Defaunation of large mammals alters understory vegetation and functional importance of invertebrates in an Afrotropical forest

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ABSTRACT

Hunting has reduced or eliminated large-bodied vertebrates in many areas across the tropics, contributing to the global process of defaunation. Elucidating the ecological consequences of hunting has important implications for managing ecosystems and for our understanding of community and ecosystem ecology. We present data collected through a combination of comparative and experimental approaches to assess how faunally-intact and heavily-hunted forests in Gabon differ in understory vegetation structure, macroinvertebrate fauna, ecological processes, and the relative importance of different taxa driving those processes. Our results show that hunted sites had denser understory vegetation and hosted approximately 170 times fewer termites compared to faunally-intact sites. While web-building spiders were positively associated with understory vegetation density, this effect did not translate to significantly higher abundances in heavily-hunted forests. Additionally, the overall rates of decomposition, insectivory, and seed predation/removal on the forest floor appeared robust to both defaunation and the associated increases in understory vegetation density. However, our exclosure experiments revealed that the contribution of invertebrates to decomposition was approximately 25% lower in hunted sites compared to faunally-intact sites. Results suggest potential resilience in this complex ecosystem such that microbial or other taxa not measured in this study may compensate for the reduced functional contribution of invertebrates to decomposition. However, while our results illustrate potential resilience, they also indicate that indirect effects following defaunation, such as increases in the density of understory vegetation, may alter invertebrate communities on the forest floor, with potential consequences for the mechanisms, and therefore the dynamics, driving critical ecosystem processes.

1. Introduction

Across the tropics, anthropogenic pressures are emptying forests of large- and medium-bodied vertebrates (Benítez-López et al., 2019; Ceballos et al., 2017; Estes et al., 2011), a phenomenon commonly referred to as *defaunation* (Dirzo et al., 2014). Through processes such as seed dispersal, trampling, herbivory, biopedturbation, and dung deposition, large vertebrates can alter the physical environment and available resources in the understory (Brodie et al., 2009; Camargo-Sanabria et al., 2015; Dunham, 2011; Rosin et al., 2017). Consequently, defaunation may have cascading effects on the communities and functional performance of understory fauna such as invertebrates (Dunham, 2008; Klink et al., 2015). However, more research is needed to understand these potential consequences of defaunation in tropical forests (but see Beckman and Muller-Landau, 2007; Peguero et al.,

2017; Wright et al., 2000), especially given the proportionally large biomass that invertebrates comprise in these systems (Wilson, 1990) and their key contributions to many ecosystem processes (Dunham and Mikheyev, 2010; Janzen, 1971; Watt et al., 1997).

Loss of large vertebrates may alter invertebrate communities via multiple pathways such that consequences are difficult to predict. In Afrotropical forests, which hold a high diversity of megafauna, the loss or decline of large herbivores such as forest elephants may increase the density of understory vegetation after it is released from herbivory and trampling pressures (Bressette et al., 2012; Rosin et al., 2017). This in turn can affect multiple microhabitat and microclimatic variables on the forest floor, altering conditions for terrestrial invertebrates. Greater understory vegetation density could benefit some invertebrate species by increasing litter input and providing more complex physical habitat structure and cover, offering resources and protection from predators

and desiccation (Ashford et al., 2013; Sayer and E.V.J.T, 2006; Fischer et al., 2013; Hansen, 2000). However, increased vegetation density could also provide more habitat structure for invertebrate predators such as spiders (Hatley and Macmahon, 1980; Robinson, 1981; Takada et al., 2008), which may then alter invertebrate communities through increased predation. It is difficult to predict how vertebrate defaunation will affect invertebrate communities because different species are likely to vary in their response to changes in microclimate and microhabitats on the forest floor. Indeed, existing studies in grassland and temperate forest ecosystems have reported varying responses of invertebrate communities following the reduction of large herbivores and the associated changes in vegetation (Bressette et al., 2012; Brousseau et al., 2013; Duguay and Farfaras, 2011; Klink et al., 2015; Miyashita et al., 2004; Roberson et al., 2016; Stewart, 2001; Suominen et al., 1999; Takada et al., 2008).

Loss of large vertebrates may also indirectly influence some invertebrate taxa by leading to a reduction in dung resources on the forest floor. Dung can be a key resource for some invertebrates, such as termites (Coe, 1977; Edwards, 1991; Holter, 2013), which are important detritivores in forest and savannah ecosystems (Bignell and Eggleton, 2000; Freymann et al., 2010; Jouquet et al., 2011; Kaiser et al., 2017). Although much remains unknown about termite dependence on dung in tropical systems (Freymann et al., 2008), existing work shows termites readily use herbivore dung in many systems (Freymann et al., 2008; Herrick and Lal, 1996; Whitford et al., 1982) and termites are reported in one study to even track herbivore dung resources (Ferrar and Watson, 1970).

If defaunation indirectly affects invertebrates, either positively or negatively, there may also be consequences for important ecosystem processes, given the large biomass and important functional role that invertebrates play in ecosystems worldwide. However, even if functional contribution of invertebrates to ecosystems is altered, complex terrestrial systems may resist changes in ecosystem processes because of the potential for functional redundancy among taxa (Ewers et al., 2015; Strong, 1992; Tenkiano and Chauvet, 2017).

To better understand the potential consequences of defaunation on understory habitat, communities, and processes, we combined experimental and comparative approaches in hunted and faunally-intact forests in Gabon. In particular, we examined differences between heavily-hunted and faunally-intact forest in terms of 1) litter depth and density of understory vegetation, 2) the abundance of different macroinvertebrate groups, and 3) the contribution of invertebrates to seed predation/removal, insectivory, and decomposition.

