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Primate responses to anthropogenic habitat disturbance: A pantropical meta-analysis

Juliana M. de Almeida-Rocha[a,*], Carlos A. Peres[b], Leonardo C. Oliveira[a,c,d]

[a] *Applied Ecology and Conservation Lab, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Ilhéus, BA 45662-900, Brazil*
[b] *Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich, Norfolk NR4 7TJ, UK*
[c] *Faculdade de Formação de Professores, Universidade do Estado do Rio de Janeiro, São Gonçalo, RJ 24435-005, Brazil*
[d] *Bicho do Mato Instituto de Pesquisa, Belo Horizonte, MG 30360-082, Brazil*

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ABSTRACT

Rapid human-induced conversion and degradation of natural habitats has severely altered patterns of species occupancy and population viability. Primates are highly vulnerable to tropical forest loss and degradation because they are highly arboreal, forest-dependent, and often highly sensitive to changes in forest structure. Here we quantify the effects of anthropogenic habitat modification on primate community structure using a global meta-analysis based on 72 studies to understand the variation in effect sizes between biogeographic regions, types of human disturbance, trophic levels of primate species, and sampling design protocols. We examined response ratios for 637 comparisons between disturbed forests and adjacent 'pseudo-control' forests with a history of little or no impact. This revealed an overall decrease of 30% (95% CI: 17–43%) in biodiversity metrics in response to habitat disturbance, which was particularly detrimental to primate assemblages in Madagascar and Southeast Asia. This effect was more severe in areas converted to agriculture (77%; 95% CI: 59–88%), while land use intensification led to far more detrimental effects than the initial degradation of forests, calling for the identification of habitat degradation thresholds. Negative effects of forest degradation were further exacerbated by ~30% under scenarios of persistent hunting pressure, emphasizing possible synergistic interactions between environmental stressors. Given that overall primate diversity was depressed in degraded habitats, our results emphasize the importance of retaining connectivity across remnants of undisturbed primary forest within human-modified landscapes to maintain full complements of primate species, and ensure their long-term persistence.

1. Introduction

Habitat loss and degradation, especially driven by agricultural expansion and intensification, are major threats to biodiversity (Maxwell et al., 2016). Over the last two decades, about one-tenth (~3.3 million km^2) of all wilderness areas worldwide were converted to anthropogenic land uses, with South America and Africa being the most affected regions (Watson et al., 2016). Given that the human footprint continues to expand relentlessly, particularly into the most species-rich biomes (Venter et al., 2016), the fate of biodiversity will increasingly rely primarily on human-modified habitats.

Anthropogenic habitat change, such as forest conversion to annual crops, cattle pastures, tree plantations, and mining, often results in forest loss, degradation and fragmentation, and these three outcomes usually interact with one another (Gardner et al., 2009). In addition to changes in forest structure and quality, including reduced canopy connectivity, availability and quality of food resources, land-use transitions are often associated with other types of interventions, such as road building, which facilitates non-structural threats to wildlife populations, such as overhunting (Wilkie et al., 2000). Furthermore, climate change exacerbated by human activities may contribute to habitat disturbance by altering patterns of fruit production that directly affect frugivores, thereby triggering cascading effects throughout the community (Morellato et al., 2015).

Human modification of natural habitats often leads to severe changes in species occurrence and population regulation mechanisms (Gardner et al., 2009). Several studies have sought to understand how different taxonomic groups cope with habitat alterations (Airoldi and Bulleri, 2011; Ribeiro-Neto et al., 2016), and to find overall patterns of species persistence following habitat disturbance (Sodhi et al., 2009;

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[*] Corresponding author at: Rodovia Ilhéus-Itabuna, km 16, UESC, Pavilhão Max de Menezes, Sala A1, Ilhéus, BA 45662-900, Brazil.
E-mail address: almeidarocha.jm@gmail.com (J.M.d. Almeida-Rocha).

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Gibson et al., 2011; Fontúrbel et al., 2014). Primates are among the vertebrate orders most affected by anthropogenic habitat disturbance, partly due to their high dependence on tropical forest ecosystems (Isaac and Cowlishaw, 2004). Anthropogenic disturbance can impact primate populations through a range of mechanisms, including reduced availability of structural resources (*e.g.* tall emergents, canopy continuity, and sleeping shelters); nutritional restrictions due to lower amount and/or quality of food resources; modified interspecific interactions due to species invasions/introductions, hunting and increased exposure to predators; and spread of diseases resulting from elevated contact with humans and domestic livestock (Irwin et al., 2010a; Schwitzer et al., 2011). Local responses to these alterations can be expressed through changes in species occupancy, abundance, demography, use of space, activity budget, health status, and body condition. There is little consensus about how different primate species are affected by specific patterns of human habitat disturbance, such as those induced by agriculture and logging, and conclusions from previous studies remain largely contradictory (Johns, 1991; Ganzhorn, 1995; Chapman et al., 2000). Co-occurring species and conspecifics in different portions of their range can diverge in their responses to the same threat, particularly if multiple threats act synergistically (Isaac and Cowlishaw, 2004). Considering that nearly 60% of all primate species are currently threatened with extinction (Estrada et al., 2017), understanding what drives this variation in species responses to human-induced environmental stressors is crucial to enhance the effectiveness of conservation actions.

To our knowledge, there are no global analyses on the effects of human-induced habitat disturbance resulting from different forms of anthropogenic activities on primate populations and/or communities. Isaac and Cowlishaw (2004) attempted to synthesize the effects of agriculture, forestry and hunting on primates, but they focused on biological traits influencing species responses. Thus, the overall effects of different human-induced forms of habitat change within different biogeographic regions remain poorly understood. Here we present a global-scale meta-analysis of studies across the New and Old World tropics that compared primate species richness and/or abundance between undisturbed forests and neighbouring forest areas that had been affected by any given pattern of human activity leading to discernible habitat change. Since the twin effects of forest habitat loss and fragmentation have been relatively well documented for primates (Harcourt and Doherty, 2005; Benchimol and Peres, 2013), we focused entirely on studies that examined the effects of human disturbance on forest habitat structure, composition and/or quality. We also examine possible causes of variation in effect sizes between studies, such as the biogeographic region where the study was conducted, the main threat under investigation, study design, species trophic level, and whether hunting pressure operated in the study region. This analysis also enabled us to identify current knowledge gaps and suggest new research priorities.

2. Materials and methods

2.1. Dataset

We systematically searched all research articles published until February 20th, 2016, that investigated the effects of human-induced habitat disturbance on primate populations and/or assemblages in tropical environments. This search was initially performed using three databases — *ISI Web of Knowledge* (www.isiwebofknowledge.com), *SciVerse SCOPUS* (www.scopus.com) and *Google Scholar* (https://scholar.google.com.br/) — using the query: [(primate*) AND ("habitat disturbance" OR "habitat degradation" OR "habitat conversion" OR "habitat alteration")]. Keywords were searched in all reference topics, except for *Web of Knowledge* searches, which were restricted to the title, abstract and keywords of the references. We then refined the searches by language (English, Spanish and Portuguese), and conducted additional searches in Google Scholar using keywords translated into both Portuguese and Spanish. As *Scopus* database is very broad, we refined our search by Subject Area (Agriculture and Biological Sciences; Environmental Sciences; and Earth and Planetary Sciences). In an attempt to include the "grey literature", we also searched for references in the *PrimateLit* (http://primatelit.library.wisc.edu/), a bibliographic primatology database that includes theses, dissertations, conference abstracts and reports, which was updated until 30 November 2010. Review articles returned by our search were used as additional bibliographic sources, and during the process of compiling, reading and sorting, we also identified new references that were assessed and added to our dataset.

