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Special Issue: Defaunation's impact in tropical terrestrial ecosystems

Cascading effects of contemporaneous defaunation on tropical forest communities

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ABSTRACT

Defaunation, driven by hunting and habitat fragmentation, poses a threat to wildlife in tropical forests worldwide and is expected to have cascading effects on other organisms, particularly plant communities. This review summarizes empirical evidence from 42 studies on the indirect effects of defaunation on plants, focusing on altered plant–animal interactions, the resulting effects on plant population demography, and finally, community-level changes in plant composition and diversity. This review confirms, as previously documented, that larger-seeded species consistently experience reduced primary seed dispersal, and increased seedling aggregation around parent trees, as a result of defaunation. Reduced seed predation and herbivory are also associated with defaunation, in some cases countering the negative effects of reduced dispersal. The net effects of these changes led to either higher or lower seedling recruitment, depending on plant species. Defaunated plant communities show consistent shifts toward lower species richness, higher species dominance, and lower diversity. More research integrating effects of defaunation on all processes from seed dispersal through plant recruitment is required to mechanistically link altered species interactions to changes in recruitment and community composition.

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1. Introduction

Animal populations are currently in decline due to both unsustainable hunting and habitat fragmentation in tropical forests throughout Asia (Corlett, 2007), Africa (Fa and Brown, 2009) and Latin America (Peres and Palacios, 2007), a phenomenon that has come to be known as defaunation (Dirzo and Miranda, 1991), or the "empty forest syndrome" (Redford, 1992), in extreme cases. Defaunation does not impact all animal species in a community equally. Rather, vertebrates respond differently to the drivers of defaunation as a function of their body size.

These responses have been articulated as a model by Wright (2003) and best demonstrated empirically in a comparison of densities of more than 30 animal taxa at three levels of hunting pressure, using 101 sites in Amazonia (Peres and Palacios, 2007). Large-bodied species, such as ungulates and large primates, tend to be preferred game species, have large home ranges, and have a higher age at first reproduction and low fecundity, traits which increase vulnerability to hunting and habitat loss (Cardillo et al., 2005). Therefore, they decline monotonically as hunting and fragmentation intensify in a system (Peres and Palacios, 2007, Appendix A). As large-bodied species begin to decline, medium-bodied species are initially expected to increase in abundance, likely due to a relaxation of competitive and predation pressures (Wright, 2003) (Appendix A). However, as large-bodied species become depleted or locally extinct, or as habitat fragments become increasingly smaller, this density compensation should cease, and medium-bodied species themselves experience the impacts of hunting and habitat loss, declining in abundance accordingly (Appendix A). Finally, small-bodied species tend to be undesireable as game species, have small habitat requirements, relatively quick maturation, and high fecundity. These traits confer high tolerance to habitat loss and harvesting, even enabling some species (e.g. rats, squirrels and small monkeys) to persist in urban, human-dominated environments. In addition, these species are also thought to benefit from reduced predation and competition as larger species decline in the system (Wright, 2003). Therefore, these species are expected to increase monotonically in abundance as hunting and fragmentation intensify in a system (Appendix A).

Because many of the animals most vulnerable to defaunation, as well as their less vulnerable competitors, are seed dispersers, seed predators, seedling predators, and herbivores, defaunation is likely to disrupt plant–vertebrate interactions (Emmons, 1989; Redford, 1992; Wright, 2003). Such disruptions are expected to negatively impact some plant species while benefitting others, and lead to an overall loss of tropical forest plant diversity. Plant species with hunted dispersers are expected to experience reduced seed dispersal, particularly the largest-seeded plant species. Changes in seed predation, seedling predation, and herbivory may have positive or negative effects on species recruitment, depending on a plant species' traits (Wright, 2003; Dirzo et al., 2007; Muller-Landau, 2007). Overall, the net effect of defaunation on plant diversity has been hypothesized to be negative (Wright, 2003; Muller-Landau, 2007), because species experiencing reduced seed dispersal will experience greater density-dependent mortality, and because seed predators and herbivores will not suppress populations of competitively dominant species.

Recent synthesis on the indirect effects of defaunation in tropical forests have focused on seed dispersal (Markl et al., 2012; McConkey et al., 2012) or seed predation (Stoner et al., 2007). However, no review has examined how different plant–animal interactions may be changing simultaneously, or evaluated the evidence linking those changes to altered recruitment or lower biodiversity. This review synthesizes 42 studies of how plant–animal interactions, plant population demography, and community diversity respond to defaunation, with the aim of evaluating how the effects of defaunation on individual species at different stages of plant recruitment contribute to changes occurring at the population or community level. In addition, I examine the heterogeneity in how defaunation is defined and studied by plant ecologists, as it relates to synthesizing results across studies.

2. Methodology

2.1. Identification of studies

Here I summarize the literature on indirect effects of tropical defaunation through 2012. (See Appendix B for methodological details.) To be included, studies had to use comparative experimental designs (e.g. defaunated vs. non-defaunated; exclosure vs. control), with raw response variables reported for both defaunated and non-defaunated conditions. In total, 42 studies (Appendix C) met all criteria for inclusion.

2.2. Standardization of response variables for comparison

Raw response values for seed dispersal, seed predation, herbivory, recruitment, diversity, and species richness were compiled from text, tables, and figures. (See Appendix B for details.) The authors' categorical characterizations of relative levels of defaunation were used to categorize sites. Reference sites generally exhibited moderate to no defaunation, while more impacted sites exhibited larger decreases in animal abundance and species richness. These sites will hereafter be referred to as "non-defaunated" and "defaunated" respectively. When studies reported response variables from multiple defaunated or non-defaunated sites, a mean value for each category was used to summarize responses and avoid introducing additional variability from individual sites. Sites experiencing the lowest levels of defaunation were grouped with "no defaunation" sites, while sites showing medium to high levels of defaunation comprised the "defaunated" sites.

To enable more direct comparisons of effects, I calculated effect sizes for each response variable. The effect size estimator used here is the percent difference in the response, as follows: Effect size = $100 * (R_D - R_{ND})/R_{ND}$, where R_D and R_{ND} are the magnitudes of the response variables in the defaunated and non-defaunated sites, respectively. (See Appendix B for additional details.) An effect size of zero indicates no difference between R_D and R_{ND}. Positive values indicate that the response variable was higher in the defaunated condition; negative values indicate that the response variable was lower in the defaunated condition. Due to the degree of heterogeneity introduced to the dataset by the variation in study design, defaunation intensities compared, and species studied, no meta-analysis of responses was conducted (cf. Hedges and Olkin, 1985). Negative results cannot reliably be attributed to true biolog-