2. Materials and methods

2.1. Study area and design

Our study was conducted May-Aug 2016 within the 5800 km^2 area surrounding the regional capital of Makokou in the Ogooue-Ivindo province in northeastern Gabon (Fig. 1). Mean annual precipitation in the region is approximately 1700 mm, with two rainy seasons (September–December and March–May) and an average temperature of 23.9 °C (Koerner et al., 2017). The study region contains the northern section of Ivindo National Park and approximately 60 small villages located along three main roads in addition to agricultural fields (livestock farming does not occur in the area) and two active logging concessions. The gradient in human activity in this area has previously been documented to coincide with a gradient in hunting pressure and of large vertebrate defaunation (Beirne et al., 2019; Koerner et al., 2017), making it an ideal region of study for our research questions.

We established a total of 11 sites within two forest categories based on defaunation status. Five sites were categorized as 'faunally-intact', and six were categorized as 'hunted' (representing a high level of defaunation). All sites were a minimum of 1.8 km apart and carefully selected to ensure habitat was similar. Each site was flat lowland old-growth rainforest > 500 m from water and dominated by tree families including Sapotaceae, Fabaceae, Myristicaceae, and Burseraceae. Soils in our study sites were sandy Oxisols and did not differ among sites based on visual and physical inspection. Previous work that overlapped with our study area, from which we based our hunted and faunally-intact forest categories, found no differences in vegetation characteristics including liana abundance, stem density, tree diameter, and tree species richness (Koerner et al., 2017). We additionally tested our sites for differences in canopy cover between forest categories and found no significant differences (Supplementary material 1).

Our faunally-intact sites were located within Ivindo National Park, a 3000 km^2 protected area with many large vertebrate species, including megafaunal herbivores (> 1000 kg) such as forest elephants (*Loxodonta cyclotis*). Our hunted sites were located outside of the park between 2 and 6 km from rural villages, where hunting was prevalent (Koerner et al., 2017) but no evidence of small-scale subsistence activities such as firewood gathering, vegetation harvesting, or gardening existed.

Koerner et al. (2017) quantified defaunation in our study region with surveys of large, diurnal vertebrate communities along transects placed at varying distances from villages. Our selected hunted and faunally-intact sites were set to correspond within their categories of 'near' (0–6 km) and 'far' (> 15 km) from villages. Koerner et al. (2017) determined that hunting pressure decreased with increasing distance from villages, while relative abundances of species targeted by hunters, such as red river hogs (*Potamochoerus porcus*) and antelope species (*Cephalophus spp.*), increased farther from villages (see Supplementary Table 1 for full species list). For example, ungulate abundances (excluding elephants with a small sample size) increased by about four-fold over a 25 km distance gradient moving away from villages.

At each site, we established three 10 × 10 m plots > 200 m apart ($n = 33$ plots). Our study was well replicated at the landscape scale within the Ogooue-Ivindo province, at distances appropriate for our main study organisms – understory macroinvertebrates – providing a sufficiently robust sampling scheme. While we were not able to replicate at the scale of multiple protected areas, our comparative study combined with experiments is useful for observing patterns and developing hypotheses useful for future research (Davies and Gray, 2015).

2.2. Habitat variable measurements

In each plot, we recorded the density of understory vegetation and leaf litter depth at 2-m intervals along three 10-m transects spaced 2-m apart. Leaf-litter depth was measured as the distance from the soil to the top of the leaf litter. To measure the density of understory vegetation, we counted the number of leaves intercepting a 1.5-m rod placed perpendicular to the ground every 2 m along the 10-m transects, with a standardized 1-m offset to the right of the transect taken before each placement (Coulloudon et al., 1999).