We restricted our database to studies that performed any reported comparison between a degraded (or more degraded) site and a relatively intact (or less degraded) old growth forest within the same study landscape. Following a strict sorting procedure (Appendix A: Fig. A.1), the final database contained 81 studies that used biodiversity metrics at the population or community level, such as species richness (including number of species, rate of species loss, and diversity index; N = 5 studies) and abundance (including density, number of records per unit of sampling effort, encounter rate, population size or capture rate; N = 77 studies). These studies amounted to a total of 662 pairwise comparisons (mean ± SD = 8.2 ± 9.7 comparisons per study) including responses for 142 primate taxa across 17 countries and three provincial territories, spanning four biogeographic regions: Southeast Asia (25 studies and 139 comparisons), Neotropics (27 studies and 245 comparisons), mainland Africa (22 studies and 225 comparisons), and Madagascar (7 studies and 45 comparisons) (Fig. 1; Appendix B). More than 50% of all studies were concentrated in tropical forests of Brazil, Indonesia and Malaysia (Fig. 1).

2.2. Meta-analytical procedure

The meta-analysis approach combines quantitative results of primary studies to investigate a general pattern (Borenstein et al., 2009). About 60% of selected references (~75% of pairwise comparisons) neither presented any error estimates (and it was not possible to extract these values indirectly) nor made it clear which sample unit had been used to calculate error estimates, preventing us from calculating a standardized mean effect size (Borenstein et al., 2009). As an alternative to perform the meta-analysis without discarding valuable data, we used a response ratio (RR) as an index of effect size (Hedges et al., 1999). Thus, for 637 comparisons derived from 72 studies, we therefore calculated RR = $\ln(\overline{X}_{\text{degraded}} / \overline{X}_{\text{control}})$, where $\overline{X}$ represents the mean biodiversity value in each treatment.

A negative RR indicates a detrimental effect of habitat disturbance and consequently a higher biodiversity value in the 'control' treatment. A median RR was calculated over all comparisons and a 95% confidence interval (CI) was estimated from 10,000 bootstrap samples (with replacement). To translate these values into percentage change, we used the equation: $(e^{RR} - 1) \cdot 100$. Since studies usually presented more than one comparison, we attempted to avoid pseudo-replication by resampling the dataset (with replacement) using only one comparison per study, and then we performed 10,000 bootstraps to generate a median effect size with a 95% CI. To support our findings, we repeated the meta-analysis for a data subset (30 studies and 155 comparisons) from which the Hedges' g effect size - the difference between the mean biodiversity metric value in disturbed treatments and their control sites weighted by the within-group standard deviation - could be calculated, using a random-effect model. We used the same approach to account for pseudo-replication in this model.

To better understand what drives the variation in effect sizes among studies, we performed additional analyses using study sub-groups defined by four categorical variables: biogeographic region, main threat, species trophic level, and study design (Table A.1). Details about studies allocation into sub-groups and species classification into trophic levels are presented in Appendices A and B. Among threat types, Agriculture

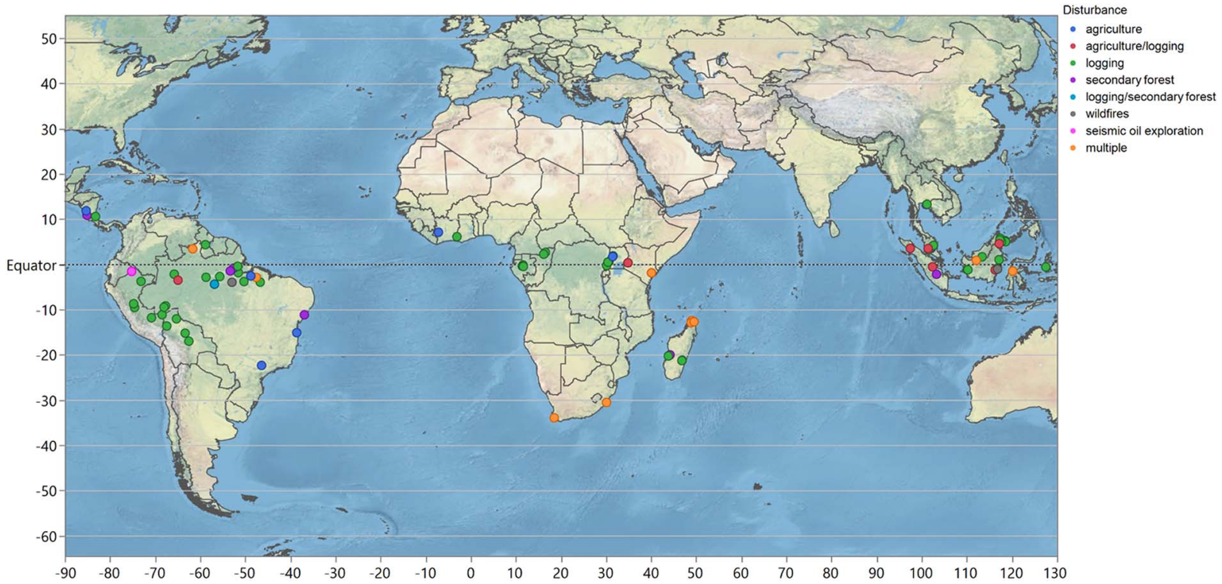

Fig. 1. Geographic distribution of study sites included in the dataset containing 81 studies. Solid circles are colour-coded according to the main patterns of land-use change reported in each study (see legend). Studies represented by two threat categories provided independent response ratios for more than one threat, while studies that did not specify a main activity, thus investigating the interaction among many stressors are represented by "multiple". (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

includes studies investigating the effects of different types of perennial plantations on primates (Table A.1). The degree to which agricultural lands can be used as primate habitat depends on the structural complexity of the converted land-use (Estrada et al., 2012), so combining different types of agriculture clearly adds heterogeneity to overall effect size estimates. Unfortunately, the limited number of studies addressing each type of agriculture prevented us from considering those effects separately, but this is revisited in the discussion. We also performed the meta-analysis for two-level factorial combinations of Main Threat and Study Design with Biogeographic Region and Trophic Level, to further examine the most important drivers of sensitivity to habitat disturbance. Finally, we performed another sub-group analysis considering primate species conservation status as defined by the IUCN (2016) to examine whether threatened species were more likely to be affected by habitat disturbance than least-concern species. We excluded species that were '*Data Deficient*' and '*Not Evaluated*', so we examined 592 comparisons from 67 studies, including responses for 116 species spanning five IUCN threat categories: *Least-Concern* (50 species), *Near-Threatened* (11), *Vulnerable* (25), *Endangered* (23) and *Critically Endangered* (7).

