

Do Ground-Dwelling Vertebrates Promote Diversity in a Neotropical Forest? Results from a Long-Term Exclosure Experiment

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Using a decade-long exclosure experiment in Panama, we tested the hypothesis that ground-dwelling vertebrate herbivores and seed predators are crucial determinants of tropical tree diversity and abundance within the understory. Our exclosure experiment is a community-level test of the Janzen–Connell hypothesis. Therefore, we predicted that vertebrate exclusion would (a) increase plant densities and (b) lower richness, diversity, and evenness. Excluding vertebrates caused a 38%–46% increase in plant densities, which, in contrast to our predictions, caused species richness to increase by 12%–15%. Because vertebrate exclusion causes plant species richness to increase, not decrease, vertebrates are unlikely to be causal agents of Janzen–Connell effects. We synthesized this and previous studies to explore why plant richness responds differently to defaunation and exclosures in tropical forests worldwide. Likely because of their contrasting effects on mesoconsumers, defaunation and exclosures cause decreases and increases in plant density respectively, which in turn cause corresponding changes in richness.

Keywords: defaunation, plant diversity, herbivory, seed predation, tropical forest

Understanding the factors that maintain the high levels of diversity characteristic of tropical forests is a central goal of tropical ecology. In old-field, grassland, and temperate forest ecosystems, many studies have demonstrated that herbivores cause changes in plant diversity and species composition, although their impacts are highly context dependent, varying with herbivore body size, herbivore densities, and productivity among other factors (Huntly 1991, Olf and Ritchie 1998, Royo et al. 2010). Still, whereas herbivores cause declines in the abundance or regeneration of dominant species or superior competitors, they typically cause increases in diversity (Huntly 1991, Carson and Root 2000, Royo et al. 2010). In contrast, although large-bodied vertebrates (e.g., white-tail deer) become overabundant, they can cause major declines in diversity in temperate forests and grasslands worldwide (McShea et al. 1997, Olf and Ritchie 1998, Nuttle et al. 2013). Oddly, far less research has critically evaluated the impact of native vertebrate herbivores and seed predators on tropical plant diversity, species composition, and forest regeneration (but see box 1). Understanding the impact of these tropical vertebrates is particularly salient,

because many of these animals are under threat of extirpation (Corlett 2007, Peres and Palacios 2007, Fa and Brown 2009).

Previous studies provide contradicting evidence for whether the effect of ground-dwelling vertebrates on tropical plant diversity is positive or negative. Studies of defaunated forests strongly suggest that where vertebrates are locally extirpated—or where they decline in abundance because of poaching or fragmentation—plant species richness and diversity often decline (box 1; Kurten 2013). This association between defaunation and declines in richness and diversity suggests that the loss of a large portion of the fauna, which includes many species of both arboreal and ground-dwelling mammals and birds, leads to declines in species richness. In contrast, the few vertebrate exclosure studies that exist have consistently revealed that excluding terrestrial seed predators and herbivores causes woody plant species richness to *increase* (box 1). In short, studies of defaunated forests suggest that vertebrates have a positive effect on tropical plant diversity, whereas experimental studies suggest that terrestrial vertebrates have a negative impact.

Box 1. What is the impact of ground-dwelling vertebrates on tropical plant diversity?

Dirzo and Miranda (1991) provided the first evidence for the potential of defaunation to cause serious declines in plant diversity. They compared the seedling diversity of two forests in Mexico, one defaunated and one intact. Adult tree diversity was similar in both forests. However in the severely defaunated forest, seedling richness was 66% lower, monodominant seedling plots were common, and vertebrate herbivory was undetectable (Dirzo and Miranda 1991). Their study suggested that vertebrate herbivores were crucial to the maintenance of tropical forest diversity. Subsequent studies have consistently shown that where poaching or fragmentation has caused severe reductions in vertebrate populations (arboreal and terrestrial), species richness of woody seedling and sapling communities often declines; there is no evidence that it ever increases (figure 1a).

However, the defaunation observed in these studies affected not only vertebrate herbivores, but also rodents and ungulates that prey on seeds and arboreal primates and large birds that disperse seeds. Manipulative experiments are the most rigorous way to determine the effects of different vertebrate guilds on plant diversity. Surprisingly, there are only a few short-term studies that have used replicated enclosures to evaluate the impact of native herbivores and granivores on plant diversity in tropical forests (Ickes et al. 2001, Royo and Carson 2005, Lizcano 2006, Camargo-Sanabria et al. 2015), and only one study lasted more than 10 years (Theimer et al. 2011). Nonetheless, in stark contrast to studies of defaunation, excluding ground-dwelling vertebrates consistently caused *increases* in species richness (figure 1a), and this is also consistent with many studies in temperate forests (see, e.g., Nuttle et al. 2013).

