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Life after logging in tropical forests of Borneo: A meta-analysis

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ABSTRACT

Selectively logged tropical forests retain high species richness and functional diversity, but species composition changes after logging, suggesting that some species are more vulnerable to logging than others. We did a meta-analysis to summarise the effect of logging on the abundance of individual bird and mammal species in tropical forests of Borneo, which have suffered some of the most intense selective logging in the tropics. We found that species classified by the International Union for Conservation of Nature (IUCN) as 'vulnerable' or 'near-threatened' are generally less abundant in logged tropical forests than those classified as 'least concern'. However, the effect of logging within each IUCN category is variable, indicating that logging is not the only or main cause of decline in abundance. While our results show that closely related species responded similarly to logging, in birds there was significant variation between responses of some closely related species. Bigger species were significantly more susceptible to logging than smaller species in both birds and mammals. We also found that cavity-nesting birds suffered more from logging than did other species. Our results highlight the importance of identifying which factors lead individual species to flourish or suffer in logged tropical forests.

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1. Introduction

A key driver of land-use change in the tropics is commercial selective logging (Edwards et al., 2014a), with more than 4 million km² of tropical forests in permanent timber estates (Blaser et al., 2011). There is serious concern over the environmental and ecological consequences of selective logging (Meijaard et al., 2005; Michalski and Peres, 2013), and the conservation value of logged tropical forests has therefore been contentious. Recent assessments have, however, shown that selectively logged tropical forests can retain many species and much functional diversity (Dent and Wright, 2009; Berry et al., 2010; Putz et al., 2012; Edwards et al., 2013b, 2014), especially when forests are logged at low intensity (Burivalova et al., 2014), via reduced-impact techniques (Bicknell et al., 2014), or under land sparing which combines higher intensity logging with the protection of primary forest tracts (Edwards et al., 2014b). Logged tropical forests are therefore increasingly valued for conservation (Edwards et al., 2014a), in addition to old-growth, unlogged tropical forests (Gibson et al., 2011).

The conservation potential of selectively logged tropical forest is strengthened for two further reasons. First, the amount of tropical forest allocated to logging is increasing rapidly (Blaser et al., 2011; Michalski and Peres, 2013). Second, the widespread conversion of logged tropical

forests to oil palm, paper-pulp, rubber and other plantation crops causes a dramatic decline in biodiversity and functional diversity (Sodhi et al., 2010; Gibson et al., 2011; Edwards et al., 2013a; Warren-Thomas et al., 2015). Forest clearance after logging caused the loss of over 1.5 million km² of tropical forests between 1980 and 2012 (Gibbs et al., 2010; Hansen et al., 2013) driving the loss of approximately 75% of bird and butterfly species (Mitra and Sheldon, 1993; Peh et al., 2006; Koh and Wilcove, 2008; Sheldon et al., 2010; Styring et al., 2011).

Although the reduction in biodiversity in tropical forests post logging is less dramatic than previously thought, some species seem to be more vulnerable to logging than others (Meijaard et al., 2005; Burivalova et al., 2014; Edwards et al., 2014c). Identification of those that are most sensitive to logging can assist development of conservation policies and logging practices to protect the most vulnerable species and will be key to further our understanding of the complex ecological impacts of logging.

In this study, we have reviewed studies that compared the abundance of bird and mammal species in unlogged tropical forests with the abundance of the same species in selectively logged tropical forests of Borneo, a global biodiversity hotspot severely threatened by land-use changes (Meijaard et al., 2005; Wilcove et al., 2013). We did a meta-analysis to estimate the magnitude of the effects of logging on species' abundance. In contrast to previous meta-analyses of integrative responses (e.g., species diversity) at a global scale (Gibson et al., 2011; Putz et al., 2012; Burivalova et al., 2014), we sought to identify which species, class (birds and mammals) and International Union for

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Conservation of Nature (IUCN) Red List status are harmed by logging, while also testing for effects of body mass, phylogeny and the time elapsed since last logging. Also, we tested whether cavity-breeding birds suffered more from logging than species with other nesting strategies, because the cutting of mature trees could decrease the availability of cavity nesting sites in logged tropical forests.

