MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master‘s Thesis

„Trophic Position determines the Persistence of Neotropical Understory Birds after Forest Disturbance“

verfasst von / submitted by

Bernhard Paces, BSc MSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2020 / Vienna, 2020

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	UA 066 879
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Naturschutz und Biodiversitätsmanagement
Betreut von / Supervisor:	Dipl. Biol. Dr. Christian H. Schulze

Acknowledgements

Throughout the whole process of data collection and writing this thesis, I received invaluable support from numerous people, and I owe my deepest gratitude to all of them. This thesis would not have been possible without the patient guidance of my great supervisor Christian Schulze. The same applies to Wolfgang Wanek, who shared his immense knowledge about stable isotopes with me, whenever needed. Thanks to Christian Voigt and his team in the stable isotope laboratory at the Leibniz Institute for Zoo and Wildlife Research in Berlin for conducting all stable isotope analyses. Saskia Schirmer patiently shared her statistical knowledge with me throughout the whole process of data analysis. Three months of fieldwork in very challenging conditions would not have been possible without my much valued friend and colleague Paulus Leidinger, whose endless motivation meant a lot to me. The team of the Tropical Research Station La Gamba provided support whenever needed. Without their help, it would not have been possible to organize the fieldwork. Also, Nina Gallmetzer, Johannes Hausharter, Daniela Krebber and Justine Vansynghel helped to successfully conduct the fieldwork. Benjamin Seaman contributed numerous useful comments on the manuscript. Thank you all!

Finally, I would like to express my deepest gratitude to my family for the never-ending support throughout all the long years of my studies!

The University of Vienna supported this study with a Needs-based Scholarship (Förderstipendium).

The German Ornithologists’ Society (DO-G) granted financial support for this research project (Forschungsförderung der DO-G).

Abstract

Habitat loss and degradation are key drivers of species extinction in the current biodiversity crisis. Therefore, research is focusing on the question which traits enable some species to utilize degraded habitats while others cannot. In particular, little is known about how a species' trophic position or niche width influences its potential to thrive in degraded habitats, and about changes in trophic interactions when forests are degraded, although the consequences of such changes can be far-reaching. Here, we used stable isotope ratios (^{15}N:^{14}N, expressed as $\delta^{15}N$) to quantify and compare trophic positions and niche widths of understory bird species inhabiting old-growth and young secondary forest in the Pacific lowlands of Costa Rica. In our dataset, a species' trophic position rather than its trophic niche width determined its persistence in disturbed secondary forest. Species feeding on lower trophic levels in old-growth forest were less likely to persist in secondary forest than those occupying a higher trophic position in old-growth forest. This pattern is likely induced by the invasion of relatively large-bodied secondary forest specialists in secondary forest that feed on various food sources high up the food chain. Secondary forest specialists thereby induced generalists occurring in secondary forest to lower their trophic position compared to those occurring in old-growth forest. To our knowledge, this is the first study to show a systematic effect of trophic position on the persistence of a wide array of bird species in a disturbed forest ecosystem, therefore providing critical new insights into species' responses to habitat degradation and the conservation value of secondary forests.

Keywords: forest disturbance, habitat degradation, secondary forest, stable isotopes, understory birds, trophic position, trophic niche width

Table of Contents

1. Introduction

Habitat loss and degradation are main drivers of species extinction in the current biodiversity crisis (Barnosky et al. 2011). In tropical biodiversity hotspot areas such as Mesoamerica (Barlow et al. 2018; Brooks et al. 2002), biodiversity seems to be even more vulnerable to habitat degradation than in temperate areas (Edwards et al. 2014; Stratford & Robinson 2005; Tobias et al. 2013). While tropical rainforest ecosystems are highly threatened by ongoing deforestation (Keenan et al. 2015; Potapov et al. 2017), secondary forest areas are expanding and therefore play an important role in the conservation of tropical forest biodiversity (Barlow et al. 2007; Chazdon et al. 2009; Wright 2005). Thus, research is increasingly focusing on the question which traits enable some species to utilize degraded habitats while others cannot do so (Koh et al. 2004; Newbold et al. 2013; Öckinger et al. 2010; Pavlacky et al. 2015; Socolar & Wilcove 2019). A general understanding of the factors involved herein is not only vital to determine a species' response to habitat degradation and its resulting conservation concern, but may enable assessments of possible consequences for the functioning of whole ecosystems and the delivery of ecosystem services (Hooper et al. 2005; Newbold et al. 2013; Sekercioğlu et al. 2004).

In particular, little is known about how a species' trophic position or trophic niche width influences its potential to live in degraded habitats, and about the way trophic interactions change due to forest degradation (Edwards et al. 2013; Hamer et al. 2015), although the consequences of changes in the network of trophic interactions can be far-reaching (Estes et al. 2011; Terborgh et al. 2001). For instance, habitat degradation as well as trophic changes in an ecosystem are among the causes which lead to the observed rise of infectious diseases all around the globe, including the ongoing COVID-19 pandemic (Lorentzen et al. 2020; Pongsiri et al. 2009; Smith et al. 2014; Whitmee et al. 2015).

For birds, which are the best studied animal taxon in tropical regions (Hill & Hamer 2004), it has been shown that a species' trophic niche width rather than its trophic position determines its persistence in intensively logged compared to unlogged forest when analysing presence-absence data for a wide array of understory bird species (Edwards et al. 2013). However, in the same study area on the island of Borneo, changes in abundances of insectivorous birds in response to logging were related to the species' trophic position (Hamer et al. 2015). These contrasting results gave rise to call for additional data on this highly relevant topic to conservation (Hamer et al. 2015). In this study we therefore investigated − to our knowledge for the first time in the Neotropical realm –disturbance effects on the trophic position and niche width of forest understory birds in another biogeographic region and also in a different forest disturbance regime. While Edwards et al. (2013) and Hamer et al. (2015) analysed the effects of selective logging on the trophic positions and trophic niche widths of understory bird species assemblages, we compared old-growth forest and young secondary forest. This difference was deliberately chosen, not only to deepen the understanding of the conservation value of this globally emerging forest type (Wright 2005), but also because bird species assemblages respond differently to different forms of forest disturbances (Durães et al. 2013; Moura et al. 2013).

The trophic position of an organism represents the number of feeding links separating it from the producer level (Thompson et al. 2007), and can be quantified using stable isotope analysis (Bearhop et al. 2004; Layman et al. 2012; Post 2002). The ratio of ^{15}N to ^{14}N (expressed as $\delta^{15}N$) in an organism's tissue is enriched by ~ 2 – 3 ‰ with each trophic transfer up the food chain (Caut et al. 2009; Perkins et al. 2014; Vanderklift & Ponsard 2003), and thus indicates the organism's trophic position during the period of synthesis of the respective tissue (Bearhop et al. 2003; Blüthgen et al. 2003; Caut et al. 2009). Consequently, the variation in the trophic position of individual birds from the same species can provide a measure for that species' population trophic niche width (Bearhop et al. 2004).

In this study, we used stable isotope analysis to compare the trophic positions and trophic niche widths of understory bird species between old-growth forest and secondary forest in the Pacific lowlands of southwestern Costa Rica, aiming to test the following three hypotheses:

1.) The trophic positions of birds in secondary forest are higher than in old-growth forest due to dietary shifts and increased trophic positions of prey species (Blüthgen et al. 2003; Edwards et al. 2013; Hamer et al. 2015; Kemp 2018; Woodcock et al. 2013).
2.) The trophic niche widths of old-growth forest bird species are larger than those of secondary forest species as the individuals of every species have access to more diverse food sources in the old-growth forest (Edwards et al. 2013; Kemp 2018).

3.) A species’ trophic niche width rather than its trophic position determines which of the old-growth forest species can persist in the secondary forest, with dietary specialists being more vulnerable to habitat destruction than generalists (Edwards et al. 2013).

2. Methods

Study area

The study area was located in southwestern Costa Rica, east of the Golfo Dulce, at the edge of the Piedras Blancas National Park and the Esquinas Rainforest in the vicinity of the village La Gamba and the Tropical Research Station La Gamba (N 08°42.063′, W 083°12.102′, 70 m a.s.l.). This area is considered both, a faunistic and floristic biodiversity hotspot (Hammel et al. 2004; Lobo & Bolaños 2005; Weissenhofer et al. 2008b), with 2700 species of vascular plants (Huber et al. 2008), about half of the butterfly species known from Costa Rica (Wiemers & Fiedler 2008), and more than 300 bird species (Tebb 2008) recorded. Among those are several range-restricted species qualifying the region as an Endemic Bird Area (EBA 021: South Central American Pacific Slope). More than 50 % of this EBA's range-restricted bird species occur abundantly in the forests around the Golfo Dulce (BirdLife International 2020; Stattersfield et al. 1998). Those forests are classified as tropical lowland wet forests and form the most common natural vegetation type in the study area (Weissenhofer et al. 2008b).

The region's climate is characterized by high annual precipitation (~6000 mm), with most rainfall from August to November (~700 mm per month) and January to March being the driest months (~200 mm per month; Weissenhofer & Huber 2008). The annual mean temperature is 28.5 °C, and is relatively constant throughout the year (Weissenhofer & Huber 2008).

