

# Logging impacts on avian species richness and composition differ across latitudes and foraging and breeding habitat preferences

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## ABSTRACT

Understanding the causes underlying changes in species diversity is a fundamental pursuit of ecology. Animal species richness and composition often change with decreased forest structural complexity associated with logging. Yet differences in latitude and forest type may strongly influence how species diversity responds to logging. We performed a meta-analysis of logging effects on local species richness and composition of birds across the world and assessed responses by different guilds (nesting strata, foraging strata, diet, and body size). This approach allowed identification of species attributes that might underlie responses to this anthropogenic disturbance. We only examined studies that allowed forests to regrow naturally following logging, and accounted for logging intensity, spatial extent, successional regrowth after logging, and the change in species composition expected due to random assembly from regional species pools. Selective logging in the tropics and clearcut logging in temperate latitudes caused loss of species from nearly all forest strata (ground to canopy), leading to substantial declines in species richness (up to 27% of species). Few species were lost or gained following any intensity of logging in lower-latitude temperate forests, but the relative abundances of these species changed substantially. Selective logging at higher-temperate latitudes generally replaced late-successional specialists with early-successional specialists, leading to no net changes in species richness but large changes in species composition. Removing less basal area during logging mitigated the loss of avian species from all forests and, in some cases, increased diversity in temperate forests. This meta-analysis provides insights into the important role of habitat specialization in determining differential responses of animal communities to logging across tropical and temperate latitudes.

*Key words:* biodiversity, birds, community ecology, habitat specialization, logging, meta-analysis, reproductive success, species composition, species richness.

## CONTENTS

I. Introduction .....	2
II. Methods .....	3
(1) Literature search and data collection .....	3
(2) Statistical analyses .....	4
III. Results .....	5
(1) Data description .....	5
(2) Logging effects on species richness across latitudes .....	5
(3) Logging effects on species composition across latitudes .....	8
(4) Logging effects differ among north-temperate forest types .....	9
IV. Discussion .....	9
V. Conclusions .....	15
VI. Acknowledgements .....	16
VII. References .....	16
VIII. Supporting Information .....	18

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## I. INTRODUCTION

Understanding the causes underlying changes in local species richness and composition is critically important for the conservation of biodiversity. Animal species richness and composition often change with decreased forest structural complexity associated with logging. Logging is an important and pervasive alteration of forest vegetation structure that occurs across most of the world (Hansen, Stehman & Potapov, 2010). Current logging practices can remove minimal amounts of timber (e.g. selective harvesting) to all or nearly all timber from the landscape (e.g. clearcut logging). Numerous local-scale studies have examined the impacts of these different types of logging on animal communities (Gray *et al.*, 2007; Vanderwel, Malcolm & Mills, 2007; Burivalova, Şekercioglu & Koh, 2014), often revealing very different effects of logging on species richness. Yet, no study has attempted to explain differential effects of logging on animal species richness and composition within and across latitudes. Such insights would be critically important to the conservation of biodiversity in a changing world.

Animal species richness can decrease as logging reduces the structural complexity of vegetation and associated breeding or foraging niches (MacArthur & MacArthur, 1961; MacArthur, Recher & Cody, 1966; Pianka, 1966*a*; Willson, 1974; Roth, 1976; Martin, 1988). Yet, the extent of change in the numbers and identities of animal species with vegetation structure may differ across latitudes depending on niche breadths. In particular, tropical species are thought to have narrower niche breadths (i.e. more habitat specialization) and to subdivide vegetation more finely than temperate species (MacArthur *et al.*, 1966; Karr & Roth, 1971; Salisbury *et al.*, 2012). If tropical species exhibit greater habitat specialization, especially in late-successional habitats, then logging in tropical forests may lead to steeper decreases in richness and greater changes in species composition compared to logging in temperate forests. However, some evidence indicates that tropical species (e.g. insects) may not exhibit greater habitat specialization than temperate counterparts (Novotny *et al.*, 2006), suggesting that responses of species richness and composition to logging may be relatively consistent among temperate and tropical forests. Alternatively, greater species diversity in the tropics may make tropical communities more resistant to logging than temperate communities (Ives & Carpenter, 2007), which might lead to stronger changes in species richness or composition in temperate forests compared with tropical forests. Thus, the effects of logging on species diversity and composition across tropical and temperate communities remains unclear.

Differences in habitat specialization and other traits may also determine which groups of species respond most strongly to logging. Logging generally removes upper forest strata (i.e. canopy trees) and allows more light to reach the forest floor, encouraging understorey growth. Thus, in the absence of other processes, logging might remove species that specialize in the canopy layer for breeding or foraging

while adding species that specialize in lower forest strata. Yet if habitat specialization is greater for tropical species, understorey- or ground-associated guilds may experience large changes in species composition or even loss of species as primary forest specialists are replaced by secondary forest specialists. Previous work suggests that lower-strata species, and especially ground-associated species, may be more affected by logging in tropical forests (Cleary *et al.*, 2007; Hamer *et al.*, 2015), but the generality of these effects across latitudes remains unknown. Dietary preferences may also determine which groups of species are most impacted by logging, for example, if logging alters the relative abundance of fruits or insects in a forest. Finally, body size influences a host of life-history traits, including dispersal ability and home-range size, and might determine differential responses to logging across species (Bowman, Jaeger & Fahrig, 2002). Yet little is known about whether body size causes differential responses to logging across latitudes.

Differences among forest types at similar latitudes may also influence responses of species richness and composition to logging. For example, changes in bird species composition with changes in vegetation structure are greater in mixed conifer–deciduous forests compared to pure conifer or deciduous forests (MacArthur *et al.*, 1966). Conifer and deciduous vegetation also differentially affect reproductive success and determine changes in bird species composition with logging in mixed conifer–deciduous forests (LaManna *et al.*, 2015). In the mixed conifer–deciduous forests that dominate northern latitudes, early-successional seres are generally deciduous with conifers dominating the late-successional seres. Thus, given that logging can drastically alter vegetation composition in these mixed-forest types, then logging might also have greater effects on the species composition of birds and other animals that breed within these forests *versus* logging in pure conifer or deciduous forests.

Responses of animal species richness and composition to logging across latitudes may be confounded by changes in regional species richness and the spatial scale of logging. Local species richness and composition are products of historical processes that influence regional richness (MacArthur & Wilson, 1963; Ricklefs, 2008; Kraft *et al.*, 2011). Regional richness decreases with latitude (Pianka, 1966*b*; MacArthur, 1972), meaning that smaller changes in species composition with logging are expected as latitude increases due to fewer species in the regional pool alone. The spatial scale at which logging effects are examined can also influence the response of animal communities to logging, most likely reflecting scale-dependent effects of habitat disturbance on habitat heterogeneity (Hill & Hamer, 2004). Thus, a comparison of the effects of logging on species richness and composition across latitudes and forest types is needed that takes into consideration differences in regional richness and spatial scale.

We conducted a meta-analysis to compare the influence of logging on local avian species richness and composition within and across latitudes. Responses of bird species to

logging have been documented in numerous individual studies, and provide an excellent system with which to examine logging effects on diversity across tropical and temperate latitudes. We also tested if logging impacts on species richness and composition differed among guilds that prefer to nest or forage in distinct vegetation layers, or among guilds defined by dietary preference and body mass. Because the majority of studies were from north-temperate latitudes, we also tested if bird species richness and composition changed more in mixed north-temperate forest types (i.e. conifer–deciduous mixed forests) compared to pure (i.e. conifer or deciduous only) forest types. A deeper understanding of the factors that explain differential logging impacts on avian communities both within and across latitudes is needed to conserve biodiversity in an era of unprecedented global change.

## II. METHODS

### (1) Literature search and data collection

We systematically searched for studies published within the past 60 years (1955–2015) examining the response of bird communities to logging. We looked for suitable peer-reviewed papers using the terms ‘birds’ and ‘logging’ on the ISI *Web of Science* online bibliographic database (accessed September 7, 2014), and also searched references within these papers. Limiting our search to published material potentially introduced a bias (Møller & Jennions, 2001) but also provided a level of quality control (Gray *et al.*, 2007). We included experiments that compared avian species composition before and after logging as well as observational studies that compared recently logged forests to nearby undisturbed controls. Studies were included only if logging was the sole difference between treatment and control sites and forests were allowed to regrow following logging (i.e. we did not examine burning or agricultural effects). Many different forms of logging exist (e.g. clearcut, shelter-wood, selective, etc.), and these practices differ primarily in the amount of basal area removed/retained on the landscape. Thus, measurements of proportion of timber basal area retained on the landscape following logging (hereafter basal area retention) were used to control for variable logging intensities across studies. Regrowth since logging occurred is also likely to influence diversity responses to logging. Thus, the number of years of successional regrowth since logging occurred (hereafter years since logging) was used to control for variable ages of logging treatments. Because these two factors (basal area retention and years since logging occurred) are expected drastically to influence responses of diversity to logging, we limited our meta-analysis to studies that provided these measurements. We further limited our search to studies that surveyed bird communities within core logged areas to avoid the confounding influence of edge effects. We also had to limit our meta-analysis to studies that provided either a measure of species turnover ( $\beta$ -diversity) or

complete species lists from unlogged and logged treatments from which  $\beta$ -diversity could be calculated (see below).

We defined regional species richness ( $\gamma$ -diversity) as all bird species detected in unlogged and logged forests. Local site richness ( $\alpha$ -diversity) was defined as the identities of bird species in either unlogged or logged forest, respectively. We then calculated the per cent change in species richness following logging as  $(S_{\text{logged}} - S_{\text{unlogged}})/S_{\text{unlogged}}$ , where  $S_{\text{logged}}$  is the number of species in the logged community and  $S_{\text{unlogged}}$  is the number of species in the unlogged community. Thus, positive values indicate a net gain of species following logging and negative values indicate a net loss of species.

