivores	Indicator	x	x	x	x	x					
Boat-billed Flycatcher	*Megarynchus pitangua*	Frugivores-insectivores	/						x		x	x	x

Chestnut-capped Brushfinch	*Arremon brunneinucha*	Frugivores-insectivores	Forest			x	x	x					
Chocó Tyrannulet	*Zimmerius albigularis*	Frugivores-insectivores	/						x		x	x	
Cinnamon Flycatcher	*Pyrrhomyias cinnamomeus*	Frugivores-insectivores	Forest		x								
Cinnamon Woodpecker	*Celeus loricatus*	Frugivores-insectivores	Forest									x	x
Club-winged Manakin	*Machaeropterus deliciosus*	Frugivores-insectivores	Indicator					x					
Collared Trogon	*Trogon collaris*	Frugivores-insectivores	Indicator							x			
Dusky Chlorospingus	*Chlorospingus semifuscus*	Frugivores-insectivores	Indicator	x	x		x						
Dusky-faced Tanager	*Mitrospingus cassinii*	Frugivores-insectivores	/										x
Ecuadorian Thrush	*Turdus maculirostris*	Frugivores-insectivores	Forest	x		x					x		
Flame-rumped Tanager	*Ramphocelus flammigerus*	Frugivores-insectivores	/					x	x		x	x	x
Golden Tanager	*Tangara arthus*	Frugivores-insectivores	Indicator	x	x	x	x	x	x				
Golden-crowned Flycatcher	*Myiodynastes chrysocephalus*	Frugivores-insectivores	/	x	x	x	x	x					
Golden-hooded Tanager	*Stilpnia larvata*	Frugivores-insectivores	/								x	x	
Golden-naped Tanager	*Chalcothraupis ruficervix*	Frugivores-insectivores	/				x						
Golden-olive Woodpecker	*Colaptes rubiginosus*	Frugivores-insectivores	/								x	x	x
Gray-and-gold Tanager	*Poecilostreptus palmeri*	Frugivores-insectivores	Indicator						x		x		
Great Thrush	*Turdus fuscater*	Frugivores-insectivores	/		x								
Guira Tanager	*Hemithraupis guira*	Frugivores-insectivores	/						x				
Masked Tityra	*Tityra semifasciata*	Frugivores-insectivores	/									x	x
Masked Trogon	*Trogon personatus*	Frugivores-insectivores	Indicator		x		x	x					
Northern Schiffornis	*Schiffornis veraepacis*	Frugivores-insectivores	Indicator										x
Ochre-bellied Flycatcher	*Mionectes oleagineus*	Frugivores-insectivores	/								x		
Ochre-breasted Tanager	*Chlorothraupis stolzmanni*	Frugivores-insectivores	Indicator						x	x			
Orange-bellied Euphonia	*Euphonia xanthogaster*	Frugivores-insectivores	/		x	x	x	x	x	x	x	x	x
Palm Tanager	*Thraupis palmarum*	Frugivores-insectivores	/					x	x		x	x	x
Piratic Flycatcher	*Legatus leucophaius*	Frugivores-insectivores	/								x	x	
Purple-throated Fruitcrow	*Querula purpurata*	Frugivores-insectivores	Indicator								x		x
Rufous-collared Sparrow	*Zonotrichia capensis*	Frugivores-insectivores	/		x								
Rufous-throated Tanager	*Ixothraupis rufigula*	Frugivores-insectivores	/						x				

