

## RESEARCH ARTICLE

# The cryptic regulation of diversity by functionally complementary large tropical forest herbivores

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## Funding information

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 2015/11521-7, 2013/50424-1 and 2014/01986-0; Conselho Nacional de Desenvolvimento Científico e Tecnológico

Handling Editor: David Edwards

## Abstract

1. Tropical forests hold some of the world's most diverse communities of plants. Many populations of large-bodied herbivores are threatened in these systems, yet their ecological functions and contribution towards the maintenance of high levels of plant diversity are poorly known. The impact of these herbivores on plant communities through antagonistic seed and seedling predation has received much attention, whilst their relevance as seed dispersal agents has been largely overlooked in experimental studies.
2. Here, we tested how two key and functionally distinct large generalist mammalian herbivore species (the tapir *Tapirus terrestris* – a solitary browser and generalist seed disperser, and the white-lipped peccary *Tayassu pecari* – a group-living generalist seed/seedling predator) affect spatiotemporal patterns of diversity of seedling communities in tropical forests. We conducted a long-term multi-region landscape-scale exclusion experiment across four regions of the Atlantic forest of Brazil, representing a functional gradient of defaunation where these species were either present and absent in isolation and in combination.
3. Our results indicate that mammalian herbivores have a substantial role in regulating beta diversity in space and time. Seedling recruitment was strongly limited by the presence of the seed/seedling predator species (the peccary), but the presence of the browser and seed disperser (the tapir) had null net effects. Alpha diversity of seedlings at the community level did not respond to large herbivore exclusion at any region, whereas beta diversity decreased only where both herbivores were simultaneously excluded. Surprisingly, the synergistic positive effect of both herbivore types on beta diversity was linked to increased evenness amongst dominant plant species, and a simultaneous decrease in alpha diversity of rare species.
4. *Synthesis.* Together, these results challenge the common perception that large tropical forest herbivores maintain tropical forest diversity through antagonistic interactions, suggesting instead a synergistic effect of antagonistic predation and mutualistic seed dispersal on regional compositional diversity and local community

assembly. We suggest that the defaunation of large-bodied herbivores with complementary functions strongly affects the structure and dynamics of plant communities through cryptic mechanisms that remain largely unexplored.

#### KEYWORDS

alpha diversity, Atlantic forest, beta diversity, defaunation, exclosure experiment, herbivory, seed dispersal, trophic cascades

## 1 | INTRODUCTION

Large consumers have large home ranges and are highly mobile and have broad diets (Harestad & Bunnell, 1979; Jetz, Carbone, Fulford, & Brown, 2004; Stephens & Krebs, 1986), and therefore are bound to have substantial effects on the structure of communities at both local and regional scales. Long-standing empirical evidence from grassland and open woodland ecosystems, for example, suggests that large ground-dwelling grazers and browsers increase local plant species diversity (alpha diversity) at high productivity and moderate herbivore densities (e.g. Augustine & McNaughton, 1998; Bakker, Ritchie, Olff, Milchunas, & Knops, 2006; Borer et al., 2014; McNaughton, 1985). Evidence about the effects on plant beta diversity, that is, the compositional variation among communities, is more cryptic and scarce, and suggest context-dependent effects of large herbivores on grassland ecosystems (Hanke et al., 2014; Masunga, Moe, & Pelekekae, 2013; Speed, Austrheim, & Mysterud, 2013).

Theoretical consumer–resource and metacommunity models also provide insights into the regulating role of large consumers. These models generally predict that generalist consumers with high dispersal rates or mobility might increase alpha diversity, but decrease beta diversity by homogenizing spatial heterogeneity and reducing differences between local communities (Gravel, Massol, Canard, Mouillot, & Mouquet, 2011; Holyoak, Leibold, & Holt, 2005; Oksanen, Fretwell, Arruda, & Niemela, 1981; Rosenzweig & MacArthur, 1963). Furthermore, by affecting the compositional turnover of communities over space and time, large consumers might affect ecosystem functions and stability at different spatial scales (Marleau, Guichard, & Loreau, 2014; Shanafelt et al., 2015; Wilcox et al., 2017).

Tropical forests are hyper-diverse ecosystems that have undergone a historic process of defaunation and trophic downgrading of large mammals (Dirzo et al., 2014; Malhi et al., 2016; Ripple et al., 2015). Yet, the role of the remaining megafauna in regulating alpha and beta diversity in space and time is still uncertain, and even less is known about the processes and mechanisms involved. The Janzen–Connell model (Connell, 1971; Janzen, 1970) proposes that density-dependent predation or parasitism of seeds and seedlings by species-specific natural enemies should increase mortality under parent trees, hence increasing alpha diversity through top-down control of local recruitment. Accordingly, it has been proposed that natural enemies might be key drivers of plant diversity in these

systems (Terborgh, 2012; 2015). However, this framework does not apply to large generalist herbivores on tropical forests, which by definition have broad diets and target common species.