We measured the change in species composition in response to logging with two  $\beta$ -diversity metrics: (i) the Jaccard dissimilarity index ( $\beta_J$ ), and (ii) the Bray–Curtis dissimilarity index ( $\beta_{BC}$ ).  $\beta_J$  measures the loss and gain of species because it only incorporates information about species presence and absence in either habitat.  $\beta_{BC}$  measures changes in the identity and relative abundance of species in multivariate space. These two metrics are recommended for examining differences in species composition among two or more sites (Anderson *et al.*, 2011; Kraft *et al.*, 2011; Myers *et al.*, 2013), and both were calculated using the ‘vegan’ package in R (Oksanen *et al.*, 2015). Both metrics range from 0 to 1, with higher values of either  $\beta$ -diversity metric representing greater change in species composition between logged and unlogged communities. Moreover, comparing these two measures provides additional information about logging effects on avian communities (Anderson *et al.*, 2011). For example, logging in a given region may result in a high value (near 1) for  $\beta_{BC}$  but a relatively low value (near zero) for  $\beta_J$ . This pattern indicates that species are not lost or gained after logging, but indicates that logging strongly alters their relative abundances. However, because  $\beta_{BC}$  requires abundance data and  $\beta_J$  does not, we could only calculate  $\beta_{BC}$  for a subset (66%) of studies.

For those studies that provided abundance data, we also used null-models to calculate the change in species composition between logged and unlogged communities not explained by differences in regional species pools among latitudes (Kraft *et al.*, 2011; Myers *et al.*, 2013). All individuals encountered in logged and unlogged forest were randomly distributed among logging treatments (i.e. logged or unlogged), while preserving the total number of individuals in each treatment (Kraft *et al.*, 2011; Myers *et al.*, 2013). Thus, these null assemblages were only the product of stochastic assembly from the species pool, and all other mechanisms that might cause additional clumping (e.g. habitat specialization, local interactions among species, dispersal limitation) were removed. The pairwise dissimilarities of these simulated communities ( $\beta_{\text{SIM}}$ ) were then compared to the observed dissimilarities ( $\beta_{BC}$ ) relative to the standard deviation of  $\beta_{\text{SIM}}$  ( $\sigma_{\text{SIM}}$ ) after 1000 iterations, and a standardized effect size of the difference was calculated as:  $\beta_{\text{SES}} = (\beta_{BC} - \beta_{\text{SIM}})/\sigma_{\text{SIM}}$ . Therefore,  $\beta_{\text{SES}}$  represents the  $\beta$ -diversity that remains unexplained by stochastic assembly from the regional species pool (Kraft *et al.*, 2011).

We recorded latitude and longitude of each study, and classified studies as tropical if they were above the tropic of Capricorn and below the tropic of Cancer. All other studies were classified as north or south temperate (including logging studies from boreal forests). This distinction was used to test for non-linear differences among tropical and temperate communities (e.g. habitat specialization) not linearly associated with latitude. Sample size (number of point counts, replicate plots, etc.) and spatial extent of each replicate sample (ha) were also recorded for each study. Because some studies used point counts (larger sample sizes, but relatively small spatial extent per sample) and others used territory-mapping techniques (smaller sample sizes, but relatively large spatial extent per sample), sample size and spatial extent per sample needed to be multiplied to calculate the total spatial extent of each study. We considered this measure of total spatial extent as the most appropriate way to compare studies that differ drastically in the spatial extent of each replicate sample. We also recorded the study method used for surveying birds (point-count, transect, spot-mapping, and mist-netting).

Bird species were classified into guilds based on the vegetation layer (or forest strata) in which they prefer to nest (cavity, canopy, understorey/shrub, or ground) and forage (aerial, canopy, understorey/shrub, or ground), based on their dietary preferences (frugivore, granivore, insectivore, nectarivore, or omnivore), and based on their body size using the *Handbook of the Birds of the World* (Del Hoyo *et al.*, 2014) and *Cornell's Birds of North America* (Poole, 2005). Accounts of all species from our selected studies were found in one of these two resources. We classified species into one of four body-mass guilds based on the median and first and third quartiles of body mass among species: (i) species in the lower 25th percentile of body mass (<11.3 g); (ii) species in the 25–50th percentile of body mass (11.3–22.7 g); (iii) species in the 50–75th percentile of body mass (22.7–57.9 g); and (iv) species with body masses greater than the 75th percentile (>57.9 g).

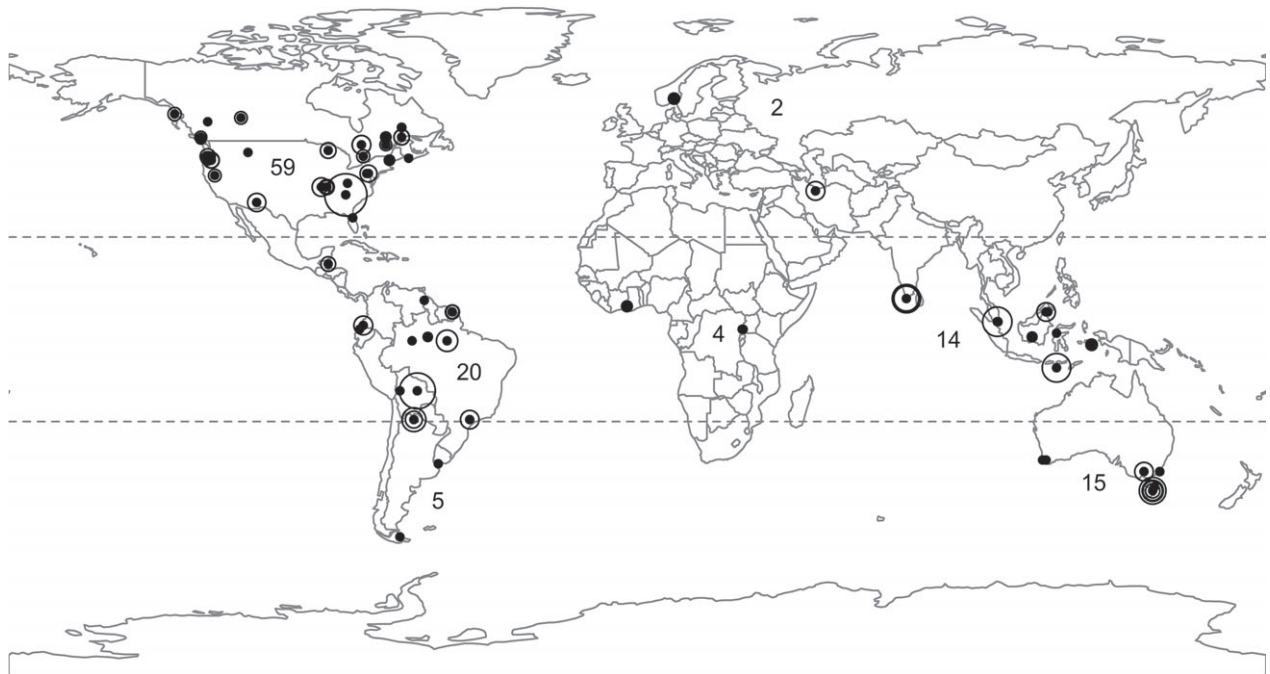
## (2) Statistical analyses

We used linear models to examine responses of avian species richness and composition to logging. If a given study examined multiple unique logging treatments (e.g. clearcut, 25, and 50% retention), then each treatment was included as a sample in our meta-analysis provided that each treatment was compared to control (undisturbed) forest. Instead of including a random effect of study (i.e. study site) to group logging treatments in our analyses, we included the relevant continuous variables of interest that differed among study sites: latitude and longitude. Specifically, we were interested in different responses of diversity to logging across latitudes. Because 75% of studies presented results from only one or two logging treatments, a random effect of study site is nearly perfectly correlated with latitude and therefore inappropriate to include in a model testing for a latitude effect (Clark & Linzer, 2015). Including latitude in all of our models appropriately groups studies by the relevant variable

of theoretical interest, and no additional random effect of study site was necessary. However, logging treatments from the same study site may be spatially auto-correlated. Thus, we tested for any spatial auto-correlation in our data set using Mantel's test ('mantel.rtest' function from R package 'ade4'; (Dray & Dufour, 2007).

We began by verifying our measure of  $\gamma$ -diversity by testing for the familiar pattern of decreasing diversity with the absolute value of latitude (hereafter absolute latitude). This measure of  $\gamma$ -diversity may be confounded with sample effort, but total spatial extent only explained <10% of variation in  $\gamma$ -diversity across studies ( $r^2 = 0.099$ ,  $P = 0.001$ ). We then examined factors influencing the change in local species richness or composition (i.e.  $\beta_J$ ,  $\beta_{BC}$ , and  $\beta_{SES}$ ) following logging with a linear model that included a categorical variable indicating tropical or temperate forest (hereafter called latitudinal zone; tropical forests were defined as being at or below the Tropics of Capricorn or Cancer), absolute latitude (the absolute value of latitude), basal area retention, years since logging,  $\gamma$ -diversity, and interactions between latitudinal zone and absolute latitude, basal area retention, and years since logging. Clearcut harvests removed >90% of tree basal area, but generally removed all standing trees. Thus, this logging technique may have drastically different effects on vegetation and animal communities compared to selective harvest (removal of <90% basal area). Moreover, clearcut harvests were only prevalent in the temperate zone. Thus, we split temperate logging into clearcut and selective harvest but kept basal area retention in the model to account for substantial variation in retention among selective harvests. Finally, before implementing each model for species richness or composition, we tested for simple correlations between total spatial extent and the change in species richness or composition (Hill & Hamer, 2004). If a relationship was detected, we incorporated total spatial extent directly into the model. If a relationship was absent, we weighted each study by their total spatial extent in order to favour those studies with greater sampling effort and precision. Variables were log-transformed if their distributions were heavily right-skewed. We then sequentially removed insignificant ( $P > 0.05$ ) interactions from this full model to arrive at a more parsimonious model. We also performed funnel plots, which test for a significant correlation between model residuals and sampling effort, to assess publication bias (Egger *et al.*, 1997). If bias is present, model residuals will be significantly correlated with sampling effort. If bias is absent, model residuals should converge to zero for those studies with the greatest sampling effort, forming a funnel shape. We also used a likelihood-ratio test to assess the effect of avian study method (i.e. point-count, transect, mist-netting, or spot-mapping), but study method did not influence our models for species richness ( $\chi^2 = 3.6$ ,  $P = 0.31$ ),  $\beta_J$  ( $\chi^2 = 1.8$ ,  $P = 0.62$ ), or  $\beta_{BC}$  ( $\chi^2 = 4.0$ ,  $P = 0.26$ ).