2. Material and methods

2.1. Data collection

A review of the literature was performed on the Web of Science using a combination of following keywords: “Logging”, “Borneo”, “Birds”, “Mammals” and “Biodiversity”. We then searched for additional studies cross-referencing from hits from this search. One author was contacted to provide data missing in the selected paper (Lammertink, 2004). Articles entered in our meta-analysis were those that compared estimates of abundance of species between unlogged and logged tropical forests. The list of study areas is reported in Table 1 and additional data are reported in the online Supplementary Table S1 (study details and abundance estimates), Supplementary Table S2 (nesting preferences of birds), Supplementary Table S3 (body mass of birds) and Supplementary Table S4 (body mass of mammals). Studies using the same dataset in two or more publications were identified and used only once. The current IUCN Red List status was collected online from <http://www.iucnredlist.org/> (last access 21/10/2014), with species categorised as least concern (LC); near-threatened (NT); or vulnerable (VU). Data for *Pongo pygmaeus* (the only species classified as endangered) were pooled within the ‘Vulnerable’ category to aid model convergence. Data on nesting preferences for birds were collected from HBWAlive (www.hbw.com; see online Supplementary Table S2).

2.2. Statistical analyses

Abundance of a species in a selectively logged versus an unlogged tropical forest, having controlled for sampling effort, was used to compare effects on logging in birds and mammals. We used the proportion of individuals of a species observed in the logged forest over the total number of individuals observed in both logged and unlogged forests as our measure of effect size. Such proportional data are best

summarized across studies using counts in a binomial (or multinomial) fashion (Hamza et al., 2008). In many cases, abundances were reported as corrected for the relative time spent surveying logged versus unlogged tropical forest (e.g., individuals per km² or number of detections per number of trap nights; see online Supplementary Table S1 for detailed study specific information). To include these data in the meta-analysis, corrected abundances were back-transformed to counts in logged and unlogged forest representative of the total sample size underlying that comparison (Eq. (1)). This approach allowed for a meta-analysis at the most primary level of the data possible and could be regarded more as a re-analysis across studies rather than classic meta-analysis (Nakagawa and Cuthill, 2007), in which secondary outputs from individual studies are summarized using effect sizes and their associated sampling variances.

For each study, calculating corrected abundances back to count data that is representative of the sample size allowed the employment of multinomial models, which are specifically designed to handle count data in proportions (Hadfield, 2010; Hadfield and Nakagawa, 2010). These statistics are immune to problems such as zero counts when using proportions to summarise data (Hamza et al., 2008), and effectively model the relative chance of observing a specific species in logged versus unlogged forest, but crucially weighted for the number of observations that make up this comparison (as in meta-analysis, Nakagawa and Cuthill, 2007). Note that this approach does not correct for inherent biases that could be present in some of the methodology employed by the studies included (Johnson, 2008; see online Supplementary Table S1 for details). We could not stratify the data set for differential methods, given the wide variety of sampling techniques used (e.g., mist netting, camera traps), corrections for time spent surveying or area used, and the relatively small number of studies.

We calculated the count in logged forest used in our analyses as:

$$\text{count in logged forest} = \left(\frac{\text{abundance in logged forest}}{\text{total abundance}} \right) \times \text{total sample size.} \quad (1)$$

The proportion of corrected abundances reported are used to construct a representative count according to the sample size of the study. For example, if the abundance reported is expressed per km² area surveyed, then assuming that 4 versus 2 individuals per km² were sampled in logged versus unlogged forest with a total number of 60 observed individuals, the underlying count in logged forest used in the analysis is $(4 / (4 + 2)) \times 60 = 40$. Due to the corrections of abundances employed and rounding issues, back-transformed counts were not always integers and in such cases were rounded to the nearest integer to allow inclusion in the multinomial models.