Selection of mist netting sites

We conducted this study at five old-growth and four young secondary forest sites (Figure 1). We chose the respective spatial replicates of the two forest types in accordance with the existing vegetation maps of the region (Höbinger et al. 2012; Weissenhofer et al. 2008b) and two maps identifying pieces of land where reforestation measures had been implemented in the last 15 years (Tropenstation La Gamba 2017; Weissenhofer et al. 2008a). Although the vegetation at the selected old-growth forest sites is classified as primary in the cited literature, we prefer to use the term 'old-growth forest' rather than 'primary forest', as it is almost impossible to still find pristine, undisturbed forest patches anywhere on earth (Vitousek 1997; Willis et al. 2004). The secondary forest sites were characterized by dense undergrowth with some old remnant trees, which served as shadow trees on these pieces of land formerly used as pastures or farmland (Tropenstation La Gamba 2017, 2020; Weissenhofer et al. 2008a). They were located in the vicinity of existing, substantially older forest fragments and were therefore selected for implementing reforestation measures, in order to close forest gaps and to serve as biological corridors (Tropenstation La Gamba 2017, 2020; Weissenhofer et al. 2008a). Studies in tropical forests have shown that mist netting sites more than 200 m apart are statistically independent (Hill & Hamer 2004; Whitman et al. 1998). In this study, the minimum distance between two sampling sites was 400 m (Figure 1) and, indeed, we did not re-catch a single bird at two different sites throughout the whole study period.

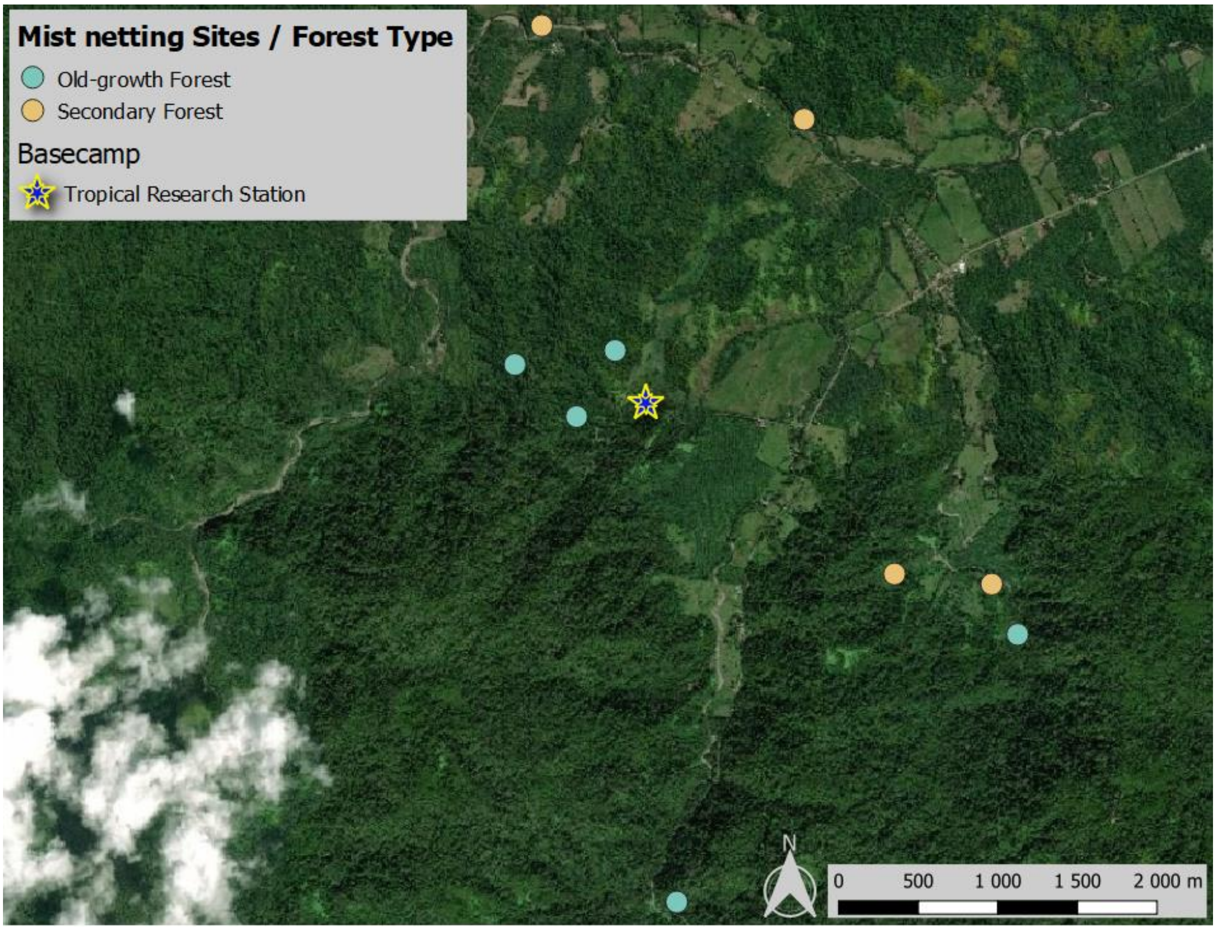

Figure 1: Map indicating the locations of the nine sampling sites and the respective forest type surrounding them. The location of the Tropical Research Station La Gamba is provided for orientational reasons only.

Avifaunal and vegetation sampling

We conducted fieldwork between 16 November 2017 and 28 January 2018. At every site, we set up six mist nets (Ecotone, Poland; length: 12 m, height: 2.5 m; number of shelves: 4, mesh size: 2 nets with 16 mm, 2 nets with 30 mm, 2 nets with 45 mm) along a linear transect to trap understory birds. Mist-netting was conducted from 05:30 AM until 03:00 PM on the first sampling day and from 05:30 AM until 11:00 AM on the second day at one site. If heavy rain forced us to close the mist nets, the missing trapping time was added to the end of the period whenever possible. After each two-day period, we moved the nets and set them up at the next site for the following two consecutive sampling days. We conducted four sampling rounds. Within those, we randomly chose the order of the sites, but we did not sample a site twice within less than eight days. In the last sampling round, we added three mist nets (Ecotone, Poland; length: 12 m long, height: 2.5 m; number of shelves: 4, mesh size: 16 mm) at every transect to increase the sample size. However, at two secondary forest sites, this was not possible due to unsuitable terrain. Nevertheless, we obtained a relatively balanced sample for data analysis (see: Results).

We identified trapped birds to species level following Garrigues & Dean (2014) and Stiles & Skutch (1989). The nomenclature used in this paper follows Garrigues & Dean (2014). English names are used throughout the text, a table with corresponding scientific names is provided in the Supplementary Material (Supplementary Table A). To avoid pseudoreplication, we marked trapped birds individually using plastic colour rings or metal bird rings. Then, we took nail clippings of each bird's central front and rear claws and stored them in labelled vials for stable isotope analysis as claw material integrates the bird's diet over a period of several weeks (Bearhop et al. 2003). Standard morphological measurements were taken, such as body weight, wing length, tarsus length as well as bill length and width following Eck et al. (2011) before we released the bird. We excluded migratory bird species and hummingbirds (Trochilidae) from nail clipping collection because claw material of the former almost certainly would not have grown entirely in the sampling area (Bearhop et al. 2003) and because of the high risk of injury to the small feet of the latter.

In addition, we collected leaves along the mist nets halfway through the sampling period to determine the baseline $\delta^{15}N$ of the primary producers at every site, against which the $\delta^{15}N$ of the collected claw material could be assessed (Woodcock et al. 2012). Every 3 m we picked a leaf, either from ankle height, waist height or 2 m above the ground. Thus, we collected 24 leaves (8 per height class) per site, placed them in a drying chamber at 40 °C to 50 °C for 24 hours and then stored them in labelled paper bags. Moreover, to facilitate data interpretation, halfway through the study period we also collected fruits, moths and spiders at every transect. These represent important food items for birds and different trophic positions in the local food webs. Moths (herbivores: trophic level two) were caught with a light-trap, which we attached to a tree in the middle of the transect and operated for one night. We collected caught animals in the early morning, put them in a freezer for several hours and dried the sample in a drying chamber at 40 °C to 50 °C for 24 hours afterwards. To reduce the heterogeneity of moth samples only individuals of groups most likely feeding on vascular plants were considered (e.g. Lithosiinae which often feed on lichens were excluded; compare Adams et al. 2016). Finally, moth samples were stored in labelled paper bags. Fruits and spiders were collected by hand around the mist netting transects. We picked all apparently different kinds of fruits we found in a radius of 50 m around the transects, placed them in a drying chamber at 40 °C to 50 °C for 24 hours and then stored fruit samples in labelled paper bags. We cut large fruits into pieces before drying and aimed to include different states of ripening in our sample. Thus, if we found a fruit type in different colourations or states of consistency, we picked one representative fruit for each colouration or state. We also collected 10 apparently different kinds of spiders (carnivores: trophic level three) within a radius of 50 m around the mist nets and handled the sample in the same way as the moth samples. We collected one composite fruit, moth and spider sample for every transect.

Stable isotope analyses

All stable isotope analyses were performed at the Stable Isotope Laboratory of the Leibniz Institute for Zoo and Wildlife Research (IZW), Berlin, Germany. We only analysed claw samples from bird species with at least $n \geq 5$ replicates in one forest type. Prior to analysis, we treated all samples from animals with a 2:1 chloroform/methanol solution (v/v) for 24 hours to remove lipids and external contaminants. For larger moths, we selected the thorax for isotopic analysis, assuming that this body part does not deviate significantly from others with respect to isotopic composition. Then, we re-dried all samples for 24 hours in a drying oven at 50 °C and ground leaves, fruits, moths, spiders and claws in a ball mill. Hereafter, we used a high-precision balance to transfer 0.5 mg of animal samples and 1.5 mg of plant samples into tin capsules. We used a Flash EA 1112 Series elemental analyser connected via a ConFlo III interface to a Delta V Advantage isotope ratio mass spectrometer (all Thermo Scientific, Bremen, Germany). We report values in $\delta^{15}N$ notation as parts per mil (‰) deviation of the ratio $^{15}N{:}^{14}N$ of the sample from that in atmospheric nitrogen. The precision of the measurements was always better than 0.15 ‰.

