

Hunting alters seedling functional trait composition in a Neotropical forest

ERIN L. KURTEN,^{1,4} S. JOSEPH WRIGHT,² AND WALTER P. CARSON³

¹*Department of Biology, Stanford University, 371 Serra Mall, Stanford, California 94305 USA*

²*Smithsonian Tropical Research Institute, Apartado 0843–03092, Balboa, República de Panamá*

³*Department of Biological Sciences, University of Pittsburgh, 4249 Fifth Avenue, Pittsburgh, Pennsylvania 15260 USA*

Abstract. Defaunation alters trophic interactions between plants and vertebrates, which may disrupt trophic cascades, thereby favoring a subset of plant species and reducing diversity. If particular functional traits characterize the favored plant species, then defaunation may alter community-wide patterns of functional trait composition. Changes in plant functional traits occurring with defaunation may help identify the species interactions affected by defaunation and the potential for other cascading effects of defaunation. We tested the hypotheses that defaunation would (1) disrupt seed dispersal, thereby favoring species whose dispersal agents are not affected (e.g., small birds, bats, and abiotic agents), (2) reduce seed predation, thereby favoring larger-seeded species, and (3) reduce herbivory, thereby favoring species with lower leaf mass per area (LMA), leaf toughness, and wood density. We examined how these six traits responded to vertebrate defaunation caused by hunters or by experimental exclosures among more than 30 000 woody seedlings in a lowland tropical moist forest. Exclosures reduced terrestrial frugivores, granivores, and herbivores, while hunters also reduced volant and arboreal frugivores and granivores. The comparison of exclosures and hunting allowed us to parse the impacts of arboreal and volant species (reduced by hunters only) and terrestrial species (reduced by both hunters and exclosures). The loss of terrestrial vertebrates alone had limited effects on plant trait composition. The additional loss of volant and arboreal vertebrates caused significant shifts in plant species composition towards communities with more species dispersed abiotically, including lianas and low wood-density tree species, and fewer species dispersed by large vertebrates. In contrast to previous studies, community seed mass did not decline significantly in hunted sites. Our exclosure results suggest this is because reducing seed predators disproportionately benefits large-seeded species, partially compensating for the reduction of seed dispersers at hunted sites. Our results demonstrate that decreased seed dispersal and seed predation are important determinants of seedling community compositional change as a consequence of defaunation. Defaunation may also negatively impact carbon storage in tropical forests, by favoring lianas and low wood density tree species.

Key words: *defaunation; dispersal; functional traits; hunting; Panama; poaching; seed predation; seedlings; tropical forest.*

INTRODUCTION

Over-hunting is causing dramatic reductions in the abundances of game species throughout the forests of tropical Africa, Asia, and the Americas and threatens many species with global extinction (Corlett 2007, Peres and Palacios 2007, Fa and Brown 2009). The loss of these species has been linked to substantial declines in plant species diversity (e.g., Dirzo and Miranda 1991, Stevenson and Aldana 2008), though this is not always observed (Roldán and Simonetti 2001, Wright et al. 2007b). Changes in plant diversity and species composition in defaunated forests might be driven by lost seed dispersers (Dirzo and Miranda 1991, Wright et al.

2007b, Nunez-Iturri et al. 2008, Stevenson and Aldana 2008, Terborgh et al. 2008, Harrison et al. 2013), seed predators (Wright et al. 2007b), or herbivores (Dirzo and Miranda 1991, Poulsen et al. 2013). However, because hunting impacts species from all of these guilds simultaneously, including primates, birds, ungulates, and large rodents (Corlett 2007, Peres and Palacios 2007, Fa and Brown 2009), these comparative studies of hunted vs. protected forests cannot identify the specific interactions or mechanisms underlying changes in plant diversity and species composition. Therefore, while the particular animal species and types of plant–animal interactions impacted by hunters are well documented, their impact on plant species composition and diversity remains speculative.

To better understand the effects of different vertebrate consumers on plant compositional change, we compare protected and heavily hunted forests and complement

Manuscript received 9 September 2014; revised 15 December 2014; accepted 19 January 2015. Corresponding Editor: T. M. Palmer.

⁴ E-mail: erinkurten@gmail.com

TABLE 1. Types of plant–vertebrate interactions impacted by hunting and by experimental exclosures and the predicted consequences for community-level plant trait composition.

Plant–vertebrate interaction and trait	Interaction impacted by		Predicted response to defaunation caused by		Varies with cause of defaunation?
	Hunting	Exclosures	Hunting	Exclosures	
Primary seed dispersal	yes	no			
Dispersal mode			↑ non-hunted agents	no change	yes
Growth Form			↑ lianas	no change	yes
Seed mass†			↓	no change	yes
Seed predation	yes	yes			
Seed mass†			↑	↑	no
Seedling herbivory	yes	yes			
Leaf toughness			↓	↓	no
Wood density			↓	↓	no
LMA			↓	↓	no

Notes: If predicted responses to hunting and exclosures differ, a statistical interaction is predicted between defaunation (control vs. defaunated) and its cause (exclosures vs. hunting). LMA, leaf mass per area.

† The net response of seed mass to defaunation depends on whether altered seed dispersal or altered seed predation has the greater impact.

this comparison with an experimental approach using fences to exclude a subset of the hunted vertebrates in protected forests. Experimental fences exclude ground-dwelling vertebrates, which include herbivores, seed predators, and secondary seed dispersers. Hunting reduces these same species, but *in addition*, reduces key primary seed dispersers including large birds, primates, and other climbing species (Wright et al. 2000). The arboreal and volant vertebrates impacted by hunters but not by fenced exclosures are implicated in observed changes if plant communities differ between hunted and protected forests, but not between exclosure and control treatments located in protected forests. In this way, our approach will, for the first time, tease apart the effects of these contrasting consumer groups on tropical forest plant communities.