Given the complex data structure of multiple reports per species across multiple studies (for which we included random terms to correct for dependence of the data, Table 3), and to also allow inclusion of phylogenetic information (see below), we employed flexible Bayesian mixed generalized models in MCMCglmm (Hadfield, 2010; Hadfield and Nakagawa, 2010) in R (R Development Core Team, 2011). Chains were run for 2,700,000 iterations, with a burn-in of 200,000 iterations and a thinning interval of 1000 iterations. Inverse Wishart priors were used ($V = 1$, $\nu = 0.002$). Models with parameter-expanded priors were also run, but these priors did not improve convergence and models with inverse Wishart priors are therefore presented. We ran a separate model to obtain estimates at the species level only, to be used for illustration purposes in Fig. 3, including a fixed effect for species and a random term for study. From these models we excluded species with zero counts and very low sample size (≤ 5) for which these fixed effects did not converge and inclusion would have yielded unreliable estimates and credible intervals, but note that models presented in Figs. 1 and 2, and Tables 2 and 3 did include these data. These models were run for 10,000,000 iterations, with burn-in of 1000,000 iterations and thinning interval of 4500 iterations.

Table 1

List of study locations for the articles included in the meta-analysis.

Study location	Article
Ulu Segama Forest Reserve, Sabah	Lambert (1992)
Ulu Segama Forest Reserve, Sabah	Heydon and Bulloh (1996)
Ulu Segama Forest Reserve, Sabah	Heydon and Bulloh (1997)
Ulu Segama Forest Reserve, Sabah	Colón (2002)
Ulu Segama Forest Reserve, Sabah	Johns in Heydon and Bulloh, 1996
Sungai Sebangau, Kalimantan	Morrogh-Bernard et al. (2003)
Lower Kinabatangan, Sabah	Ancrenaz et al. (2004)
Gunung Palung National Park, Kalimantan	Lammertink (2004)
Gunung Palung National Park, Kalimantan	Johnson et al. (2005)
Gunung Palung National Park, Kalimantan	Felton et al. (2003)
Berau and East Kutai, Kalimantan	Marshall et al. (2006)
Danum Valley Conservation Area, Kinabalu, Tawau Hills, Luasong Field Centre, Kg. Monggis, Kg. Tumbalang, Sabah	Wells et al. (2007a)
Tabin Wildlife Reserve, Sabah	Bernard et al. (2009)
Sela'an-Linau, Sarawak	Mathai et al. (2010)
Ulu Segama Forest Reserve, Sabah	Edwards et al. (2011)
Maliau Basin Conservation Area, Sabah	Brodie and Giordano (2012)
Maliau Basin Conservation Area and Kalabakan Forest Reserve, Sabah	Cusack et al. (2015)

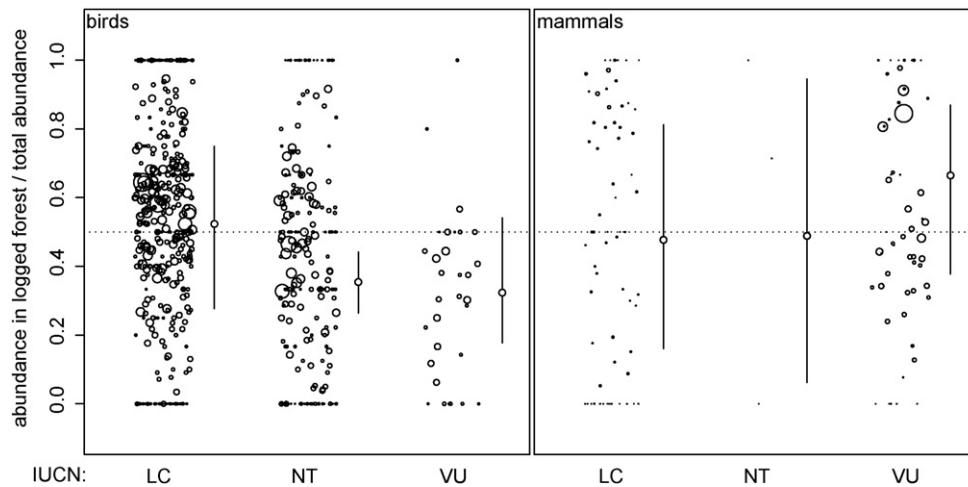


Fig. 1. IUCN category plotted against the abundance of a species in a logged forest over total abundance. LC = least concern, NT = near threatened, VU = vulnerable. Bubble area reflects total sample size in a single comparison and individual comparisons are jittered on the x-axis within each category to show all raw data. Overall estimates with 95% credible intervals are from models as presented in Table 2, see text for more details.