Rarefaction analyses in both this study and previous work suggest that excluding terrestrial vertebrates via enclosures causes changes in plant densities, which in turn causes changes in species richness (figure 2a–2f; Theimer et al. 2011). Indeed, changes in plant density are positively correlated with changes in species richness among enclosure and defaunation studies that quantify both responses (figure 1b). Together these results demonstrate that overhunting and enclosures likely have contrasting effects on plant species richness because overhunting tends to cause declines in plant densities, which in turn lead to declines in richness (figure 1b). Excluding vertebrates has the opposite effect on density and richness (figure 1b).

Our data do not explain why defaunated forests often have lower seedling densities than their intact counterparts. However, conceptual models predict that at intermediate levels of defaunation, medium and small-bodied herbivores and seed predators may actually increase in abundance, because they benefit from reduced resource competition and suffer less predation from larger carnivores (Wright 2003, Dirzo et al. 2007). Empirical evidence from Amazonia supports this prediction (Bodmer et al. 1997, Peres and Palacios 2007). Higher abundances of mesoconsumers may increase seed predation and herbivore pressure in these forests, leading to the lower recruitment rates and seedling densities observed in those forests (figure 1a). A decline in stem densities would then lead to a decline in species richness (figure 1b).

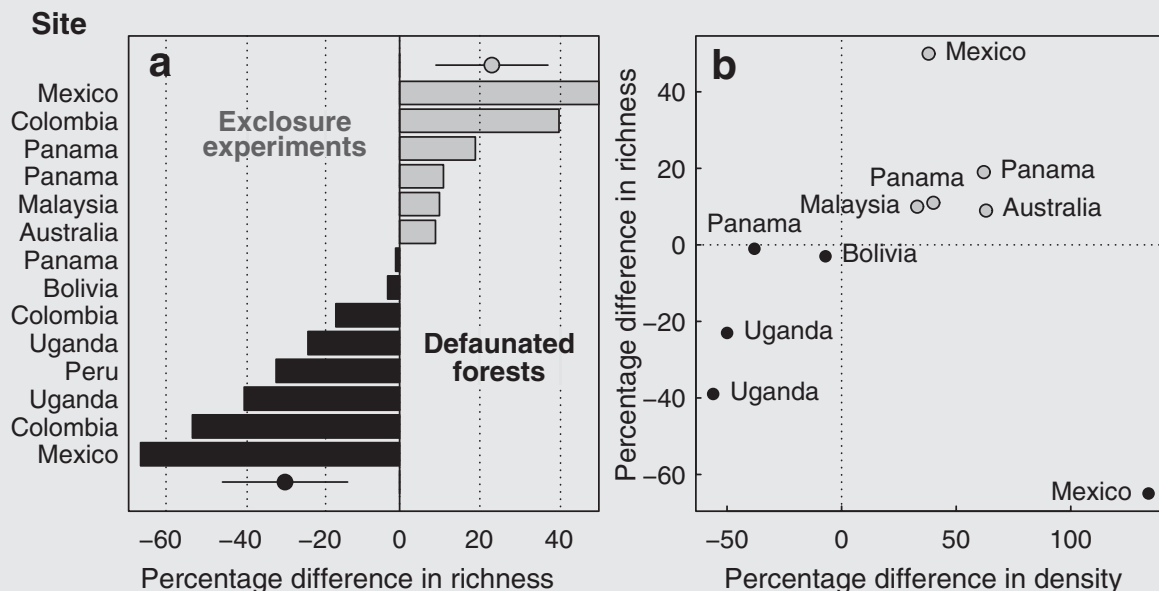


Figure 1. (a) The percent difference in species richness in tropical forests where vertebrates populations have been reduced, versus where vertebrate communities are intact. Studies included here focus on seedlings or saplings of woody species. Observational studies of forests which have been defaunated by hunting or fragmentation are in black, whereas manipulative enclosure experiments are in grey. The bars represent individual results; the circles represent the group means, and the error bars represent 95% confidence intervals. (b) The magnitude of the change in richness is positively correlated with the change in stem density, but only when the Mexican defaunation study is excluded ($p = .88$ with Mexican defaunation study, $p = .041$ without). Details of how the percent difference values for each study were determined are described by Kurten (2013).