2.3. Invertebrate sampling

We concentrated our study on macroinvertebrates (> 5 mm) because they are often used as indicators of environmental changes across many systems (Haskell, 2000; Hodkinson and Jackson, 2005; Walters et al., 2009). We particularly focused on sampling epigean (litter-dwelling) macroinvertebrates because we anticipated this to be the group most affected by changes in understory vegetation and litter on the forest floor. To measure macroinvertebrate communities, we placed five pitfall traps 1 m apart across the center of each plot (created a 5-m transect bisecting each of the three 10 × 10 m plots within each site; $n = 165$ pitfall traps). The traps were approximately 200 ml in volume. We suspended roofs made of plastic sheeting over the pitfall traps to block falling debris and rain. Each trap contained a solution of 30 ml of 95% ethanol, a drop of Dawn© dish soap, and 50 ml of water. We collected traps after five days in the field. Traps were set out between 9 and 11 AM on the first day and retrieved between 9 and 11 AM on the
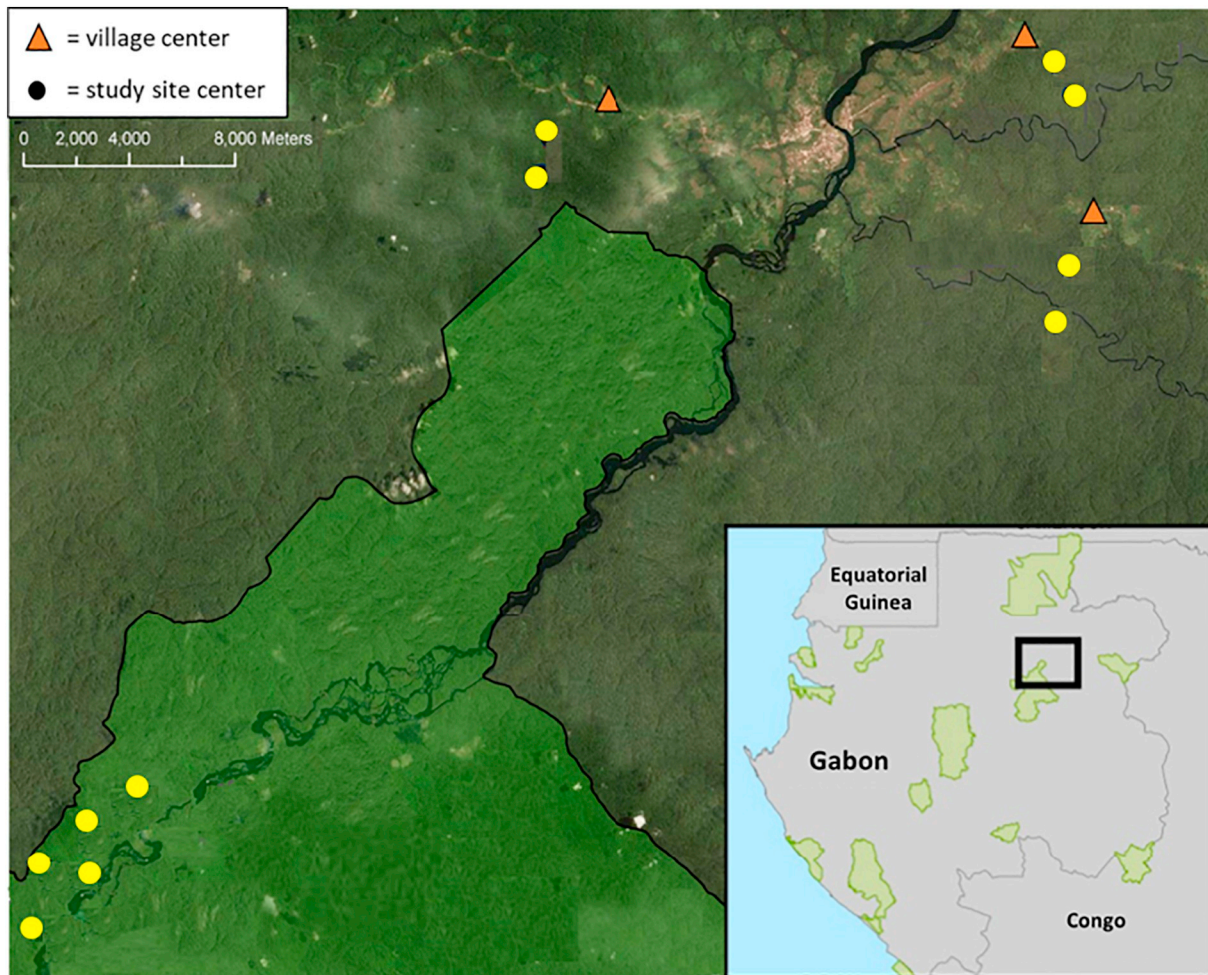
Fig. 1. Map of study area. The inset depicts the location of our study area (black rectangle) within Gabon. Each study site (depicted as yellow circles) consists of three 10 m × 10 m plots situated > 200 m apart (not shown). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

fifth day (5 pitfall traps × 5 days × 33 plots = 19,800 pitfall trap hours). We identified all macroinvertebrates to order and, where possible, to family. Two hunted plots and one faunally-intact plot were excluded from analyses because the traps were destroyed by ant swarms or red river hogs, but the data from the remaining plots in each of those sites were recorded.

We were also interested in the effects of defaunation on web-building spiders in the understory, which we expected to be affected by changes in understory vegetation structure. To measure web-building spider abundance in each plot, we counted spiders during the day in webs within 3 m of the ground along four 10-m transects, each 2 m apart and 1-m wide.

2.4. Ecological processes: decomposition, insectivory, and seed predation/removal

To better understand how defaunation might affect the functional role that understory macroinvertebrates play in ecosystem processes, we employed macroinvertebrate exclosure experiments. We filled 1-mm nylon mesh litter bags with 2.50 g of dried, freshly senesced leaves cut into 2 cm^2 pieces from a common tree in the study area, *Santiria trimera*. Control bags were similar except that we cut six 1 cm^2 perforations on each side to allow entry by macroinvertebrates (Ewers et al., 2015). Three macroinvertebrate exclosure bags and three control bags were scattered within each plot (*n* = 99 bags per treatment). We collected, dried, and re-weighed the bags after approximately 32 days.

We also conducted exclosure experiments to examine seed predation/removal and insectivory by invertebrates in hunted and faunally-intact forests. We evaluated insectivory using dehydrated intact beetle larvae, *Tenebrio molitor*, and seed predation/removal rates with raw peanuts. For the latter, we required seeds that were attractive to invertebrate taxa that could be obtained in large numbers. Raw peanuts were selected after we conducted preliminary seed predation trials using raw sunflower seeds, raw pumpkin seeds, and raw peanuts to determine which were the most readily eaten by invertebrates. In each plot, we set up one insectivory exclosure experiment and one seed predation/removal exclosure experiment comprised of: (1) a control treatment in which 10 larvae (for insectivory experiments) or 10 peanuts (for seed predation experiments) were placed on a leaf from a common shrub, *Megafluniom macrostachys* (Marantaceae), with large, waxy leaves well-suited for creating a natural 'floor' for our experimental setup; and (2) a terrestrial invertebrate exclosure treatment in which 10 larvae or 10 peanuts were placed on the same type of leaf and surrounded by a 2-cm high barrier coated in insect-trapping glue (Tanglefoot©, Grand Rapids, MI) (*n* = 33 replicates per treatment of each insectivory and seed predation/removal experiments). After 24 h, we recorded how many larvae and peanuts were removed or consumed to some degree.