We also tested for differential impacts of logging on species richness or composition of guilds that nest or forage in different forest strata, have different dietary preferences, or have different body mass. We used identical approaches to



**Fig. 1.** Map showing locations of 119 logged–unlogged paired replicates from 62 published studies across the globe used in meta-analyses. Locations are shown with a point; a circle around that point indicates relative sample size and spatial extent of the study. Boundaries of the tropics (Tropics of Capricorn and Cancer) are shown by dashed lines. Numbers indicate the count of replicates within a continent and latitudinal zone (i.e. north-temperate America = 59; tropical America = 20; south-temperate America = 5; north-temperate Eurasia = 2; tropical Africa = 4; tropical Asia = 14; and south-temperate Australia = 15).

those above with an added fixed factor of guild and an interaction between guild and latitudinal-zone/logging-type (i.e. tropical selective harvest, temperate selective harvest, temperate clearcut harvest). Again, a random effect of study site was unnecessary because logging treatments were already grouped by location (i.e. latitude and longitude).

We then tested if the impacts of logging on local avian species richness or composition differed among north-temperate forest types (i.e. pure deciduous or conifer forest *versus* mixed conifer–deciduous forest). Identical approaches to those described above were used to test for a difference in species richness and composition across pure and mixed forest types. We also tested for interactions of forest type with logging type (clearcut *versus* selective harvest), basal area retention and years since logging to evaluate if forest type influenced diversity responses to logging. All analyses were performed using program R (R Core Development Team, 2014).

### III. RESULTS

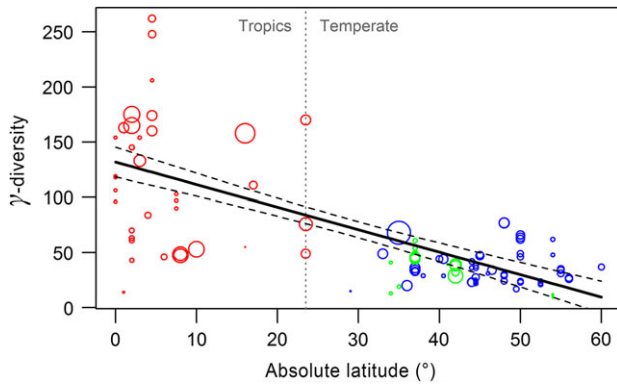
#### (1) Data description

Sixty-two studies matched our search criteria (Fig. 1, see online Supporting Information, Table S1). Unfortunately, Africa and temperate Eurasia were under-represented in our analyses because most studies in these regions focused solely on richness and few published the

necessary data to calculate changes in species composition. Thirty-three of the 62 studies examined multiple logging treatments, resulting in 119 control–treatment replicates for our meta-analysis. These studies spanned a wide range of logging intensities (0.0–93.0% basal area retention; mean  $\pm$  S.D. =  $33.0 \pm 27.8\%$ ) and years since logging (1.0–80.0 years; mean  $\pm$  S.D. =  $11.9 \pm 15.2$  years). Thirty-three replicates were from clearcut forests (all in the temperate zone) and 86 were from selectively logged forests (38 from tropical and 48 from temperate latitudes). Most studies were published to report logging effects on species richness, and 60% of studies reported statistically insignificant effects of logging on richness. Thus, publishing bias should not be a major factor influencing the meta-analyses. Indeed, funnel plot regression tests indicated that publication bias did not influence our global models for species richness ( $t = 0.38$ ,  $P = 0.71$ ) nor either compositional measure ( $\beta_J$ :  $t = 1.12$ ,  $P = 0.27$ ;  $\beta_{BC}$ :  $t = -0.63$ ,  $P = 0.54$ ) (see online Supporting Information, Fig. S1). Spatial auto-correlation was not present in datasets for changes in species richness ( $r = -0.064$ ,  $P = 0.96$ ) or species composition ( $\beta_J$ :  $r = 0.028$ ,  $P = 0.21$ ;  $\beta_{BC}$ :  $r = 0.013$ ,  $P = 0.37$ ). As expected,  $\gamma$ -diversity ( $r^2 = 0.460$ ) decreased with increasing latitude (Fig. 2).

#### (2) Logging effects on species richness across latitudes

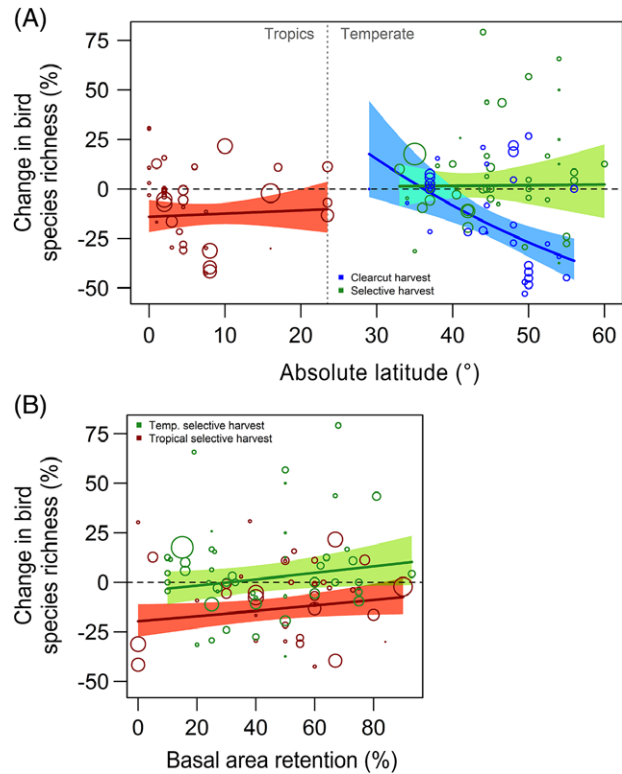
Effects of selective logging on bird species richness differed strongly among tropical and temperate forests and among



**Fig. 2.** Relationship between the absolute value of latitude (absolute latitude) and regional diversity ( $\gamma$ -diversity). Tropical studies are red, north temperate studies are blue, and south temperate studies are green. Larger points indicate increased total spatial extent (sample size  $\times$  spatial extent per sample) of a study. The linear relationship (slope estimate  $\pm$  95% C.I.) between regional diversity and latitude is shown in black.

harvest type in the temperate zone (Fig. 3). Logging reduced species richness across the tropics, with an average loss of 11% of species 6 years after a 50% basal-area retention harvest (Fig. 3A). Retaining less basal area increased these losses (Fig. 3B), with an average loss of 22% of species 1 year following low basal-area retention ( $\sim$ 5%) logging in the tropics. On average, all levels of basal-area retention in the tropics resulted in loss of species (Fig. 3B). More importantly, species richness never approached pre-logging levels in tropical forests over time, with an average loss of 10.3% of species 40 years after a 50% basal-area retention harvest (Table 1). In contrast to selective logging in the tropics, selective logging in temperate forests did not reduce bird species richness and corresponded with slightly increased richness if at least 60% of basal area was retained (Fig. 3B). Not surprisingly, temperate clearcut logging had strong impacts on bird diversity, with an average loss of 16% of species 6 years after harvest. These losses were even greater at higher latitudes, with an average loss of 27% of species 6 years following clearcuts at or above  $50^\circ$  latitude (Fig. 3A). Thus, logging generally reduced species richness in the tropics. Limited disturbance *via* logging yielded increases in species richness in temperate forests, but clearcut logging yielded reductions in richness.

We were able to classify over 1450 bird species into guilds based on the vegetation layer (or forest strata) in which they nest or forage, dietary preferences, and body mass from 41 of the studies used above. This represented all species documented in these 41 studies. We were only able to classify species from these 41 studies because other studies failed to provide detailed species lists. Logging effects on species richness of these guilds differed across latitudes and harvest types (Fig. 4, Table 2). Logging in tropical forests generally decreased avian richness across all nesting, foraging, dietary, and body-mass guilds except for omnivores (Fig. 4). Ground-nesting, ground-foraging, and large-sized



**Fig. 3.** Per cent change in bird species richness ( $\pm$ 95% CI) due to different logging types (clearcut *versus* selective harvests) across (A) latitudes and (B) different levels of basal area retention. Tropical selective-logging studies are in red, temperate clearcut-logging studies are in blue, and temperate selective-logging studies are in green. Tropical forests were only selectively logged, but at varying intensities. Effects of logging on bird species richness are shown at mean absolute latitudes ( $7^\circ$  for tropics and  $45^\circ$  for temperate) and regional richness (96 species for tropics and 32 species for temperate) for each latitudinal zone. Years since logging was log transformed. Effects of latitude are shown at mean basal area retention for each logging type, and effects of basal area retention are shown at the mean of log-transformed years since logging (6 years). Larger points indicate increased total spatial extent (sample size  $\times$  spatial extent per sample) of a study.