Although studies of defaunated forests and exclosure experiments may seem analogous, they have important differences, which may explain why defaunated forests develop understories that contrast with the understories that regenerate inside exclosures. One key difference is that excluding vertebrates via fences often causes increases in seedling and sapling densities, whereas defaunation from hunting does not (box 1; Kurten 2013). Therefore, excluding vertebrates via exclosures increases seedling and sapling recruitment and density, and this, in turn, increases species richness, likely by enhancing the abundance of less common species (Theimer et al. 2011) or by increasing opportunities for niche differences and the resource partitioning of new recruits of multiple species in distinct microsites (Schnitzer and Carson 2010). A second key difference is that many tropical forests have been overhunted for decades and therefore have been defaunated for extensive periods, whereas exclosure studies typically last for only a few years (but see Theimer et al. 2011 for a long-term study). Consequently, it remains unclear whether exclosure studies report only short-term transient responses and whether changes in density and species richness ultimately will be sustained over longer periods.

The third, and perhaps most important, key difference between defaunated forests and exclosure experiments is their contrasting effects on animal communities. Whereas fences substantially reduce nearly all terrestrial seed predators and herbivores, defaunation additionally leads to the near extirpation of primate and avian seed dispersers, primarily because of excessive hunting. Indeed, several studies of defaunated forests argue that the loss of these larger-bodied arboreal vertebrate seed dispersers is primarily responsible for declines in woody species diversity, because these animals mitigate distance- and density-dependent mortality (Stevenson and Aldana 2008, Nunez-Iturri et al. 2008, Terborgh et al. 2008, Vanthomme et al. 2010, Effiom et al. 2013). Indeed, the loss of large-bodied seed dispersers in tropical forests has been linked to the reduced seed dispersal of larger-seeded woody species in at least 11 different studies (e.g., Wright et al. 2000, McConkey and Drake 2006, Wang et al. 2007, Holbrook and Loiselle 2009, Brodie et al. 2009; see Kurten 2013 for a recent review). Consequently, declines in primate and avian seed dispersers, rather than in terrestrial consumers, may be partially or primarily responsible for plant species losses. However, defaunation also affects terrestrial consumers differently than exclosures. Although exclosures reduce terrestrial vertebrates, low to intermediate levels of defaunation can actually lead to *increases* of some mesoherbivores and seed predators, likely because of reduced competition, release from predation, or both (box 1). This increase in mesoherbivores and seed predators, which does not occur in exclosure experiments, may explain why some defaunated forests experience declines in stem densities, whereas vertebrate exclosures cause increases in stem densities. These differences in stem densities, in turn, may contribute to observed differences in richness and diversity responses.

Here, we examine the impact of excluding ground-dwelling vertebrates for 12 years on plant density, richness, diversity, and evenness. In addition, we explore whether the contrasting effects of defaunation versus vertebrate exclusion on plant community richness and diversity can be reconciled as being a consequence of their differing effects on ground-dwelling vertebrate consumers, as we described above. We also argue that our experimental use of exclosures tests a community-level prediction of the Janzen–Connell hypothesis, whereby these herbivores and seed predators are keeping the most fecund and competitive woody species in check during seedling and sapling regeneration within the understory (Janzen 1970, Connell 1971, Carson et al. 2008). Connell (1971) proposed just such an experiment: “if all enemies of trees were removed from an entire forest, each species would probably form small groves, and the more rapidly growing species would gradually spread over the habitat . . . The final result would be a lower pattern diversity . . . and as a consequence fewer species in any local area of forest” (p. 302). The use of fences to exclude ground-dwelling vertebrates (primarily white-tailed deer) in temperate forests has repeatedly shown that they cause declines in species richness and diversity when they are at a relatively high abundance (Kain et al. 2011, Nuttle et al. 2013, Begley-Miller et al. 2014; see Cole et al. 2012 for a tropical example with feral pigs) but may promote diversity when in low abundance by preferentially damaging dense layers of a few fast-growing trees and shrubs (Royo et al. 2010). Although it is not clear what their impact would be in a long-term study in a tropical forest, we predicted that excluding native terrestrial vertebrates would cause stem densities to increase and species richness and diversity to decline, both in absolute terms and on a per capita basis (i.e., rarefied species richness). Finally, we predicted strong interactions of time and exclusion, whereby changes in density and diversity metrics would be more likely to occur only after many years.

Methods

Our study took place in the Barro Colorado National Monument (BCNM; 9 degrees [°] 10 minutes ['] north, 79°51' west) is a group of mainland peninsulas and islands located in Lake Gatun in the Republic of Panama. The forest is semideciduous moist forest, receiving approximately 2600 millimeters of rainfall per year, with a dry season from January through April (Wright and Calderón 2006). See Leigh (1999) for a detailed description of the biota, climate, and geology of the site. Hunting is prohibited, and regular patrols by game wardens have dramatically reduced the incidence of poaching (Wright et al. 2000, 2007).