Excluding studies comparing the same site before and after a degradation event, there is always the possibility that intrinsic differences between any two sites will affect the final response ratio. We assume that authors investigated the most prevalent threats in their study areas, and since we restricted the dataset to studies comparing sites in the same region, it is unlikely that this represents a prohibitive problem in within-study estimates. However, this may add heterogeneity in between-study estimates, making it difficult to assign an overall effect. Primates are often targeted by subsistence and commercial hunters (Cowlishaw and Dunbar, 2000) and hunting can amplify effects of habitat degradation (Remis and Robinson, 2012). Thus, we compared the median effect size among studies at sites that were exposed to and without a history of hunting pressure to examine any possible synergistic effects between hunting and habitat disturbance. We classified study areas as *hunted* (253 comparisons from 26 studies) when authors declared that hunting on local primate assemblages was ubiquitous, even if they failed to test responses to hunting. Conversely, study areas were classified as *unhunted* (167 comparisons from 24 studies) if authors clearly stated that hunting was negligible, absent in the study area or if the study species was not usually hunted. We excluded from this analysis studies that failed to mention anything about hunting pressure (217 comparisons from 24 studies), and we used the same approach to account for pseudo-replication in all analyses.

2.3. Publication bias

We tested for publication bias using the dataset for which Hedges' g effect sizes could be calculated using two methods: (1) the Trim-and-Fill Method estimates the number of missing studies required to make a funnel plot (effect sizes plotted against standard errors) symmetric and recalculates an adjusted overall effect size including those missing studies (Duval and Tweedie, 2000); and (2) the Fail-Safe Number Rosenthal Approach estimates the number of unpublished studies with no effect (Hedges' $g = 0$) that would be required to render the overall effect size non-significant (Rosenthal, 1991). As for all previous analyses, we accounted for pseudo-replication biases (see details in Appendix A).

2.4. Model selection approach

We fitted Generalized Linear Models (GLMs) using 518 comparisons from 64 studies to compare candidate models that could best predict the effect sizes. Since geographically restricted species are expected to be more vulnerable to extinction than widespread species (Payne and Finnegan, 2007), we included species range size as an additional explanatory variable, resulting in 23 plausible models encompassing all combinations of moderator variables (region, threat, trophic level, study design, hunting pressure and range size) plus a null model containing only the intercept and error parameters. We removed outliers (77 comparisons from 8 studies) and used the absolute response ratio ($\overline{X}_{\text{degraded}}/\overline{X}_{\text{control}}$) as the dependent variable, assuming a Gamma distribution. We accounted for pseudo-replication by using only one comparison per study to find the top-ranked models (the most selected within 10,000 sample fits) based on the Akaike Information Criterion corrected for small samples (AIC_c; Burnham and Anderson, 2002). For each candidate model, we calculated the percentage of simulations in which it was top-ranked (AICc-πi), the mean Akaike weight (w), and the mean goodness-of-fit (adjusted R^2).

All analyses were performed using R 3.3.1. (R Core Team, 2016). We used the *Metafor* package (Viechtbauer, 2010) to perform the meta-analysis with Hedges' g effect size and to check for publication bias.

3. Results

3.1. Overall effect of habitat disturbance

The overall RR effect size for 637 comparisons across all 72 primate studies was − 0.19 [95%CI: − 0.29, − 0.08], and increased to − 0.36 [− 0.56, − 0.19] when we considered only one comparison per study. Since pseudo-replication substantially affected the estimates, all results presented here are based on bootstrapped effect sizes (see Table A.3 for complete results). All forms of habitat disturbance led to a median decrease of 30% (17–43%) in biodiversity metrics across all primate assemblages. Negative effect was corroborated by the meta-analysis performed with Hedges' g effect size (− 0.47; 95%CI: − 0.75, − 0.20; T^2 = 0.42 + − 0.09 SE; I^2 = 74%), and the results were robust to publication biases (see Section 4 of Appendix A).

3.2. Biogeographic regions

There was significant variation in effect sizes across biogeographic regions (Fig. 2A). Madagascar experienced the most severe effect size (48% decrease; 95%CI: 39–60%), followed by Southeast Asia (25% decrease; 10–54%), for which the negative effects were largely induced by logging and agriculture (Fig. 3A; Table A.4). Surprisingly, the median effect size for the Neotropics (44% decrease; 70% decrease to 1% increase) and Africa (15% decrease; 37% decrease to 30% increase) were not statistically significant (Fig. 2A). African primates were apparently the least sensitive to habitat disturbance, showing positive responses to logging, multiple threats, and secondary forests (Fig. 3A).

3.3. Anthropogenic activities

All forms of *agriculture* were by far the most detrimental patterns of habitat disturbance to primate communities (77% decrease; 59–88%), followed by *logging* (22% decrease; 8–37%) (Figs. 2B and 3). There was no overall effect for both *secondary forests* (30% decrease; 63% decrease to 42% increase) and *multiple threats* (27% decrease; 63% decrease to 15% increase). The effects of agriculture were consistently negative for Southeast Asia, where tree monocultures, such as rubber and oil palm plantations, accounted for a limited number of five studies, and for the Neotropics, for which degraded systems included agromosaics, agroforests and monocultures (Table A.4; Appendix B). A larger sample size would be required to investigate the specific impact of different