2.5. Statistical analysis

We analyzed our data using generalized linear mixed models

(GLMM), following guidelines from Bolker et al. (Bolker et al., 2009). For all analyses, we modeled the response variables with the appropriate underlying probability distribution (Poisson, binomial, Gaussian, negative binomial and gamma) and included a random effect of plot nested within site to replicate our nested study design. Model fit was assessed by examining residuals for normality and, when necessary, checking for overdispersion (variance ≫ mean of count data). When appropriate, we accounted for overdispersion by using a negative binomial distribution, which includes an extra parameter that allows both the mean and variance to be estimated. For most models, we evaluated the main effects and interaction of covariates employing a backwards model selection process to find the best fitting model based on the lowest Akaike Information Criterion (AIC) score. When interaction terms were not biologically meaningful, we report only the main effects (detailed below).

To evaluate the effect of forest defaunation status on the density of understory vegetation, we built a negative binomial GLMM. To assess the effect of forest defaunation status on litter depth, we log-transformed litter depth to achieve normality and employed a Gaussian distribution. Because understory density and litter depth were significantly, positively related (linear mixed effects model: $\beta = 0.04 \pm 0.02$ SE, $t = 2.31$, $p < .05$), we only used understory vegetation density as a habitat variable to examine predictors of macroinvertebrate abundances.

To analyze effects of the density of understory vegetation and defaunation status on the abundances of the major invertebrate taxonomic groups collected in our pitfall traps, we built two negative binomial GLMMs with counts of invertebrates as the response variable. The first model included the main effects and interaction between taxonomic group and understory density as independent variables, and the second model included taxonomic group and defaunation status. We also examined the effects of defaunation status and understory density on the abundance of web-building spiders through Poisson GLMMs.

To examine the effects of defaunation status on litter decomposition overall and litter decomposition specifically by macroinvertebrates, we modeled the proportion of litter that decomposed in each litter bag for each treatment (control and macroinvertebrate exclusion) with a gamma distribution, the continuous distribution counterpart to the negative binomial (Bolker, 2008). We included the number of days a bag was left in the field (27–36 days) as an offset term. Fixed effects were treatment type (control or macroinvertebrate exclusion), forest defaunation status, and their interaction.

To analyze the effects of defaunation status on our experiments involving insectivory and seed predation/removal, we assessed the effects of treatment type (control or terrestrial invertebrate exclusion), forest defaunation status, and their interaction on the response variables of either proportion of seeds removed (in the case of our seed predation/removal experiments) or the proportion of beetle larvae removed (for our insectivory experiments). For both experiments, we excluded one replicate of the experiment because the barrier around one invertebrate exclusion treatment in the hunted forest was broken. For seed predation, we built a binomial GLMM to model probability of seed removal. For insectivory, we arcsine square-root transformed the proportions of larvae removed so that they were approximately normally distributed, and then modeled insectivory using a Gaussian distribution (linear mixed model).

We conducted all statistical analyses in R version 3.6.1 (R Core Team, 2019) using the 'glmmTMB' package (Brooks et al., 2017).

3. Results

3.1. Habitat variables

Hunted sites were associated with significantly higher densities of understory vegetation ($\beta = 0.49 \pm 0.19$, $z = 2.62$, $p < .01$) (Fig. 2A) and nearly significantly higher litter depth ($\beta = 0.15 \pm 0.08$, $z = 1.75$,

$p = .07$) (Fig. 2B).

3.2. Epigean macroinvertebrate communities and web-building spiders

Pitfall traps yielded > 8600 macroinvertebrates in at least 15 taxonomic groups (Supplementary Table 2). Our macroinvertebrate data can be split into the following most common groups: *Formicidae* (Hymenoptera), *Araneidae* (Araneae, web-building spiders), *Lycosidae* (Araneae, ground-dwelling wolf spiders), *Blattodea* (cockroaches), *Termitoidae* (Blattodea; infraorder: Isoptera), *Coleoptera* (beetles), and *Acrididae and Gryllidae* (Orthoptera; grasshoppers and crickets).

Termites were the only invertebrate group that differed significantly in abundance between the hunted and faunally-intact sites, having a strong negative response to defaunation ($\beta = -4.98 \pm 0.65$, $z = -7.62$, $p < .001$), with faunally-intact sites hosting approximately 170 times more termites than hunted sites (Fig. 3).

The density of understory vegetation was positively related to the abundance of web-building spiders ($\beta = 0.66 \pm 0.27$, $z = 2.44$, $p < .05$), although forest defaunation status had no significant effect on their abundance ($\beta = 0.25 \pm 0.29$, $z = 0.87$, $p = .38$). Understory density showed a significant negative relationship with termite abundance ($\beta = -2.85 \pm 0.67$, $z = -4.24$, $p < .001$) and near-significant positive relationship with ant abundance ($\beta = 0.81 \pm 0.47$, $z = 1.73$, $p = .08$) (Table 1).

3.3. Ecosystem processes and invertebrate functional contribution

Defaunation had no significant effect on the proportion of litter mass that decomposed in our experimental litter bags ($\beta = 0.06 \pm 0.21$, $z = 0.28$, $p = .78$) (Fig. 4A, B). However, excluding macroinvertebrates from our experimental litter bags decreased the proportion of litter mass that decomposed significantly ($\beta = -1.50 \pm 0.28$, $z = -5.37$, $p < .001$) (Supplementary Fig. S3) and the interaction term between defaunation and our macroinvertebrate exclosure treatment was significant, such that defaunation reduced the negative effect that excluding macroinvertebrates had on the proportion of litter that decomposed relative to the faunally-intact forest ($\beta = -0.73 \pm 0.34$, $z = -2.17$, $p = .03$) (Fig. 4A, B; Table 2).