Three separate chains were run to establish convergence using Gelman-Rubin statistics (Gelman and Rubin, 1992), of which the first chain is reported in the results. The resulting autocorrelations across iterations were low (<0.1) and potential scale reduction was lower than 1.05 among chains for all parameters indicating adequate convergence, except for a few models where the random term study showed some divergence between chains that was moderate ~ 1.2 . Note, however, that the estimated variance for study was very close to zero and hence minor stochastic deviations from zero in separate chains easily results in an apparent divergence in the potential scale reduction across chains. Examination of plots of the chain indicated adequate convergence. Therefore chains were not run for longer and doubts on proper convergence should not affect any of the conclusions presented.

In addition to examining patterns across the whole dataset, we also tested for phylogenetic signal and the effect of body mass using separate phylogenies, and thus models, for birds and for mammals. From a distribution of 1000 trees extracted from the recent bird supertree project (www.birdtree.org, Jetz et al., 2012) the most parsimonious tree was extracted using BEAST (Drummond et al., 2012). We purposely did not investigate phylogenetic uncertainty (Simons et al., 2014), because of the computational demands of MCMCglmm. For mammals, we used a

recent maximum-likelihood based supertree (Bininda-Emonds et al., 2007). When 95% credible intervals did not overlap zero for the fixed estimates we considered them significant. Model interpretation was based on DIC, which behaves similarly to AIC, meaning that models with lower DIC are preferred and that a reduction of ≥ 2 indicates substantial support for the alternative model (Burnham and Anderson, 2004; Horvathova et al., 2011).

3. Results

There was strong evidence of an effect of IUCN status on species abundance in selectively logged versus unlogged tropical forest (Table 2). Near-threatened and vulnerable birds fared worse after logging, whereas there was a suggestion that vulnerable mammals do better after logging (Fig. 1). However, there was no significant statistical support for such a difference in the effect of IUCN status between birds and mammals as judged by DIC (Table 2). The number of years since last logging, as tested within the context of the preferred model, did not explain the observed abundance response to logging (estimate: -0.0023 , 95%CI: -0.0105 – 0.0072).

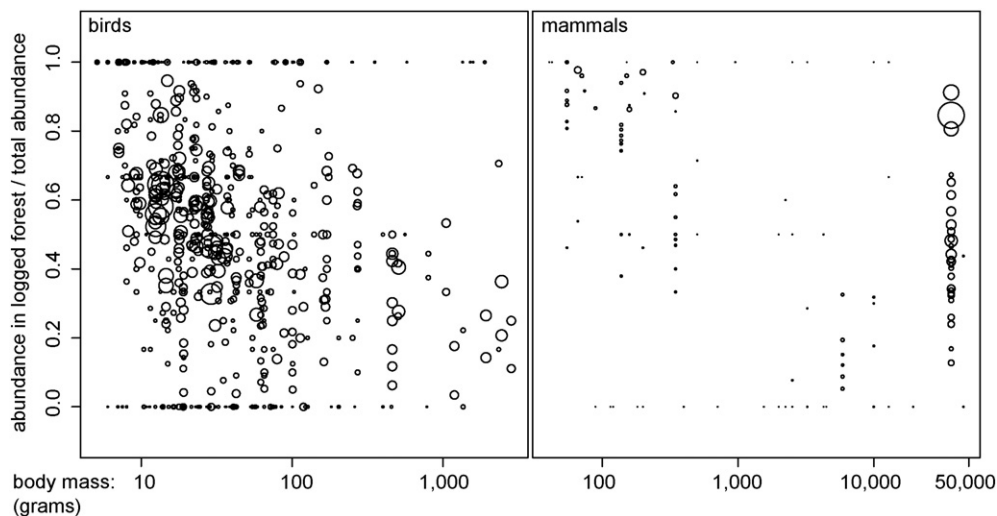


Fig. 2. Raw body mass plotted against abundance in logged forest over the total (x-axis is a \log_{10} axis). See text for estimates from phylogenetically controlled analyses which revealed a significant negative relationship between body mass and response to logging, with bigger species showing a stronger reduction in abundance in logged forest in both birds and mammals. Bubble areas represent different sample sizes per comparison.