Our focus is on how functional traits of plant species (*sensu* McGill et al. 2006) change when these contrasting vertebrate groups are either present or absent. Seed dispersers, seed predators, and herbivores select plants for different reasons, which are reflected by plant functional traits (Wardle et al. 2001, Wright et al. 2007b, Terborgh et al. 2008). For example, folivores select plants on the basis of leaf toughness, while frugivores and granivores do not. Thus, we focus on functional trait shifts to identify the interactions responsible for the changes in plant community composition that follow defaunation. We tested three hypotheses.

Hypothesis 1.—The loss of vertebrate seed dispersers will disfavor plant species with large seeds dispersed by game species (Table 1). The loss of primates and large birds should cause this group of plant species to decline in abundance because of intense density-dependent mortality that occurs around parent trees, loss of directed dispersal, and decreased frugivore seed han-

dling, which can enhance germination and survival (Traveset and Verdú 2002, Brodie et al. 2009, Comita et al. 2010, Heer et al. 2010, Mangan et al. 2010, Swamy et al. 2011, de Barros Leite et al. 2012). A corollary of our first hypothesis is that lianas should increase in importance where large-bodied dispersers are reduced (Table 1). While the growth form of a species does not influence its palatability to frugivores per se, trees tend to have biotic dispersal agents and lianas tend to have abiotic dispersal agents in Panama and throughout the Neotropics (Gentry 1983, Muller-Landau and Hardesty 2005).

Hypothesis 2.—The loss of vertebrate seed predators will favor plant species with large seeds that are consumed by game species (Table 1). Our first and second hypotheses will often have conflicting effects because the seeds dispersed by game species are often also consumed by other game species. The net effect of the loss of both dispersers and seed predators varies among studies that compare hunted and protected forests. For example, species with large seeds are more abundant in hunted forests in Panama (Wright et al. 2007b), but less abundant in hunted forests in Peru and Colombia (Nunez-Iturri et al. 2008, Stevenson and Aldana 2008, Terborgh et al. 2008). Our approach, which contrasts results from experimental exclosures with results from a comparison of hunted and protected forests, will allow us to evaluate the effects of the loss of terrestrial seed predators in the presence and absence of arboreal and volant seed dispersers.

Hypothesis 3.—The loss of vertebrate herbivores will favor species with traits associated with increased palatability or low tolerance of herbivory, specifically low leaf mass per unit area (LMA), low leaf toughness, and low wood density (Wardle et al. 2002, Alvarez-Clare and Kitajima 2009) (Table 1). If herbivory is an

important driver of species composition, then these trait changes should occur both where herbivores have been nearly extirpated by hunting as well as inside exclosures (Table 1).

METHODS

Study sites.—The Barro Colorado National Monument (BCNM; 9°10' N, 79°51' W) is a 59-km² preserve comprised of islands and mainland peninsulas located in Lake Gatun in Panama. Leigh (1999) describes its biota, climate, and geology. Hunting is prohibited and regular patrols by game wardens have dramatically reduced the incidence of poaching (Wright et al. 2000, 2007b). The Parque Nacional Soberanía (PNS) is a 225-km² preserve that is contiguous with the BCNM, but it is not actively patrolled.

The intensity of poaching is much greater throughout the PNS than within the BCNM. Sign of hunters encountered was approximately five times greater in the PNS than in the BCNM (Wright et al. 2000). Several commonly hunted mammals have densities in the PNS that are 52–77% lower than their densities within the BCNM, including howler monkeys (*Alouatta palliata*), white-face capuchin monkeys (*Cebus capucinus*), peccaries (*Tayassu tajacu*), brocket deer (*Mazama americana*), and agoutis (*Dasyprocta punctata*) (Wright et al. 2000). Other game species occurring within the BCNM have been locally extirpated from PNS, including spider monkeys (*Ateles geoffroyi*), tapir (*Tapirus bairdii*), and Crested Guan (*Penelope purpurascens*) (Wright et al. 2000). White-lipped peccary (*Tayassu pecari*) is the only game species that has been extirpated from both the BCNM and PNS.

Experimental design.—Between late 1993 and mid 1994, eight fenced, exclosure plots were constructed and paired with eight open, control plots within the BCNM (Appendix A: Fig. A1) (Royo and Carson 2005). Each plot is 30 × 45 m in size. Fences were of 12.7-cm mesh galvanized steel fencing 2.2 m tall and buried 0.25 m deep. An additional 1.3-cm mesh surrounded the lower 70 cm and also extended 0.25 m below ground. Twenty-eight 0.5 × 0.5 m subplots were established in each of the 16 plots in a stratified random fashion to census seedlings. To avoid fence effects, subplots were at least 5 m from plot edges. Within each subplot, all woody plants less than 50 cm in height were tagged, measured, and identified in 2006.

Exclosure effectiveness.—We assessed differences in the animal communities between open and exclosure treatments using Reconyx RC-55 infrared cameras (Reconyx, Holmen, Wisconsin, USA) between August and October 2008. Each plot was monitored at six to seven locations, for a total of 41 camera trap days per plot. A camera trigger was counted as a new “visit” if (1) it was a different species than the prior trigger, or (2) if 60 minutes had elapsed between triggers (di Bitetti et al. 2008). We chose this method of quantification because unmarked individuals of most vertebrates in this

community cannot be distinguished by photograph, and because this measure of activity likely describes local animal impact on each plot more accurately than an abundance estimate. Because it was difficult to count individuals for social animals such as peccaries (*T. tajacu*) and coatis (*Nasua narica*), activity by these species was analyzed as the number of visits by social groups rather than visits by individuals.

Plant censuses at hunted vs. protected sites.—At nine protected sites (BCNM) and 11 intensely hunted sites (PNS; Appendix A: Fig. A1), all trees larger than 20 cm diameter at breast height (dbh) within a 1-ha plot were mapped and identified (Wright et al. 2007b). Between June and December 2004, all woody plants less than 50 cm tall were censused in a central 8 × 8 m subplot (Wright et al. 2007b).

Plant traits.—Data on dispersal agents have been assembled from published studies and long-term personal observations by Wright and colleagues (Muller-Landau and Hardesty 2005, Wright et al. 2007b). Woody species were assigned to one of three seed dispersal modes: hunted, non-hunted, or mixed. The hunted dispersal mode included species dispersed by large birds (≥300 g body mass) and non-volant mammals (≥3 kg body mass). The non-hunted dispersal mode included species dispersed by small birds (<300 g body mass), bats, small rodents (≤1 kg body mass), and abiotically (wind, explosive, water). The mixed dispersal mode included species dispersed by animals from both the hunted and non-hunted categories (Wright et al. 2007b).