We calculated the trophic position of each sampled understory bird as $\lambda + (\delta^{15}N_{bird} - \delta^{15}N_{baseline\ organism}) / E$, where λ is the trophic level of the organisms used to estimate

$\delta^{15}N_{\text{baseline organism}}$ (λ = 1 for plants used in this study) and E is the enrichment in $\delta^{15}N$ per trophic level (Post et al. 2000). For the value of $\delta^{15}N_{\text{baseline organism}}$ we used the $\delta^{15}N$ for the 24 leaves collected from the same mist netting site from where the bird's claw material was collected (Woodcock et al. 2012). According to two extensive reviews, we chose a value of E = 2.5 as an appropriate trophic enrichment factor for our study system (Caut et al. 2009; Edwards et al. 2013; Vanderklift & Ponsard 2003). We calculated the trophic niche widths for each species as the standard deviation of the sampled individuals' mean trophic position. We used the same equation and the $\delta^{15}N$ from the fruit, moth and spider samples to calculate the respective trophic position of these samples.

Statistical analyses

Statistical analyses were conducted to test for differences in trophic position and niche width, both between the two forest types and the three species categories 'old-growth forest specialists', 'secondary forest specialists' and 'generalists'. Therefore, we assigned species to these categories by their respective presence in old-growth forest, secondary forest or both. A species was classified as characteristic of one of the forest types only if it occurred at more than one study site of that specific forest type, because records at a single site might occur by chance. As we only analysed claw samples from species with $n \geq 5$ samples in one forest type, those with a smaller sample size were neither assigned to a species category nor included in any statistical analyses.

We used phylogenetically informed Gaussian Bayesian Markov chain Monte Carlo generalized linear mixed models (MCMCglmms) in R v. 3.5.1 (package: MCMCglmm v. 2.29) to test for differences in the trophic positions of individual birds between the two forest types and three species categories (Hadfield 2010, 2019; Hadfield & Nakagawa 2010; R Core Team 2018). To account for respective species affiliation and phylogenetic non-independence between species in the models, we used two samples, each consisting of 1000 phylogenetic trees, downloaded from the BirdTree project (http://birdtree.org; Jetz et al. 2012), once using the backbone by Hackett et al. (2008) and once using the backbone by Ericson et al. (2006). We generated two 50 % consensus trees based on these samples using the least-squares method in the R package phytools v. 0.6-99 (Revell 2012). Consequently, we ran the MCMCglmms twice, with the species-specific edge lengths of the two consensus trees included as random effect – first the one and then the other. As the results differed only marginally, we calculated all reported outputs using the backbone by Hackett et al. (2008). To test for differences in trophic position of bird species between forest types, we built a model with forest type included as fixed effect and phylogeny as random effect (Trophic Position Model 1 = TPM1). We added species category as a second fixed effect in a second model to test for differences in trophic position of individual birds between forest types and species categories (TPM2). In order to calculate all pairwise comparisons between the factors forest type and species category necessary for final data interpretation, we ran this model two more times: once with reversed factor level order for forest type (TPM3) and once only with species category as fixed effect (TPM4). For all models, we used weakly informative priors (V = 1, nu = 0.002) corresponding to an inverse-Gamma distribution and specified 5 000 000 Monte Carlo iterations with a burn-in of 1000 and thinning of 500. All models converged according to visual inspection of their trace plots, and the Gelman-Rubin statistic was always < 1.1 for all parameters (Gelman et al. 2014; Roy 2020). We used the parameter estimations from TPM2 and the "predict"-function implemented in the MCMCglmm package to calculate the mean trophic position for every species category and its 95 % credible intervals (Hadfield 2010; Hadfield & Nakagawa 2010).

To test for differences in species' trophic niche widths between forest types and species categories, we also used four MCMCglmms in R v. 3.5.1 (Hadfield 2010, 2019; Hadfield & Nakagawa 2010; R Core Team 2018): one with forest type as fixed effect (trophic niche width model 1 = TNWM1), one with forest type and species category as fixed effect (TNWM2), which we ran a second time with reversed factor level order for forest type (TNWM3), and one with only species category as fixed effect (TNWM4). The model specifications were the same as above. All models converged according to visual inspection of their trace plots, and the Gelman-Rubin statistic was always < 1.1 for all parameters (Gelman et al. 2014; Roy 2020). However, we did not include a phylogenetic tree as random effect in these analyses, because our sample size was too small and model convergence was otherwise not achieved. Instead, to check for phylogenetic non-independence, we calculated pairwise Mantle tests with 9999 permutations in Past v. 4.02 between the phylogenetic relatedness matrices of each set of species and their respective Euclidean distances in trophic niche widths (12 Mantle tests, all $p > 0.3$; Hammer et al. 2001). We calculated every pairwise comparison twice, once with the phylogeny based on the backbone by Hackett et al. (2008) and once by Ericson et al. (2006). We used the parameter estimations from TNWM2 and the "predict"-function implemented in the MCMCglmm package to calculate the mean trophic niche width for every species category and its 95 % credible intervals (Hadfield 2010; Hadfield & Nakagawa 2010).

To check for spatial autocorrelation in this dataset, we calculated a linear model of the species' mean trophic positions at every sampling site within each forest type in R v. 3.5.1 (R Core Team 2018). We used the site-specific model residuals hereafter to calculate a matrix with Euclidean distances between those, and checked for a significant correlation with a matrix containing all pairwise linear distances between the sites using a Mantle test with 9999 permutations in Past v. 4.02 ($p = 0.85$; Hammer et al. 2001). We repeated this procedure three times, testing the site-specific residuals of the mean trophic positions of the three most caught bird species for a significant correlation with the pairwise linear distance matrix (all p-values > 0.09). Therefore, we are confident that the spatial arrangement of our study sites did not affect our analyses.

All obtained p-values were adjusted using the “p.adjust”-function and the method proposed by Benjamini & Hochberg (1995) in R v. 3.5.1 (R Core Team 2018). None of the obtained p-values < 0.05 were > 0.05 after the adjustment.

3. Results

We obtained $\delta^{15}N$ values from 22 bird species (n = 275 birds) in old-growth forest (6 species categorized as habitat specialists: n = 57 birds, 14 species as habitat generalists: n = 218 birds) and from 23 species (n = 293 birds) in secondary forest (7 species categorized as habitat specialists: n = 67 birds, 14 species as habitat generalists: n = 226 birds; Figure 2).

Birds had a significantly higher trophic position in old-growth forest than in secondary forest (MCMCglmm, TPM1: $p < 0.0001$; Table 1). When taking species categories into account, old-growth forest specialists had a lower trophic position than generalists occurring in old-growth forest (MCMCglmm, TPM2: $p = 0.017$; Table 1, Figure 3). These generalists significantly lowered their trophic position when occurring in secondary forest (MCMCglmm, TPM2: $p < 0.0001$), where they had a lower trophic position than secondary forest specialists (MCMCglmm, TPM3: $p < 0.0001$; Table 1, Figure 3). Therefore, trophic position determined species persistence in secondary forest. Old-growth forest specialists also had a lower trophic position than secondary forest specialists (MCMCglmm, TPM4: $p < 0.0001$; Table 1, Figure 3). Hence, the overall higher trophic position of birds in old-growth forest is not a result of species turnover, but rather a consequence of habitat generalists changing their trophic position when occurring in different forest types.

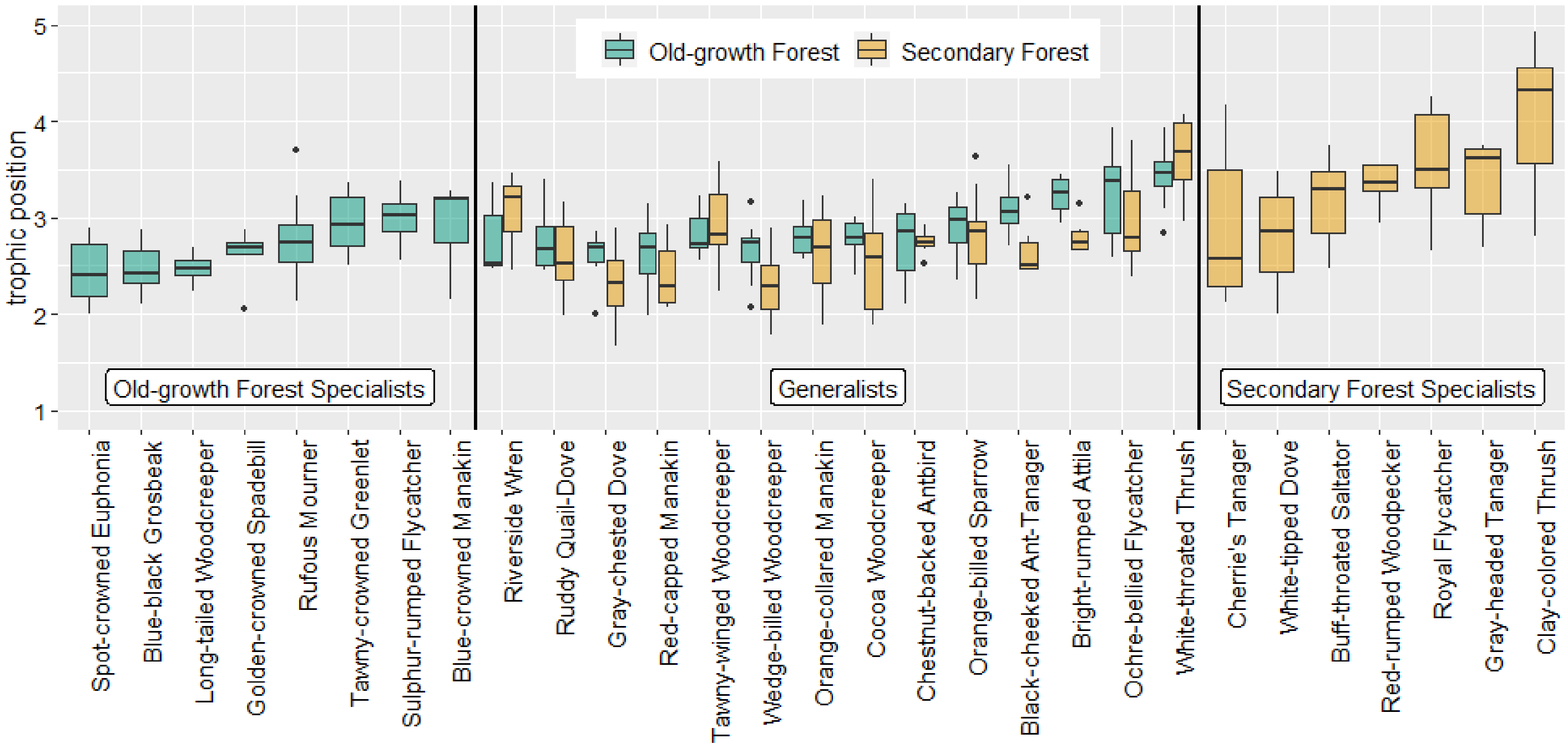

Figure 2: Calculated median trophic positions of all birds and respective species analysed in this study. Boxes depict the interquartile range, whiskers minimum/maximum values within 1.5 times the interquartile range. Species categories relevant for data interpretation are separated by continuous black vertical lines. Within these, species are ordered by increasing median trophic position in old-growth forest or secondary forest, respectively. n ≥ 5 claw samples for every species in each forest type.