Excluding terrestrial invertebrates reduced insectivory significantly regardless of forest defaunation status ($\beta = -1.30 \pm 0.09$, $z = -14.11$, $p < .001$), and defaunation did not significantly affect the outcomes of our invertebrate exclosure treatment (defaunation status and exclosure interaction term: $\beta = -0.25 \pm 0.18$, $z = -1.39$, $p = .17$) (Fig. 5A, B). The insectivory experiments yielded 100% predation in all control treatments regardless of forest defaunation status. Because the defaunation term in our models, along with the interaction term of forest defaunation status with the invertebrate exclosure treatment, did not improve model fit, these terms were not included in our final model.

Similarly, excluding terrestrial invertebrates significantly reduced seed predation/removal regardless of forest defaunation status ($\beta = -3.81 \pm 0.0.36$, $z = -10.56$, $p < .001$), and defaunation also had no significant effect overall on seed predation/removal ($\beta = -0.33 \pm 0.43$, $z = 0.78$, $p = .43$), nor did it affect the outcomes of the terrestrial invertebrate exclosure treatment (defaunation status and exclosure interaction term: $\beta = -0.86 \pm 0.71$, $z = 1.22$, $p = .22$) (Fig. 5C, D). Neither defaunation status nor the interaction term between defaunation and the exclosure treatment improved model fit and were not included in our final model.

4. Discussion

4.1. Summary

Tropical forests in Africa hold one of the last remaining refuges for relatively intact assemblages of forest megafauna worldwide; however,
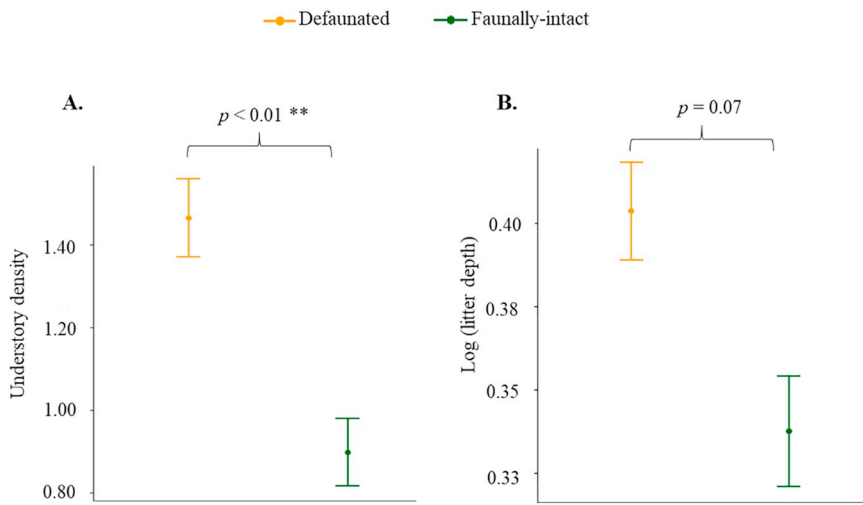
Fig. 2. (A.) Mean understory density with bars depicting ± standard error in the faunally-intact and defaunated forest; p-value taken from the negative binomial GLMM testing differences in understory vegetation density between forest defaunation statuses. Understory vegetation density measured as the number of leaves that overlapped at a given vertical point (see methods). (B.) Log-transformed mean leaf litter depth with bars depicting ± standard error in the faunally-intact and defaunated forest; p-value taken from log-transformed linear mixed model testing the difference in litter depth between defaunation statuses. (Data also displayed in box-and-whisker plots in the Supplementary material, Fig. 1.)
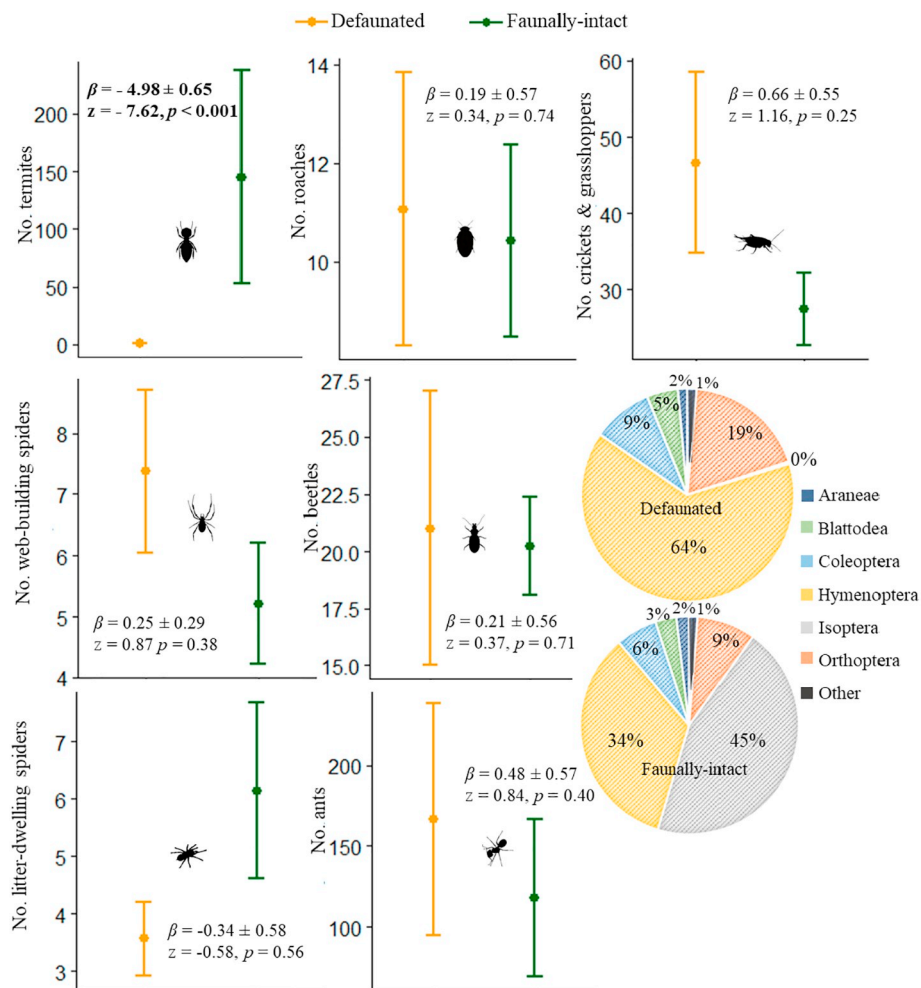