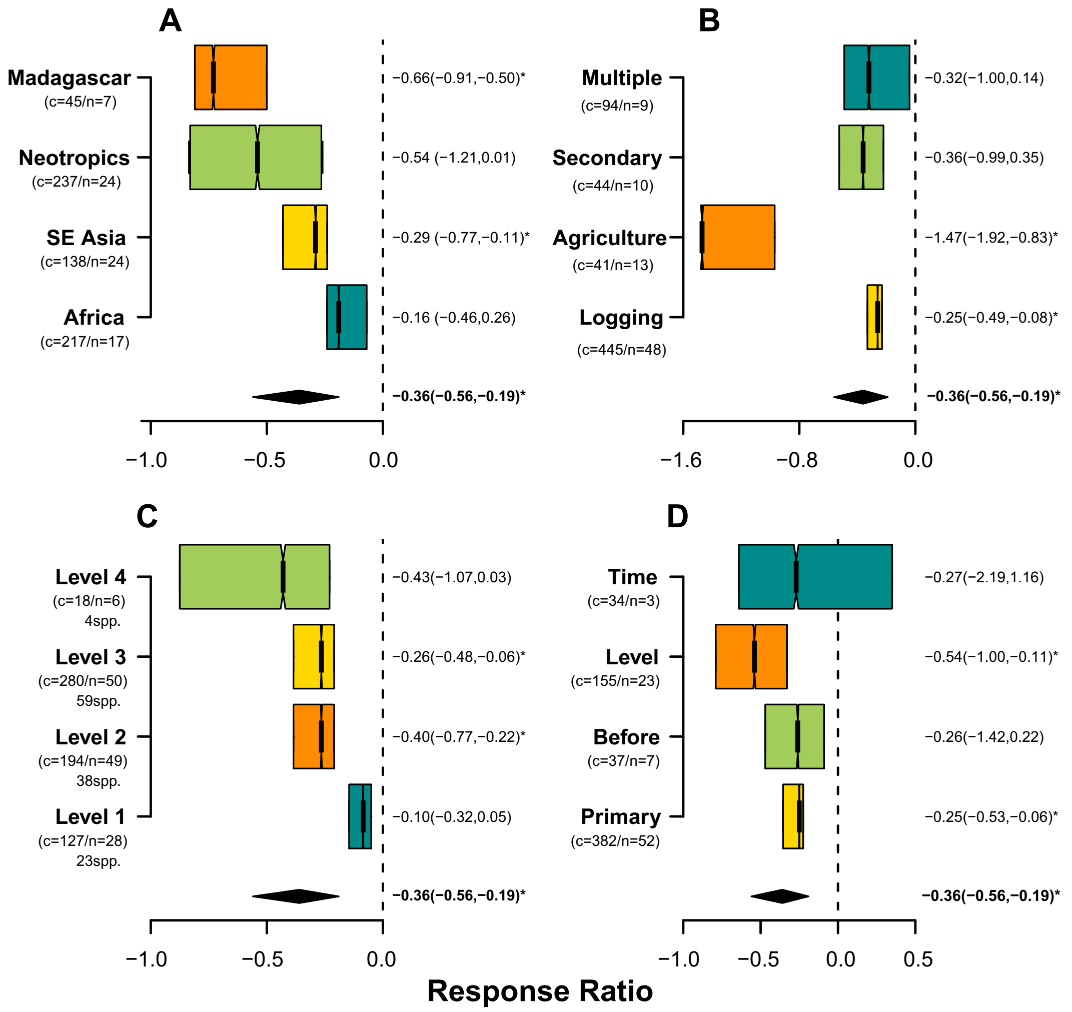

Fig. 2. Bootstrapped response ratios broken-down by (A) biogeographic region, (B) study design (names along the y-axis represent the control treatment; "time" and "level" represent comparisons between old- and recently-degraded sites, and less- and more-degraded sites, respectively), (C) main threat, and (D) trophic level. The black diamond represents the overall bootstrapped effect size obtained for the entire dataset without moderators, and the black dashed line indicates no effect of habitat disturbance. Box plots show the median values, and first and third quartiles of 10,000 resampled (with replacement) effect sizes for each category. Notches in boxes approximate 95% CIs. Values on the left of each panel show the total number of comparisons (c) and the number of studies (n; which represents the number of comparisons used in each bootstrap). Values on the right represent the median effect size and the 95% CI for the median effect size in each category (asterisks indicate statistically significant effect sizes).

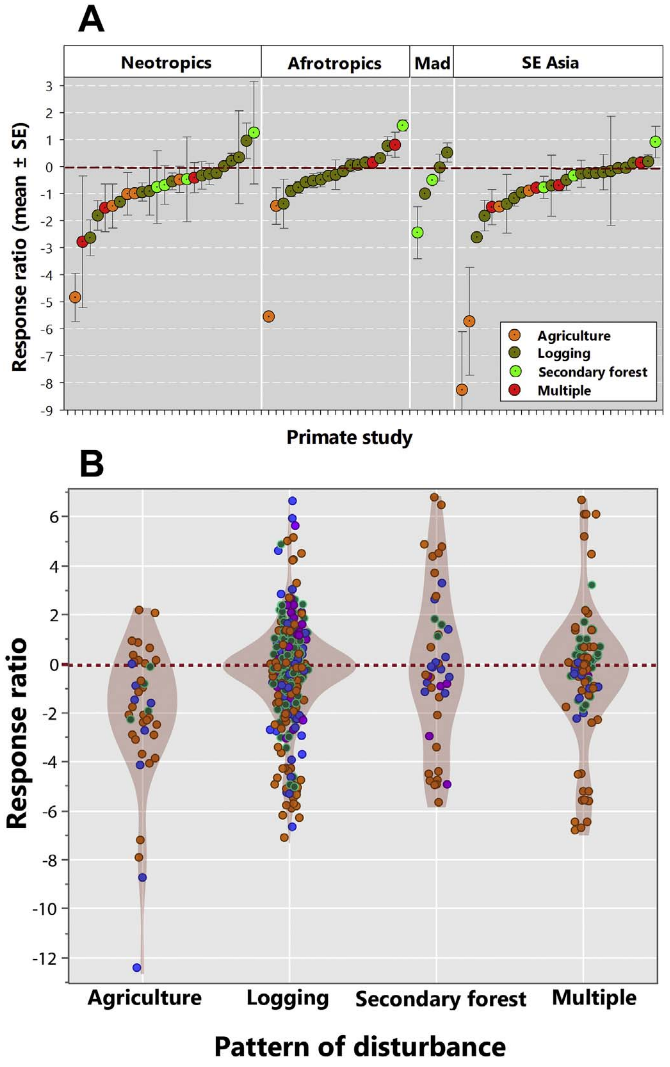

Fig. 3. (A) Mean and standard error of primate response ratios at the scale of individual study sites, broken-down by major biogeographic realms (left to right, Neotropics, Afrotropics, Madagascar, and Southeast Asia) and type of anthropogenic habitat disturbance examined here; threat; and (B) the overall distribution of response ratios at the scale of individual primate populations for major patterns of disturbance. Background dark brown shading indicates violin density plots, indicating the distribution space of the data in which violin widths show data frequency. Orange, green, lilac and blue circles indicate study sites in the Neotropics, Afrotropics, Madagasgar, and Southeast Asia, respectively. Dashed red lines indicate neutral response ratios. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

agricultural production systems for each region. Also, Southeast Asian primates were apparently most sensitive to logging, compared to those in other regions (Table A.4).

3.4. *Species trophic level*

We found consistently negative effect sizes for the second trophic level (33% decrease; 20–54%), consisting primarily of frugivores and frugivore-folivores, and the third trophic level (23% decrease; 6–38%), consisting primarily of frugivore-faunivores (Fig. 2C). These species were particularly affected by agriculture and logging (Table A.4). We failed to find consistent effects of forest degradation for species in the lowest level (10% decrease; 27% decrease to 4% increase), comprised primarily of folivores, and the fourth level (35% decrease; 66% decrease to 3% increase), comprised mainly of insectivores. However, robust generalizations for this last category would require a larger sample size (Fig. 2C).

3.5. *Study design*

When primary forests were compared to disturbed forests, there was an overall decrease of 23% [6–42%] in the biodiversity metrics (Fig. 2D). However, when areas that had already succumbed to some degree of disturbance were compared to more disturbed areas, the effect was more negative (42% decrease; 10–63%) (Fig. 2C), a pattern particularly evident in Southeast Asia (Table A.4). There was no overall effect for studies comparing the same sites before-and-after degradation (23% decrease; 76% decrease to 25% increase) or between long-degraded and recently-degraded forests (24% decrease; 89% decrease to 219% increase), but the latter category encompassed only one African and two Southeast Asian landscapes, so estimates are unreliable.

3.6. *IUCN status*

We excluded *Data Deficient* and *Not Evaluated* species, so we examined 592 comparisons from 67 studies, including responses for 116 species spanning five IUCN threat categories: *Least-Concern* (50 species), *Near-Threatened* (11), *Vulnerable* (25), *Endangered* (23) and *Critically Endangered* (7). We detected overall negative effects for both near-threatened and threatened species, but not for *Least-Concern* species (14% decrease; 0–36%). The most negative effects were detected for *Vulnerable* species (55% decrease; 30–63%), followed by *Critically Endangered* species (37% decrease; 7–95%), *Near-threatened* species (23% decrease; 6–52%) and *Endangered* species (21% decrease; 13–39%) (Fig. A.2).