Table 1: Model outputs of the four trophic position models (TPM1 - 4) calculated in this study. All models were phylogenetically informed Markov chain Monte Carlo (MCMC) generalized linear mixed models. eff. samp. = effective sample size, G = generalist, l-95% CI = lower 95 % credible interval, u-95% CI = upper 95 % credible interval, OF = old-growth forest, OS = old-growth forest specialists, post. = posterior, SF = secondary forest, SS = secondary forest specialists.

TPM1: Location effects: trophic_position ~ forest					
	post. mean	l-95% CI	u-95% CI	eff. samp.	*pMCMC*
(Intercept)	3.0306	2.4484	3.5829	9998	< 0.0001
forestSF	-0.1703	-0.2436	-0.0921	9998	< 0.0001
G - structure: ~ species					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
species	0.3966	0.1716	0.6715	9998	
R - structure: ~ units					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
units	0.1422	0.1253	0.1591	10417	
TPM2: Location effects: trophic_position ~ forest + species_category					
	post. mean	l-95% CI	u-95% CI	eff. samp.	*pMCMC*
(Intercept)	2.9114	2.5403	3.2737	9998	< 0.0001
forestSF	-0.2011	-0.2766	-0.1265	9998	< 0.0001
species_categoryOS	-0.2461	-0.4531	-0.0489	9998	0.0172
species_categorySS	0.5685	0.3466	0.7884	9998	< 0.0001
G - structure: ~ species					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
species	0.1473	0.0617	0.2516	10259	
R - structure: ~ units					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
units	0.1416	0.1251	0.1585	9998	
TPM3: Location effects: trophic_position ~ factor(forest, levels = c("SF", "OF") + species_category)					
	post. mean	l-95% CI	u-95% CI	eff. samp.	*pMCMC*
(Intercept)	2.7096	2.3257	3.0606	9998	< 0.0001
forestOF	0.2022	0.1264	0.2752	9998	< 0.0001
species_categoryOS	-0.2461	-0.4436	-0.0348	9998	0.0204
species_categorySS	0.5694	0.3465	0.7866	9998	< 0.0001
G - structure: ~ species					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
species	0.1482	0.0625	0.2534	9998	
R - structure: ~ units					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
units	0.1415	0.1251	0.1588	9998	
TPM4: Location effects: trophic_position ~ factor(species_category, levels=c("OS", "SS", "G"))					
	post. mean	l-95% CI	u-95% CI	eff. samp.	*pMCMC*
(Intercept)	2.6565	2.2658	3.0322	9653	< 0.0001
species_categorySS	0.6122	0.3520	0.8831	9424	< 0.0001
species_categoryG	0.1536	-0.0433	0.3585	9694	0.134
G - structure: ~ species					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
species	0.1461	0.0596	0.2478	9998	
R - structure: ~ units					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
units	0.1486	0.1309	0.1662	9998	

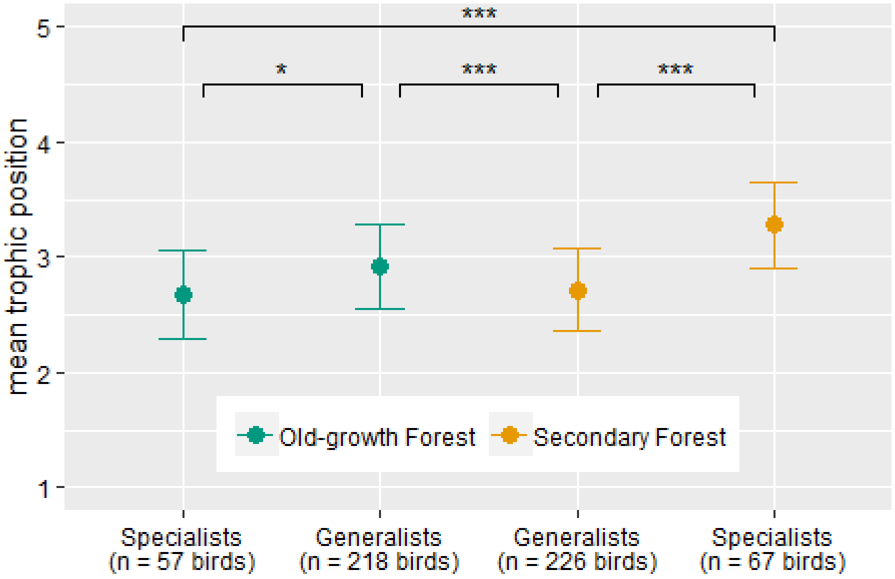

Figure 3: Posterior means (± 95 % credible intervals) of the trophic positions of the four bird species categories. Values were calculated using trophic position model 2 (TPM2; Table 1). Indicated *p*-values correspond to the respective pairwise species category comparisons (TPM2 - TPM4; Table 1). * = $p < 0.05$, *** = $p < 0.001$.

The species' trophic niche widths were smaller in old-growth forest than in secondary forest (MCMCglmm, TNWM1: $p = 0.005$; Table 2). Old-growth forest specialists did not differ from generalists occurring in old-growth forest in their trophic niche widths (MCMCglmm, TNWM2: $p = 0.409$; Table 2, Figure 4). Also, generalists did not significantly change their trophic niche widths when occurring in different forest types (MCMCglmm, TNWM2: $p = 0.101$; Table 2, Figure 4). However, generalists occurring in secondary forest had smaller trophic niche widths than secondary forest specialists (MCMCglmm, TNWM3: $p < 0.0001$; Table 2, Figure 4). Old-growth forest specialists had smaller trophic niche widths than secondary forest specialists (MCMCglmm, TNWM4: $p = 0.001$; Table 2, Figure 4). Hence, the overall smaller trophic niche widths observed in old-growth forest species are mainly a consequence of the partial species turnover between the two habitat types and are not caused by habitat generalists changing their trophic niche widths when occurring in old-growth forest or secondary forest, respectively.

Table 2: Model outputs of the four trophic niche width models (TNWM1 - 4) calculated in this study. All models were Markov chain Monte Carlo (MCMC) generalized linear mixed models. eff. samp. = effective sample size, G = generalist, l-95% CI = lower 95 % credible interval, u-95% CI = upper 95 % credible interval, OF = old-growth forest, OS = old-growth forest specialists, post. = posterior, SF = secondary forest, SS = secondary forest specialists.

TNWM1: Location effects: trophic_width ~ forest					
	post. mean	l-95% CI	u-95% CI	eff. samp.	*pMCMC*
(Intercept)	0.2966	0.2439	0.3490	9998	< 0.0001
forestSF	0.1133	0.0392	0.1908	9998	0.0054
R - structure: ~ units					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
units	0.0155	0.0092	0.0228	9998	
TNWM2: Location effects: trophic_width ~ forest + species_category					
	post. mean	l-95% CI	u-95% CI	eff. samp.	*pMCMC*
(Intercept)	0.2819	0.2242	0.3404	9998	< 0.0001
forestSF	0.0693	-0.0133	0.1520	9998	0.1006
species_categoryOS	0.0397	-0.0576	0.1354	9998	0.4089
species_categorySS	0.1758	0.0726	0.2753	9998	0.0018
R - structure: ~ units					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
units	0.0122	0.0072	0.0182	9998	
TNWM3: Location effects: trophic_width ~ factor(forest, levels = c("SF", "OF") + species_category)					
	post. mean	l-95% CI	u-95% CI	eff. samp.	*pMCMC*
(Intercept)	0.3515	0.2952	0.4104	9998	< 0.0001
forestOF	-0.0690	-0.1522	0.0097	9998	0.0904
species_categoryOS	0.0396	-0.0571	0.1347	8855	0.4173
species_categorySS	0.1755	0.0744	0.2721	9998	< 0.0001
R - structure: ~ units					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
units	0.0121	0.0072	0.0179	9998	
TNWM4: Location effects: trophic_width ~ factor(species_category, levels=c("OS", "SS", "G"))					
	post. mean	l-95% CI	u-95% CI	eff. samp.	*pMCMC*
(Intercept)	0.3220	0.2458	0.4010	9998	< 0.0001
species_categorySS	0.0206	0.0933	0.3240	10677	0.0012
species_categoryG	-0.0050	-0.0976	0.0800	10732	0.9064
R - structure: ~ units					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
units	0.0128	0.0077	0.0188	9998	