Wright et al. (2010) determined dry seed mass, leaf mass per area (LMA), laminar toughness (Westbrook et al. 2011), and wood density for species in central Panama. Here, dry seed mass equals endosperm plus embryo mass after oven drying to constant mass at 60°C. Leaf mass per unit area equals the mass of a leaf disc after oven drying to constant mass at 60°C divided by the area of the disc. Laminar fracture toughness equals the energy necessary to cut through the lamina (excluding the midvein) normalized by the area cut or the product of the length of the cut and the thickness of the lamina (Lucas 2000). All leaf measurements were for shade leaves because two thirds of the free-standing woody species in our site are shrubs and treelets that never reach the forest canopy and therefore lack sun-exposed leaves (King et al. 2006). Wood density equaled mass after drying at 100°C divided by fresh volume determined by water displacement. Appendix B: Table B1 summarizes the number of individuals and species for which trait data was available.

Statistical analyses.—We used a MANOVA to evaluate the effect of the fenced exclosures for the activity levels of vertebrate species. We used linear models (LMs) and generalized linear models (GLMs) with one main effect (control vs. defaunated) to evaluate trait differences between hunted vs. protected sites. We used mixed effects models, with one fixed effect (control



PLATE 1. Camera traps captured a variety of animals in the experimental plots including (A) ocelots, (B) brocket deer, (C) collared peccaries, and (D) spiny rats. Camera trap images provided by E. L. Kurten.

vs. defaunated) and one random effect (plot pair), to evaluate trait differences in the enclosure experiment. To determine whether trait responses to enclosure and hunting were statistically significantly different, we next performed an analysis of the enclosure experiment and hunting comparison together. These LMs and GLMs included two main effects and their interaction. The main effects were defaunation (control vs. defaunated) and cause of defaunation (enclosures vs. hunting). Because the results were very similar when the enclosure experiment and hunting comparison were analyzed separately or together, we focus on the results from the combined analyses in the main text for most traits. We also provide the results of the separate analyses (Appendix B: Table B10), but report these results in the main text only for one case, in which the results differed qualitatively from the combined analyses (i.e., a significant vs. nonsignificant effect).

Response variables were the number of seedlings of two growth forms (free-standing vs. climbing) or three seed-dispersal modes (hunted, non-hunted, and mixed) out of the total number of seedlings, and plot mean trait values of the four continuous traits. Growth form and dispersal mode responses were analyzed with binomial error distributions; continuous functional trait responses were analyzed with normal error distributions. Where interaction terms were significant, Tukey HSD and

pairwise GLM tests were used to conduct multiple comparisons for normally and binomially distributed variables, respectively. The proportional representation of liana and tree growth forms sums to one; therefore the results for the two growth forms are equivalent, and we only report the analysis for climbing species. We report the statistical tests for the three dispersal groups, but note that their relative abundances are likewise not independent.

Where responses to enclosures and hunting were significantly different from expectation (Table 1), we examine post-hoc whether these differences may be knock-on effects of altered seed dispersal. Specifically, we used ANOVAs, followed by Tukey HSD post-hoc tests, to test whether species with different dispersal agents differed significantly in seed mass and wood density. Seed dry mass and laminar toughness were not normally distributed and were log-transformed for all analyses. Statistical analyses were performed with R version 2.15.2 (R Development Core Team 2011).

RESULTS

Seedling censuses.—We censused 20 231 seedlings comprising 279 species in our survey of heavily poached vs. protected sites. We censused 12 075 seedlings comprising 249 species in the enclosure experiment.

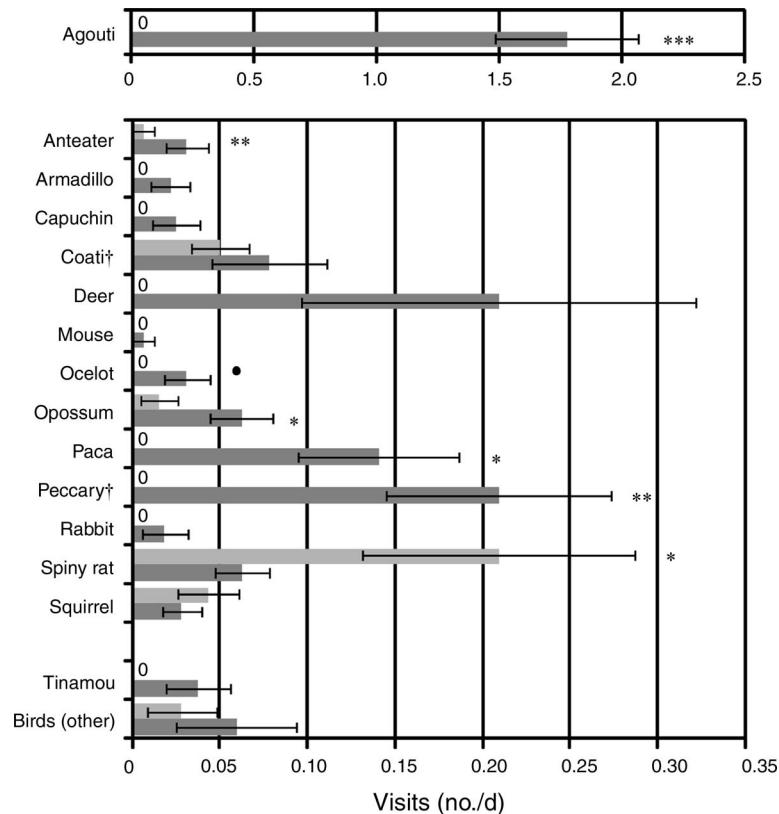


FIG. 1. Visits per day (mean \pm SE) for control plots (dark gray) and exclusion plots (light gray). Cameras were operated for 41 days in each of 16 plots. Zeros denote no individuals observed in exclusions.