Table 2

A. Model selection based on DIC shows that there were significant differences in effect size among different “IUCN status” categories. B. DIC comparisons of the null model (including IUCN status) with a model that included either phylogeny showed that shared ancestry explained variation in the response to logging in both birds and mammals.

Model	DIC	
A		
IUCN status	34,723.7	
Class + IUCN status	34,723.9	
Null	34,726.6	
IUCN status * class	34,727.9	
B		
	Birds	Mammals
IUCN status	16,656.7	18,069.6
+ Phylogeny	16,652.2	18,068.8

Phylogeny explained a substantial proportion of responses to selective logging (birds: 0.30, mammals: 0.62; Tables 2B and 3), suggesting that closely related species respond similarly to logging. Note that a substantial proportion of the variation was explained by the random intercept of species in birds, demonstrating that irrespective of phylogeny, bird species differed in their response to logging due to unknown causes (Table 3). These effects are also illustrated in Fig. 3, in which we plotted the estimated relative abundance in logged forest per species (see Methods), showing substantial heterogeneity among species (Tables 2 and 3) and a limited effect of logging across species. The latter is in accordance with the overall estimates presented in Fig. 1: only species with a specific IUCN status suffer from logging. We sought to further explain these species differences focussing on body mass in both birds and mammals, and breeding behavior in birds (i.e., natural cavity dependence).

In the models containing the separate phylogenies, we tested for an effect of body mass on species response to logging. We found that bigger species were significantly more susceptible to logging than smaller species in both birds and mammals, whilst controlling for phylogeny (scaled $\log_{10}(\text{body mass})$; birds: -0.24 , 95%CI: -0.47 to -0.03 ; mammals: -1.1 , 95%CI: -1.9 to -0.17 ; Fig. 2).

Cavity breeding birds were bigger ($t = -4.6$, $df = 76$, $p < 0.001$) and cavity breeders suffered more from selective logging, although credible intervals overlapped zero considerably (-0.30 , 95%CI: -0.91 – 0.34). However, body mass still showed a very similar relationship with response to logging (-0.21 , 95%CI: -0.45 – 0.01) in a model including a factor coding for cavity breeding. Moreover, the posterior distributions for body mass from these two models were almost identical, showing 93% overlap, suggesting a consistent relationship between the response to logging and body mass independent from natural cavities requirements for breeding.

Table 3

Fraction of variance explained by the random part of the preferred model including IUCN status and phylogeny (Table 2B) (sensu Nakagawa and Santos, 2012). Residual variance can be interpreted here as heterogeneity in classic meta-analysis, meaning the higher this fraction is the larger the heterogeneity. The rule of thumb for this fraction is that 0.25 is considered low with 0.50 to 0.75 considered moderate to high heterogeneity (Nakagawa and Santos, 2012). The phylogenetic fraction is equivalent to Pagel's λ (Nakagawa and Santos, 2012).

	Birds	Mammals
Phylogeny	0.30 (0.05–0.60)	0.62 (0.24–0.89)
Species	0.43 (0.14–0.70)	0.05 (0.00–0.37)
Residual	0.26 (0.11–0.71)	0.32 (0.10–0.64)

4. Discussion

We found that the effect size of logging impacts on local abundance of Bornean birds and mammals differs among species, is higher in larger species, and is similar between closely related species. We also found that Bornean species (especially birds) classified by IUCN as vulnerable or near-threatened declined in abundance in logged tropical forests compared to those classified as least concern. Cavity-breeding birds tended to suffer more from logging than others; however, cavity breeders were also bigger, making it hard to disentangle the effect of body mass from that of breeding habits per se. Finally, all these findings were independent from years since last logging.

Although our results show that closely related species responded similarly to logging, there was still variation in how they responded (Fig. 3). For example, a visual examination of Fig. 3 suggests that there might be variation in effect size among bird species within the same genus. One reason for within genus differences might lie with variation in feeding habits or trophic flexibility (Wong, 1986; Edwards et al., 2013b; Burivalova et al., 2015; Hamer et al., 2015). Second, reduced inter-species competition could explain higher numbers of some species in logged tropical forests released from competition from species abundant in primary tropical forests (e.g., Hussin, 1994).