3.7. *Hunting pressure*

Primate assemblages at hunted sites experienced more negative effects across pairwise comparisons of habitat disturbance (49% decrease; 19–65%) than those in unhunted sites (20%; 3–41%). Hunting pressure therefore almost certainly aggravated the detrimental effects of habitat disturbance by further reducing biodiversity metrics by ~30% compared to habitat disturbance alone. However, it remains unclear whether these effects were induced by hunting *per se* or by an interaction between hunting and any co-occurring pattern of structural habitat disturbance.

3.8. *Model selection*

The best model predicting effect sizes was *hunting* (AICc = 121.04; w = 0.33; AICc-πi = 29%), followed by the *null* model (AICc = 127.56; w = 0.26; AICc-πi = 16%) and the *region* + *range* model (AICc = 118.89; w = 0.46; AICc-πi = 11%) (Table A.5). The *hunting* model explained 11–14% of the overall deviance, whereas the *region* + *range* model had a higher explanatory power of 23–27%. Regarding species range sizes, we failed to find an overall pattern of geographically restricted species experiencing more detrimental effects than widespread species, although this was apparently the case of Malagasy primates (Fig. A3).

4. Discussion

4.1. *Overall effect of habitat disturbance*

Human-induced habitat change had an overall negative effect on primate assemblages, reducing population or community-wide metrics by 16–42%. These results extend those of previous global-scale meta-analyses on the effects of land-use on biodiversity considering multiple taxa (Gibson et al., 2011; Murphy and Romanuk, 2014; Newbold et al., 2015). We further shed light on apparent contradictions exposed by other studies. For example, Gibson et al. (2011) failed to find an overall effect of habitat change for tropical forest mammals but acknowledged that their results may have been masked by combining all mammalian orders, despite the wide variation in their sensitivity to habitat modification.

4.2. Biogeographic regions

Madagascar showed the most negative responses to habitat disturbance, despite the small number of studies in this land mass. Several studies have shown that Malagasy primate species persistence or local extinction in altered habitats is usually associated with behavioural, dietary and/or physiological plasticity (Irwin et al., 2010b; Junge et al., 2011), but these were not included in our dataset because we focused on population or community-wide responses. Madagascar has succumbed to the highest deforestation rates over the last century (Harper et al., 2007) and the accelerated rate of forest loss of ~1500 km^2 per year (Moat and Smith, 2007) poses a real threat to all forest-dwelling species. Although our effect size estimate for this region is imprecise, our result suggests high levels of sensitivity to habitat change, which is consistent with the fact that nearly 94% of all lemur species are currently threatened with extinction (Schwitzer et al., 2013).

Considering a wide range of taxa, Gibson et al. (2011) identified Southeast Asia as the most sensitive region to tropical forest disturbance. Our overall 24% reduction in response metrics to disturbed forests in this region is comparable with the 22% detected in a previous meta-analysis that did not consider primate responses (Sodhi et al., 2009). Our effect size estimate for Southeast Asia was the most precise, suggesting little species flexibility in confronting habitat changes. Because of the recent disturbance history of Southeast Asian forests (Sodhi and Brook, 2006), this fauna may be less pre-adapted to habitat alterations than those elsewhere (Sodhi et al., 2009), which may explain the narrow variation in responses. Currently, Southeast Asia is under the highest anthropogenic pressure of all major tropical forest regions, and the human footprint is increasing mainly due to high human density and expansion of oil palm monoculture (Koh and Wilcove, 2008; Venter et al., 2016). Phillips et al. (2016) also identified the Asian fauna as the most affected by land-use effects, particularly in the case of tree monocultures. Oil palm plantations are largely incompatible with forest-dwelling species (Danielsen and Heegaard, 1995; Fitzherbert et al., 2008) representing a major threat to primates, which is especially alarming in Southeast Asia, where ~80% of all primate species are threatened with extinction (Cotton et al., 2016).

Neotropical primate assemblages exhibited the widest variation in response ratios. The median effect size was high, which may reflect the dominance of studies addressing species from intermediate trophic levels that consume mostly fruits, which are highly sensitive to habitat changes. Also, ~60% of all Neotropical studies coincided with hunted areas, which aggravated the detrimental effects of habitat disturbance. However, there was no overall effect for this region, probably because this dataset included studies across different types of human-induced habitat disturbance, but only agricultural practices returned a consistently negative effect within this sub-group of studies.

African primates were apparently less affected by existing patterns of habitat disturbance, ranging from negative and neutral responses to logging (Chapman et al., 2000; Mammides et al., 2009), to positive responses to multiple threats (Lawes, 1992) and secondary forests (Decker, 1994). This apparent tolerance to habitat disturbance could be attributed to the higher ecological plasticity of Afrotropical primates in dealing with habitat changes. The paleoecological record shows that the overall drier African climate has predisposed the fragmentation of Afrotropical forests over millions of years (Hamilton and Taylor, 1991), exposing species to edge habitats typical of natural forest-savannah mosaics. This may have resulted in an evolutionary filter leading to pre-adaptations to contemporary forms of human-induced habitat alterations (Balmford, 1996). However, African primates are faring no better than those elsewhere: currently, 44% of all species are threatened, and great apes are the most endangered primate clade, with all species defined as threatened (Cotton et al., 2016). Deforestation has also drastically reduced forest areas, mainly in East and West Africa (Chapman et al., 1999), and hunting has been singled out as the main driver of extinction of some species (Struhsaker, 1999).

4.3. Anthropogenic activities

As observed for other taxa (Gibson et al., 2011), forest conversion into agricultural lands represents the most detrimental human activity for primates, leading to drastic population declines. Indeed, agricultural expansion and intensification impart the greatest current impact on species assessed by the IUCN Red List (Maxwell et al., 2016). Yet we found a limited number of studies comparing primate populations/communities in agricultural systems and primary forests. These studies indicate that agromosaics (Johns, 1991) and agroforests, such as shade-cocoa (Oliveira et al., 2011) and teak plantations (Oliveira, 2015), can support or subsidize some primate populations, but more structurally simplified systems, such as rubber and oil palm plantations retain a significantly lower biodiversity value than natural forests (Danielsen and Heegaard, 1995; van Schaik et al., 2001). This suggests that polyculture systems and intervening forest areas around agricultural patches can effectively maintain landscape heterogeneity to mitigate the negative effects of agriculture. Unfortunately, we failed to uncover studies comparing variable-aged agricultural systems to assess the time trajectory of persisting primate populations in the aftermath of initial habitat perturbation. Although some studies documented wholesale primate extinctions in cultivated areas such as oil palm and eucalyptus plantations (van Schaik et al., 2001; Dotta and Verdade, 2011), species richness is a weaker metric to evaluate the conservation value of modified habitats for primates because responses were more frequently related to abundance than occupancy. Also, while some systems such as agroforestry may function as primate habitat, other simplified systems such as monocultures can only be used as corridors between forest habitat patches (Estrada et al., 2012), thus using species richness as a response metric would return a similar biodiversity value for very different modified habitats.