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; • $P < 0.1$; † groups, not individuals.

Exclusion effectiveness.—Fenced plots excluded non-climbing, terrestrial granivores and herbivores, including agoutis (*D. punctata*), pacas (*Agouti paca*), deer (*M. americana* and *O. virginianus*), and peccaries (*T. tajacu*) (Fig. 1; see Plate 1). Most climbing animals and birds were undeterred by the exclusion treatment (Fig. 1). Tinamous (*Tinamus major*), which are seed predators (Erard et al. 1991), did not occur in the exclusions, but the decrease relative to control plots was not significant (Fig. 1). Only spiny rats (*Proechimys semispinosus*) showed significantly higher activity in exclusions vs. controls.

Dispersal mode.—The response of seed dispersal traits to vertebrate exclusion contrasted sharply with their response to hunting (Fig. 2; Appendix B: Tables B2–B4, B10). The relative abundance of plant species with seeds dispersed by game species increased by 14% inside fenced exclusions (Fig. 2A) and decreased by 30% with hunting (Fig. 2B; two-way interaction, $P < 0.001$; Tables B2 and B10). The relative abundance of plant species with seeds dispersed by non-hunted dispersal agents (e.g., small birds, bats, wind, explosion) decreased by 24% inside fenced exclusions (Fig. 2E) and increased by 67% with hunting (Fig. 2F; two-way interaction, $P < 0.001$; Tables B4 and B10). The relative abundance of plant species with seeds dispersed by game and non-game

species increased by 21% and by 8% inside fenced exclusions and with hunting, respectively (Fig. 2C and 2D; two-way interaction, $P < 0.001$; Tables B3 and B10).

Life forms.—Trees and lianas had significantly different associations with seed dispersal agents ($\chi^2 = 58.1$, $df = 2$, $P < 0.001$). Nearly one-third of tree species, but only a small fraction of liana species, were dispersed exclusively by game animals (hunted dispersal agents; Table 2). The relative abundance of lianas decreased by 26% inside fenced exclusions (Fig. 3A) and increased by 89% with hunting (Fig. 3B; two-way interaction, $P < 0.001$; Tables B5 and B10).

Seed mass, wood density, and leaf traits.—Community mean seed mass increased by 47% inside fenced exclusions (Fig. 4A) and decreased by 11% with hunting (Fig. 4B). Analyzed separately, the exclusion experiment caused a significant increase in seed mass ($P < 0.001$, Table B10), while the effect of hunting was not significant ($P = 0.69$, Table B10). However, when analyzed together, seed mass responses to exclusions and hunting were not significantly different (two-way interaction, $P = 0.156$, Table B6).

Community mean wood density did not change significantly in fenced exclusions (Fig. 4C), but decreased by 6% with hunting (Fig. 4D; two-way

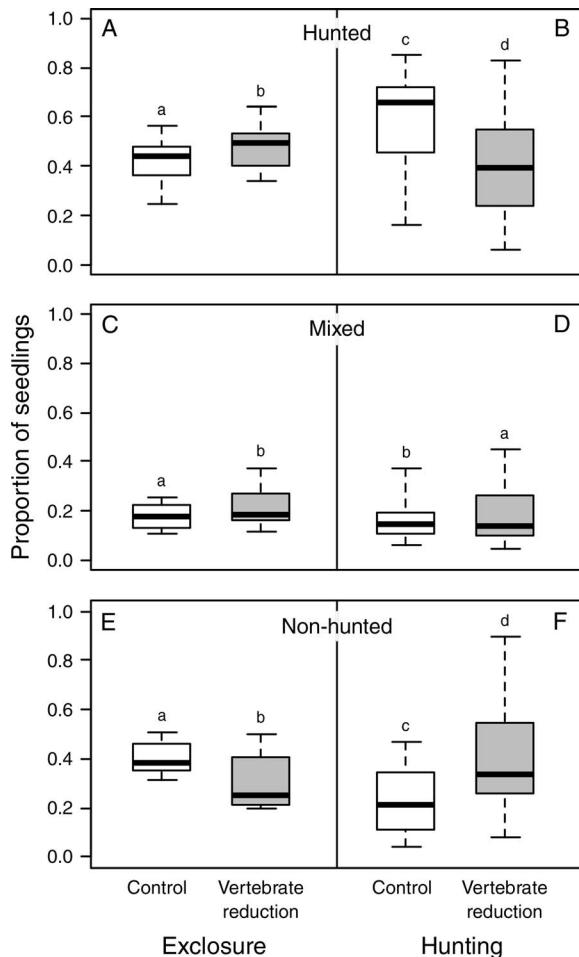


FIG. 2. Changes in the proportion of seedlings characterized by different seed dispersal agents in response to vertebrate reduction caused by exclosures (left) and hunting (right). (A, B) Seeds dispersed by large frugivores that are hunted, (C, D) seeds dispersed by both hunted and non-hunted frugivores, and (E, F) seeds only dispersed abiotically or by small frugivores that are not hunted. The heavy horizontal lines represent medians, boxes represent first and third quartiles, and whiskers represent extreme values. Lower-case letters distinguish groups that are significantly different from one another ($P < 0.05$), where a two-way analysis of exclosure and hunting data together identified a significant interaction between main effects.

TABLE 2. Percentage of tree and liana species that have hunted dispersal agents, non-hunted dispersal agents, or both types of dispersal agents (mixed).

Agents	Trees (%)	Lianas (%)
Hunted	35.2	7.5
Mixed	40.4	14.9
Non-hunted	24.4	77.6

Note: Trees ($N = 176$ species) and lianas ($N = 67$ species) had significant associations with different types of dispersal agents ($\chi^2 = 58.1$, $df = 2$, $P < 0.001$).