Exclosure experimental design. In 1994, we established eight pairs of plots within the BCNM. One plot in each pair was randomly selected to be fenced, whereas the other was left as an adjacent control plot. All plots were located in areas of primary forest, half on Barro Colorado Island (BCI) and

half on the Gigante Peninsula (Royo and Carson 2005). Plots were 30 × 45 meters (m) and approximately 5–10 m apart from their paired plot. Exclosure fences were 2.2 m in height and constructed from 12.7 × 12.7-centimeter (cm) galvanized steel fencing. A secondary 1.3 × 1.3-cm mesh surrounded the lower 70 cm. All fencing extended 0.25 m below ground. Using camera traps, we verified that fences eliminated all nonclimbing, terrestrial vertebrates from exclosure plots, including agoutis (*Dasyprocta punctata*), pacas (*Agouti paca*), deer (*Mazama americana* and *Odocoileus virginianus*), and peccaries (*Tayassu tajacu*) (Kurten et al. 2015). Tinamous (*Tinamus major*), large, ground-dwelling avian seed predators, also did not occur within the exclosures. Most climbing vertebrates were also reduced by exclosures, except spiny rats (*Proechimys steerei*), which had higher activity inside exclosures (Kurten et al. 2015).

In each of the 16 plots, all saplings 40–200 cm in height were mapped, measured, and identified to species in each plot. A 3-m buffer was placed around the interior perimeter to avoid fence and edge effects. Twenty-eight 1 × 1-m seedling subplots were established in each of the 16 plots in a stratified random manner; each plot was divided into four quadrats and seven seedling subplots were randomly placed within each quadrat. Within each seedling subplot, each plant less than 40 cm in height was tagged, measured, and identified. Saplings were censused six times between 1994 and 2003. Seedlings were censused annually from 1997–2006. Sapling and seedling censuses included only woody tree and liana species.

Statistical Analyses. Because we expected the response variables inside exclosures to continue to change over the time scale of our experiment, we treated time as a continuous covariate. Therefore, linear mixed effects (LME) models were used to test for the fixed effects of exclosure and time on plant density, species richness, evenness (Pielou's index), and diversity (Shannon–Wiener index), while accounting for the plot pair as a random factor. For seedlings, which were sampled at the level of subplot, a model with the subplot factor nested in the main plot was used, except where indices were undefined at the subplot level (e.g., Pielou's evenness for subplots containing only one species). In that case, subplots were pooled, the response metric was calculated at the whole plot level, and subplot was not included in the model. We also examined two other diversity metrics, the probability of interspecific encounter and the effective number of species. Because these alternative metrics corroborated results from the Shannon–Wiener index, we report them only in the supplemental material (supplemental figure S1). For the synthesis of studies, an LME was also used to test for a correlation between change in density and change in species richness among studies. To account for the nonindependence of data points coming from the same study (i.e., different size classes or community types), “study” was included as a random factor.

Models were fit using the “lme4” package in R version 2.15.2 (R Development Core Team 2011). Parameters were estimated using a restricted maximum likelihood approach, whereas *p*-values were estimated with the package “lmerTest.” Because observed species richness is positively correlated with the number of stems sampled, and exclosure plots generally had more stems than control plots, we also conducted a rarefaction analysis to determine the estimated species richness at the lowest observed stem densities across the time series (0.7 saplings per square meter [m²] and 11.1 seedlings per m²), for each plot at each time point. To examine changes in community composition over time, we conducted nonmetric multidimensional scaling (NMDS) analyses of plot-level species composition using Bray–Curtis similarities. Rarefaction and NMDS analyses were conducted with the package “vegan” (Oksanen et al. 2013).

Impact of excluding of ground-dwelling vertebrates in Panama

In total, we censused 34,962 saplings (369 species), and 45,639 seedlings (321 species) in the exclosure experiment.

Stem densities and species richness. Excluding terrestrial vertebrates caused a 46% increase in sapling densities over time (figure 2a; *p* < .001 for the interaction of time and treatment; supplemental table S1). Seedling densities were more variable over time, reflecting a pulse of seedling recruitment, followed by high mortality in both control and exclosure plots (figure 2b). However, even after that mortality, excluding vertebrates still caused a 38% increase in seedling densities (figure 2b; *p* < .001 for the interaction of time and treatment; table S1). Excluding vertebrates also caused similar and significant increases in species richness, although effect sizes were smaller (figure 2c, 2d). Excluding vertebrates led to a 15% increase (more than 20 additional species) in sapling species richness (figure 2c; *p* < .001 for the interaction of time and treatment; supplemental table S2), and a 12% increase (more than 15 additional species) in seedling species richness (figure 2d; *p* < .001 for the interaction of time and treatment; table S2). For both seedlings and saplings, excluding vertebrates did not increase rarefied species richness (figure 2e, 2f; supplemental table S3); therefore, increases in species richness were driven by increases in seedling and sapling density.