Logging had an overall negative effect on primates, with variable responses across biogeographic regions, but selective logging had a less severe impact than agriculture (see also Edwards et al., 2010; Gibson et al., 2011; Sodhi et al., 2009). However, although logging is often seen as biodiversity-friendly, the degree to which population impacts are expressed depends on timber removal techniques, selectivity of timber species in conventional and reduced-impact logging (RIL) operations, length of the felling cycle, and design of skid trails and logging roads (Gullison and Hardner, 1993; Burivalova et al., 2014). Population impacts may be lower if target tree species are not key food resources for primate consumers, nor abundant emergent trees which would lead to profound changes in forest structure (Meijaard and Sheil, 2008). It is therefore largely possible to predict the effects of logging if the ecology of the local fauna is well documented and RIL techniques can be introduced (Sist, 2000). Moreover, the abundance of some primate species in logging concessions is often negatively correlated with distance from unlogged forests (Clark et al., 2009), emphasizing the critical landscape role of intact primary forests.

The biodiversity conservation role of tropical secondary forests has generated much debate (Chazdon et al., 2009). Previous analyses have shown that biodiversity retention of secondary forests is much lower than that in undisturbed forests, suggesting that primary forests are irreplaceable (Gibson et al., 2011; Newbold et al., 2015). Although vertebrate, invertebrate and plant species richness was not significantly different between primary and secondary forests, there was a tendency towards biotic homogenization (Phillips et al., 2016). Although we failed to uncover an overall effect of secondary forests, this does not necessarily mean that second-growth sites can support full complements of species typical of old-growth forests. Patterns of species richness and composition tend to converge with those of undisturbed old-growth as forest regeneration advances into late succession (Chazdon et al., 2009; Norden et al., 2009), so community effects in older secondary forests are expected to be less severe than those in early successional forests. Finally, different land uses may have arisen either independently or simultaneously, leading to highly variable vegetation structures, which can result in either stronger or weaker impacts on species. Age of secondary forests, previous land use history, and landscape context are therefore crucial considerations in better predicting the successional pathways and conservation role of tropical secondary forests (Melo et al., 2013; Arroyo-Rodríguez et al., 2017).

We failed to detect an overall effect of multiple threats. Although this may reflect a limited sample size, we expected a lack of consistency since multiple threats may interact in different ways. Nearly 80% of all currently threatened species are affected by more than a single major threat (Maxwell et al., 2016), so efficient conservation strategies must consider the synergistic effects among these threats (Brook et al., 2008). For example, hunting amplified the negative effects of structural habitat disturbance by ~30%, which is consistent with the synergistic effects between hunting and forest fragmentation on platyrrhine primates (Benchimol and Peres, 2013). Developing studies that dissect tropical forest wildlife responses to multiple threats is therefore a pressing research priority. Prospective meta-analyses, in which investigators develop independent primary studies sharing the same protocol with the common objective of integrating findings (Berlin and Ghersi, 2005), can be a good approach to achieve more conclusive evidence on how synergistic human activities erode tropical biodiversity.

4.4. Species trophic level

Part of the variance in response ratios can be attributed to species trophic level. Frugivores were most sensitive to forest degradation, corroborating previous findings (Purvis et al., 2000). Since ripe fruits are more patchily distributed in space and time than leaves, changes in habitat structure are expected to affect frugivores more than folivores (Isaac and Cowlishaw, 2004). Additionally, logging disturbance to the forest canopy tends to elevate young-leaf production but depress fruit availability in large canopy trees, particularly if those include commercially-valuable timber (Ganzhorn, 1995). Our results suggest that the impact of habitat disturbance on trophic levels can be non-linear, but a larger sample size is required to obtain more precise estimates for insectivores.

4.5. Study design

Only studies comparing primary *vs* degraded forests and less-degraded *vs* more-degraded forests returned consistently negative effect sizes. Interestingly, effects of disturbance were more negative in areas that had already been degraded to some degree. It is widely known that ecological systems are intrinsically resilient to some disturbance (Holling, 1973), so effects of disturbance could be cumulative and aggravated above a resiliency threshold whenever the extent or intensity of forest disturbance is elevated. For example, some primate species may thrive in some agricultural systems (Raboy et al., 2004; Merker et al., 2005), but are intolerant to others due to management intensification resulting in more severe changes in forest structure (Danielsen and Heegaard, 1995; van Schaik et al., 2001). Burivalova et al. (2014) found a higher species richness for some taxonomic groups in lightly-logged forests compared to unlogged forests, but as logging intensity increased, the richness of all taxa decreased linearly to values below those in primary forest until they reach a specific threshold. Mammals, for example, can tolerate a timber extraction rate of 10 m^3 ha^{-1}, but an additional increase to 20 m^3 ha^{-1} resulted in a loss of ~35% in species richness (Burivalova et al., 2014). Land-use intensification may therefore pose an additional threat to wild primates, calling for additional research to identify operational thresholds above which net population growth rates become negative. Only studies comparing different levels of exploitation over time or across sites can derive tolerance thresholds, which could be used to design biodiversity-friendly management of production forests.

Temporal comparisons of the same site before-and-after degradation are likely to return the most reliable signals since they preclude biases associated with intrinsic differences between sites. Unfortunately, only ~10% of all studies in our dataset adopted this design, so we failed to detect an overall effect. Likewise, studies monitoring responses to disturbance over time could throw further light into population recovery from degradation, but these represented only ~5% of our dataset, leading to inconclusive results. We strongly encourage longitudinal study designs, which can take advantage of research opportunities involving episodic disturbance events including wildfires, selective logging and mining operations.

4.6. IUCN status

The IUCN threat categories generally reflected species vulnerability to human disturbance: we detected an overall negative effect size for all threatened and near-threatened categories but not for *Least-Concern* species. However, the degree to which a species is sensitive to habitat disturbance could not be directly inferred through its IUCN status as the magnitude of the effect size was uncorrelated with threat categories. For instance, *Vulnerable* species apparently experienced the most detrimental effects. A greater research effort focused on *Critically Endangered* species would help clarify these findings.

4.7. Predicting effect sizes

Our model selection approach identified hunting pressure as the most important stressor influencing primate responses to habitat disturbance. The *null* model was the second best ranked, suggesting that habitat disturbance effects are essentially universal, as no single variable had a decisive impact on response ratios. Finally, a significant portion of sample fits returned *Region + Geographic range* as the top-ranked model, supporting the notion that species responses have a strong geographic context. However, the explanatory power of these models was weak (11–27%), suggesting that other important factors that were not investigated here may play a role. We did not consider the influence of landscape context and 'spill-over' effects from neighbouring undisturbed forest in our analysis, although it clearly played a role in most studies, calling for the inclusion of landscape variables into predictive models.