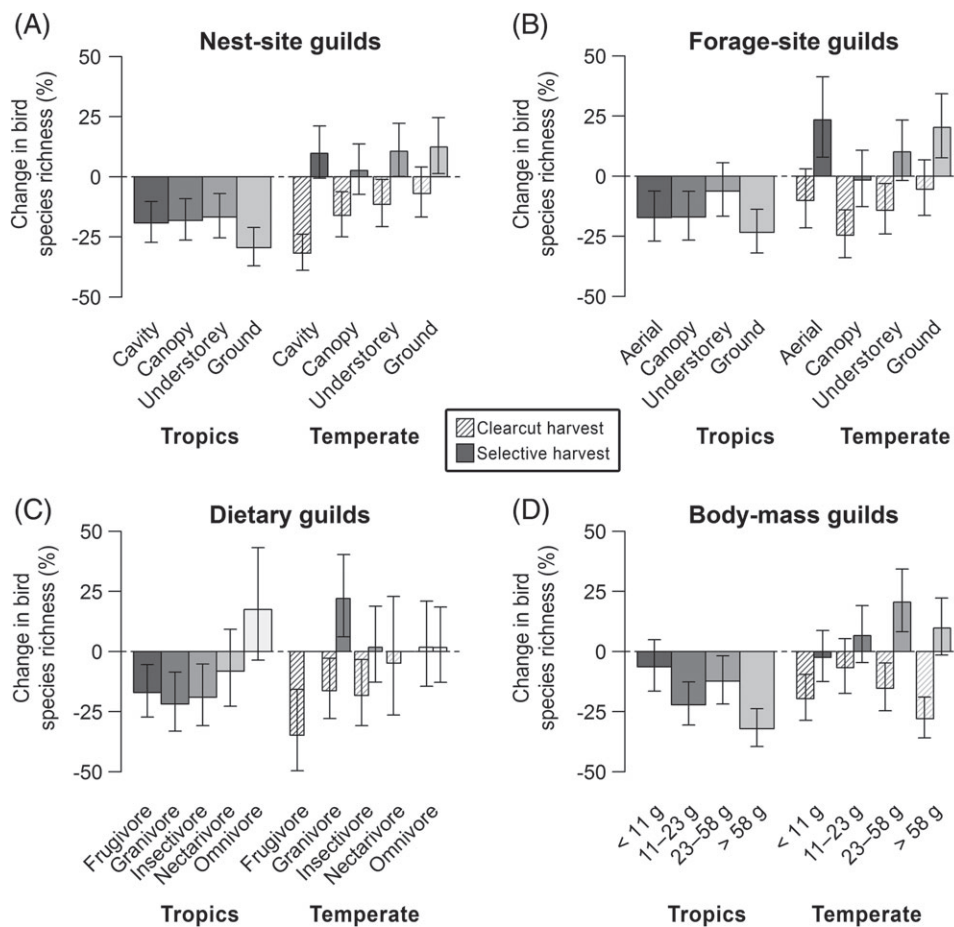
(>75th percentile body mass) guilds experienced the largest declines in species richness with tropical logging (Fig. 4). By contrast, nearly all guilds had increases in species richness following selective logging in temperate latitudes, especially ground- and aerial-foraging guilds, granivores, and birds between 22.7 and 57.9 g body mass (Fig. 4). Clearcut logging in temperate latitudes resulted in a net loss of species from nearly all guilds, especially frugivores, large-sized species, and guilds that nest or forage in the canopy (Fig. 4). Therefore, habitat and dietary preferences of species determined their responses to logging. Effects of logging on species richness of guilds occupying lower vegetation layers differed starkly among latitudes, with lower-strata tropical birds decreasing in richness and lower-strata temperate birds increasing in richness following logging (Fig. 4A, B).

Table 1. Model describing logging effects on avian species richness across latitudes. Degrees of freedom (d.f.), slope estimates, 95% confidence intervals (C.I.), *F* statistics, and *P*-values are presented. Overall model fit ( $r^2$ ) is also shown. Slope estimates represent the change in per cent species richness per standardized unit change in the variable. Slopes for logging type are mean responses. Slopes for each categorical variable are provided for significant interactions

Model	Variable	d.f.	Slope	Slope C.I.	<i>F</i>	<i>P</i> -value
<b>Change in species richness</b> $r^2 = 0.314$ $N = 119$	Years since logging	1	0.02	(-0.02,0.06)	1.0	0.309
	Basal area retention <sup>†</sup>	1	0.04	(-0.004,0.09)	3.2	0.075
	Regional species pool size ( $\gamma$ )*	1	0.10	(0.03,0.16)	9.3	0.003
	Absolute latitude	1	—	—	2.1	0.151
	Logging type*	2	—	—	11.0	<0.001
	Tropics selective harvesting*	—	-0.12	(-0.17,-0.06)	—	—
	Temperate clearcut harvesting*	—	-0.17	(-0.24,-0.10)	—	—
	Temperate selective harvesting	—	0.03	(-0.04,0.10)	—	—
	Absolute latitude × logging type*	2	—	—	5.7	0.004
	Tropics selective harvesting	—	0.04	(-0.13,0.20)	—	—
	Temperate clearcut harvesting*	—	-0.44	(-0.68,-0.20)	—	—
	Temperate selective harvesting	—	0.01	(-0.18,0.19)	—	—

\*Significant at  $P < 0.05$ .

<sup>†</sup>Marginally significant at  $P < 0.10$ .



**Fig. 4.** Latitudinal differences in the effect of logging on bird species richness across guilds of species that differ in (A) nest-site location, (B) forage-site location, (C) dietary preferences, and (D) body mass. Guild means ( $\pm 95\%$  CI) for effects of logging on species richness were calculated at the mean absolute latitude for each latitudinal zone ( $7^\circ$  for tropics and  $45^\circ$  for temperate).

Table 2. Model describing logging effects on avian species richness of nest-site, forage-site, dietary, and body-mass guilds across latitudes. See Table 1 for description of parameters. Slopes for each categorical variable are provided for significant interactions

Model	Variable	d.f.	Slope	Slope C.I.	<i>F</i>	<i>P</i> -value
<b>Change in species richness of nest-site guilds</b> $r^2 = 0.352$ $N = 79$	Years since logging	1	0.01	(-0.02,0.04)	0.8	0.366
	Basal area retention*	1	0.04	(0.002,0.08)	4.2	0.041
	Regional species pool size ( $\gamma$ )*	1	0.07	(0.03,0.11)	10.0	0.002
	Absolute latitude*	1	—	—	4.3	0.039
	Logging type*	2	—	—	28.2	<0.001
	Absolute latitude $\times$ logging type*	2	—	—	8.5	<0.001
	Tropics selective harvesting	—	-0.03	(-0.17,0.10)	—	—
	Temperate clearcut harvesting*	—	-0.38	(-0.54,-0.21)	—	—
	Temperate selective harvesting	—	0.07	(-0.07,0.20)	—	—
	Nest-site guild	3	—	—	1.6	0.184
	Nest-site guild $\times$ logging type*	6	—	—	3.6	0.002
	<b>Change in species richness of forage-site guilds</b> $r^2 = 0.255$ $N = 79$	Years since logging	1	0.02	(-0.02,0.05)	0.7
Basal area retention*		1	0.05	(0.01,0.10)	5.0	0.027
Regional species pool size ( $\gamma$ )		1	0.03	(-0.03,0.08)	1.1	0.300
Absolute latitude		1	—	—	1.8	0.184
Logging type*		2	—	—	17.9	<0.001
Absolute latitude $\times$ logging type <sup>†</sup>		2	—	—	2.9	0.056
Tropics selective harvesting		—	-0.02	(-0.18,0.13)	—	—
Temperate clearcut harvesting*		—	-0.25	(-0.44,-0.07)	—	—
Temperate selective harvesting		—	0.04	(-0.12,0.19)	—	—
Forage-site guild*		3	—	—	2.8	0.042
Forage-site guild $\times$ logging type*		6	—	—	2.3	0.038
<b>Change in species richness of dietary guilds</b> $r^2 = 0.235$ $N = 79$		Years since logging <sup>†</sup>	1	0.04	(0.001,0.08)	3.6
	Basal area retention	1	0.03	(-0.02,0.09)	1.4	0.240
	Regional species pool size ( $\gamma$ )	1	0.03	(-0.06,0.11)	0.3	0.568
	Absolute latitude	1	—	—	1.0	0.309
	Logging type*	2	—	—	6.9	0.001
	Absolute latitude $\times$ logging type*	2	—	—	5.9	0.003
	Tropics selective harvesting	—	0.11	(-0.05,0.26)	—	—
	Temperate clearcut harvesting*	—	-0.41	(-0.66,-0.16)	—	—
	Temperate selective harvesting	—	-0.06	(-0.26,0.14)	—	—
	Dietary guild	4	—	—	1.9	0.116
	Dietary guild $\times$ logging type*	7	—	—	3.1	0.004
	<b>Change in species richness of body-mass guilds</b> $r^2 = 0.321$ $N = 79$	Years since logging	1	0.02	(-0.01,0.05)	1.4
Basal area retention <sup>†</sup>		1	0.04	(-0.002,0.09)	3.5	0.063
Regional species pool size ( $\gamma$ )*		1	0.06	(0.02,0.10)	7.3	0.007
Absolute latitude*		1	—	—	4.4	0.037
Logging type*		2	—	—	23.8	<0.001
Absolute latitude $\times$ logging type*		2	—	—	11.5	<0.001
Tropics selective harvesting		—	0.03	(-0.11,0.17)	—	—
Temperate clearcut harvesting*		—	-0.46	(-0.64,-0.29)	—	—
Temperate selective harvesting		—	0.03	(-0.12,0.18)	—	—
Body-mass guild*		3	—	—	4.6	0.004
Body-mass guild $\times$ logging type*		6	—	—	3.8	0.001

\*Significant at  $P < 0.05$ .<sup>†</sup>Marginally significant at  $P < 0.10$ .