Fig. 3. Mean number of macroinvertebrates in most commonly-occurring groups collected in pitfall traps across sites in the faunally-intact and defaunated forest. Bars depict standard error ± the mean. Note different y-axis scales of invertebrate abundances. The results from our negative binomial mixed model examining the effects of defaunation on group abundances are included under the boxplots. β indicates the magnitude of the effect of defaunation on invertebrate counts, and the sign indicates the direction of the effect (negative or positive). (Data also displayed in box-and-whisker plots in the Supplementary material, Fig. 2).

unsustainable hunting is resulting in rapid loss of large herbivorous mammals (Cormier-Salem et al., 2018). In our study of the consequences of defaunation in Gabon's rainforest, we found that faunally-intact sites were associated with, on average, a 170-fold higher abundance of termites than hunted sites. This difference in termite abundance was in part predicted by higher understory vegetation density in hunted sites, which overall was also associated with marginally higher ant abundances and significantly higher web-building spider abundances. In hunted sites, the contribution of macroinvertebrates to decomposition was approximately 25% lower than in

Table 1
Output from our negative binomial GLMM examining the effects of understory vegetation density on the abundance of invertebrates captured in pitfall traps for each of the common taxonomic groups. β indicates the magnitude of effect, and the sign indicates the direction of the effect (negative or positive). Significant effects (termites) are in bold.

Response variable: counts of individuals Fixed effect: density of understory vegetation				
	β	SE	z	p
Araneae (litter-dwelling spiders)	0.45	0.50	0.90	0.37
Blattodea (roaches)	− 0.31	0.49	− 0.63	0.53
Coleoptera (beetles)	− 0.43	0.50	− 0.85	0.39
Hymenoptera (ants)	0.81	0.47	1.73	0.08
Isoptera (termites)	**− 2.85**	**0.67**	**− 4.24**	**< 0.001**
Orthoptera (crickets, grasshoppers)	− 0.10	0.49	− 0.20	0.84

Table 2
Results of the gamma GLMM model examining the effects of defaunation and treatment on the proportion of litter bags that decomposed. The model included the main effects of defaunation (hunted versus faunally-intact sites), treatment (exclosures versus controls), and their interaction. β values indicate the magnitude of effects, where negative β values indicate a decrease in decomposition in response to the covariates and positive β indicate an increase in decomposition.

Response variable: proportion of litter decomposed				
Fixed effects:	β	SE	z	p
Defaunation	0.06	0.21	0.28	0.78
Macroinvertebrate exclosure	-1.50	0.28	-5.37	< 0.001
Interaction of defaunation and macroinvertebrate exclosure	-0.73	0.34	-2.17	0.03

faunally-intact sites; however, forest defaunation status was not predictive of rates of decomposition, insectivory or seed predation/removal overall, suggesting the potential resilience of these ecosystem processes to the loss of large mammals. The dramatic differences in both vegetation structure and the populations of a naturally abundant invertebrate taxa between hunted and faunally-intact sites could suggest potentially far-reaching consequences of defaunation on a large scale, particularly for organisms sensitive to understory environmental conditions or who rely on termites for food.

4.2. Connections between defaunation, understory vegetation, and macroinvertebrates

Associations we found between forest defaunation status and understory vegetation density are consistent with findings from previous work in other systems (Harrison et al., 2013; Rosin et al., 2017). In our system, a probable driver of higher understory vegetation cover in hunted sites compared to faunally-intact sites is the substantial decline in herbivorous elephant, ape, and ungulate population numbers associated with commercial and subsistence hunting throughout the Congo–Ogooué Basin (Beirne et al., 2019; Koerner et al., 2017). Elephants and other large, herbivorous vertebrates physically shape habitat structure through the trampling, breakage, and consumption of stems and leaves, the impacts of which are strongest at the understory level (Asner and Levick, 2012; Bakker et al., 2016; Maron and Crone, 2006; Poulsen et al., 2018). Consequently, large herbivore loss may result in large scale changes in the physical structure of the understory habitat in both savanna and tropical forest systems (Asner et al., 2016; Keesing and Young, 2014; Rosin et al., 2017).