Diversity and evenness. Excluding vertebrates did not cause significant changes in Shannon–Wiener diversity (*H'*) for saplings (figure 2g, supplemental table S4). Diversity increases for seedlings were significant, but modest (*H'* increased 1.7% in control plots and 2.9% in exclosure plots; figure 2h; *p* < .001 for the interaction of time and treatment; table S4). Alternative diversity metrics yielded similar results (figure S1). For saplings and seedlings, excluding vertebrates did not alter evenness (figure 2i, 2j; supplemental table S5).

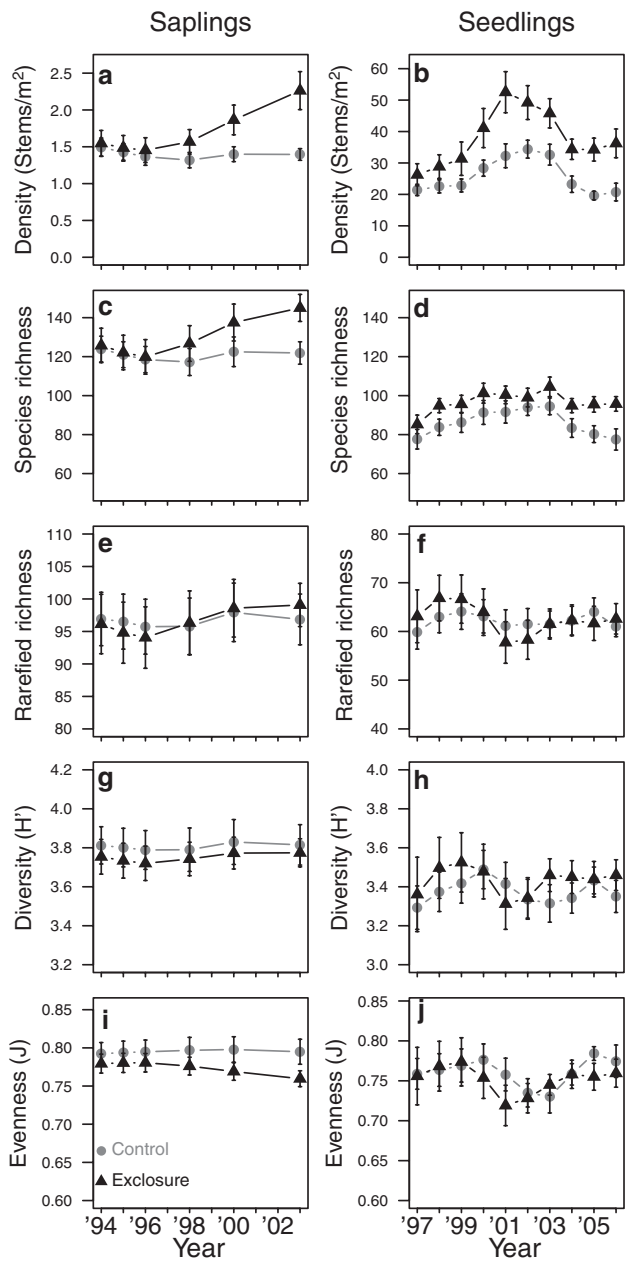


Figure 2. Responses of community-level (a, b) stem densities, (c, d) species richness, (e, f) rarefied richness, (g, h) Shannon–Weiner diversity, and (i, j) Pielou’s evenness to terrestrial vertebrate exclusion for saplings (left) and seedlings (right). Circles represent control plots; triangles represent exclusions. Error bars represent standard errors. Abbreviations: m^2 , square meters.

Synthesis

We demonstrated that the relatively long-term exclusion of ground-dwelling vertebrates led to a sustained increase in plant species richness for both seedlings and saplings. On average exclusion plots had about 20 more sapling species and about 15 more seedling species than paired control plots had after nine and twelve years respectively.

Our results strongly suggest that the *net effect* of excluding ground-dwelling vertebrates is to increase seedling and sapling establishment, because at least some of these vertebrates function predominantly as seed and seedling predators and herbivores. Therefore, our study suggests that these vertebrates are not responsible for Janzen–Connell effects (Janzen 1970, Connell 1971, Terborgh 1988, 1992), because their exclusion did not lead to a seedling and sapling layer dominated by a few highly competitive or fecund species capable of forming a dense and low diversity seedling layer (but cf. Dirzo and Miranda 1991, Camargo-Sanabria et al. 2015).

