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

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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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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