Empirical studies demonstrate that ground-dwelling seed and seedling predators in tropical forests indeed have a strong impact on plant recruitment, but whether this generates higher or lower plant diversity is still unclear, partly due to the scarcity of long-term experimental studies and compositional differences between sites (Clark, Poulsen, & Levey, 2012; Kurten & Carson, 2015; Paine & Beck, 2007; Paine, Beck, & Terborgh, 2016). Small mammals, for example, act as efficient seed and seedling predators, and evidence suggests that they might increase beta diversity but not alpha diversity (Paine et al., 2016). Large- and medium-sized mammals also cause strong declines in seedling abundance, but subsequent changes in alpha or beta diversity are less predictable, with compositional changes among the mammal herbivore community thought to play an important role in explaining this uncertainty (Kurten & Carson, 2015; Paine et al., 2016). Yet, a common assumption of these studies is that antagonistic effects mediate the impact of large herbivores on tropical forest diversity.

On the other hand, many large mammalian herbivores in tropical forests are seed dispersers and about 89% of the woody species are animal-dispersed (Almeida-Neto, Campassi, Galetti, Jordano, & Oliveira-Filho, 2008; Jordano, 2000). Recent empirical evidence supports a strong case for consumer–resource coevolution and a potential large influence of assisted seed dispersal in the evolution and dynamics of tropical forests (Brodie, 2017; Carvalho, Galetti, Colevatti, & Jordano, 2016; Galetti et al., 2013). Accordingly, it has been suggested that mutualistic seed dispersal by large herbivores might be a relevant process in the maintenance of diversity structure in these systems (Kurten, 2013; Kurten, Wright, Carson, & Palmer, 2015; Terborgh et al., 2008). However, the quantification of its true relevance or the outcome of its interaction with antagonistic large herbivore predation has not been formally tested. Furthermore, large herbivore species vary substantially in their predation versus dispersal role, even within functional guilds (Brodie, Helmy, Brockelman, & Maron, 2009; Bueno et al., 2013; McConkey et al., 2018). Thus, there is a strong need for exclusion experiments that isolate effects of different functional types of large herbivores in tropical forests. Such experiments could help to characterize the relative role of different types of enemies and mutualists in shaping diversity at local and regional scales, so as to inform on how functional complementarities

amongst these consumers and associated ecological mechanisms shape tropical forest diversity and community assembly.

Here, we report the results of a 7-year replicated exclusion experiment across a functional defaunation gradient spanning different regions, aiming to evaluate how two key and functionally distinct large herbivore species affect spatiotemporal patterns of diversity of seedling communities in the hyper-diverse Atlantic Forest of Brazil. In these forests, like in other areas of the Neotropics, two mammalian herbivores dominate the understory of terrestrial ecosystems in terms of biomass: the white-lipped peccary (WLP; *Tayassu pecari*) and the lowland tapir (*Tapirus terrestris*; Galetti et al., 2017). Both species are generalist herbivores with remarkable broad diets, the WLP mainly as a seed and seedling predator and the lowland tapir as seed disperser and browser (Beck, 2006; Bueno et al., 2013; Keuroghlian & Eaton, 2009; O'Farrill, Galetti, & Campos-Arceiz, 2013; Silman, Terborgh, & Kiltie, 2003). WLPs gather in large herds often exceeding 100 individuals, posing a strong predatory impact on plants (Beck, 2006; Keuroghlian & Eaton, 2009; Silman et al., 2003). At the other extreme of the predator–mutualist continuum, tapirs have solitary habit and are amongst the world's most relevant generalist seed dispersers (O'Farrill et al., 2013).

We first validated the assumption of different functional roles of both focal species by testing the hypothesis that the WLP limits seedling recruitment, whereas tapir effects on recruitment are negligible. We then tested the prediction that predation from WLP and assisted seed dispersal from tapirs would increase alpha diversity but decrease beta diversity amongst plant communities (e.g. homogenizing effect). We predicted a possible synergic effect of both herbivore types in combination, leading to a non-additive increase

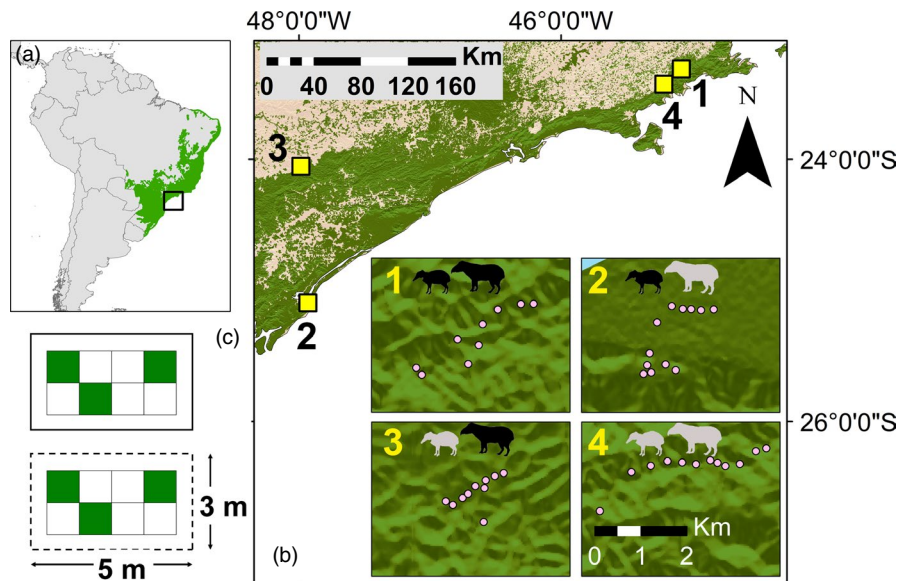
in alpha diversity and a decrease in beta diversity compared to a net additive effect expected from regions where only one species is present. This would suggest a functional complementary role of both herbivores in the maintenance of diversity. Lastly, taking our predictions to the community assembly level, we further tested that increases in alpha and decreases in beta diversity were caused by a decrease in the abundance and/or diversity of dominant plant species and a concomitant increase among rare plant species.