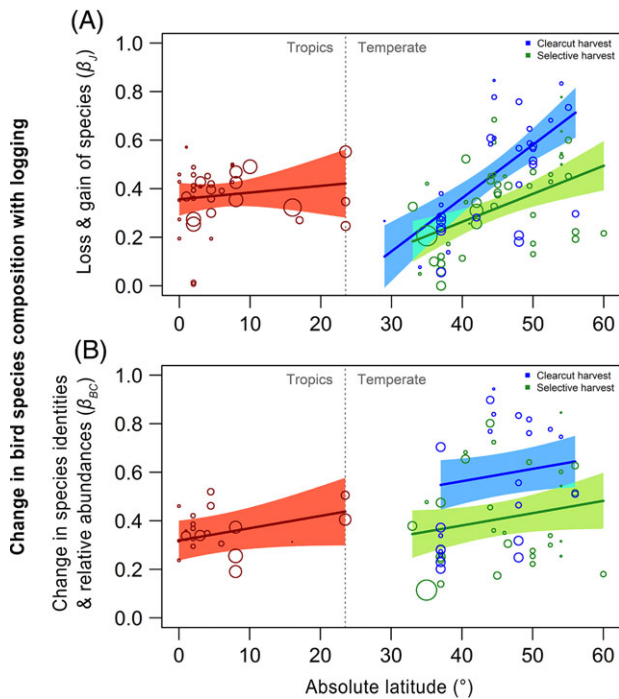
### (3) Logging effects on species composition across latitudes

The effect of logging on bird species composition also differed across latitudes and harvest types (Fig. 5, Table 3).  $\beta_J$ , which measures the loss and gain of species following logging, was nearly constant across tropical latitudes, dropped steeply at lower temperate latitudes, and then increased again at higher temperate latitudes (Fig. 5A). Thus,  $\beta_J$  was roughly constant following selective harvests in tropical and temperate latitudes except between 30° and 40° latitude. This pattern

indicates that relatively fewer species were lost or gained following logging in lower-temperate latitudes compared with either tropical or higher-latitude temperate logging. Temperate clearcut harvests showed steeper increases in  $\beta_J$  with latitude than temperate selective harvests (Fig. 5A), corresponding with substantial loss of species following clearcut logging at higher latitudes (Fig. 3A).

By contrast,  $\beta_{BC}$  (which measures changes in species relative abundances) was approximately constant across latitudes following selective logging in tropical and temperate





**Fig. 5.** Effects of logging on bird species composition measured by (A) the loss and gain of species ( $\beta_J$ ) and (B) the change in species relative abundances ( $\beta_{BC}$ ) across latitudes. Tropical selective-logging studies are in red, temperate clearcut-logging studies are in blue, and temperate selective-logging studies are in green. Larger points indicate increased total spatial extent (sample size  $\times$  spatial extent per sample) of a study. Linear relationships (slope estimate  $\pm$  95% CI) between the change in species composition and latitude for each logging type in each latitudinal zone are also shown.

forests (Fig. 5B). This indicates that while few species were lost or gained following selective logging in lower-latitude temperate forests, the change in the relative abundances of these species was similar to that in tropical and higher-latitude regions.  $\beta_{BC}$  changed more dramatically following temperate clearcut harvests (Fig. 5B, Table 3). The change in bird species composition following temperate clearcut logging tended to converge with the change in bird species composition following temperate and tropical selective logging after roughly 30 years of forest regrowth (Fig. 6, Table 3). Nonetheless, species composition was still distinct from unlogged forests (i.e.  $\beta_{BC} > 0$ ) even 80–90 years after logging (Fig. 6). Analyses of  $\beta_{SES}$ , which represents changes in species composition that remain unexplained by stochastic assembly from the regional species pool, revealed quantitatively similar patterns as analyses of  $\beta_{BC}$  (Table 3) and were positively correlated with  $\beta_{BC}$  ( $r = 0.60, P < 0.001$ ). Thus, observed patterns in the change in species composition following logging across latitudes did not appear to be driven by differences in regional species pools across latitudes.

Effects of logging on species composition, especially  $\beta_{BC}$ , were strong but less variable among nest-site, forage-site, dietary, and body-mass guilds than effects of logging on species richness of these guilds (Fig. 7, Tables 4 and

5). Selective logging appeared disproportionately to alter the species composition of tropical canopy-nesting species, tropical ground-foraging species, tropical granivores, and tropical large-bodied species more than other guilds at any latitude (Fig. 7). Temperate clearcut harvesting had substantial impacts on avian species composition across guilds, but especially on cavity- and canopy-nesting species, canopy- and aerial-foraging species, frugivores, insectivores, and large-bodied species (Fig. 7). Thus, despite differential effects of logging on species richness across latitudes and guilds, the composition of bird species in all guilds changed substantially following logging at all latitudes.

#### (4) Logging effects differ among north-temperate forest types

Effects of logging on avian species richness and composition varied substantially among pure and mixed north-temperate forest types (Fig. 8). Logging in either pure conifer or deciduous forests types tended to reduce bird species richness on average, but logging in mixed conifer–deciduous forests resulted in no net change in species richness (Fig. 8A). Furthermore, forest type appeared to explain the decline in  $\beta_J$  at lower north-temperate latitudes. Logging caused more loss/gain of species ( $\beta_J$ ) in higher-latitude north-temperate forests than in lower-latitude north-temperate forests (Fig. 5A). However, variation in  $\beta_J$  was better explained by forest type than by latitude in the north-temperate zone (Table 6, Figs 5 and 8B), suggesting that greater changes in species identities following logging at higher latitudes may be associated with the general transition from pure deciduous or conifer forest to mixed conifer–deciduous forest. However, the change in species relative abundances following logging ( $\beta_{BC}$ ) did not differ among pure and mixed north-temperate forest types (Fig. 8C), indicating that pre- and post-logging communities in lower north-temperate latitudes had similar species but differed in the relative abundances of those species. Thus, the observed pattern of increasing  $\beta_J$  but constant  $\beta_{BC}$  across temperate latitudes may be caused by geographic shifts in the abundances of conifer and deciduous trees.

## IV. DISCUSSION

Logging in tropical *versus* temperate latitudes had notably different effects on species richness and composition. Logging in tropical forests caused substantial loss of avian species (up to 22% of species). Another recent review of tropical logging studies found that the richness of mammals, amphibians, and invertebrate species also decreased with tropical logging (Burivalova *et al.*, 2014). However, we found that avian richness was largely unaffected by selective logging in north- and south-temperate forests (Fig. 3). Previous reviews have focused primarily on logging impacts to animal species richness and diversity at either temperate (Vanderwel *et al.*, 2007) or tropical latitudes (Gray *et al.*, 2007; Burivalova

Table 3. Models describing logging effects on avian species composition across latitudes. Model predicting changes in the identities of species (based on presence–absence data, or  $\beta_J$ ) and changes in the identities and relative abundances of species (based on abundance data, or  $\beta_{BC}$ ) following logging are shown. See Table 1 for description of parameters. Logging effects on species composition after correcting for expected differences in species composition due to changes in species pools across latitudes ( $\beta_{SES}$ ) are also shown (see text for further details)

Model	Variable	d.f.	Slope	Slope C.I.	<i>F</i>	<i>P</i> -value
<b>Change in species composition (<math>\beta_J</math>)</b> $r^2 = 0.408$ $N = 119$	Years since logging	1	−0.02	(−0.05,0.01)	1.3	0.249
	Basal area retention	1	−0.01	(−0.05,0.03)	0.1	0.768
	Regional species pool size ( $\gamma$ ) <sup>†</sup>	1	−0.04	(−0.08,0.002)	3.5	0.064
	Absolute latitude*	1	—	—	34.8	<0.001
	Total spatial extent <sup>†</sup>	1	−0.03	(−0.06,0.003)	3.2	0.078
	Logging type*	2	—	—	23.2	<0.001
	Tropics selective harvesting*	—	0.38	(0.33,0.42)	—	—
	Temperate clearcut harvesting*	—	0.47	(0.42,0.52)	—	—
	Temperate selective harvesting*	—	0.32	(0.28,0.37)	—	—
	Absolute latitude × logging type*	2	—	—	6.2	0.003
	Tropics selective harvesting	—	0.05	(−0.09,0.20)	—	—
	Temperate clearcut harvesting*	—	0.42	(0.28,0.57)	—	—
	Temperate selective harvesting*	—	0.22	(0.11,0.34)	—	—
<b>Change in species composition (<math>\beta_{BC}</math>)</b> $r^2 = 0.440$ $N = 74$	Years since logging*	1	—	—	9.8	0.003
	Basal area retention	1	−0.02	(−0.08,0.04)	0.5	0.468
	Regional species pool size ( $\gamma$ )	1	−0.03	(−0.09,0.03)	0.8	0.368
	Absolute latitude	1	0.10	(−0.02,0.21)	2.8	0.102
	Total spatial extent	1	−0.03	(−0.07,0.02)	1.4	0.236
	Logging type*	2	—	—	4.8	0.011
	Tropics selective harvesting*	—	0.36	(0.28,0.44)	—	—
	Temperate clearcut harvesting*	—	0.61	(0.53,0.68)	—	—
	Temperate selective harvesting*	—	0.39	(0.33,0.45)	—	—
	Years since logging × logging type*	2	—	—	5.2	0.008
	Tropics selective harvesting	—	−0.003	(−0.08,0.07)	—	—
	Temperate clearcut harvesting*	—	−0.16	(−0.24,−0.09)	—	—
	Temperate selective harvesting*	—	−0.04	(−0.10,0.02)	—	—
<b>Change in species composition (<math>\beta_{SES}</math>)</b> $r^2 = 0.329$ $N = 74$	Years since logging*	1	−0.10	(−0.16,−0.04)	9.5	0.003
	Basal area retention	1	−0.06	(−0.14,0.03)	1.8	0.187
	Absolute latitude <sup>†</sup>	1	0.16	(−0.02,0.35)	3.0	0.087
	Logging type*	2	—	—	9.3	<0.001
	Tropics selective harvesting*	—	14.1	(10.6,18.7)	—	—
	Temperate clearcut harvesting*	—	29.0	(21.3,39.4)	—	—
Temperate selective harvesting*	—	11.1	(8.5,14.4)	—	—	

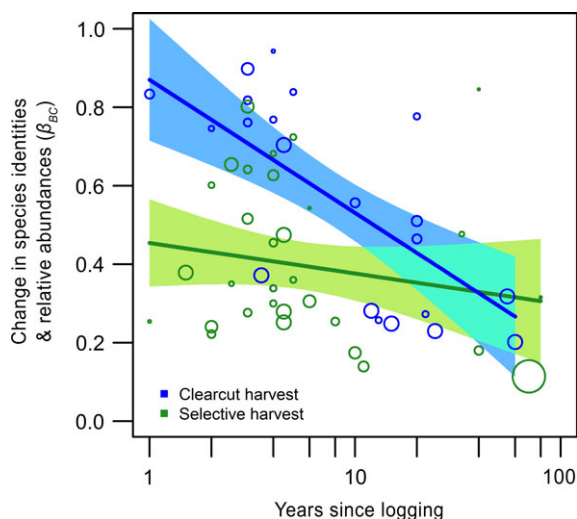
\*Significant at  $P < 0.05$ .

