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

David Costantini [a,b,*], David P. Edwards [c], Mirre J.P. Simons [c]

[a] Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium
[b] Institute for Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK
[c] Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK

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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.

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 millon 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

* Corresponding author at: Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium.
E-mail address: davidcostantini@libero.it (D. Costantini).

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 km^2 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:

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

(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 km^2 area surveyed, then assuming that 4 versus 2 individuals per km^2 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 1,000,000 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)