Both our results and previous studies in Malaysia, Colombia, Australia, and Mexico demonstrated that excluding terrestrial seed predators and herbivores caused seedling and sapling densities to increase (figure 2a, 2b; Ickes et al. 2001, Lizcano 2006, Theimer et al. 2011, Camargo-Sanabria et al. 2015), suggesting that these results may apply broadly. It is important to recognize that the increase in species richness we observed was driven by an increase in stem density, which we verified via rarefaction (cf. Theimer et al. 2011). Changes in species richness tracked changes in density (figure 2c, 2d). Taken together, these data suggest that one impact of vertebrate herbivores on tropical understory plant communities is to reduce stem densities, thereby reducing the opportunity for uncommon species to occur in the community and lowering local richness.

Herbivores were primarily responsible for changes in the sapling community, whereas a broader array of terrestrial consumers likely contributed to changes in the seedling community. In the final census, approximately 92% of saplings in the plots had established prior to constructing the exclosures. Therefore, terrestrial secondary seed dispersers and seed predators, which shape seed shadows prior to seedling establishment, contributed little to the changes in the sapling community that occurred over time. Instead, increases in sapling density and richness were primarily driven by herbivores, postestablishment. In contrast to the saplings, 83% of seedlings in the final census recruited *after* the exclosures were built. Therefore, increases in seedling density and richness reflect the net effects of removing terrestrial seed dispersers, seed predators and herbivores. Shifts in functional traits in exclusion communities suggest that the removal of seed predators contributed most to changes in the seedling community (Kurten et al. 2015). Spiny rats were the only species to show higher activity inside exclosures (Kurten et al. 2015). However, increases in stem densities (figure 2a, 2b) and shifts in functional traits (Kurten et al. 2015) suggest that their ability to compensate for the removal of larger seed predators and herbivores was limited (cf. Kurten et al. 2015).

Seedling densities in both control and exclusion plots increased dramatically in the first five years of the experiment, but these increases attenuated thereafter (figure 3b, box 2). Long-term monitoring showed that overall increases in seedling densities caused by vertebrate exclusion were more modest than they initially appeared (figure 2b).

Box 2. How did species composition in the exclosures change over time?

In our study, exclosure plot location explained much of the variation in community composition (figures 3a, 3b). The first NMDS axis separated plots on BCI and the Gigante peninsula; the second NMDS axis separated areas within BCI and Gigante. Changes in species composition over time were generally smaller than initial differences between paired plots, particularly for saplings (figures 3a, 3b). One might predict that excluding vertebrates would consistently favor the same species, thereby producing similar compositional shifts among plots, but we did not observe this. Only within a plot location were compositional changes in exclosure plots generally similar, and often distinct from the compositional changes that occurred in paired control plots. One might also expect competitively dominant species to increase in abundance disproportionately inside exclosures. However, species relative abundances showed little change over time (figure S2).

The species showing the greatest changes in abundance in response to vertebrate exclosure varied by location and size class. Among saplings, excluding vertebrates on BCI led to increases in several genera, particularly in the families Rubiaceae (*Randia*, *Faramea*, and *Psychotria*), Burseraceae (*Tetragastris* and *Protium*), Moraceae (*Brosimum* and *Sorocea*), and Malpighiaceae (*Hiraea* and *Mascagnia*), as well as the genera *Lacmellea* (Apocynaceae), *Doloiocarpus* (Dilleniaceae), *Virola* (Myristicaceae), and *Beilschmiedia* (Lauraceae) (figure 3c). Excluding vertebrates on the Gigante peninsula caused large increases in the genera *Chamaedorea* (Arecaceae), *Piper* (Piperaceae), and *Quararibea* (Malvaceae), as well as increases in some of the same genera that increased on BCI (e.g., *Sorocea*, *Virola*, *Psychotria*) (figure 3c). Most of these taxa are shade-tolerant species, many are among the most abundant species on BCI, and a few are relatively large seeded (Croat 1978).

Among seedlings, compositional changes were affected both by vertebrate exclosures, as well as by a pulse of seedling recruitment and subsequent mortality likely driven by La Niña and El Niño events (Wright and Calderón 2006). Several taxa which increased rapidly in the first half of the exclosure experiment remained more abundant in the exclosures, despite subsequent heavy mortality. These included *Quararibea* and *Doloiocarpus* on BCI, *Pithecoctenium* (Bignoniaceae) on Gigante, and *Tetragastris* and *Trichillia* (Meliaceae) at both sites (figure 3d). On BCI, *Faramea* and *Pouteria* (Sapotaceae) increased during the pulse of recruitment, but later suffered even higher mortality (figure 3d), resulting in an overall decrease in abundance over time inside the exclosures (data not shown). Other taxa increased more in control plots than in exclosures (e.g., *Faramea*, *Doloiocarpus* on Gigante; data not shown). *Hybanthus* (Violaceae) showed the opposite recruitment pattern of many groups, declining in abundance during the seedling pulse and then subsequently recovering (figure 3d). Changes in some taxa occurred independently of the pulse, either increasing (e.g., *Lacmellea* and *Maripa* [Convolvulaceae] on BCI, *Gustavia* [Lecythidaceae] on Gigante, *Virola* in both sites) or decreasing (e.g., *Beilschmiedia* on BCI) consistently in exclosures throughout the experiment (figure 3d). Such highly variable responses to vertebrate exclosure make it difficult to make general predictions about which plant species, and consumers dependent on them, may be most negatively affected by terrestrial defaunation.