5. Conclusions and recommendations

Human-induced habitat disturbance in tropical forests has a consistently negative effect on local primate faunas, leading to significant reductions in species richness and abundance. The biodiversity value of degraded habitats can be very low, underpinning the critical role of large tracts of primary forests in maintaining the full integrity of biotic assemblages through landscape supplementation, complementation and/or source-sink dynamics (Dunning et al., 1992). Differences in species responses are associated with the four major biogeographic realms, likely reflecting the interaction between historical and ecological context, particularly resilience to disturbance conferred over evolutionary time scales and contemporary trophic requirements. Among all threats examined here, forest conversion to agricultural practices induced the most detrimental effects on primates, often leading to population extirpations, even if some species can adjust to agroforests and agro-mosaics. Although some studies suggest a role of selective logging in contributing for biodiversity conservation (Edwards et al., 2010), we found logging to be the second most severe threat for primates. It is possible, however, to mitigate the effects of selective logging by combining ecological knowledge about local faunas with reduced-impact logging (RIL) techniques.

Increasingly intensified land-use systems gradually reduced the baseline character of primate faunas typical of undisturbed primary forests, thereby calling for the identification of acceptable forest degradation thresholds. We also recommend a greater research focus on multiple co-occurring threats, which remain poorly understood in terms of at local scales how they affect different species. Hunting pressure, for example, exacerbated the negative effects of habitat structural degradation, so it should be considered, for example, when granting environmental licenses for forest management plans. Finally, since some degraded habitats could still retain populations of several primate species, we suggest the adoption of a 'countryside biogeography framework', which recognizes the importance of human-modified habitats for the fate of wildlife (Mendenhall et al., 2014). However, because of the overall low biodiversity value of degraded forests, retaining primary forest patches remains critical in safeguarding more resilient populations through individual fluxes among neighbouring patches.

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Supplementary data

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References

Airoldi, L., Bulleri, F., 2011. Anthropogenic disturbance can determine the magnitude of opportunistic species responses on marine urban infrastructures. PLoS One 6, e22985.

Arroyo-Rodríguez, V., Melo, F.P.L., Martínez-Ramos, M., Bongers, F., Chazdon, R.L., Meave, J.A., et al., 2017. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. Biol. Rev. 92, 326–340.

Balmford, A., 1996. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. Trends Ecol. Evol. 11, 193–196.

Benchimol, M., Peres, C.A., 2013. Anthropogenic modulators of species-area relationships in Neotropical primates: a continental-scale analysis of fragmented forest landscapes. Divers. Distrib. 19, 1339–1352.

Berlin, J.A., Ghersi, D., 2005. Preventing publication bias: Registeries and prospective meta-analysis. In: Rothstein, H.R., Sutton, A.J., Borenstein, M. (Eds.), Publication Bias in Meta Analysis: Prevention, Assessment, and Adjustments. Wiley, West Sussex, pp. 35–48.

Borenstein, M., Hedges, L., Higgins, J., Rothstein, H., 2009. Introduction to Meta-analysis. Wiley, Chichester, UK.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. 123, 453–460.

Burivalova, Z., Şekercioğlu, Ç.H., Koh, L.P., 2014. Thresholds of logging intensity to maintain tropical forest biodiversity. Curr. Biol. 24, 1893–1898.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer, New York.

Chapman, C.A., Gautier-hion, A., Oates, J.F., Onderdonk, D.A., 1999. African primate communities: determinants of structure and threats to survival. In: Feagle, J.G., Janson, C.H., Reed, K.E. (Eds.), Primate Communities. Cambridge University Press, Cambridge, pp. 1–37.

Chapman, C.A., Balcomb, S.R., Gillespie, T.R., Skorupa, J.P., Struhsaker, T.T., 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. Conserv. Biol. 14, 207–217.

Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., et al., 2009. The potential for species conservation in tropical secondary forests. Conserv. Biol. 23, 1406–1417.

Clark, C.J., Poulsen, J.R., Malonga, R., Elkan, P.W., 2009. Logging concessions can extend the conservation estate for central African tropical forests. Conserv. Biol. 23, 1281–1293.

Cotton, A., Clark, F., Boubli, J.P., Schwitzer, C., 2016. IUCN red list of threatened primate species. In: Wich, S.A., Marshall, A.J. (Eds.), An Introduction to Primate Conservation. Oxford University Press, Oxford, UK, pp. 31–38.

Cowlishaw, G., Dunbar, R., 2000. Hunting. In: Cowlishaw, G., Dunbar, R. (Eds.), Primate Conservation Biology. The University of Chicago Press, Chicago, pp. 242–288.

Danielsen, F., Heegaard, M., 1995. Impact of logging and plantation development on species diversity: a case study from Sumatra. In: Sandbukt, O. (Ed.), Management of Tropical Forests: Towards an Integrated Perspective. Centre for Development and the Environment, University of Oslo, Oslo, pp. 73–92.

Decker, B.S., 1994. Effects of habitat disturbance on the behavioral ecology and demographics of the Tana river red colobus (*Colobus badius rufomitratus*). Int. J. Primatol. 15, 703–737.

Dotta, G., Verdade, L.M., 2011. Medium to large-sized mammals in agricultural landscapes of south-eastern Brazil. Mammalia 75, 345–352.

Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. Oikos 65, 169–175.

Duval, S., Tweedie, R., 2000. A nonparametric 'trim and fill' method of accounting for publication bias in meta-analysis. J. Am. Stat. Assoc. 95, 89–98.

Edwards, D.P., Larsen, T.H., Docherty, T.D.S., Ansell, F.A., Hsu, W.W., Derhé, M.A., et al., 2010. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. Proc. R. Soc. B 278, 82–90.

Estrada, A., Raboy, B.E., Oliveira, L.C., 2012. Agroecosystems and primate conservation in the tropics: a review. Am. J. Primatol. 74, 696–711.

Estrada, A., Garber, P.A., Rylands, A.B., Roos, C., Fernandez-duque, E., Fiore, A. Di, et al., 2017. Impending extinction crisis of the world's primates: why primates matter. Sci. Adv. 3, e1600946.

Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F., Phalan, B., 2008. How will oil palm expansion affect biodiversity? Trends Ecol. Evol. 23, 538–545.

Fontúrbel, F.E., Candia, A.B., Salazar, D.A., Malebrán, J., González-Browne, C., Botto-Mahan, C., 2014. How forest marsupials are affected by habitat degradation and fragmentation? A meta-analysis. Naturwissenschaften 101, 599–602.

Ganzhorn, J., 1995. Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. Ecology 76, 2084–2096.

Gardner, T.A., Barlow, J., Chazdon, R., Robert, M., Harvey, C.A., 2009. Prospects for tropical forest biodiversity in a human-modified world. Ecol. Lett. 12, 561–582.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., et al., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.

Gullison, R.E., Hardner, J.J., 1993. The effects of road design and harvest intensity on forest damage caused by selective logging: empirical results and a simulation model from the Bosque Chimanes, Bolivia. For. Ecol. Manag. 59, 1–14.

Hamilton, A.C., Taylor, D., 1991. History of climate and forests in Tropical Africa during the last 8 million years. Clim. Chang. 19, 65–78.

Harcourt, A.H., Doherty, D.A., 2005. Species-area relationships of primates in tropical forest fragments: a global analysis. J. Appl. Ecol. 42, 630–637.

Harper, G.J., Steininger, M.K., Tucker, C.J., Juhn, D., Hawkins, F., 2007. Fifty years of deforestation and forest fragmentation in Madagascar. Environ. Conserv. 34, 1–9.

Hedges, L., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4, 1–23.