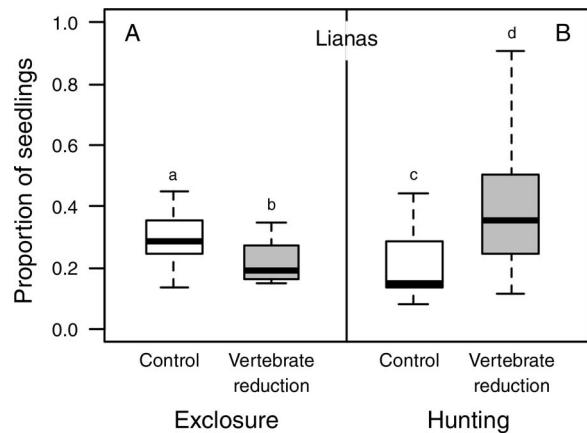


FIG. 3. Changes in the proportion of woody seedlings comprised of lianas in response to vertebrate reduction caused by (A) exclosures and (B) hunting. The caption to Fig. 2 explains the bar-and-whisker plots and lower case letters.

interaction, $P = 0.005$; Tables B7 and B10). Community mean leaf traits (LMA and laminar toughness) did not change significantly in response to exclosures or hunting (Fig. 4E–H; Tables B8–B10).

Correlated trait responses.—Changes in plant species composition with respect to seed dispersal modes and wood density associated with exclosures and hunting differed from our predictions (Table 1). We examined post-hoc whether correlated trait responses, or shifts in one trait producing shifts in a correlated trait, might have contributed to these outcomes. Species with non-hunted dispersal agents had significantly lower mean wood density than either species with hunted dispersal agents or species dispersed by a mix of hunted and non-hunted agents (Fig. 5A, $F_{2,214} = 7.328$, $P = 0.001$). In particular, wind-dispersed species had significantly lower mean wood density than species dispersed by mammals and large birds (Fig. 5B, $F_{6,348} = 3.393$, $P = 0.003$). Similarly, species with hunted dispersal agents had significantly higher mean seed mass than either species with non-hunted dispersal agents, or species dispersed by both hunted and non-hunted agents (Fig. 5C, $F_{2,164} = 12.82$, $P < 0.001$). In particular, wind-dispersed species and species dispersed by small birds had significantly lower seed mass compared to species dispersed by mammals and large birds (Fig. 5D, $F_{6,265} = 9.511$, $P < 0.002$).

DISCUSSION

Defaunation has been linked to major declines in woody species diversity. The underlying causes for these declines have been elusive because defaunation causes the simultaneous loss of seed dispersers, seed predators, and herbivores. Consequently, the degree to which these different interactions drive compositional changes and diversity declines remains poorly understood. Here we demonstrate that defaunation elicits a multitude of changes in the functional trait composi-

tion of the seedling layer in a tropical forest. Both arboreal and terrestrial animal species contribute to these changes, but in different ways. Our results strongly suggest that losses of arboreal seed dispersers cause large shifts in the functional trait composition of the seedling community. These effects are further modified by the loss of seed predators. We also provide the strongest support to date for a novel mechanism for the increase in lianas in Neotropical forests, namely that the defaunation of seed dispersers favors plant species with non-game and abiotic dispersal agents (Wright et al. 2007b).

Vertebrate herbivory did not have a strong impact on seedling community composition. Neither LMA nor leaf toughness showed any response to hunting or vertebrate exclosures (Fig. 4E–H). Mean wood density at hunted sites was significantly lower than at protected sites (Fig. 4D), and this was true even when lianas were excluded from the analysis (Appendix B: Fig. B1). However, exclosures had no significant effect on wood density (Fig. 4C), which is unexpected if vertebrate herbivores control wood density responses. We believe the significant difference in wood density between hunted and protected sites (Fig. 4D) is an indirect effect of defaunation.

We distinguish direct effects of defaunation, which involve plant traits selected actively by animals, from indirect effects, which involve plant traits *associated* with those traits selected actively by animals. The defaunation responses that we interpret as indirect effects depend on associations of other traits with seed dispersal modes. For example, wood density is significantly lower among species whose seeds are dispersed by wind than species dispersed by large birds and mammals (Fig. 5B). Where hunters removed large frugivores, the relative abundance of plants with seeds dispersed only by large birds and mammals fell significantly (Fig. 2B), and the relative abundance of plants with wind-dispersed seeds rose from 9% of seedlings to 31% of seedlings (data not shown, but see Fig. 2F). This shift in representation of species with different dispersal modes is sufficient to explain the entire decrease in mean wood density (Fig. 4D), and also accounts for the lack of a decline in wood density in exclosures (Fig. 4C). We conclude defaunation affects mean wood density indirectly through effects mediated by dispersal mode.

We also observed offsetting effects of defaunation, which can occur when different animals select different plant traits, with opposing effects on plant functional trait composition. For example, large granivores select large seeds (Dirzo et al. 2007, Mendoza and Dirzo 2007) while large frugivores select large fruits, which tend to have large seeds (Wright et al. 2007a). Hunters remove large frugivores that disperse large seeds and large granivores that kill those same large seeds. Comparisons of hunted and protected forests show the net effect of reducing both these groups for community seed mass. In contrast, our exclosures removed terrestrial granivores,