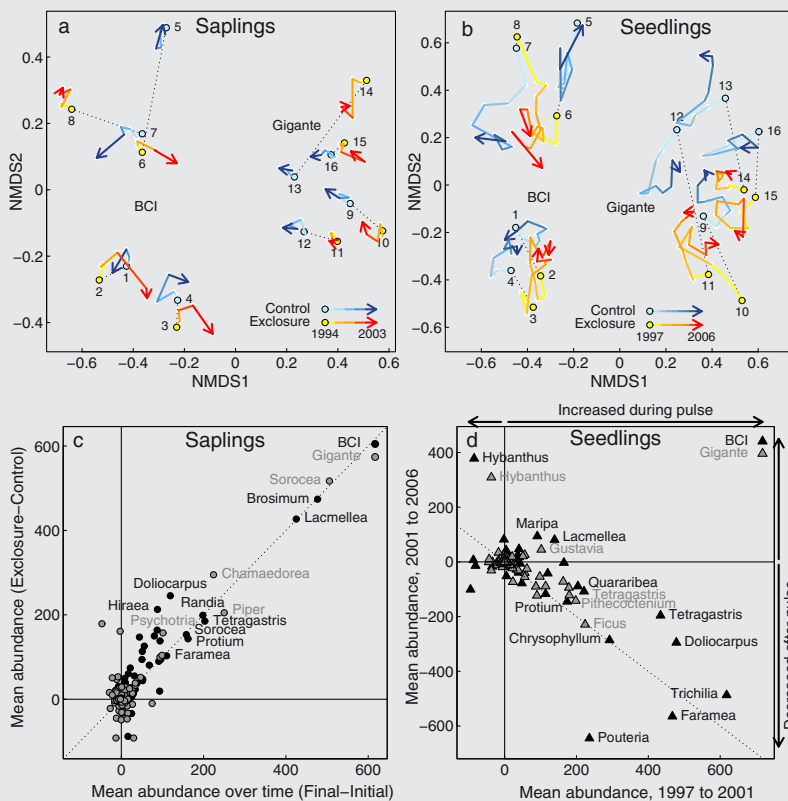


Figure 3. (a) Community similarity over time in control plots (blue) and exclosure plots (orange-red) for saplings from 1994–2003. Dashed lines between plots show paired control plots and exclosures. (b) Seedling community similarity from 1997–2006. (c) The difference in sapling abundance between exclosures and control plots in the final census versus sapling change in abundance over time (1994–2003). The dashed 1:1 line shows where the total change in abundance of a species over time is equal to the difference between control and exclosure abundances in the final census. (d) The change in seedling abundance before and after the pulse in seedling recruitment. The dashed negative 1:1 line represents zero net change in abundance over time—that is, where the total increase in abundance during the recruitment pulse is equal to the total decrease in abundance after the pulse.

Seedlings declined from their peak densities even inside the exclosures during the later years of the experiment (figure 2b). This suggests that factors other than vertebrate consumers were contributing to these dynamics. Because competition is known to be weak among tropical seedlings, even at extremely high densities (Paine et al. 2008), other natural enemies (i.e., pathogens and invertebrates; Howe et al. 1985, Augspurger and Kitajima 1992) or abiotic factors were likely responsible. Drought is an important agent of seedling mortality in this forest (Bunker and Carson 2005, Engelbrecht et al. 2007). We suggest that a wet La Niña period from 1998 to 2001 may have facilitated higher seedling recruitment, which was offset by higher seedling mortality when drier conditions returned beginning in 2002 (Wright and Calderón 2006).

Excluding vertebrates caused a substantial increase in species richness for seedlings and saplings but caused little to no change in Shannon–Wiener diversity (figure 2g, 2h). Increases in species richness without corresponding increases in species diversity have also been observed in other tropical exclosure studies (Ickes et al. 2001, Theimer et al. 2011). This result could occur if a few species benefit disproportionately from excluding vertebrates; decreased evenness would lower Shannon–Wiener diversity, countering any positive effects resulting from increased species richness. However, excluding vertebrates did not cause significant changes in seedling or sapling evenness (figure 2i, 2j; cf. Theimer et al. 2011). Instead, it appears that Shannon–Wiener diversity did not increase because patterns of relative abundance among species inside the exclosures were largely unchanged over time (supplemental figure S2). Although the exclosure plots did have higher species richness, the additional species were too rare, and their relative abundances too small, to cause an increase in Shannon–Wiener diversity (figure S2). Furthermore, although one may have predicted that excluding terrestrial vertebrates would cause large and consistent shifts in species composition over time, our results suggest that excluding vertebrates caused changes in species composition that were highly variable and location dependent (box 2). The effect of time and exclosure on species composition was generally smaller than the effect of location (box 2), and the magnitude of compositional change over time was not generally greater in exclosure plots than in control plots (box 2).