In the case of mammals, small species (e.g., *Leopoldalmys*, *Maxomys*, *Niviventer*, *Tupaia*) were generally more abundant in logged than in primary tropical forests. This is in contrast to a previous study, which found that *Maxomys* rat species in Peninsula Malaysia were significantly more common in primary than in old-regenerating forests (Yasuda et al., 2003). Previous studies on Bornean small mammals have revealed that shifts in microhabitat use and prevalence of parasites do not show coherent trends in congeneric species between unlogged and logged tropical forests despite their strong convergence in morphology and habitat use (Wells et al., 2006, 2007b). Further studies are needed to clarify why congeneric species are differentially affected by selective logging.

In our meta-analysis, the longest period since logging was 26 years, whereas in Yasuda et al. (2003) forests were logged 40 years prior. Although we found that the effect size of logging was independent from the years since logging, we cannot rule out that detrimental effects of logging on *Maxomys* and some other vertebrate species may take longer times to emerge. For example, time since last logging had a negative impact on woodpecker abundances (Styring and Ickes, 2001; Styring and Hussin, 2004). This pattern of decreasing cavity-nester (specifically woodpecker) abundance with time since logging spanned sites ranging from 5 to 40 years since logging (Styring and Ickes, 2001; Styring and Hussin, 2004). Similarly, Burivalova et al. (2015) showed that granivorous birds increase in abundance after logging in the short to medium-term, but decline significantly in the long-term as grasses are replaced by forest regrowth.

The importance of trophic ecology for responses to logging of both birds and mammals are to some extent corroborated by our results on body mass. When correcting for shared ancestry, bigger species were significantly more susceptible to logging than smaller species (see also Gray et al., 2007; Hamer et al., 2015). It could be that the larger metabolic needs of bigger species mean that they require higher resource availability and larger foraging areas, two aspects that are likely to be negatively impacted by logging (Styring and Ickes, 2001; Styring and Hussin, 2004) and which have combined to reveal a shift in mass-abundance scaling of birds in logged forests in Northeast India (Srinivasan, 2013). Moreover, larger species have slower reproductive rates, which might make them more vulnerable to environmental changes due to logging (Price and Gittleman, 2007).

Cavity-nesting birds suffered more from logging than other nesting groups, probably because old trees that have more abundant and larger cavities are also those trees preferentially selected for harvest. However, because cavity breeders were also bigger, we cannot rule out that something other than breeding habits negatively impacts their abundance.