While a majority of invertebrate taxa did not show significant associations with defaunation or understory vegetation density in our study, there were two notable exceptions. The significant relationships that we detected between the density of understory vegetation with termites and web-building spiders suggest that factors affecting vegetation density might indirectly affect their abundances. The negative association we found between termite abundances and both understory vegetation density and defaunation may be driven by links between open understory and increased levels of deadwood, uprooted plant biomass, and dung in the presence of megafaunal herbivores including elephants in faunally-intact areas (Holdo and McDowell, 2004). The positive association we found between understory vegetation density and web-building spiders is consistent with studies linking understory structural diversity and density to spider diversity and abundances (Campuzano et al., 2016; Miyashita et al., 2004; Roberson et al., 2016). Despite these findings, however, our results did not indicate a significant association between vertebrate defaunation and web-building spider abundances. We posit that this could be due to diffuse associations between variables, such that indirect effects may be undetectable at the scale of our study or are overwhelmed by other important ecological factors. A deeper understanding of this interaction may be important for future studies because spiders are impactful predators (Floren et al., 2002; Nyffeler and Birkhofer, 2017; Philpott and Armbrecht, 2006; Way and Khoo, 1992), and an increase in their abundance with high understory density could have substantial implications for insectivory patterns and understory foodwebs.

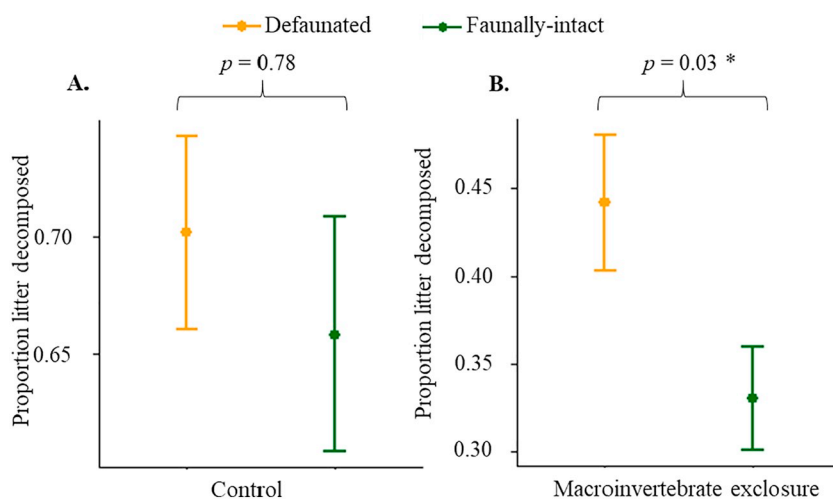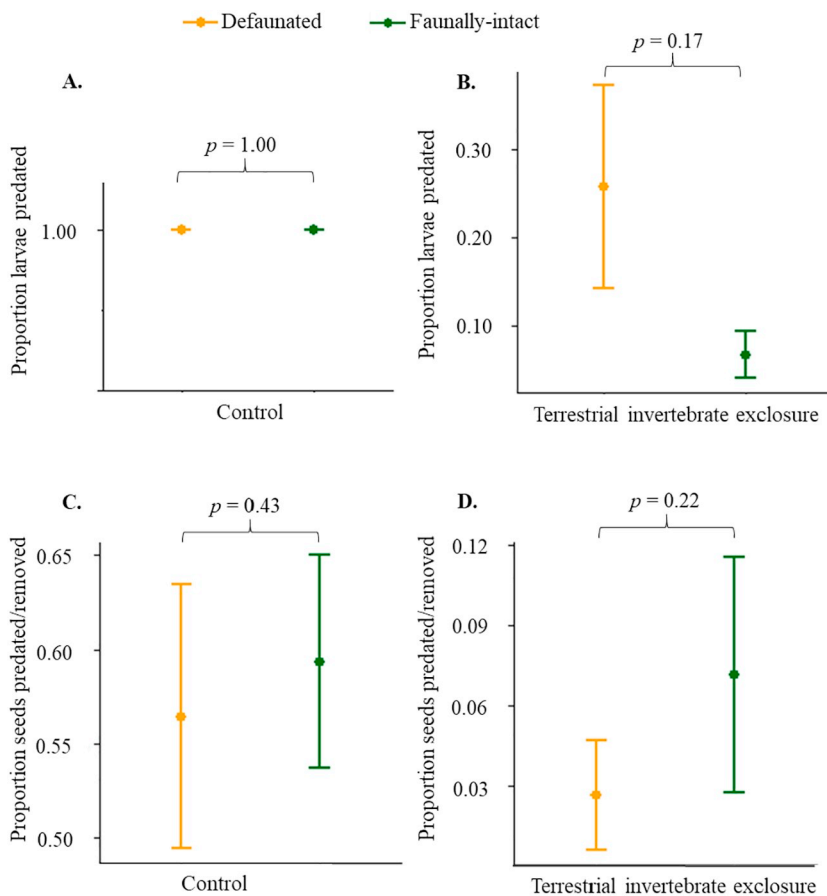The dramatically lower termite abundances in our hunted sites

Fig. 4. Mean proportion of litter decomposed in control (A.) and invertebrate exclosure (B.) treatments across sites in the faunally-intact and defaunated forest. Bars depict standard error ± the mean. *p*-values are from our Gamma mixed model examining differences in decomposition under different treatments, defaunation statuses, and the interaction between the two. (Data also displayed in box-and-whisker plots in the Supplementary material, Fig. 3).