Our results demonstrate that the exclusion of ground-dwelling vertebrates caused sustained increases in species richness. Because the increase in species richness is the result of increased stem densities in exclosures, it is possible that stem thinning in later stages of recruitment may attenuate the increase in species richness. However, if these additional species were to reach reproductive size before they are lost from the community, these individuals would have the opportunity to alter the regeneration pool and increase richness in the next generation. This could occur for shrub or subcanopy tree species that reach reproductive maturity at a relatively small size (e.g., *Psychotria* spp.), or via

an interaction with light gaps which allow these individuals to reach reproductive size before extensive thinning occurs (Schnitzer et al. 2008).

However, these conclusions must remain somewhat tenuous. It is not clear, even after more than a decade of monitoring, the degree to which these increases in species richness will be sustained over the next half century. There is some evidence that the presence of vertebrate herbivores may enhance or promote negative density-dependent seedling mortality. Indeed, the exclusion of vertebrates led to an absence of negative density-dependent seedling mortality in one case (Webb and Peart 1999) and positive density-dependent mortality in another (Theimer et al. 2011), suggesting that in the absence of vertebrate herbivores, negative-density dependent mortality from invertebrates and pathogens alone is not sufficient for keeping the populations of competitive plant species in check (cf. Camargo-Sanabria et al. 2015). Consistent with this, increases in the abundance of fast-growing, poorly defended, low-wood density tree species, and monodominant seedling plots have been observed in hunted forests in the Republic of Congo and Mexico, respectively (Dirzo and Miranda 1991, Poulsen et al. 2013). In our experiment, some species that increased in density (box 2) are among the most abundant species throughout the BCNM (e.g., *Tetragastris panamensis*, *Faramea occidentalis*, *Trichilia tuberculata*, *Brosimum alicastrum*, *Beilschmiedia pendula*, *Virola sebifera*; Hubbell et al. 2005), and many are shade tolerant or have large seeds (e.g., *B. pendula*, *V. sebifera*; Croat 1978, Wright et al. 2010). If these species eventually formed dense layers or spatially aggregated small groves within the understory (Connell 1971, Carson et al. 2008), which in turn exclude other woody species, then species richness could eventually decline via this process, although these dynamics would likely take many decades. Nonetheless, our results strongly suggest that ground-dwelling vertebrates suppress local species richness rather than enhance it over the duration of our experiment and at least for the following few decades (but cf. Camargo-Sanabria et al. 2015).

Studies of defaunated forests have suggested that vertebrate herbivores and seed predators have positive effects on tropical plant diversity whereas excluding terrestrial vertebrates alone have suggested the opposite (box 1). Our study demonstrates that excluding vertebrate herbivores and seed predators increases stem densities via a reduction in seed and seedling predation and herbivory, which in turn increases plant species richness. In contrast, studies of defaunated forests have either shown declines in seedling and sapling densities and richness, or no change in densities and richness, relative to forests with relatively intact fauna (Chapman and Onderdonk 1998, Roldán and Simonetti 2001, Terborgh et al. 2001, Wright et al. 2007). Vertebrate exclosures eliminate terrestrial consumers, whereas intermediate levels of defaunation lead to *higher* abundances of mesoherbivores and seed predators (Bodmer et al. 1997, Peres and Palacios 2007). It is likely that the contrasting

effects of vertebrate exclusion and defaunation on terrestrial vertebrate communities are responsible, at least in part, for their distinct and contrasting effects on stem densities, and in turn species richness (box 1). Our synthesis of these data with prior studies suggests that arboreal seed dispersers are necessary for the maintenance of tropical diversity (Nunez-Iturri et al. 2008, Stevenson and Aldana 2008, Terborgh et al. 2008, Vanthomme et al. 2010, Effiom et al. 2013). However, intermediate levels of defaunation which reduce abundances of large terrestrial primary consumers and carnivores may release mesoherbivores and seed predators, thereby also decreasing richness and diversity. In contrast, the near extirpation of terrestrial vertebrates (or exclusion via fences) is likely to enhance species richness, at least over the course of several decades.

Supplemental material

The supplemental material is available online at <http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biv110/-/DC1>.

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