<sup>†</sup>Marginally significant at  $P < 0.10$ .

*et al.*, 2014). Yet changes in species richness cannot capture changes in the identities or relative abundances of species. Changes in species identities were relatively small in south-temperate forests and lower-latitude north-temperate forests, where logging also had little influence on net species richness. The presence of mostly similar species in logged and unlogged forests indicates that bird species in these forests are likely habitat generalists. However, the relative abundances of these species changed with logging as much as the relative abundances of species in forests at other latitudes (Fig. 5). This pattern suggests that while most species are able to occupy both logged and unlogged lower-latitude temperate forests, many species achieve higher abundance and likely have higher fitness in one habitat over the other (Fretwell & Lucas, 1970). By contrast, selective logging caused substantial changes in the identities and relative abundances of bird species in north-temperate mixed conifer–deciduous forests

despite having little to no effect on net species richness. This result indicates that a roughly equivalent number of species specialize in either earlier- or later-successional habitat in higher-latitude temperate forests and that these species replace each other to yield stable richness. A historic regime of large-scale, high-intensity wildfires in north-temperate forests, especially in boreal forests, might account for the large number of early-successional specialist species in these forests (Johnson, Miyanishi & Bridge, 2001). Overall, tropical logging appeared generally to reduce animal species richness, while selective logging in temperate latitudes had greater effects on species composition than on species richness.

Changes in species identities ( $\beta_J$ ) with logging were greater in tropical forests, where logging also caused substantial reductions in richness (Figs 3 and 5). The reduction in tropical bird-species richness reflected that many bird species using older forests disappeared following logging



**Fig. 6.** Effects of logging on bird species composition measured by the change in species relative abundances ( $\beta_{BC}$ ) as a function of the number of years since logging occurred. Temperate clearcut-logging studies are in blue and temperate selective-logging studies are in green. Larger points indicate increased total spatial extent (sample size  $\times$  spatial extent per sample) of a study. Linear relationships (slope estimate  $\pm$  95% CI) between the change in species composition and years since logging for each logging type are also shown. Years since logging is on a log scale.

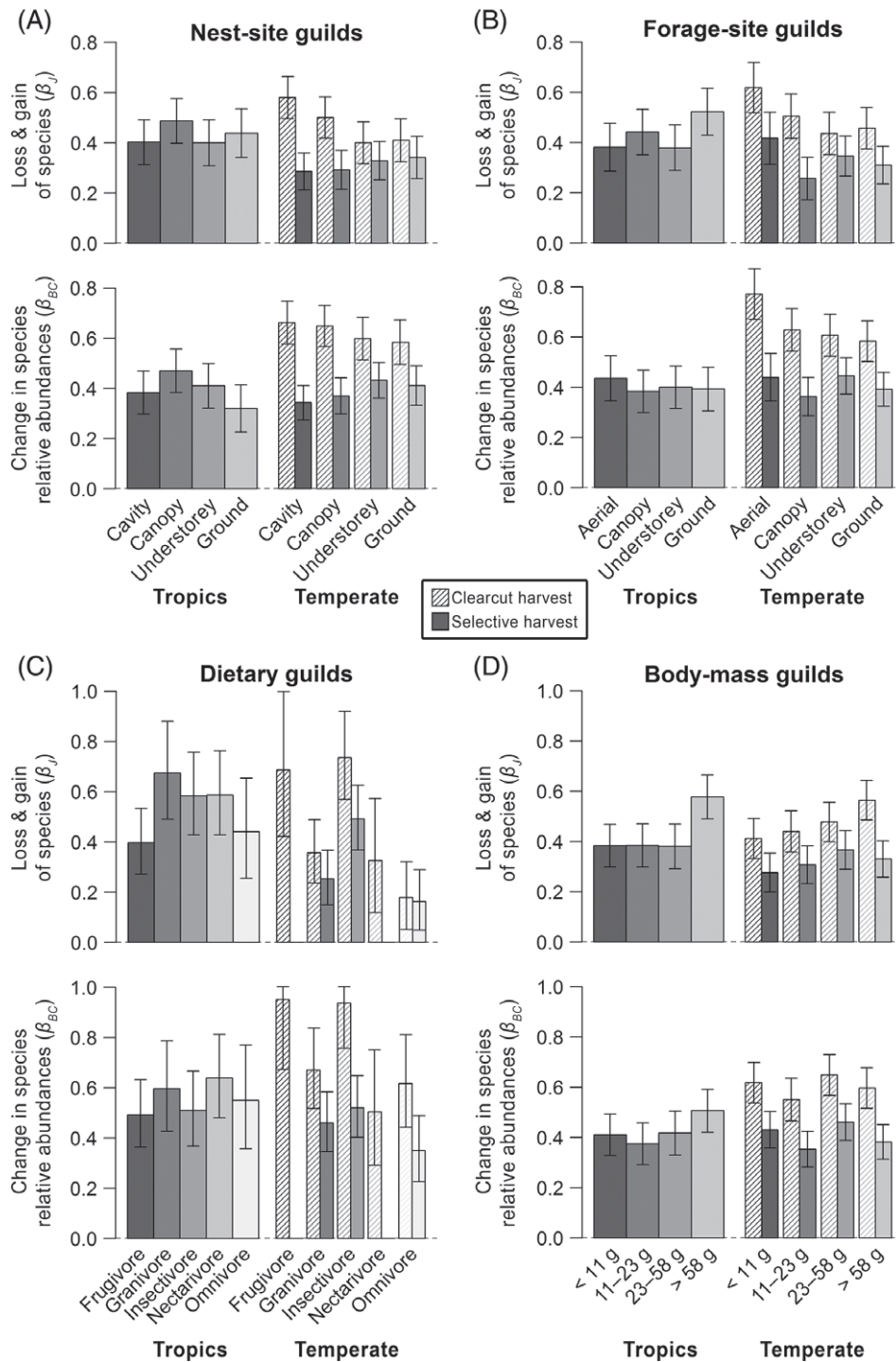
and is consistent with a coarser-scale analysis showing that abundances of tropical mammal and bird habitat-specialist species are most dependent on primary forests (Newbold *et al.*, 2014). These results suggest substantial specialization in late-successional habitat among tropical species and support similar results from local-scale tropical studies (Salisbury *et al.*, 2012; Edwards *et al.*, 2013). Yet these results contrast with the idea that habitat specialization is equivalent among tropical and temperate species (Novotny *et al.*, 2006). The variable responses of species richness and composition to logging support long-standing speculation (MacArthur *et al.*, 1966; Karr & Roth, 1971; MacArthur, 1972) that the numbers of habitat specialists and generalists differ between tropical and temperate forests. Moreover, the latitudinal patterns detected here (Figs 3 and 5) suggest that tropical species predominantly specialize in late-successional habitats, that lower-latitude temperate species can generally occupy both early- and late-successional habitats, and that a roughly equivalent number of higher-latitude temperate species specialize in either early- or late-successional habitats. Thus, results from this meta-analysis are consistent with the idea that strong habitat specialization, especially specialization in late-successional habitat types, leads to substantial loss of animal species following logging in the tropics.

Increased animal species richness with increased vegetation structure has been associated with the addition of species that prefer to nest or forage in higher vegetation layers (MacArthur *et al.*, 1966; Willson, 1974; Martin, 1988). Thus, we expected logging to remove species that forage or

breed in the canopy and possibly add species that forage or breed in lower vegetation layers because of post-logging successional regrowth. Temperate selective logging most closely resembled this expected pattern, having no net effect on richness of canopy species and adding species to nearly all other forest strata (Fig. 4A, B). Temperate clearcut logging removed species from nearly all forest strata, especially from the canopy (Fig. 4A, B). Tropical logging also caused a loss of species that forage in the canopy, but caused an equal or greater loss of species that forage in lower forest strata (Fig. 4A, B). In particular, the net loss of tropical species that nest on the ground was greater than the loss of species in any other strata following selective logging (Figs 4 and 7). This result supports the idea that ground-dwelling tropical species are more strongly impacted by logging than species occupying other forest strata (Cleary *et al.*, 2007; Hamer *et al.*, 2015). Thus, steep declines in tropical species diversity with logging appear to result from a loss of species occupying all forest strata, but especially ground-nesting species. By contrast, selective logging in temperate forests appears to add species occupying lower forest strata. Such differential effects of logging across species that prefer to nest and forage in distinct forest strata, as well as across species with different dietary preferences, also support the idea that habitat specialization can determine changes in diversity following anthropogenic disturbances such as logging.

While we focused on patterns in species richness and composition across logged and unlogged forests, logging effects on demographic rates may be an important but understudied impact of logging on animal populations. Occupation of a habitat does not necessarily mean that population growth rates in that habitat are sustainable ( $\lambda > 1.0$ ). Specifically, some species that occupy logged habitats may have poor demographic performance (reduced survival or reproductive success) relative to conspecifics in unlogged habitats (Fretwell & Lucas, 1970; Pulliam, 2000). Yet the number of studies that have examined logging effects on animal species survival or reproduction is much lower than the number of studies examining logging effects on animal diversity or community composition. We therefore recognize the need for more studies that go beyond effects on species diversity and examine the fitness impacts of logging and other changes in vegetation structure on animals that occupy logged forests.