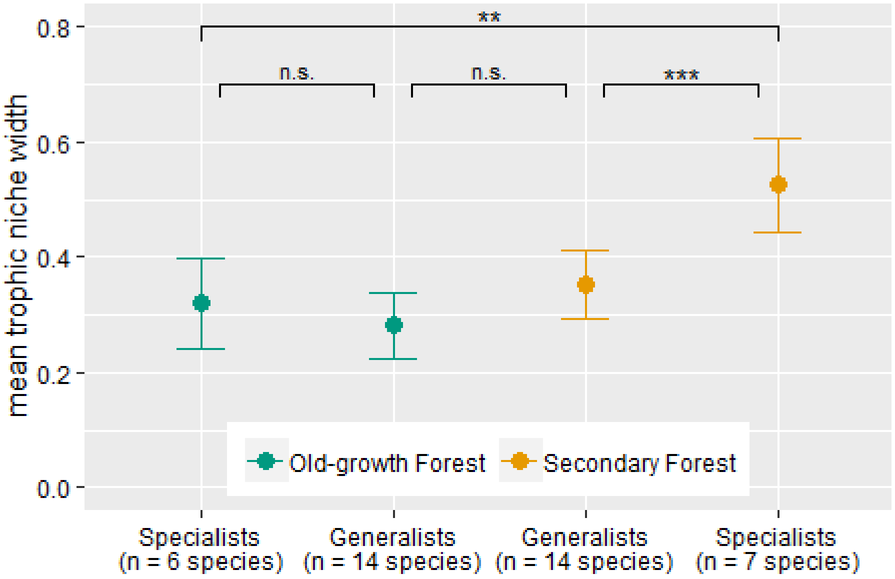

Figure 4: Posterior means (± 95 % credible intervals) of the trophic niche widths of the four bird species categories. Values were calculated using trophic niche width model 2 (TNWM2; Table 2). Indicated *p*-values correspond to the respective pairwise species category comparisons (TNWM2 - TNWM4; Table 2). n.s. = not significant, ** = $p < 0.01$, *** = $p < 0.001$.

4. Discussion

Mean trophic positions of species analysed in this study ranged from 2.29 ± 0.30 to 4.09 ± 0.67 (mean ± SD), which is generally in line with literature classifying the sampled species as frugivorous, omnivorous or insectivorous (Garrigues & Dean 2014; Stiles & Skutch 1989). Krebber (2019) analysed faecal samples of the understory bird species in the same study area and frequently found arthropod parts in the faeces of all bird species investigated, even those regarded as obligate frugivores such as all Manakin species (Pipridae). For Manakins, similar results were also found in eastern Ecuador (Fair et al. 2013). Therefore, mean trophic positions > 2 appear to be plausible even for frugivorous bird species such as Manakins (Edwards et al. 2013; Ferger et al. 2013). Insectivorous bird species are known to feed on fruits occasionally, especially in the rainforest understory, therefore trophic positions < 3 for presumed insectivores are frequently encountered in similar studies, as is a substantial overlap in static feeding guilds (Edwards et al. 2013; Ferger et al. 2013; Hamer et al. 2015; Herrera et al. 2003; Schleuning et al. 2011). However, it should be noted that inaccuracies in the estimations of birds' trophic positions are an inherent issue in bulk stable isotope datasets (Martínez del Rio et al. 2009; Nielsen et al. 2018). Those can only be overcome by applying multiple methods of diet tracing to the same set of species (Nielsen et al. 2018), which was beyond the scope of this study. However, as species' diets and trophic niches are often difficult to assess, especially for small bird species occurring in dense rainforest understory, and as our resulting trophic positions are generally in line with the literature, we are confident that our approach is suitable to shed light on the outlined research hypotheses (Edwards et al. 2013; Hamer et al. 2015; Herrera et al. 2003; Layman et al. 2012).

Unexpectedly, we found lower trophic positions in secondary forest birds compared to those occurring in old-growth forest. Changes in trophic position do not necessarily indicate dietary shifts or prey species changing their trophic positions, but can also arise from variation in the nitrogen isotopic signature of the baseline organisms used for the calculation of trophic positions, or from varying body conditions between groups (Gorokhova 2017; Hobson et al. 1993; Martínez del Rio et al. 2009; Woodcock et al. 2012). However, we accounted for local differences in baseline isotopic ratios by using sampling site-specific $\delta^{15}N$ values of plants in the calculation of trophic positions (Woodcock et al. 2012). In addition, there was no difference in size-corrected body mass between generalists occurring either in old-growth forest or secondary forest, indicating no substantial difference in body condition between forest types (MCMCglmm: $p = 0.75$; Supplementary Table B). Therefore, we are confident that our findings represent fundamental changes in birds' trophic position after habitat degradation. Importantly, the observed overall decrease in birds' trophic positions was caused by habitat generalists, which had a lower trophic position when occurring in secondary forest than in old-growth forest. This pattern is opposite to findings for birds, bats and ants from the island of Borneo, where species and/or individuals occurring in selectively-logged rainforest had a higher trophic position than those in unlogged forest (Edwards et al. 2013; Hamer et al. 2015; Kemp 2018; Woodcock et al. 2013). Blüthgen et al. (2003) also documented increased trophic positions of ants from naturally regenerating forest compared with mature wet forest in Australia, and this pattern is also known from the aquatic realm (Power et al. 2008). However, disturbance was also shown to decrease trophic positions in ants and aquatic organisms (Fox et al. 2009; Gibb & Cunningham 2011; Kim et al. 2019; McHugh et al. 2010).

In this study, we documented disturbance-induced decreased trophic positions in understory birds for the first time. A reduction in avian trophic position can be observed when birds feed from lower trophic levels and/or when their prey reduced its trophic position (Edwards et al. 2013; McHugh et al. 2010; Post et al. 2000; Post & Takimoto 2007). Although the sample size was small, trophic positions of fruits, moths and spiders sampled around the study sites showed no systematic difference between forest types (3 Mann-Whitney-U-Tests: $p > 0.28$: Supplementary Table C). Thus, there is no reason to assume substantial changes in trophic positions of important avian dietary components. Interestingly, specialists in old-growth forest had significantly lower body mass than those in secondary forest (old-growth forest: $n = 8$, median = 12.48 g; secondary forest: $n = 7$, median = 30.71 g; *Mann-Whitney-U* = 9, $p = 0.032$), had a smaller trophic niche width than those in secondary forest and a lower trophic position than generalists occurring in old-growth forest. But the heavier secondary forest specialists had a higher trophic position than generalists in the same habitat and wider trophic niche widths. Therefore, it is more likely that the observed changes in trophic positions of habitat generalists are a result of competitively induced dietary shifts than a consequence of trophic changes in main food sources. However, this needs to be confirmed in future studies.

Following the definition of food chain length by Post & Takimoto (2007), we found a marked increase in food chain length from old-growth forest (highest mean trophic position of all bird species: 3.46 ± 0.29) towards secondary forest (highest mean trophic position of all bird species: 4.09 ± 0.67). This is similar to findings by Hamer et al. (2015) and Woodcock et al. (2013) for birds and ants, respectively, who found an increase in food chain length from unlogged towards selectively logged forest on the island of Borneo. The reason for these observations could be the high productivity of certain disturbed rainforest types, such as selectively logged forest on the island of Borneo or secondary forest in the Pacific lowlands of Costa Rica (Berry et al. 2010; Hamer et al. 2015; Oberleitner 2016; Takimoto & Post 2013; Wanek et al. 2008).

As we could measure trophic niche width on the species level only and not on the individual level, as was the case for trophic position, sample size was small for the comparison of trophic niche widths between forest types and species categories. Therefore, it may well be possible that additional sampling could yield even more insights into changes in trophic niche widths due to forest disturbance. In our dataset, we found significantly smaller trophic niche widths in bird species occurring in old-growth forest compared to those occurring in secondary forest. This means that birds consumed a more diverse diet in secondary forest, at least in terms of the trophic positions of their ingested food items (Edwards et al. 2013). This difference was largely due to secondary forest specialists having larger trophic niche widths than old-growth forest specialists. As dietary specialists are less likely to persist in disturbed habitats (Edwards et al. 2013; Newbold et al. 2013), large trophic niche widths in secondary forest specialists should be expected. Interestingly, generalists also had slightly larger trophic niche widths when occurring in secondary forest, although this difference was not significant. Our data, therefore, do not support the hypothesis that trophic niche widths are compressed due to a restricted resource diversity at lower trophic levels in disturbed habitats, which is well documented for other taxa and ecosystems (Burdon et al. 2020; Crowley et al. 2012; Edwards et al. 2013; Kemp 2018; Layman et al. 2007). While data of the cited studies are – to our knowledge – most likely not affected by corridor effects, the secondary forest patches studied here were selected for reforestation measures because of their suitability to serve as biological corridors (Weissenhofer et al. 2008a). As corridors increase the movement of organisms between habitat patches (Gilbert-Norton et al. 2010), it is likely that mobile organisms using these temporarily increase the available resource diversity for birds (Resasco et al. 2012). Additionally, the catchment area around the mist nets from where we sampled birds may also be increased due to corridor effects. Competition is another factor which can influence dietary breadth, with a higher amount of competitors leading to a narrower dietary or trophic niche (Fründ et al. 2013; Inouye 1978; Kim et al. 2019; Pacala & Roughgarden 1982). In our dataset, mean trophic positions of the 22 bird species in old-growth forest ranged from 2.45 ± 0.37 to 3.46 ± 0.29. Only 15 bird species occupied the same trophic range in secondary forest, with the 6 remaining species having a trophic position above or below this range. Therefore, a wider occupied range of trophic positions and reduced interspecific competition could have resulted in non-contracted trophic niche widths in generalists occurring in secondary forest despite forest disturbance. Another possible explanation for the missing niche width contraction in this dataset could again be provided by the high primary productivity in the studied secondary forest ecosystem, analogues to what Miller et al. (2019) recently documented, i.e. niche width expansion along a primary productivity gradient in coral reef fish. Whatever the underlying reasons for the observed patterns in trophic niche widths are, non-contracted trophic niche-widths in bird species persisting in secondary forest highlight the already described high conservation value of this habitat (Schulze et al. 2019). Because studies showed that species with small trophic niche widths are less likely to persist after disturbance events, non-contracted trophic niche widths render these species more resilient to future impacts compared to those persisting with contracted trophic niche widths, as documented in selectively logged forest in Borneo (Boyles & Storm 2007; Edwards et al. 2013; Öckinger et al. 2010).