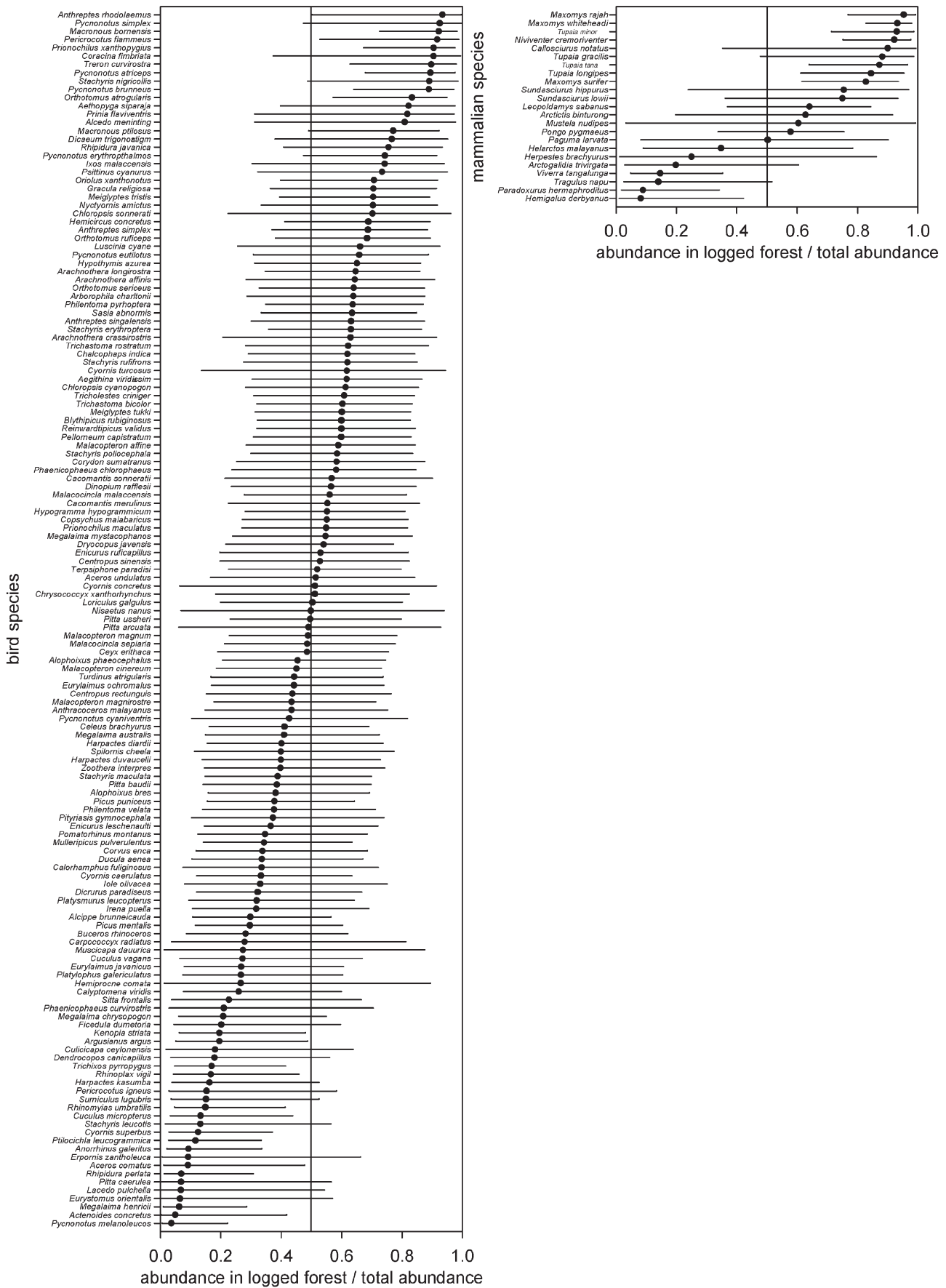


Fig. 3. Species-specific estimates of the response to logging on Borneo, fitted as a fixed predictor in the model. Estimates are given with their 95% credible intervals and presented sorted for magnitude.

One strategy to help buffer the decline of cavity-nesting bird populations is the installation of nest-boxes in selectively logged tropical forests. Recent studies on birds in South America (Liévana and Sarasola, 2013; Olah et al., 2014) and New Guinea (Warakai et al., 2013) reveal a positive effect of artificial nest boxes for cavity-nesting birds, suggesting a causal link between the reduced availability of natural cavities in logged forests and response in species diversity and abundance, highlighting a promising conservation tool for cavity-nesting birds.

We found that the effect of logging on species abundance varied among IUCN statuses. In addition to IUCN category, we also found independent effects of phylogeny (especially in birds) and body mass in predicting responses to logging among species (Fig. 2, Table 2B). The effect of logging on mammals was less dependent on their conservation status, so other factors (e.g., poaching, post-logging fires) might be more important than logging. Note that the increases in abundance recorded in logged versus unlogged tropical forests could stem from differences in the environment (e.g., tree species composition, fruit availability, thickness of vegetation, height of the canopy) that is not fully corrected for in original studies. For example, previous work suggested that tropical forests that support higher species richness might also support more sensitive species (Sheldon and Styring, 2011).

In conclusion, our meta-analysis has enabled us to identify heterogeneity in the short-term responses of Bornean bird and mammal species to selective logging. Such heterogeneity in response resulted in apparently little effect of logging on overall abundance across all species (Fig. 1), while species with similar ecologies and evolutionary relatedness differed strongly in how they are affected by logging, indicating the importance of studies on individual species. The substantial heterogeneity present in our final models (Table 3) suggests that there are as yet unidentified moderating variables that determine a species response to selective logging. Unpicking this variation is a major frontier in understanding which species will be winners and losers from logging, and thus planning selective logging that prevents species extinctions. There is presently both insufficient life-history data for many Bornean species and surprisingly limited knowledge about the physiological and population genetic responses of species to selective logging. Future work in this direction will be pivotal if we wish to identify the proximate factors that drive species to success or failure after logging.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.02.020>.

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