We searched thoroughly for papers studying the effects of logging on avian communities across the globe. While all of the western hemisphere, tropical Asia, and Australia were well represented in our meta-analysis, Africa and temperate Eurasia were unfortunately underrepresented in our meta-analysis (Fig. 1). Two reasons might account for Africa and temperate Eurasia being poorly represented here. First, our search was restricted to papers that were published or have been translated into English, and this might limit the number of studies from Russia or China. Second, most studies from Africa and temperate Eurasia focused solely on richness and few published species lists from logged and unlogged forests, which were required to calculate changes in species



**Fig. 7.** Latitudinal differences in the effect of logging on bird species composition measured by the loss and gain of species ( $\beta_j$ ) and the change in species relative abundances ( $\beta_{BC}$ ) across guilds of species that differ in (A) nest-site location, (B) forage-site location, (C) dietary preferences, and (D) body mass. Guild means ( $\pm 95\%$  CI) for effects of logging on species richness were calculated at the mean absolute latitude for each latitudinal zone ( $7^\circ$  for tropics and  $45^\circ$  for temperate).

composition. Thus, we encourage future studies of land-use effects to publish full species lists and as much of the original data whenever possible. Also, we must emphasize that the scope of inference of this meta-analysis, while covering most

of the inhabited world (Fig. 1), may not necessarily apply to Africa or temperate Eurasia.

This meta-analysis highlights the role of habitat specialization and preferences in determining effects of

Table 4. Models describing logging effects on avian species composition of nest-site, forage-site, dietary, and body-mass guilds across latitudes. Model predicting changes in the identities of species (based on presence–absence data, or  $\beta_j$ ) following logging are shown. See Table 1 for description of parameters

Model	Variable	d.f.	Slope	Slope C.I.	<i>F</i>	<i>P</i> -value
<b>Change in species composition (<math>\beta_j</math>) of nest-site guilds</b> <i>r</i> <sup>2</sup> = 0.275 <i>N</i> = 79	Years since logging*	1	−0.03	(−0.05,−0.004)	5.2	0.023
	Basal area retention	1	−0.02	(−0.05,0.02)	0.8	0.385
	Regional species pool size ( $\gamma$ )	1	0.00	(−0.03,0.03)	0.0	0.984
	Absolute latitude*	1	—	—	14.5	<0.001
	Total spatial extent*	1	−0.06	(−0.09,−0.03)	19.4	<0.001
	Logging type*	2	—	—	17.9	<0.001
	Absolute latitude × logging type*	2	—	—	7.4	0.001
	Tropics selective harvesting	—	0.05	(−0.06,0.17)	—	—
	Temperate clearcut harvesting*	—	0.34	(0.21,0.46)	—	—
	Temperate selective harvesting	—	0.05	(−0.05,0.15)	—	—
	Nest-site guild	3	—	—	0.8	0.496
	Nest-site guild × logging type*	6	—	—	2.2	0.040
	<b>Change in species composition (<math>\beta_j</math>) of forage-site guilds</b> <i>r</i> <sup>2</sup> = 0.303 <i>N</i> = 79	Years since logging*	1	−0.04	(−0.06,−0.01)	7.6
Basal area retention		1	−0.02	(−0.06,0.02)	0.8	0.361
Regional species pool size ( $\gamma$ )		1	−0.01	(−0.05,0.03)	0.5	0.492
Absolute latitude*		1	—	—	13.0	<0.001
Total spatial extent*		1	−0.07	(−0.09,−0.04)	20.9	<0.001
Logging type*		2	—	—	17.6	<0.001
Absolute latitude × logging type*		2	—	—	6.0	0.003
Tropics selective harvesting		—	0.02	(−0.10,0.14)	—	—
Temperate clearcut harvesting*		—	0.32	(0.19,0.45)	—	—
Temperate selective harvesting		—	0.08	(−0.02,0.19)	—	—
Forage-site guild		3	—	—	0.9	0.427
Forage-site guild × logging type*		6	—	—	2.7	0.013
<b>Change in species composition (<math>\beta_j</math>) of dietary guilds</b> <i>r</i> <sup>2</sup> = 0.300 <i>N</i> = 79		Years since logging	1	−0.01	(−0.04,0.02)	0.4
	Basal area retention	1	−0.03	(−0.07,0.02)	1.5	0.221
	Regional species pool size ( $\gamma$ )*	1	−0.06	(−0.12,−0.01)	4.8	0.030
	Absolute latitude*	1	—	—	10.2	0.002
	Total spatial extent*	1	−0.05	(−0.08,−0.02)	11.3	0.001
	Logging type*	2	—	—	14.9	<0.001
	Absolute latitude × logging type	2	—	—	1.5	0.230
	Tropics selective harvesting	—	0.08	(−0.03,0.19)	—	—
	Temperate clearcut harvesting*	—	0.24	(0.08,0.40)	—	—
	Temperate selective harvesting	—	0.09	(−0.03,0.21)	—	—
	Dietary guild*	4	—	—	5.9	<0.001
	Dietary guild × logging type*	7	—	—	3.3	0.002
	<b>Change in species composition (<math>\beta_j</math>) of body-mass guilds</b> <i>r</i> <sup>2</sup> = 0.319 <i>N</i> = 79	Years since logging	1	−0.01	(−0.04,0.01)	1.2
Basal area retention		1	−0.01	(−0.04,0.03)	0.1	0.716
Regional species pool size ( $\gamma$ )		1	−0.02	(−0.04,0.01)	1.1	0.294
Absolute latitude*		1	—	—	13.9	<0.001
Total spatial extent*		1	−0.07	(−0.10,−0.05)	28.5	<0.001
Logging type*		2	—	—	19.1	<0.001
Absolute latitude × logging type*		2	—	—	9.0	<0.001
Tropics selective harvesting		—	0.03	(−0.08,0.14)	—	—
Temperate clearcut harvesting*		—	0.35	(0.22,0.47)	—	—
Temperate selective harvesting		—	0.05	(−0.05,0.15)	—	—
Body-mass guild*		3	—	—	5.4	0.001
Body-mass guild × logging type		6	—	—	1.5	0.179

\*Significant at *P* < 0.05.

†Marginally significant at *P* < 0.10.

logging on animal species richness and composition across latitudes and forest types. Such preferences should have evolved due to the reliability of certain vegetation types or structures as indicators of successful reproductive or foraging outcomes (Fretwell & Lucas, 1970; Pulliam, 2000). Yet logging followed by agricultural development,

livestock grazing, or other human activities often decouples once-reliable habitat cues from the actual reproductive or survival consequences of settling in such degraded habitats (Schlaepfer, Runge & Sherman, 2002; Gibbs *et al.*, 2010; Chalfoun & Schmidt, 2012). Our meta-analysis was restricted to logging practices that allowed forests

Table 5. Models describing logging effects on avian species composition of nest-site, forage-site, dietary, and body-mass guilds across latitudes. Model predicting changes in the identities and relative abundances of species (based on abundance data, or  $\beta_{BC}$ ) following logging are shown. See Table 1 for description of parameters

Model	Variable	d.f.	Slope	Slope C.I.	<i>F</i>	<i>P</i> -value
<b>Change in species composition (<math>\beta_{BC}</math>) of nest-site guilds</b> $r^2 = 0.360$ $N = 74$	Years since logging*	1	—	—	39.1	<0.001
	Basal area retention	1	-0.03	(-0.06,0.01)	2.2	0.138
	Regional species pool size ( $\gamma$ ) <sup>†</sup>	1	-0.03	(-0.06,0.003)	3.1	0.082
	Absolute latitude*	1	0.09	(0.03,0.16)	7.8	0.006
	Total spatial extent*	1	-0.02	(-0.04,0.01)	2.0	0.156
	Logging type*	2	—	—	16.1	<0.001
	Years since logging × logging type*	2	—	—	9.6	<0.001
	Tropics selective harvesting	—	-0.02	(-0.06,0.02)	—	—
	Temperate clearcut harvesting*	—	-0.15	(-0.19,-0.11)	—	—
	Temperate selective harvesting*	—	-0.06	(-0.10,-0.02)	—	—
	Nest-site guild	3	—	—	0.9	0.434
Nest-site guild × logging type	6	—	—	1.6	0.155	
<b>Change in species composition (<math>\beta_{BC}</math>) of forage-site guilds</b> $r^2 = 0.389$ $N = 74$	Years since logging*	1	—	—	31.1	<0.001
	Basal area retention*	1	-0.04	(-0.07,-0.01)	5.1	0.025
	Regional species pool size ( $\gamma$ )	1	-0.02	(-0.06,0.02)	1.0	0.313
	Absolute latitude*	1	0.12	(0.05,0.19)	12.5	<0.001
	Total spatial extent <sup>†</sup>	1	-0.02	(-0.05,0.002)	3.2	0.076
	Logging type*	2	—	—	15.9	<0.001
	Years since logging × logging type*	2	—	—	11.3	<0.001
	Tropics selective harvesting	—	0.002	(-0.04,0.04)	—	—
	Temperate clearcut harvesting*	—	-0.14	(-0.18,-0.10)	—	—
	Temperate selective harvesting*	—	-0.07	(-0.10,-0.03)	—	—
	Forage-site guild	3	—	—	1.7	0.167
Forage-site guild × logging type	6	—	—	1.0	0.427	
<b>Change in species composition (<math>\beta_{BC}</math>) of dietary guilds</b> $r^2 = 0.300$ $N = 74$	Years since logging*	1	—	—	19.2	<0.001
	Basal area retention	1	-0.03	(-0.07,0.01)	2.1	0.145
	Regional species pool size ( $\gamma$ )	1	-0.04	(-0.10,0.01)	2.7	0.010
	Absolute latitude*	1	0.12	(0.05,0.20)	11.3	<0.001
	Total spatial extent	1	-0.01	(-0.04,0.02)	0.6	0.447
	Logging type*	2	—	—	14.2	<0.001
	Years since logging × logging type*	2	—	—	7.6	0.001
	Tropics selective harvesting	—	-0.01	(-0.05,0.03)	—	—
	Temperate clearcut harvesting*	—	-0.14	(-0.18,-0.09)	—	—
	Temperate selective harvesting*	—	-0.05	(-0.09,-0.002)	—	—
	Dietary guild	4	—	—	1.5	0.204
Dietary guild × logging type*	7	—	—	2.3	0.027	
<b>Change in species composition (<math>\beta_{BC}</math>) of body-mass guilds</b> $r^2 = 0.379$ $N = 74$	Years since logging*	1	—	—	33.1	<0.001
	Basal area retention	1	-0.02	(-0.06,0.01)	2.0	0.160
	Regional species pool size ( $\gamma$ )	1	-0.01	(-0.04,0.01)	1.0	0.316
	Absolute latitude*	1	0.10	(0.04,0.17)	10.3	0.002
	Total spatial extent*	1	-0.05	(-0.08,-0.03)	17.4	<0.001
	Logging type*	2	—	—	14.6	<0.001
	Years since logging × logging type*	2	—	—	12.2	<0.001
	Tropics selective harvesting	—	-0.02	(-0.07,0.02)	—	—
	Temperate clearcut harvesting*	—	-0.15	(-0.20,-0.11)	—	—
	Temperate selective harvesting <sup>†</sup>	—	-0.03	(-0.07,0.005)	—	—
	Body-mass guild <sup>†</sup>	3	—	—	2.5	0.058
Body-mass guild × logging type	6	—	—	1.0	0.453	

\*Significant at  $P < 0.05$ .

