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Special Issue: Defaunation's impact in tropical terrestrial ecosystems

Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass

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Unprecedented rates of logging and hunting threaten to transform the remaining primary tropical forest into a degraded mosaic, emptied of wildlife. Defaunation is expected to interrupt plant–animal interactions with cascading effects for forest structure, composition, and ecosystem services. In a Central African forest first logged 35 years ago, we evaluated this process of ecological erosion in 30 study sites distributed across forest disturbed by logging and hunting, logging alone, and neither logging nor hunting. Both logging and hunting tended to reduce abundances of large mammals, together shifting the relative abundance of the animal community towards squirrels and small birds. Through a series of experiments, we evaluated the effects of logging and hunting on seed dispersal, seed predation and herbivory. We demonstrate that complete defaunation is not necessary to significantly alter the strength of plant-animal interactions. Hunting reduced the mean dispersal distances of nine mammal-dispersed tree species by 22%. Rates of seed predation were similar among forest types, but hunted forest had significantly lower rates of herbivory that we attribute to the lower abundance of meso-herbivores. Hunted forest also had significantly lower above-ground biomass (301 Mg ha^{-1}) than the logged only (358 Mg ha^{-1}) and undisturbed (455 Mg ha^{-1}) forest types, but similar numbers of tree species and individuals. Lower biomass in hunted forest is likely attributable to significantly lower wood densities at small tree size classes (<40 cm). We hypothesize that over time the human-mediated modification of plant-animal interactions can alter the composition of the forest to have a higher proportion of fast-growing, low wood density tree species, diminishing the long-term potential for carbon storage.

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1. Introduction

Worldwide, tropical forests are being emptied of their large vertebrate populations (Brook et al., 2003; Fa et al., 2003; Peres and Palacios, 2007). Defaunation, the local extirpation of large vertebrates, is driven by myriad activities, including rural population growth, artisanal mining, logging and road construction; but the proximate factor is overhunting. Subsistence and commercial hunting take an enormous toll on populations of tropical mammals, birds and reptiles, with annual losses of animals estimated at 6 million in Southeast Asia, 16 million in the Brazilian Amazon, and 18 million in Central Africa (Butler, 2013).

It is widely recognized that losses of vertebrate populations can disrupt plant–animal interactions, threatening the integrity of natural ecosystems. Hunting can alter rates of pre-dispersal predation (Beckman and Muller-Landau, 2007), seed dispersal (Wright et al., 2000; Galetti et al., 2006; Brodie et al., 2009; Holbrook and Loiselle, 2009), seed predation (Wright et al., 2000, 2007a,b), seedling predation (Vanthomme et al., 2010), and herbivory (Dirzo and Miranda, 1991). Changes in these processes should have cascading effects for species composition, diversity, and structure of plant communities (Muller-Landau, 2007; Wright et al., 2007a,b). One of the few generalizations to have emerged from these studies is the prediction that defaunation will be most detrimental for large-seeded tree species (Kurten, this issue); however there is disagreement over the consequences of these changes for the plant community (e.g., Wright et al., 2007a,b; Vanthomme et al., 2010). While the short-term responses of forests to hunting are beginning to be understood, the long-term ecological consequences remain a matter of speculation.

Defaunation in Central Africa would probably be a localized problem if not for extractive industries whose operations take place over millions of hectares (Butler and Laurance, 2008; Clark and Poulsen, 2012). With deeper roots than other industries, timber extraction is a good example of how large-scale extractive industries set the stage for defaunation. Logging operations open

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roads and provide access for slash-and-burn farmers and hunters to remote forests (Wilkie et al., 2000; Robinson et al., 1999). Logging requires a labor force to inventory, extract, and refine logs; thus villages and towns are built in the forest, increasing hunting pressure on wildlife (Poulsen et al., 2009).

Defaunation generally occurs in size-based increments, with hunters first taking the largest species, and then working down to lower size classes of animals (Peres and Palacios, 2007; Poulsen et al., 2011); most Central African forests are located somewhere between the extremes of complete defaunation and a fully intact vertebrate community. Hunting therefore initiates a process we call *ecological erosion* – the incremental deterioration or alteration of ecological communities and processes. This term captures the nature of the phenomenon, as most interactions are not completely lost, but rather eroded and weakened as the animal community is modified. The degree of change for plant-animal interactions and the plant community will depend on the intensity of hunting and sensitivity of the faunal community. This raises questions of whether: (1) different disturbances, such as logging and hunting, impact animal guilds in different ways and potentially offset each other's negative effects on wildlife; and (2) whether ecological processes are maintained in the absence of complete defaunation.