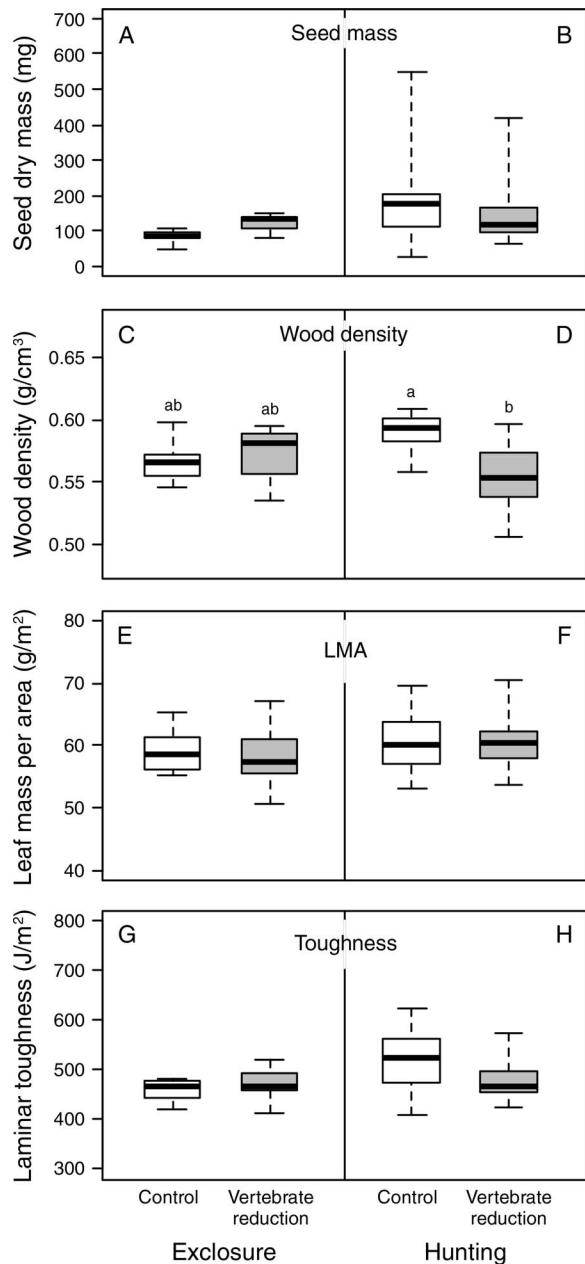


FIG. 4. Responses of community mean (A, B) seed mass, (C, D) wood density, (E, F) leaf mass per area (LMA), and (G, H) leaf toughness to vertebrate reduction caused by exclosures (left) and hunting (right). The caption to Fig. 2 explains the bar-and-whisker plots, and the lower case letters in panels (C) and (D).

but had no effect on arboreal frugivores responsible for primary seed dispersal (Fig. 1). Inside exclosures, mean seed mass increased by 47%, demonstrating the negative impact of those terrestrial granivores (Fig. 4A). The relative abundance of species dispersed by hunted frugivores also increased significantly inside exclosures (Fig. 2A), which we interpret as an indirect effect of missing granivores. In contrast, in our comparison of

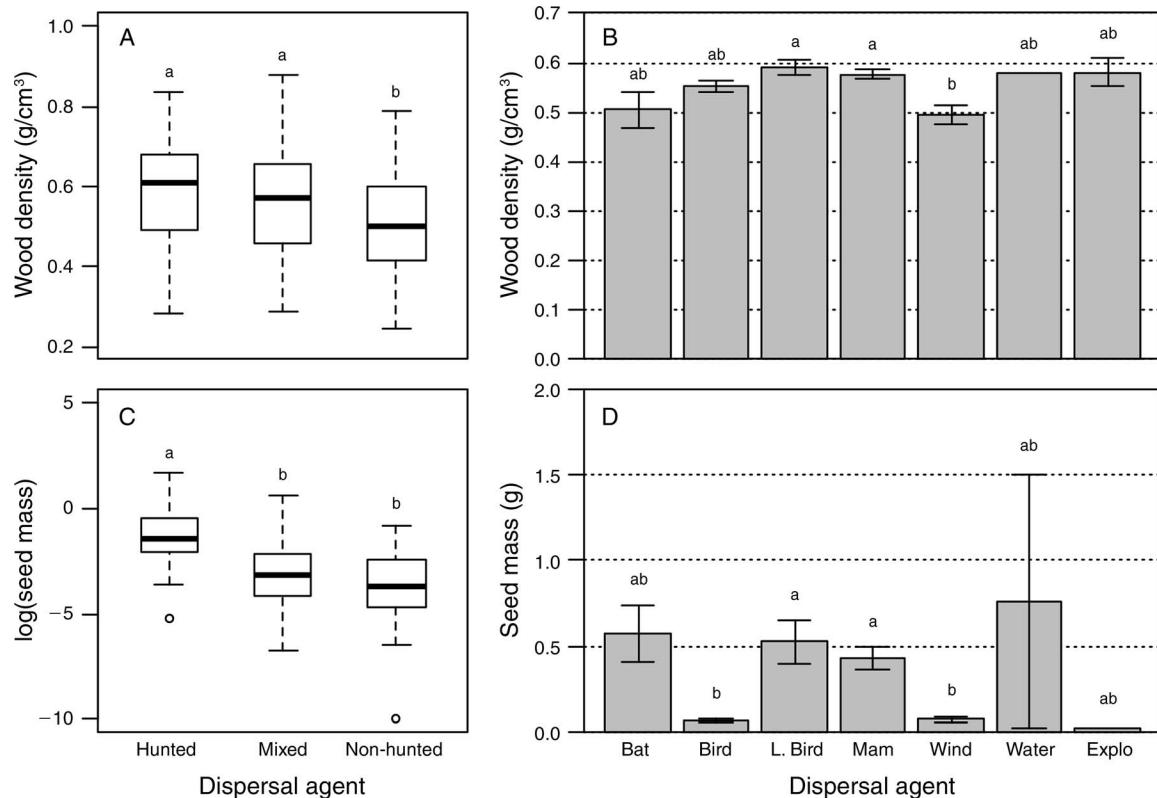


FIG. 5. Species with non-hunted seed dispersal agents have (A) lower wood densities, while those with hunted dispersal agents have (C) higher seed masses (measured in grams). Wind-dispersed species have significantly lower (B) wood density and (D) seed mass than both mammal-dispersed and large-bird-dispersed species. Bars with the same lower case letters were not significantly different ($P < 0.05$) in Tukey post hoc comparisons. Components of box-and-whisker plots in panels (A) and (C) are as in Fig. 2. Bars in panels (B) and (D) are means and error bars represent standard errors. Abbreviations are L. Bird, large bird; Mam, mammal; Explo, explosive.

hunted and protected forests, hunting was associated with a highly significant reduction in the relative abundance of seedlings with frugivore-dispersed seeds (Fig. 2B), but there was no corresponding effect on seed mass (Fig. 4B). We believe this reflects the compensatory effects of missing granivores. The loss of large frugivores is generally thought to disfavor large-seeded plant species (Nunez-Iturri et al. 2008, Stevenson and Aldana 2008, Terborgh et al. 2008). The impact of the loss of large frugivores for plant community composition might be even larger than is generally appreciated because comparisons of hunted and protected forests can only document the net effect of missing frugivores and granivores.