Fig. 5. The mean proportion of larvae predated in control (A.) and invertebrate exclosure (B.) treatments across sites in the faunally-intact and defaunated forest. The mean proportion of seeds predated/removed in the control (C.) and invertebrate exclosure (D.) treatments across sites in the faunally-intact and defaunated forest. Bars depict standard error ± the mean. *p*-values shown in (A.) and (B.) are from our linear mixed model and *p*-values shown in (C.) and (D.) are from our binomial mixed model examining differences in predation under each treatment, defaunation status, and the interaction between treatment and defaunation status. (Data also displayed in box-and-whisker plots in the Supplementary material, Fig. 4).

compared to our faunally-intact sites are concerning, given that termites are among the most abundant insects in tropical terrestrial ecosystems, with a density that can reach 10,400 individuals per m² (Bignell, 2019; Eggleton et al., 1994; Eggleton and Bignell, 2000). Termites have important effects on plant decomposition, carbon flux and physical properties of the soil (Bignell, 2019) and are a key food resource for some vertebrates (Sanz et al., 2004; Tutin and Fernandez, 1983). Termites are also often considered indicator species because of their sensitivity to anthropogenic disturbances, such as changes in vegetation, habitat degradation and selective logging (Burghouts et al., 1992; Eggleton et al., 1996, 2002; Ewers et al., 2015; Nunes et al., 2017). We posit that loss of large vertebrates could precipitate termite declines as a result of less available fallen woody debris and animal dung for termites to consume (Ferrar and Watson, 1970; Holdo and McDowell, 2004; but see Lagendijk et al., 2016). Dung can be a critical resource for termites in many systems and even wood-consuming and phytophagous termite species have been found to feed on dung (Coe, 1977; Freymann et al., 2008). Supporting this potential connection, dung abundance decreased by > 2.5 times in our study region's hunted areas compared to faunally-intact areas, despite termite presence in faunally-intact sites presumably operating to remove dung (data collected by Koerner et al. (2017) and used with permission; negative binomial GLMM: $\beta = -0.83 \pm 0.28$, $z = -3.01$, $p = .0026$) (Supplementary Fig. S5). This finding indicates a large reduction in a potentially important food and nutrient resource for termites and other taxa as well.

In light of the critical roles termites play in tropical systems as ecosystem engineers and also as a key resource for animals such as chimpanzees, gorillas, and other insects (Eggleton and Bignell, 2000; Tutin and Fernandez, 1983), their declines could negatively impact a diverse suite of animals that rely on them for prey. Further research must be pursued to understand the potential connection between

termite decline and defaunation. Additionally, although our pitfall trap data indicate a decline in one important detritivorous group, termites, in response to defaunation, we note that the pitfall trapping method may be biased for some taxonomic groups and does not provide a good metric for all invertebrates in the understory that may be experiencing indirect effects following defaunation.

4.3. Ecological resilience: robust ecological processes despite lower macroinvertebrate contribution to decomposition

We did not find differences in decomposition, seed predation or insectivory between hunted and faunally-intact sites; however, excluding macroinvertebrates from our litter bags revealed a lower functional contribution of targeted invertebrate groups to decomposition in hunted habitat. This result is similar to findings by Ewers et al. (2015) which showed that logging was associated with a lower functional contribution by invertebrates despite a lack of any overall change in the ecological processes studied. We hypothesize that changes in microclimate, resource availability, and possibly increases in the activities of understory insectivorous mammal or bird communities, as a result of defaunation, may have reduced the abundance or activity of detritivorous macroinvertebrate guilds, such as termites which we found were at much lower abundances in defaunated areas, thereby reducing the effect of their functional role as decomposers.

The functional contribution of focal invertebrate groups to insectivory and seed predation/removal did not significantly change in response to defaunation. It is important to note, however, that the use of dried beetle larvae (mealworms) for our study of insectivory is likely to have primarily measured the effects of ants as insect predators and may not have captured the effect of taxa that feed only on live prey such as spiders, wasps and mantids. Experiments with live prey or an array of insect prey items may reveal different results and should be considered

for future studies. Similarly, our seed predation/removal experimental results may have been influenced by our use of peanuts as a proxy for local seeds. Because peanuts are high reward and easy to process for many vertebrate and invertebrate seed predators, we hypothesize that there was enough redundancy among taxa to maintain static rates of predation/removal regardless of potential changes in species community compositions between forest types. Experiments conducted with a lower-reward seed may yield less redundancy among taxa to maintain seed predation/removal and are worth exploring.

4.4. Conclusion

The loss of large vertebrate taxa can have complex and cascading consequences for ecosystems that we are just starting to understand. Given the unprecedented rates of defaunation occurring in tropical ecosystems worldwide, understanding these consequences is critical for ecosystem conservation and management. Africa's Congo–Ogooué Basin is the second most expansive region of tropical forest globally (Cormier-Salem et al., 2018) and within that region, Gabon is one of the last rainforest sites in the world that has maintained a diverse community of megafauna. Time is running out to understand the potential ecosystem consequences of losing this region's large terrestrial herbivores. Our study suggests that the decline of large vertebrates from a diverse rainforest ecosystem may alter understory vegetation and a multitude of species interactions, including the functional contributions of invertebrates. However, functional redundancy and compensation among the diverse taxa present in tropical forests may buffer some ecological processes from overall negative effects. Declines similar to what we detected in termite numbers could have consequences for many other taxa that utilize these animals for food, further exacerbating biodiversity declines. Research at a higher taxonomic resolution than that captured by our study would be beneficial for understanding changes in understory invertebrate communities triggered by defaunation and the potential side effects. Further work is also needed to explore changes in the relative contribution of taxa to key ecosystem processes with more resolution, as our results indicate in a broad way that changes are occurring in invertebrate functional roles in defaunated forests. Additionally, future research should also explore how understory ecological processes may change in systems with more complete defaunation and whether there is a tipping point beyond which redundancy among taxa no longer acts to buffer these important processes.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.108329.

Declaration of competing interest

All authors (Therese Lamperty, Kai Zhu, John Poulsen, Amy Dunham) declare that there are no financial and personal relationships with other people or organizations that could inappropriately influence (bias) this work.

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