A species’ trophic position rather than its trophic niche width determined species persistence after disturbance in our dataset, contrary to our research hypothesis (Edwards et al. 2013). Hamer et al. (2015) already observed that insectivorous bird abundance post-logging is related to trophic position, with species occupying high trophic positions in primary forest being most negatively affected by selective logging. Farneda et al. (2015) documented a similar effect of trophic position on the prevalence and abundance of Amazonian bats in forest fragments, again with bat species occupying a high trophic position being most adversely affected. However, Gray et al. (2007) and Newbold et al. (2013) identified frugivorous as well as insectivorous forest specialists as the bird species groups most susceptible to tropical forest disturbance and intensified land use, respectively. Recently, a worldwide analysis showed that small herbivorous bird species are disproportionally affected by human habitat alteration (Atwood et al. 2020), and Sekercioğlu et al. (2002) pointed out that, among tropical forest birds, small understory insectivores are most sensitive to forest disturbance and fragmentation. The set of species categorized as old-growth forest specialists in our study corresponds to these findings, as it consists of 2 species of frugivores (Blue-crowned Manakin, Spot-crowned Euphonia), 4 insectivorous species (Golden-crowned Spadebill, Long-tailed Woodcreeper, Sulphur-rumped Flycatcher, Tawny-crowned Greenlet) and two omnivores (Blue-black Grosbeack, Rufous Mourner; Garrigues & Dean 2014; Stiles & Skutch 1989). Another factor which can explain tropical forest bird species' extinction histories and current distribution patterns is dispersal limitation (Moore et al. 2008). However, if dispersal limitations played a role in the presence-absence pattern of bird species in our dataset, it would be extremely unlikely to record such a clear pattern of trophic position determining species persistence in secondary forest after disturbance. In addition, we recorded Chestnut-backed Antbirds in both habitat types, a species which is among the most reluctant tested to cross open-water gaps 100 m wide (Moore et al. 2008).

Therefore, we conclude that species which fed on low trophic levels in old-growth forest were less likely to persist in secondary forest than those occupying a higher trophic position in old-growth forest. This pattern is most likely induced by the invasion of relatively large-bodied secondary forest specialists in disturbed forest feeding on various food sources high up the food chain, thus inducing generalists also occurring in secondary forest to lower their trophic position compared to those occurring in old-growth forest. This probably resulted in the competitive exclusion of some species occupying low trophic positions in old-growth forest, which were not able to lower their trophic position in secondary forest as habitat generalists occurring in secondary forest did.

To our knowledge, this is the first study to show a systematic effect of trophic position on the persistence of a wide array of bird species in a disturbed forest ecosystem. Thus, data on species' trophic positions should be incorporated in future assessments of species vulnerability to environmental changes whenever possible. In line with Edwards et al. (2013) and Hamer et al. (2015) we call for the use of flexible measures of trophic position instead of static feeding guilds, as they cannot resolve most disturbance-induced trophic changes in a food web, such as those documented in this study. Based on our findings, we strongly recommend continuing and intensifying the ongoing conservation and reforestation efforts in the region. Reforestation measures implemented in the past have already resulted in well-connected secondary forest supporting numerous old-growth forest bird species and supplying them with a broad variety of food sources. In order to improve habitat quality for old-growth forest specialists not yet occurring in these sites, forest edge and gap situations – the preferred habitat of secondary forest specialists (Garrigues & Dean 2014; Stiles & Skutch 1989) – should be minimized, and the creation of the largest possible coherent forest patches should be prioritized.

5. References

Adams, M.-O., C. L. Seifert, L. Lehner, C. Truxa, W. Wanek and K. Fiedler. 2016. Stable isotope signatures reflect dietary diversity in European forest moths. Frontiers in Zoology **13**:37.

Atwood, T. B., S. A. Valentine, E. Hammill, D. J. McCauley, E. M. P. Madin, K. H. Beard and W. D. Pearse. 2020. Herbivores at the highest risk of extinction among mammals, birds, and reptiles. Science Advances **6**:eabb8458.

Barlow, J., et al. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences of the United States of America **104**:18555–18560.

Barlow, J., et al. 2018. The future of hyperdiverse tropical ecosystems. Nature **559**:517–526.

Barnosky, A. D., et al. 2011. Has the Earth's sixth mass extinction already arrived? Nature **471**:51–57.

Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller and H. Macleod. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. Journal of Animal Ecology **73**:1007–1012.

Bearhop, S., R. W. Furness, G. M. Hilton, S. C. Votier and S. Waldron. 2003. A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. Functional Ecology **17**:270–275.

Benjamini, Y. and Y. Hochberg. 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. Journal of the Royal Statistical Society: Series B (Methodological) **57**:289–300.

Berry, N. J., et al. 2010. The high value of logged tropical forests: lessons from northern Borneo. Biodiversity and Conservation **19**:985–997.

BirdLife International. 2020. Endemic Bird Areas factsheet: South Central American Pacific slope. Available from http://www.birdlife.org/.

Blüthgen, N., G. Gebauer and K. Fiedler. 2003. Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. Oecologia **137**:426–435.

Boyles, J. G. and J. J. Storm. 2007. The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. PLoS ONE **2:** https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0000672.

Brooks, T. M., et al. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology **16**:909–923.

Burdon, F. J., A. R. McIntosh and J. S. Harding. 2020. Mechanisms of trophic niche compression: Evidence from landscape disturbance. Journal of Animal Ecology **89**:730–744.

Caut, S., E. Angulo and F. Courchamp. 2009. Variation in discrimination factors (Δ 15 N and Δ 13 C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology **46**:443–453.

Chazdon, R. L., C. A. Peres, D. Dent, D. Sheil, A. E. Lugo, D. Lamb, N. E. Stork and S. E. Miller. 2009. The potential for species conservation in tropical secondary forests. Conservation Biology **23**:1406–1417.

Crowley, B. E., L. R. Godfrey, T. P. Guilderson, P. Zermeño, P. L. Koch and N. J. Dominy. 2012. Extinction and ecological retreat in a community of primates. Proceedings of the Royal Society B: Biological Sciences **279**:3597–3605.

Durães, R., L. Carrasco, T. B. Smith and J. Karubian. 2013. Effects of forest disturbance and habitat loss on avian communities in a Neotropical biodiversity hotspot. Biological Conservation **166**:203–211.

Eck, S., T. Töpfer, J. Fiebig, I. Heynen, W. Fiedler, B. Nicolai, R. van den Elzen, R. Winkler and F. Woog. 2011. Measuring birds. Christ Media Natur, Minden, Germany.

Edwards, D. P., et al. 2013. Trophic flexibility and the persistence of understory birds in intensively logged rainforest. Conservation Biology **27**:1079–1086.

Edwards, D. P., J. A. Tobias, D. Sheil, E. Meijaard and W. F. Laurance. 2014. Maintaining ecosystem function and services in logged tropical forests. Trends in Ecology & Evolution **29**:511–520.

Ericson, P. G. P., D. Zuccon, J. I. Ohlson, U. S. Johansson, H. Alvarenga and R. O. Prum. 2006. Higher-level phylogeny and morphological evolution of tyrant flycatchers, cotingas, manakins, and their allies (Aves: Tyrannida). Molecular Phylogenetics and Evolution **40**:471–483.

Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. Science **333**:301–306.

Fair, J. M., T. B. Ryder, B. A. Loiselle, J. G. Blake, T. E. Larson, P. Davis, J. Syme, G. B. Perkins and J. M. Heikoop. 2013. Estimates of dietary overlap for six species of Amazonian manakin birds using stable isotopes. Isotopes in Environmental and Health Studies **49**:420–435.

Farneda, F. Z., R. Rocha, A. López-Baucells, M. Groenenberg, I. Silva, J. M. Palmeirim, P. E. D. Bobrowiec and C. F. J. Meyer. 2015. Trait-related responses to habitat fragmentation in Amazonian bats. Journal of Applied Ecology **52**:1381–1391.

Ferger, S. W., K. Böhning-Gaese, W. Wilcke, Y. Oelmann and M. Schleuning. 2013. Distinct carbon sources indicate strong differentiation between tropical forest and farmland bird communities. Oecologia **171**:473–486.

Fox, S. E., M. Teichberg, Y. S. Olsen, L. Heffner and I. Valiela. 2009. Restructuring of benthic communities in eutrophic estuaries: lower abundance of prey leads to trophic shifts from omnivory to grazing. Marine Ecology Progress Series **380**:43–57.

Fründ, J., C. F. Dormann, A. Holzschuh and T. Tscharntke. 2013. Bee diversity effects on pollination depend on functional complementarity and niche shifts. Ecology **94**:2042–2054.

Garrigues, R. and R. Dean. 2014. The birds of Costa Rica. Cornell University Press, Ithaca, New York, United States.

Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari and D. B. Rubin. 2014. Model checking. Bayesian data analysis. Boca Raton, FL: Chapman & Hall/CRC.

Gibb, H. and S. A. Cunningham. 2011. Habitat contrasts reveal a shift in the trophic position of ant assemblages. Journal of Animal Ecology **80**:119–127.

Gilbert-Norton, L., R. Wilson, J. R. Stevens and K. H. Beard. 2010. A meta-analytic review of corridor effectiveness. Conservation Biology **24**:660–668.

Gorokhova, E. 2017. Individual growth as a non-dietary determinant of the isotopic niche metrics. Methods in Ecology and Evolution **9**:269–277.