The strong shift in growth form composition between hunted and protected forests (Fig. 3B) represents another indirect effect of hunting associated with dispersal mode. Large frugivores seek large fruits, regardless of whether they grow on trees or lianas. However, the fruits that these frugivores prefer are strongly associated with trees, and rarely occur among lianas in the Neotropics (Gentry 1983, Muller-Landau and Hardesty 2005). Where hunters removed large frugivores, the relative abundance of plants with seeds

dispersed by large frugivores fell by 30% (Fig. 2B), and the relative abundance of plants with seeds dispersed abiotically and by smaller, non-game frugivores increased (Fig. 2F). The latter increase included an 89% increase among lianas (Fig. 3B). The enclosure experiment reinforces the interpretation that primary seed dispersal drives the increase among lianas in hunted forests. The enclosures mimicked the negative impact of hunters on terrestrial vertebrates (c.f. Fig. 1 and Wright et al. 2000), but had no effect on the arboreal frugivores that disperse large seeds and fruits. Lianas actually decreased in importance inside the enclosures (Fig. 3A).

One concern regarding the enclosures is that climbing vertebrates were not excluded. The higher spiny rat activity observed inside enclosures (Fig. 1) may have resulted from decreased competition (Fig. 1), increased vegetation cover, or fewer predators, in particular ocelots (Fig. 1). Regardless of the cause, one may ask whether spiny rats in enclosures may have compensated for the removal of other seedling predators, leading to the lack of differences in wood density and leaf traits in the enclosure experiment. Spiny rats alone *can* achieve seedling predation rates similar to those of a more diverse community of vertebrate herbivores (Asquith et

al. 1997). However, this has only been documented where their densities were 11-fold higher (Adler 1996) than those on Barro Colorado Island (Glanz 1990), among the highest spiny rat densities ever recorded. In contrast, spiny rat activity in our exclosures only increased 3.4-fold (Fig. 1). Moreover, final seedling densities were 38% greater in exclosure plots relative to control plots (Kurten and Carson, *in press*), an increase that would not be expected if spiny rats were fully compensating for other herbivores.

Our study results would have been strengthened by replicating our forest comparison over multiple hunted and protected reserves. However, as is the case in most comparative studies of defaunation, such replication was not logistically feasible, in the absence of other protected forests in the area. Nevertheless, the high replication and spatial extent of our sampling (over a 100-km² area in PNS, and over a 50-km² area in the BCNM) is greater than in most studies of the indirect impact of hunting on plants, and ensures that the differences observed represent true differences between the hunted and protected areas (Fig. A1).

Overall, our results offer strong support to previous studies that concluded that the loss of dispersers were key to declines of certain plant species (Nunez-Iturri et al. 2008, Stevenson and Aldana 2008, Terborgh et al. 2008, Harrison et al. 2013), but which could not distinguish between the loss of seed predators vs. dispersers as we have done here.

Implications.—Defaunation might reduce forest carbon sequestration. In particular, the loss of large-bodied seed dispersers has the potential to alter the ability of forests to store carbon by (1) decreasing the abundance of trees relative to lianas (Fig. 3B) and (2) shifting the tree community toward lower wood density species (Fig. 4D). If changes in carbon sequestration were proportional to the decrease in community mean wood density in the tree seedling community alone (5.6%; Fig. B1), this would translate to a 17 Mg/ha decrease in aboveground biomass at our site. Increased competition from lianas would likely cause further declines in biomass (Wright et al. 2007b, Schnitzer and Carson 2010). Our results complement an African study, which found that 35 years of hunting led to a 8–9% decrease in community mean wood density and a loss of 57 Mg/ha in above ground biomass, relative to protected forests (Poulsen et al. 2013). That study, which focused on larger trees (>10 cm dbh), suggests that the changes we documented in the seedling layer are unlikely to attenuate as seedlings mature. If the changes in carbon storage potential represented here are as widespread as over-hunting itself, the potential global impact will be great.

ACKNOWLEDGMENTS

We extend our gratitude to the Autoridad Nacional del Ambiente (ANAM) for permitting us to conduct research within the Parque Nacional Soberanía. D. Brassfield, D. Ureña, and J. Balbuena conducted the seedling censuses in the hunting

comparison. A competitive research grant from the Smithsonian Tropical Research Institute to S. J. Wright funded seedling censuses in hunted and protected forests. Comments from D. Ackerly, R. Dirzo, and two anonymous reviewers improved the manuscript. NSF grants DEB-9527729 and DEB-0212054 to WPC funded the exclosure experiment. NSF DEB-0808338, the Theresa Heinz Environmental Scholars program, and the STRI short-term fellowship program provided support to E. L. Kurten.