<sup>†</sup>Marginally significant at  $P < 0.10$ .

to regrow following disturbance. Thus, logging followed by human land use likely leads to greater reductions in species richness and changes in species composition than we report here (Edwards *et al.*, 2010; Newbold *et al.*, 2015). Furthermore, proliferations of human land-use activities as

well as climate change are threatening an unprecedented level of vegetation change across the globe (Gibbs *et al.*, 2010; Gottfried *et al.*, 2012). A thorough understanding of the global impacts these changes will have on species richness and composition of animal communities, as well as on animal

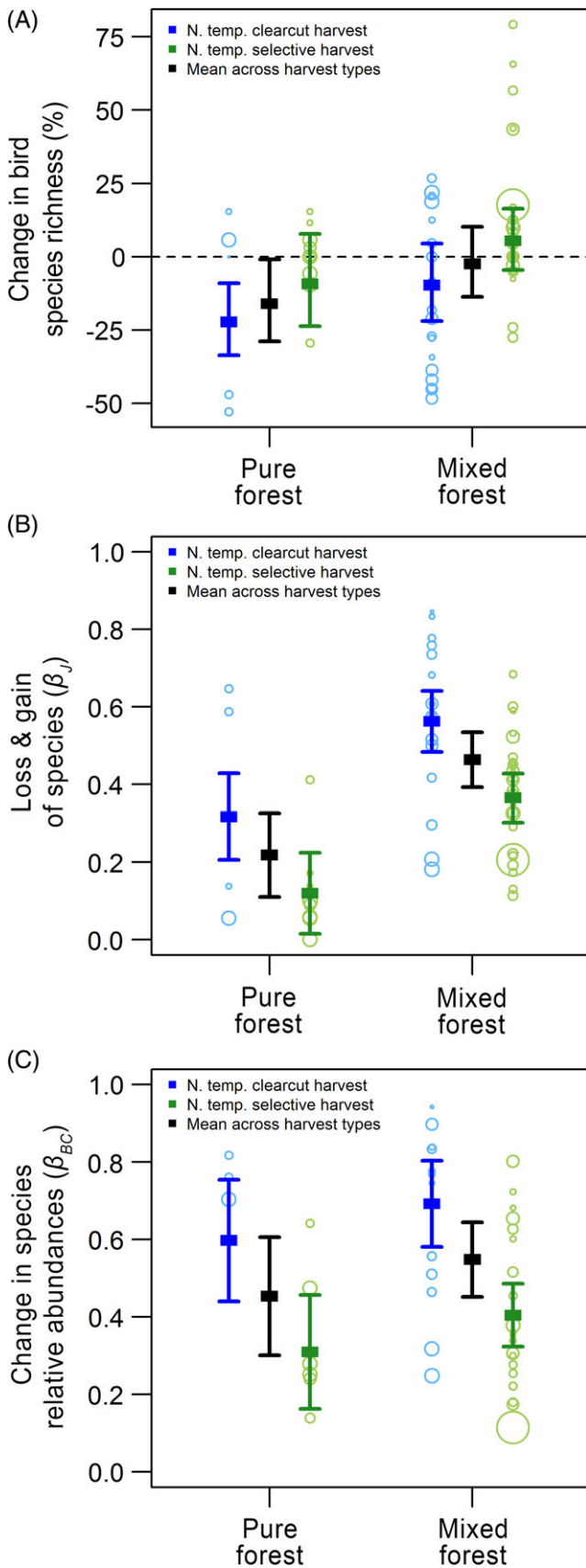


Fig. 8. Legend on next column.

fitness, will be essential to conserving biodiversity around the world.

## V. CONCLUSIONS

(1) This meta-analysis has shown that logging has dramatically different effects on animal species richness and composition in tropical compared to temperate forests as evidenced by differential responses of avian species richness and composition to logging across latitudes. This is the first comprehensive assessment of logging effects on species richness and composition across tropical and temperate latitudes for any animal taxonomic group.

(2) Logging in tropical forests led to a loss of species that breed and forage in all forest strata (ground to canopy), causing severe reductions in bird species richness. This result suggests that many tropical species across all forest strata specialize in late-successional forest habitat.

(3) Logging in lower latitude north- and south-temperate forests generally did not affect the richness or identities of avian species. While most forest-dwelling species in these latitudes appeared to be habitat generalists, logging in these latitudes did change their relative abundances. This suggests that existence of both logged and unlogged forests would ensure that all species have healthy regional population abundances.

(4) Logging in higher-latitude north-temperate forests did not alter species richness, but did alter the identities and relative abundances of avian species. Logging at higher latitudes generally replaced lost late-successional specialist species with early-successional specialist species. This pattern suggests that a landscape including both logged and unlogged forests would support maximal regional diversity. A historic regime of large-scale, stand-replacing wildfires in high-latitude compared to lower-latitude forests may account for the increase in species that specialize in early-successional habitat at higher latitudes.

(5) Clearcut harvesting was devastating to avian communities in higher-latitude temperate forests and dramatically altered the relative abundances of bird species in lower-latitude temperate forests. Thus, clearcut-logging practices should be avoided if possible.

Fig. 8. Effects of logging on (A) bird species richness, (B) bird species composition measured by the loss and gain of species ( $\beta_j$ ), and (C) bird species composition measured by the change in species relative abundances ( $\beta_{BC}$ ) across pure (conifer or deciduous only) and mixed (conifer mixed with deciduous) north-temperate forest types. Temperate clearcut-logging studies are in blue and temperate selective-logging studies are in green. Means ( $\pm 95\%$  C.I.) are indicated for each logging type (clearcut and selective harvest) in their respective colour, and overall forest type means (across harvest types) are in black. Larger points indicate increased total spatial extent (sample size  $\times$  spatial extent per sample) of a study.

Table 6. Models describing effects of logging on local avian species richness and composition across pure (conifer or deciduous only) and mixed (conifer and deciduous) north-temperate forest types. See Table 1 for description of parameters

Model	Variable	d.f.	Slope	Slope C.I.	<i>F</i>	<i>P</i> -value
<b>Change in species richness</b> $r^2 = 0.424$ $N = 61$	Years since logging	1	0.01	(-0.05,0.07)	0.2	0.682
	Basal area retention	1	0.03	(-0.05,0.12)	0.7	0.396
	Regional species pool size ( $\gamma$ )	1	0.03	(-0.04,0.11)	0.8	0.383
	Absolute latitude*	1	—	—	4.1	0.048
	Logging type (clearcut vs. selective) <sup>†</sup>	1	—	—	3.0	0.089
	Absolute latitude $\times$ logging type*	1	—	—	7.9	0.007
	Temperate clearcut harvesting*	—	-0.25	(-0.39,-0.11)	—	—
	Temperate selective harvesting	—	-0.03	(-0.11,0.05)	—	—
<b>Change in species composition (<math>\beta_f</math>)</b> $r^2 = 0.645$ $N = 61$	Forest type (pure vs. mixed forest) <sup>†</sup>	1	—	—	2.9	0.095
	Years since logging*	1	-0.06	(-0.10,-0.02)	9.2	0.004
	Basal area retention	1	0.01	(-0.05,0.06)	0.04	0.843
	Regional species pool size ( $\gamma$ )	1	-0.01	(-0.06,0.04)	0.2	0.688
	Absolute latitude	1	—	—	1.1	0.294
	Logging type (clearcut vs. selective)*	1	—	—	13.5	0.001
	Absolute latitude $\times$ logging type*	1	—	—	6.6	0.013
	Temperate clearcut harvesting*	—	0.10	(0.03,0.17)	—	—
<b>Change in species composition (<math>\beta_{BC}</math>)</b> $r^2 = 0.637$ $N = 41$	Temperate selective harvesting	—	-0.01	(-0.07,0.04)	—	—
	Forest type (pure vs. mixed forest)*	1	—	—	18.8	<0.001
	Years since logging*	1	—	—	10.0	0.003
	Basal area retention	1	-0.01	(-0.08,0.06)	0.1	0.702
	Regional species pool size ( $\gamma$ ) <sup>†</sup>	1	-0.06	(-0.12,0.005)	3.3	0.079
	Absolute latitude	1	-0.03	(-0.09,0.04)	0.6	0.451
	Logging type (clearcut vs. selective)*	1	—	—	14.9	0.001
	Years since logging $\times$ logging type	1	—	—	0.5	0.503
	Temperate clearcut harvesting*	—	-0.12	(-0.20,-0.03)	—	—
	Temperate selective harvesting*	—	-0.08	(-0.16,-0.003)	—	—
	Forest type (pure vs. mixed forest) <sup>†</sup>	1	—	—	1.6	0.217

\*Significant at  $P < 0.05$ .<sup>†</sup>Marginally significant at  $P < 0.10$ .

(6) Removing less basal area during logging did not eliminate, but mitigated the loss of species from tropical forests. In some cases, removing less basal area during logging increased avian diversity in temperate forests.

(7) This meta-analysis provides insights into the important role of habitat specialization in determining differential responses of animal communities to logging across tropical and temperate latitudes.

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## VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Table S1.** Published studies used in meta-analyses examining logging effects on local turnover of avian communities.

**Fig. S1.** Funnel plots showing model residuals plotted against total spatial extent (sample size × spatial extent per sample) of a study.

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