Gray, M. A., S. L. Baldauf, P. J. Mayhew and J. K. Hill. 2007. The response of avian feeding guilds to tropical forest disturbance. Conservation Biology **21**:133–141.

Hackett, S. J., et al. 2008. A phylogenomic study of birds reveals their evolutionary history. Science **320**:1763–1768.

Hadfield, J. D. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. Journal of Statistical Software **33:** http://www.jstatsoft.org/v33/i02/.

Hadfield, J. D. 2019. MCMCglmm course notes. Available from https://stat.ethz.ch/CRAN/web/packages/MCMCglmm/vignettes/CourseNotes.pdf.

Hadfield, J. D. and S. Nakagawa. 2010. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. Journal of Evolutionary Biology **23**:494–508.

Hamer, K. C., R. J. Newton, F. A. Edwards, S. Benedick, S. H. Bottrell and D. P. Edwards. 2015. Impacts of selective logging on insectivorous birds in Borneo: The importance of trophic position, body size and foraging height. Biological Conservation **188**:82–88.

Hammel, B. E., M. H. Grayum, C. Herrera and N. Zamora, editors. 2004. Manual de Plantas de Costa Rica Volumen I Introduccion. Missouri Botanical Garden.

Hammer, Ø., D. A. T. Harper and P. D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica **4**:9.

Herrera, L. G., K. A. Hobson, M. Rodríguez and P. Hernandez. 2003. Trophic partitioning in tropical rain forest birds: insights from stable isotope analysis. Oecologia **136**:439–444.

Hill, J. K. and K. C. Hamer. 2004. Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. Journal of Applied Ecology **41**:744–754.

Höbinger, T., S. Schindler, B. S. Seaman, T. Wrbka and A. Weissenhofer. 2012. Impact of oil palm plantations on the structure of the agroforestry mosaic of La Gamba, southern Costa Rica: potential implications for biodiversity. Agroforestry Systems **85**:367–381.

Hobson, K. A., R. T. Alisauskas and R. G. Clark. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: Implications for isotopic analyses of diet. The Condor **95**:388.

Hooper, D. U., et al. 2005. Effects pf biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs **75**:3–35.

Huber, W., A. Weissenhofer, N. Zamora and A. Weber. 2008. Plant diversity and biogeography of the Golfo Dulce region, Costa Rica. Stapfia **88**:97–104.

Inouye, D. W. 1978. Resource partitioning in bumblebees: Experimental studies of foraging behavior. Ecology **59**:672–678.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature **491**:444–448.

Keenan, R. J., G. A. Reams, F. Achard, J. V. de Freitas, A. Grainger and E. Lindquist. 2015. Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015 **352**:9–20.

Kemp, V. A. 2018. The effects of forest degradation on trophic interactions and elemental fluxes in an experimental landscape, Malaysian Borneo. Doctoral thesis, London, United Kingdom.

Kim, T., S. Bartel and C. Gratton. 2019. Grassland harvesting alters ant community trophic structure: An isotopic study in tallgrass prairies. Ecology and Evolution **9**:9815–9826.

Koh, L. P., N. S. Sodhi and B. W. Brook. 2004. Ecological Correlates of Extinction Proneness in Tropical Butterflies. Conservation Biology **18**:1571–1578.

Krebber, D. 2019. Resource partitioning in frugivorous understory birds. Master's thesis, Vienna, Austria.

Layman, C. A., et al. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Reviews of the Cambridge Philosophical Society **87**:545–562.

Layman, C. A., J. P. Quattrochi, C. M. Peyer and J. E. Allgeier. 2007. Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecology Letters **10**:937–944.

Lobo, J. and F. Bolaños. 2005. Historia Natural de Golfito, Costa Rica. Santo Domingo: INBio.

Lorentzen, H. F., T. Benfield, S. Stisen and C. Rahbek. 2020. COVID-19 is possibly a consequence of the anthropogenic biodiversity crisis and climate changes. Danish Medical Journal **67**:A205025.

Martínez del Rio, C., N. Wolf, S. A. Carleton and L. Z. Gannes. 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biological Reviews of the Cambridge Philosophical Society **84**:91–111.

McHugh, P. A., A. R. McIntosh and P. G. Jellyman. 2010. Dual influences of ecosystem size and disturbance on food chain length in streams. Ecology Letters **13**:881–890.

Miller, S. D., B. J. Zgliczynski, M. D. Fox, L. S. Kaufman, R. H. Michener, S. A. Sandin and S. L. Hamilton. 2019. Niche width expansion of coral reef fishes along a primary production gradient in the remote central Pacific. Marine Ecology Progress Series **625**:127–143.

Moore, R. P., W. D. Robinson, I. J. Lovette and T. R. Robinson. 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. Ecology Letters **11**:960–968.

Moura, N. G., A. C. Lees, C. B. Andretti, B. J.W. Davis, R. R.C. Solar, A. Aleixo, J. Barlow, J. Ferreira and T. A. Gardner. 2013. Avian biodiversity in multiple-use landscapes of the Brazilian Amazon. Biological Conservation **167**:339–348.

Newbold, T., J. P. W. Scharlemann, S. H. M. Butchart, C. H. Sekercioğlu, R. Alkemade, H. Booth and D. W. Purves. 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proceedings of the Royal Society B: Biological Sciences **280**:20122131.

Nielsen, J. M., E. L. Clare, B. Hayden, M. T. Brett and P. Kratina. 2018. Diet tracing in ecology: Method comparison and selection. Methods in Ecology and Evolution **9**:278–291.

Oberleitner, F. 2016. Recovery of aboveground biomass, species richness and species composition in tropical secondary forests in SW Costa Rica. Master's thesis, Vienna, Austria.

Öckinger, E., et al. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters **13**:969–979.

Pacala, S. and J. Roughgarden. 1982. Resource partitioning and interspecific competition in two two-species insular anolis lizard communities. Science **217**:444–446.

Pavlacky, D. C., H. P. Possingham and A. W. Goldizen. 2015. Integrating life history traits and forest structure to evaluate the vulnerability of rainforest birds along gradients of deforestation and fragmentation in eastern Australia. Biological Conservation **188**:89–99.

Perkins, M. J., R. A. McDonald, F. J. F. van Veen, S. D. Kelly, G. Rees and S. Bearhop. 2014. Application of nitrogen and carbon stable isotopes (δ(15)N and δ(13)C) to quantify food chain length and trophic structure. PLoS ONE **9**:e93281.

Pongsiri, M. J., J. Roman, V. O. Ezenwa, T. L. Goldberg, H. S. Koren, S. C. Newbold, R. S. Ostfeld, S. K. Pattanayak and D. J. Salkeld. 2009. Biodiversity loss affects global disease ecology. BioScience **59**:945–954.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology **83**:703–718.

Post, D. M., M. L. Pace and N. G. Hairston. 2000. Ecosystem size determines food-chain length in lakes. Nature **405**:1047–1049.

Post, D. M. and G. Takimoto. 2007. Proximate structural mechanisms for variation in food-chain length. Oikos **116**:775–782.

Potapov, P., et al. 2017. The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Science Advances **3**:e1600821.

Power, M. E., M. S. Parker and W. E. Dietrich. 2008. Seasonal reassembly of a river food web: Floods, droughts, and impacts of fish. Ecological Monographs **78**:263–282.

R Core Team. 2018. R: A language and environment for statistical computing, Vienna, Austria.

Resasco, J., D. J. Levey and E. I. Damschen. 2012. Habitat corridors alter relative trophic position of fire ants. Ecosphere **3**:art100.

Revell, L. J. 2012. phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution **3**:217–223.

Roy, V. 2020. Convergence diagnostics for Markov Chain Monte Carlo. Annual Review of Statistics and Its Application **7**:387–412.

Schleuning, M., N. Blüthgen, M. Flörchinger, J. Braun, H. M. Schaefer and K. Böhning-Gaese. 2011. Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. Ecology **92**:26–36.

Schulze, C. H., P. Leidinger, B. Paces and A. F. R. Páez. 2019. The importance of reforested and naturally regenerating young forest patches as secondary habitats for forest birds in the Biological Corridor La Gamba, Costa Rica. Acta ZooBot Austria **156**:79–98.

Sekercioğlu, C. H., G. C. Daily and P. R. Ehrlich. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences of the United States of America **101**:18042–18047.

Sekercioğlu, C. H., P. R. Ehrlich, G. C. Daily, D. Aygen, D. Goehring and R. F. Sandi. 2002. Disappearance of insectivorous birds from tropical forest fragments. Proceedings of the National Academy of Sciences of the United States of America **99**:263–267.

Smith, K. F., M. Goldberg, S. Rosenthal, L. Carlson, J. Chen, C. Chen and S. Ramachandran. 2014. Global rise in human infectious disease outbreaks. Journal of the Royal Society, Interface **11**:20140950.

Socolar, J. B. and D. S. Wilcove. 2019. Forest-type specialization strongly predicts avian responses to tropical agriculture. Proceedings of the Royal Society B: Biological Sciences **286**:20191724.

Stattersfield, A. J., M. J. Crosby, A. J. Long and D. C. Wege. 1998. Endemic bird areas of the world-Priorities for biodiversity conservation. BirdLife International, Cambridge.

Stiles, F. G. and A. F. Skutch. 1989. Guide to the birds of Costa Rica. Cornell University Press, Ithaca, United States.

Stratford, J. A. and W. D. Robinson. 2005. Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. Frontiers in Ecology and the Environment **3**:85–92.

Takimoto, G. and D. M. Post. 2013. Environmental determinants of food-chain length: a meta-analysis. Ecological Research **28**:675–681.

Tebb, G. 2008. The birds of La Gamba. Stapfia **88**:353–380.

Terborgh, J., et al. 2001. Ecological meltdown in predator-free forest fragments. Science **294**:1923–1926.