LITERATURE CITED

- Adler, G. H. 1996. The island syndrome in isolated populations of a tropical forest rodent. *Oecologia* 108:694–700.
- Alvarez-Clare, S., and K. Kitajima. 2009. Susceptibility of tree seedlings to biotic and abiotic hazards in the understory of a moist tropical forest in Panama. *Biotropica* 41:47–56.
- Asquith, N. M., S. J. Wright, and M. J. Clauss. 1997. Does mammal community composition control recruitment in Neotropical forests? Evidence from Panama. *Ecology* 78: 941–946.
- Brodie, J. F., O. E. Helmy, W. Y. Brockelman, and J. L. Maron. 2009. Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecological Applications* 19:854–863.
- Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329:330–332.
- Corlett, R. T. 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica* 39:292–303.
- de Barros Leite, A., P. H. S. Brancalion, R. Guevara, and M. Galetti. 2012. Differential seed germination of a keystone palm (*Euterpe edulis*) dispersed by avian frugivores. *Journal of Tropical Ecology* 28:615–618.
- di Bitetti, M. S., C. A. Ferrari, C. de Angelo, and Y. di Blanco. 2008. Differential responses to hunting in two sympatric species of brocket deer (*Mazama americana* and *M. nana*). *Biotropica* 40:636–645.
- Dirzo, R., E. Mendoza, and P. Ortiz. 2007. Size-related differential seed predation in a heavily defaunated Neotropical rain forest. *Biotropica* 39:355–362.
- Dirzo, R., and A. Miranda. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. Pages 273–287 in P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, editors. *Plant–animal interactions: evolutionary ecology in tropical and temperate regions*. John Wiley & Sons, New York, New York, USA.
- Erard, E., M. Théry, and D. Sabatier. 1991. Régime alimentaire de *Tinamus major* (Tinamidae), *Crax alector* (Cracidae) et *Psophia crepitans* (Psophiidae), en Forêt Guyanaise. *Gibier Faune Sauvage* 8:183–210.
- Fa, J. E., and D. Brown. 2009. Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. *Mammal Review* 39:231–264.
- Gentry, A. H. 1983. Dispersal ecology and diversity in Neotropical forest communities. Pages 303–314 in K. Kubitzki, editor. *Dispersal and distribution: an international symposium*. Paul Parey, Hamburg, Germany.
- Glanz, W. E. 1990. Neotropical mammal densities: How unusual is the community on Barro Colorado Island, Panama? Pages 287–313 in A. H. Gentry, editor. *Four Neotropical rainforests*. Yale University Press, New Haven, Connecticut, USA.
- Harrison, R. D., S. Tan, J. B. Plotkin, F. Slik, M. Detto, T. Brenes, A. Itoh, and S. J. Davies. 2013. Consequences of defaunation for a tropical tree community. *Ecology Letters* 16:687–694.

- Heer, K., L. Albrecht, and E. K. V. Kalko. 2010. Effects of ingestion by neotropical bats on germination parameters of native free-standing and strangler figs (*Ficus* sp., Moraceae). *Oecologia* 163:425–435.
- King, D., S. J. Wright, and J. H. Connell. 2006. The distribution of maximum tree heights in tropical vs. temperate forests: cause or consequence of tropical diversity? *Journal of Tropical Ecology* 22:11–24.
- Kurten, E. L. and W. P. Carson. *In press*. Do ground-dwelling vertebrates promote diversity in a Neotropical forest? Results from a long-term experiment. *BioScience*.
- Leigh, E. G. 1999. *Tropical forest ecology: a view from Barro Colorado Island*. Oxford University Press, New York, New York, USA.
- Lucas, P. 2000. Mechanical defences to herbivory. *Annals of Botany* 86:913–920.
- Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever. 2010. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* 466:752–755.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21:178–185.
- Mendoza, E., and R. Dirzo. 2007. Seed-size variation determines interspecific differential predation by mammals in a neotropical rain forest. *Oikos* 116:1841–1852.
- Muller-Landau, H. C., and B. D. Hardesty. 2005. Seed dispersal of woody plants in tropical forests: concepts, examples, and future directions. Pages 267–309 in D. F. R. P. Burslem, M. A. Pinard, and S. E. Hartley, editors. *Biotic interactions in the tropics: their role in the maintenance of species diversity*. Cambridge University Press, New York, New York, USA.
- Nunez-Iturri, G., O. Olsson, and H. F. Howe. 2008. Hunting reduces recruitment of primate-dispersed trees in Amazonian Peru. *Biological Conservation* 141:1536–1546.
- Peres, C. A., and E. Palacios. 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. *Biotropica* 39:304–315.
- Poulsen, J. R., C. J. Clark, and T. M. Palmer. 2013. Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. *Biological Conservation* 163:122–130.
- R Development Core Team. 2011. *R: a language and environment for statistical computing*. R Project for Statistical Computing, Vienna, Austria. www.r-project.org
- Roldán, A. I., and J. A. Simonetti. 2001. Plant-mammal interactions in tropical Bolivian forests with different hunting pressures. *Conservation Biology* 15:617–623.
- Royo, A. A., and W. P. Carson. 2005. The herb community of a tropical forest in central Panamá: dynamics and impact of mammalian herbivores. *Oecologia* 145:66–75.
- Schnitzer, S. A., and W. P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology Letters* 13:849–857.
- Stevenson, P. R., and A. M. Aldana. 2008. Potential effects of ateline extinction and forest fragmentation on plant diversity and composition in the Western Orinoco Basin, Colombia. *International Journal of Primatology* 29:365–377.
- Swamy, V., J. Terborgh, K. G. Dexter, B. D. Best, P. Alvarez, and F. Cornejo. 2011. Are all seeds equal? Spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest. *Ecology Letters* 14:195–201.
- Terborgh, J., G. Nuñez-Iturri, N. C. A. Pitman, F. H. Cornejo Valverde, P. Alvarez, V. Swamy, E. G. Pringle, and C. E. T. Paine. 2008. Tree recruitment in an empty forest. *Ecology* 89:1757–1768.
- Traveset, A., and M. Verdú. 2002. A meta-analysis of the effect of gut treatment on seed germination. Pages 339–530 in D. J. Levey, W. R. Silva, and M. Galetti, editors. *Seed dispersal and frugivory: ecology, evolution, and conservation*. CAB International, Oxford, UK.
- Wardle, D. A., G. M. Barker, G. W. Yeates, K. I. Bonner, and A. Ghani. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecological Monographs* 71:587–614.
- Wardle, D. A., K. I. Bonner, and G. M. Barker. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology* 16:585–595.
- Westbrook, J., K. Kitajima, J. Burleigh, W. Kress, D. Erickson, and S. J. Wright. 2011. What makes a leaf tough? Patterns of correlated evolution between leaf toughness traits and demographic rates among 197 shade-tolerant woody species in a neotropical forest. *American Naturalist* 177:800–811.
- Wright, I. J., et al. 2007a. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99:1003–1015.
- Wright, S. J., A. Hernández, and R. Condit. 2007b. The bushmeat harvest alters seedling banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica* 39:363–371.
- Wright, S. J., et al. 2010. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* 91:3664–3674.
- Wright, S. J., H. Zeballos, I. Domínguez, M. M. Gallardo, M. C. Moreno, and R. Ibáñez. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology* 14:227–239.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-1735.1.sm>