In this paper, we evaluate the potential consequences of ecological erosion for the species composition and structure of a Central African forest. We synthesize the results of several experiments conducted across a gradient of hunting and logging in Republic of Congo. Intensive hunting in the area likely began with the onset of logging 35 years before this study: its effects are now manifested by significantly higher abundances of small-bodied species in disturbed forest compared to undisturbed forest (Poulsen et al., 2011). We examine the effects of reduced populations of large-bodied species on ecological processes by comparing (1) seed rain abundance and seed dispersal patterns, (2) post-dispersal seed predation, and (3) herbivory among forest disturbed by logging and hunting, logging alone, and neither logging nor hunting. To assess the possible repercussions of changes to ecological processes, we compare tree species composition and biomass among forest types.

2. Materials and methods

2.1. Study site description and design

In 2005, we initiated a research program to monitor the impact of logging and hunting on tropical forest dynamics in Republic of Congo (Clark et al., 2009; Poulsen et al., 2009, 2011; Fig. 1). This area includes the Nouabalé-Ndoki National Park (NNNP) and the adjacent Kabo logging concession (KLC) managed by the Congolaise Industrielle des Bois company (CIB). The NNNP has never been commercially logged and has not recently contained permanent villages; although hunter-gatherer populations inhabited the region for approximately 40,000 years and evidence of iron smelting sites and burning date from 1240 BP (Lanfranchi et al., 1998; Brncic et al., 2007). The KLC was first selectively logged (<2 trees/ha) approximately 35 years before our study. We estimate that the effects of both hunting and logging likely date back this long, as logging operations included the construction of a worker's camp (~3000 people in 2005) and a sawmill at Kabo village (CIB, 2006).

As part of this research program, we established the Sangha Plot Network (SPN) consisting of 30 sites in an area of 3000 km^2 (Fig. 1). Each site includes a 1-ha tree plot for measuring forest diversity and structure at the midpoint of a 2.5 km transect for quantifying animal densities. The SPN stretches over a gradient of undisturbed forest to logged, hunted forest near the town of Kabo. We randomly located the sites in mixed lowland tropical forest within each of the three different forest types: logged and hunted forest, logged and unhunted forest, and unlogged and unhunted forest (see Poulsen et al. (2011) for details). Here we refer to the forest types as "hunted", "logged only" and "undisturbed".

None of our study sites are defaunated: they all retain the full complement of forest species, but at different densities, with the hunted site on a trajectory to defaunation. Although hunting and logging can sometimes impact animal guilds in different ways (logging reduced the density of squirrels, whereas hunting increased densities of squirrels), when combined they exacerbated declines in populations of medium- and large-bodied mammals and shifted the relative abundance of the community towards small-bodied squirrels and birds (Fig. 2, Poulsen et al., 2011). Elephants were an exception to this pattern: their densities did not differ significantly between hunted and undisturbed forests. We attribute this to active law enforcement efforts to protect elephants and logging-induced habitat modification (Clark et al., 2009). Elephant densities were highest in logged only forest, probably because the opening of forest during timber extraction results in a surge of seedling and saplings that are browse for elephants (Clark et al., 2009). However, our snapshot of the animal community, conducted 5 years after the creation of an armed eco-guard unit, likely does not represent the history of the area. In the past, poaching of elephants for ivory was intense in large forest clearings: elephant carcasses were often seen in clearings during fly-overs in the1990s (B. Curran, pers. comm.). That is to say, we believe that elephant populations were lower in the past (maybe substantially so), particularly in the hunted forest, and this may have contributed to present day differences in forest structure.

We designed our study to detect the individual effects of logging, hunting, and the combination of logging and hunting. We estimate these effects for different responses (e.g., animal density, seed dispersal distances) by comparing the value at the disturbed site from the value where that disturbance was not present:

$$Effect_l = Site_{l,uh}/Site_{ul,uh}$$

$$Effect_h = Site_{l,h}/Site_{l,uh}$$

$$Effect_{l+h} = Site_{l,h}/Site_{ul,uh}$$

where subscript "l" indicates logged, subscript "h" indicates hunted, subscript "uh" indicates unhunted, and subscript "ul" represent unlogged. Note that due to the missing forest type (unlogged, hunted), our estimate of the effect of hunting is actually the estimate of hunting in logged forest.

2.2. Seed rain and dispersal

To determine the impact of changes in the vertebrate community on seed rain patterns, we erected 21-1 m^2 seed traps in each forest plot ($N = 630$ traps in 30 plots). Seed traps were constructed of plastic mesh attached to 1 × 1 m wooden frames elevated to a height of 1 m from the ground. Traps were centered along three lines at 25, 50, and 75 m from the plot border, with 10 m separating each trap so that all traps were at least 20 m from the plot borders. During the two-year duration of this study, we collected all seeds and fruits that fell into the traps every two weeks and counted and identified them to species.

To estimate seed dispersal patterns across the three forest types, we used an inverse modeling method that models the density of seeds at a single location (seed trap) as the summed contribution of seeds dispersed from all conspecific adult trees in the plot. We assumed that the contribution of each adult tree to the seed rain at a location depends only on its individual fecundity

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