Thompson, R. M., M. Hemberg, B. M. Starzomski and J. B. Shurin. 2007. Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. Ecology **88**:612–617.

Tobias, J. A., C. H. Sekercioğlu and F. H. Vargas. 2013. Bird conservation in tropical ecosystems. Pages 258–276 in D. W. Macdonald and K. J. Willis, editors. Key topics in conservation biology 2. John Wiley & Sons, Oxford.

Tropenstation La Gamba. 2017. Der biologische Korridor (COBIGA). Available from https://www.lagamba.at/naturschutzsoziales/biologischer-korridor/.

Tropenstation La Gamba. 2020. Properties of the Tropical Station La Gamba. Available from https://www.lagamba.at/tropenstation/grundstuecke-der-station/.

Vanderklift, M. A. and S. Ponsard. 2003. Sources of variation in consumer-diet delta 15N enrichment: a meta-analysis. Oecologia **136**:169–182.

Vitousek, P. M. 1997. Human domination of earth's ecosystems. Science **277**:494–499.

Wanek, W., S. Drage, N. Hinko, F. Hofhansl, E.-M. Pölz, A. Ratzer and A. Richter. 2008. Primary production and nutrient cycling in lowland rainforests of the Golfo Dulce region. Stapfia **88**:155–178.

Weissenhofer, A., M. Barquero, W. Huber, V. Mayer and J. Nájera Umaña. 2008a. The Biological Corridor Project in the Piedras Blancas National Park, Costa Rica.- A project to preserve the biodiversity by reforestation and alternative culture, with support of the community La Gamba by new marketing strategies. Stapfia **88**:715–723.

Weissenhofer, A. and W. Huber. 2008. The climate of the Esquinas rainforest. Stapfia **88**:59–62.

Weissenhofer, A., W. Huber, T. Koukal, M. Immitzer, E. Schembera, S. Sontag, N. A. Zamora-Villalobos and A. Weber. 2008b. Ecosystem diversity in the Piedras Blancas National Park and adjacent areas (Costa Rica), with the first vegetation map of the area. Stapfia **88**:65–96.

Whitman, A. A., J. M. Hagan and N. V. L. Brokaw. 1998. Effects of selection logging on birds in Northern Belize. Biotropica **30**:449–457.

Whitmee, S., et al. 2015. Safeguarding human health in the Anthropocene epoch: report of The Rockefeller Foundation–Lancet Commission on planetary health. The Lancet **386**:1973–2028.

Wiemers, M. and K. Fiedler. 2008. Butterfly diversity of the Piedras Blancas National Park and its vicinity a preliminary assessment (Lepidoptera: Papilionoidea & Hesperioidea). Stapfia **88**:277–294.

Willis, K. J., L. Gillson and T. M. Brncic. 2004. How 'virgin' is virgin rainforest? Science **304**:402–403.

Woodcock, P., D. P. Edwards, R. J. Newton, F. A. Edwards, C. V. Khen, S. H. Bottrell and K. C. Hamer. 2012. Assessing trophic position from nitrogen isotope ratios: effective calibration against spatially varying baselines. Die Naturwissenschaften **99**:275–283.

Woodcock, P., D. P. Edwards, R. J. Newton, C. Vun Khen, S. H. Bottrell and K. C. Hamer. 2013. Impacts of intensive logging on the trophic organisation of ant communities in a biodiversity hotspot. PLoS ONE **8**:e60756.

Wright, S. J. 2005. Tropical forests in a changing environment. Trends in Ecology & Evolution **20**:553–560.

6. Supporting Materials

Supplementary Table A: Overview of English and Latin names of the bird species from which we analysed claw material in this study. Nomenclature follows Garrigues & Dean (2014).

English species name	Latin species name
Black-cheeked Ant-Tanager	*Habia atrimaxillaris*
Blue-black Grosbeak	*Cyanocompsa cyanoides*
Blue-crowned Manakin	*Lepidothrix coronata*
Bright-rumped Attila	*Attila spadiceus*
Buff-throated Saltator	*Saltator maximus*
Cherrie's Tanager	*Ramphocelus costaricensis*
Chestnut-backed Antbird	*Myrmeciza exsul*
Clay-colored Thrush	*Turdus grayi*
Cocoa Woodcreeper	*Xiphorhynchus susurrans*
Golden-crowned Spadebill	*Platyrinchus coronatus*
Gray-chested Dove	*Leptotila cassini*
Gray-headed Tanager	*Eucometis penicillata*
Long-tailed Woodcreeper	*Deconychura longicauda*
Ochre-bellied Flycatcher	*Mionectes oleagineus*
Orange-billed Sparrow	*Arremon aurantiirostris*
Orange-collared Manakin	*Manacus aurantiacus*
Red-capped Manakin	*Ceratopipra mentalis*
Red-rumped Woodpecker	*Veniliornis kirkii*
Riverside Wren	*Cantorchilus semibadius*
Royal Flycatcher	*Onychorhynchus coronatus*
Ruddy Quail-Dove	*Geotrygon montana*
Rufous Mourner	*Rhytipterna holerythra*
Spot-crowned Euphonia	*Euphonia imitans*
Sulphur-rumped Flycatcher	*Myiobius sulphureipygius*
Tawny-crowned Greenlet	*Hylophilus ochraceiceps*
Tawny-winged Woodcreeper	*Dendrocincla anabatina*
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*
White-throated Thrush	*Turdus assimilis*
White-tipped Dove	*Leptotila verreauxi*

Supplementary Table B: Model output of a Gaussian Bayesian Markov chain Monte Carlo generalized linear mixed model (MCMCglmm) investigating the difference in size-corrected body mass between forest types in habitat generalists. Model parameters were the same as for the trophic position models 1 - 4 (see: Methods). Size-corrected body mass was calculated as (body mass / tarsus length) * (mean tarsus length of species). eff. samp. = effective sample size, l-95% CI = lower 95 % credible interval, u-95% CI = upper 95 % credible interval, post. = posterior, SF = secondary forest.

MCMCglmm: Location effects: corr_mass ~ forest					
	post. mean	l-95% CI	u-95% CI	eff. samp.	*pMCMC*
(Intercept)	65.9945	25.5894	105.2819	9998	0.0024
forestSF	0.1553	-0.7688	1.1048	9998	0.7542
G-structure: ~ species_lat					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
species_lat	1543	526	2893	9998	
R-structure: ~ units					
	post. mean	l-95% CI	u-95% CI	eff. samp.	
units	21.16	18.28	23.93	9998	

Supplementary Table C: Summary of the trophic positions calculated for fruit, moth and spider samples collected at the study sites. Old-growth forest sites (OF, n = 5) are separated from secondary forest sites (SF, n = 4) by a dashed line. Three Mann-Whitney-U-Tests were calculated to test for significant differences between forest types. M = median, *M-W-U* = *Mann-Whitney-U*, TP = trophic position.

SiteID	**TP: Fruits**	**TP: Moths**	**TP: Spiders**
CT01	1.31	2.44	2.92
FT06	0.67	3.18	2.52
LB02	1.29	2.60	2.68
OT02	0.83	2.74	3.15
SG01	0.95	2.48	2.58
LB01	1.59	2.05	2.60
LB03	1.25	2.37	3.02
VB01	0.38	2.28	2.33
VB02	0.88	3.43	3.03
Forest	**M: Fruits**	**M: Moths**	**M: Spiders**
OF	0.95	2.60	2.68
SF	1.06	2.34	2.81
M-W-U	10.00	5.00	10.00
p	0.90	0.27	0.90

7. Appendix: Zusammenfassung

Lebensraumzerstörung und -degradation sind entscheidende Ursachen für das Aussterben von Arten in der aktuellen Biodiversitätskrise. Deshalb konzentriert sich die Forschung zunehmend auf die Frage, welche Eigenschaften es einigen Arten ermöglichen, degradierte Lebensräume zu nutzen, während andere dies nicht können. Besonders wenig ist darüber bekannt, wie die trophische Position einer Art oder deren Nischenbreite ihre Fähigkeit beeinflusst, in degradierten Habitaten fortzubestehen und darüber, wie sich trophische Interaktionen verändern, wenn Waldökosysteme gestört werden, obwohl die Konsequenzen solcher Änderungen weitreichend sein können. In dieser Studie verwenden wir stabile Stickstoffisotopenverhältnisse (^{15}N:^{14}N, angegeben als $\delta^{15}N$), um trophische Positionen und Nischenbreiten von Unterwuchsvogelarten, die im Altwald oder Sekundärwald in den pazifischen Tieflagen Costa Ricas vorkommen, zu quantifizieren und zu vergleichen. Unsere Daten zeigen, dass die trophische Position einer Art und nicht ihre Nischenbreite darüber entscheidet, ob diese nach einer Waldstörung dort weiter vorkommt oder nicht. Arten, die im Altwald eine niedrige trophische Position hatten, sind im Sekundärwald eher verschwunden als Arten mit höherer trophischer Position im Altwald. Dieses Muster wurde höchstwahrscheinlich durch die Einwanderung relativ großer, spezialisierter Sekundärwaldvogelarten in die Sekundärwälder verursacht, die sich dort sehr vielseitig von Nahrungsressourcen mit hoher trophischer Position ernähren. Das führt dazu, dass die Generalisten im Sekundärwald ihre trophische Position im Vergleich zu ihren Artgenossen im Altwald reduzieren. Dies ist – soweit uns bekannt - die erste Studie, die einen systematischen Effekt der trophischen Position auf den teilweisen Fortbestand einer Vogelartengemeinschaft in einem gestörten Waldökosystem aufzeigt. Sie trägt daher dazu bei, die Konsequenzen von Lebensraumdegradation auf Arten und den naturschutzfachlichen Wert von Sekundärwäldern besser zu verstehen.

Schlagwörter: Störung des Waldes, Habitatzerstörung, Sekundärwald, stabile Isotopen, Unterwuchsvögel, trophische Position, trophische Nischenbreite