Irwin, M.T., Junge, R.E., Raharison, J.L., Karen, E.S., 2010a. Variation in physiological health of diademed sifakas across intact and fragmented forest at Tsinjoarivo, eastern Madagascar. Am. J. Primatol. 72, 1013–1025.

Irwin, M.T., Wright, P.C., Birkinshaw, C., Fisher, B.L., Gardner, C.J., Glos, J., et al., 2010b. Patterns of species change in anthropogenically disturbed forests of Madagascar. Biol. Conserv. 143, 2351–2362 (Elsevier Ltd.).

Isaac, N.J.B., Cowlishaw, G., 2004. How species respond to multiple extinction threats. Proc. R. Soc. B 271, 1135–1141.

IUCN, 2016. The IUCN Red List of Threatened Species. Version 2016-3. http://www.iucnredlist.org.

Johns, A., 1991. Forest disturbance and Amazonian primates. In: Box, H.O. (Ed.), Primate Responses to Environmental Change. Chapman & Hall, London, UK, pp. 115–135.

Junge, R.E., Barrett, M.A., Yoder, A.D., 2011. Effects of anthropogenic disturbance on indri (*Indri indri*) health in Madagascar. Am. J. Primatol. 73, 632–642.

Koh, L.P., Wilcove, D.S., 2008. Is oil palm agriculture really destroying tropical biodiversity? Conserv. Lett. 1, 60–64.

Lawes, M.J., 1992. Estimates of population density and correlates of the status of the samango monkey *Cercopithecus mitis* in Natal, South Africa. Biol. Conserv. 60, 197–210.

Mammides, C., Cords, M., Peters, M.K., 2009. Effects of habitat disturbance and food supply on population densities of three primate species in the Kakamega Forest, Kenya. Afr. J. Ecol. 47, 87–96.

Maxwell, S.L., Fuller, R.A., Brooks, T.M., Watson, J.E., 2016. The ravages of guns, nets and bulldozers. Nature 536, 143–145.

Meijaard, E., Sheil, D., 2008. The persistence and conservation of Borneo's mammals in lowland rain forests managed for timber: observations, overviews and opportunities. Ecol. Res. 23, 21–34.

Melo, F.P.L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., Tabarelli, M., 2013. On the hope for biodiversity-friendly tropical landscapes. Trends Ecol. Evol. 28, 461–468.

Mendenhall, C.D., Karp, D.S., Meyer, C.F.J., Hadly, E.A., Daily, G.C., 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509, 213–217.

Merker, S., Yustian, I., Mühlenberg, M., 2005. Responding to forest degradation: altered habitat use by Dian's tarsier *Tarsius dianae* in Sulawesi, Indonesia. Oryx 39, 189–195.

Moat, J., Smith, P., 2007. Atlas of the Vegetation of Madagascar. Kew Publishing, Royal Botanical Gardens, Kew.

Morellato, L.P.C., Alberton, B., Alvarado, S.T., Borges, B., Buisson, E., Gabriela, M., et al., 2015. Linking plant phenology to conservation biology. Biol. Conserv. 195, 60–72 (Elsevier B.V.).

Murphy, G.E.P., Romanuk, T.N., 2014. A meta-analysis of declines in local species richness from human disturbances. Ecol. Evol. 4, 91–103.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., et al., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50.

Norden, N., Chazdon, R.L., Chao, A., Jiang, Y.H., Vílchez-Alvarado, B., 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. Ecol. Lett. 12, 385–394.

Oliveira, A.T.M., 2015. Uso do Sistema Agroflorestal de Teca (*Tectona grandis* L.f) por Vertebrados Terrestres de Médio e Grande Porte, na Amazônia Meridional de Mato Grosso. Universidade do Estado de Mato Grosso.

Oliveira, L.C., Neves, L.G., Raboy, B.E., Dietz, J.M., 2011. Abundance of jackfruit (*Artocarpus heterophyllus*) affects group characteristics and use of space by golden-headed lion tamarins (*Leontopithecus chrysomelas*) in Cabruca agroforest. Environ. Manag. 48, 248–262.

Payne, J.L., Finnegan, S., 2007. The effect of geographic range on extinction risk during background and mass extinction. PNAS 104, 10506–10511.

Phillips, H., Newbold, T., Purvis, A., 2016. Land-use effects on local biodiversity in tropical forests vary between continents. Biodivers. Conserv. 26 (9), 2251–2270.

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proc. R. Soc. B 267, 1947–1952.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austriahttps://www.r-project.org/.

Raboy, B.E., Christman, M.C., Dietz, J.M., 2004. The use of degraded and shade cocoa forests by endangered golden-headed lion tamarins *Leontopithecus chrysomelas*. Oryx 38, 75–83.

Remis, M.J., Robinson, C.A.J., 2012. Reductions in primate abundance and diversity in a multiuse protected area: synergistic impacts of hunting and logging in a Congo basin forest. Am. J. Primatol. 74, 602–612.

Ribeiro-Neto, D., Arnan, X., Tabarelli, M., Leal, I.R., 2016. Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. Biodivers. Conserv. 25, 943–956.

Rosenthal, R., 1991. Meta-Analytic Procedures for Social Research. SAGE, Newbury Park.

Schwitzer, C., Glatt, L., Nekaris, K., Ganzhorn, J., 2011. Responses of animals to habitat alteration: an overview focussing on primates. Endanger. Species Res. 14, 31–38.

Schwitzer, C., Mittermeier, R., Davies, N., Johnson, S., Ratsimbazafy, J., Razafindramanana, J., et al., 2013. Lemurs of Madagascar - A Strategy for their Conservation. IUCN SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International, Bristol, UK, pp. 2013–2016.

Sist, P., 2000. Reduced-impact logging in the tropics: objectives, principles and impacts. Int. For. Rev. 2, 3–10.

Sodhi, N.S., Brook, B.W., 2006. Southeast Asian Biodiversity in Crisis. Cambridge University Press, Cambridge, UK.

Sodhi, N.S., Lee, T.M., Koh, L.P., Brook, B.W., 2009. A meta-analysis of the impact of anthropogenic forest disturbance on southeast Asia's biotas. Biotropica 41, 103–109.

Struhsaker, T.T., 1999. Primate communities in Africa: the consequence of long-term evolution or the artifact of recent hunting? In: Feagle, J.G., Janson, C.H., Reed, K.E. (Eds.), Primate Communities. Cambridge University Press, Cambridge, pp. 289–294.

van Schaik, C.P., Monk, K.A., Robertson, J.M.Y., 2001. Dramatic decline in orang-utan numbers in the Leuser Ecosystem, Northern Sumatra. Oryx 35, 14–25.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., et al., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat. Commun. 7, 12558.

Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. J. Stat. Softw. 36, 1–48.

Watson, J.E.M., Shanahan, D.F., Marco, M. Di, Sanderson, E.W., Mackey, B., 2016. Report catastrophic declines in wilderness areas undermine global environment targets. Curr. Biol. 26, 2929–2934 (Elsevier Ltd.).

Wilkie, D., Shaw, E., Rotberg, F., Morelli, G., Auzel, P., 2000. Roads, development, and conservation in the Congo Basin. Conserv. Biol. 14, 1614–1622.