Rufous-winged Tanager	*Tangara lavinia*	Frugivores-insectivores	Forest										x
Rusty-margined Flycatcher	*Myiozetetes cayanensis*	Frugivores-insectivores	/					x	x		x	x	x
Scaled Fruiteater	*Ampelioides tschudii*	Frugivores-insectivores	Indicator			x							
Slaty-capped Flycatcher	*Leptopogon superciliaris*	Frugivores-insectivores	/				x	x	x	x	x		
Snowy-throated Kingbird	*Tyrannus niveigularis*	Frugivores-insectivores	/									x	
Sooty-headed Tyrannulet	*Phyllomyias griseiceps*	Frugivores-insectivores	/									x	
Southern Beardless Tyrannulet	*Camptostoma obsoletum*	Frugivores-insectivores	/									x	
Streak-necked Flycatcher	*Mionectes striaticollis*	Frugivores-insectivores	Forest				x						
Swallow Tanager	*Tersina viridis*	Frugivores-insectivores	/						x				
Tawny-crested Tanager	*Tachyphonus delatrii*	Frugivores-insectivores	Indicator								x		x
Tricolored Brushfinch	*Atlapetes tricolor*	Frugivores-insectivores	/				x	x					
White-bearded Manakin	*Manacus manacus*	Frugivores-insectivores	/								x	x	x
White-crested Elaenia	*Elaenia albiceps*	Frugivores-insectivores	/		x								
White-tailed Trogon	*Trogon chionurus*	Frugivores-insectivores	Indicator										x
White-winged Tanager	*Piranga leucoptera*	Frugivores-insectivores	/					x	x				
Yellow Tyrannulet	*Capsiempis flaveola*	Frugivores-insectivores	/									x	
Yellow-bellied Elaenia	*Elaenia flavogaster*	Frugivores-insectivores	/						x				
Yellow-crowned Tyrannulet	*Tyrannulus elatus*	Frugivores-insectivores	/									x	
Yellow-throated Chlorospingus	*Chlorospingus flavigularis*	Frugivores-insectivores	/					x	x	x			
Yellow-bellied Siskin	*Spinus xanthogastrus*	Predominantly granivorous	/		x				x				
Blue Ground-dove	*Claravis pretiosa*	Predominantly granivorous	/								x	x	
Blue-headed Parrot	*Pionus menstruus*	Predominantly granivorous	/									x	x
Chestnut-fronted Macaw	*Ara severus*	Predominantly granivorous	/										x
Red-billed Parrot	*Pionus sordidus*	Predominantly granivorous	/	x	x	x	x	x			x		
Slate-colored Grosbeak	*Saltator grossus*	Predominantly granivorous	Forest							x	x	x	x
Thick-billed Seed-Finch	*Sporophila funerea*	Predominantly granivorous	/									x	
Variable Seedeater	*Sporophila corvina*	Predominantly granivorous	/						x			x	
Yellow-bellied Seedeater	*Sporophila nigricollis*	Predominantly granivorous	/									x	
Barred Hawk	*Morphnarchus princeps*	Predominantly vertebrate-eaters	/				x		x				

Collared Forest-Falcon	*Micrastur semitorquatus*	Predominantly vertebrate-eaters	Indicator	x									
Gray-headed Kite	*Leptodon cayanensis*	Predominantly vertebrate-eaters	/						x				x
Great Antshrike	*Taraba major*	Predominantly vertebrate-eaters	/									x	
Laughing Falcon	*Herpetotheres cachinnans*	Predominantly vertebrate-eaters	/										x
Roadside Hawk	*Rupornis magnirostris*	Predominantly vertebrate-eaters	/				x		x			x	x
Ruddy Foliage-gleaner	*Clibanornis rubiginosus*	Predominantly vertebrate-eaters	Indicator										x
Striped Woodhaunter	*Automolus subulatus*	Predominantly vertebrate-eaters	Indicator							x			x
White-whiskered Puffbird	*Malacoptila panamensis*	Predominantly vertebrate-eaters	/								x		x
Bananaquit	*Coereba flaveola*	Predominantly nectarivorous	/						x		x		
Booted Racket-tail	*Ocreatus underwoodii*	Predominantly nectarivorous	/			x		x					
Lesser Violetear	*Colibri cyanotus*	Predominantly nectarivorous	/		x	x	x						
Rufous-tailed Hummingbird	*Amazilia tzacatl*	Predominantly nectarivorous	/									x	
Sparkling Violetear	*Colibri coruscans*	Predominantly nectarivorous	/			x							
Speckled Hummingbird	*Adelomyia melanogenys*	Predominantly nectarivorous	Indicator	x	x		x						
Violet-tailed Sylph	*Aglaiocercus coelestis*	Predominantly nectarivorous	/		x		x						
White-sided Flowerpiercer	*Diglossa albilatera*	Predominantly nectarivorous	/		x		x						
White-whiskered Hermit	*Phaethornis yaruqui*	Predominantly nectarivorous	/						x	x	x	x	x
Fawn-breasted Tanager	*Pipraeidea melanonota*	Omnivores	/						x				
Masked Flowerpiercer	*Diglossa cyanea*	Omnivores	/		x								
Mealy Parrot	*Amazona farinosa*	Omnivores	/									x	x
Orange-billed Sparrow	*Arremon aurantiirostris*	Omnivores	/						x	x			
Rufous Motmot	*Baryphthengus martii*	Omnivores	Forest										x

Appendix table 1. Common and scientific species names are given for each of the species recorded. Each species has been assigned to a functional group based on its main diet. Some species belong to a sensitivity group, either being a forest species, either an indicator species. The right part of the table shows in which habitats within each of the three strata the species were found (indicated with x). SR: Reforested area Santa Rosa, PSR: pasture Santa Rosa, PU: natural forest Puyucunapi, LY: reforested area La Yumbada, PN: reforested area Piedras Negras, PMI: pasture Milpe, MI: natural forest Milpe, SU: reforested area Suamox, PSI: pasture Silanche, SI: natural forest Silanche.