## 2 | MATERIALS AND METHODS

### 2.1 | Study regions

The study was carried out at four regions in a continuous protected area of the Atlantic Forest along the Serra do Mar corridor in the State of São Paulo, Brazil: Itamambuca and Vargem Grande bases (ITA and VGM respectively, located at the municipalities of Ubatuba and São Luiz do Paraitinga), at the Serra do Mar State Park – Santa Virgínia, the largest continuous reserve area of Atlantic forest in Brazil (332,000 ha); Carlos Botelho State Park (CBO, São Miguel Arcanjo, 37,633 ha); Ilha do Cardoso State Park (CAR, Cananéia, 13,500 ha). In CAR the climate is Af (tropical zone, without dry season) and in the other areas it is Cwb.

Landscape fragmentation and unregulated hunting practices on these regions have contributed towards the local extinction of either WLPs, tapir or both (Galetti et al., 2017), generating a “natural experiment” where to test for functional complementarity amongst these herbivores (Figure 1). At ITA, both peccaries and tapirs are present and abundant, whereas at VGM both species are locally extinct. At



**FIGURE 1** Location of study area and experimental design. (a) Broad region of study (highlighted in black) within the Brazilian Atlantic Forest biome (in green). (b) The exact location of each of the studied regions, each with a different combination of white-lipped peccary [WLP] and tapir: region 1 (Itamambuca), both species present; region 2 (Ilha do Cardoso), only WLP present; region 3 (Carlos Botelho), only tapir present; region 4 (Vargem Grande), both species absent. Panels in (b) show locations of replicate experimental plot pairs within every region. Every replicate pair (c) consisted of one exclusion plot (top) adjacent to one open plot (bottom), within which all seedlings on three 1 m<sup>2</sup> subplots were monitored every 6 months

CAR only WLPs occur, whereas at CBO only tapirs are present and WLPs absent.

We inferred the net effect of WLPs and tapirs in isolation or in combination by comparing results of experimentally excluding large and medium-sized herbivores in different regions. Despite the geographical distance, all regions are within the same protected area, share similar vegetation composition and, as previous studies suggest, background assemblages of medium- and large-sized ground-dwelling mammals including seed dispersers, seed and seedling predators, and carnivores are similar across the regions considered (Brocardo, Rodarte, Bueno, Culot, & Galetti, 2012; Galetti et al., 2017; Lima et al., 2017; Rocha-Mendes et al., 2015). Small mammals are also abundant and extraordinarily diverse at all sites, showing particularly large abundances at VGM, the site where both WLPs and tapirs remain locally extinct (Bovendorp et al., 2017; Galetti et al., 2015; Rocha-Mendes et al., 2015). The absence of WLPs and tapirs from this site allows testing how experimentally excluding assemblages of remaining medium- and large-sized mammals affect plant communities in the absence of the two focal species. These include agoutis (*Dasyprocta* spp.), pacas (*Cuniculus paca*), brocket deer (*Mazama* spp.) and collared peccaries (*Pecari tajacu*), amongst other species.

## 2.2 | Experimental set up and plant sampling

In 2009, 15 paired open control plots and experimental exclusion plots (5 m long × 3 m wide = 15 m<sup>2</sup> each) were installed at CBO, and in 2010 at the rest of the regions. Because some of these plots were lost through the years due to fallen trees, the data reported here includes nine paired-plots in ITA, 12 in CAR, 10 in CBO, and 12 in VGM, which add up to a total of 86 plots. Within every region, replicate plots were located at least 200 m from the closest pair to reduce spatial autocorrelation. The exclusion plots were fenced off using a 1.6-m-high metal fence, 5 cm wire mesh, excluding all terrestrial mammals other than small rodents and marsupials, which could permeate through the fence. The control plots remained open with their area demarcated by plastic piles. Open and closed plots were separated 2–7 m from each other to ensure homogeneity between microenvironments. We left a border of 0.5 m inside every plot to ease access into the plots while minimizing disturbance and spurious results related to, for example, the use of fences as perches by birds and edge effects.

At the beginning of the experiment, every plot was subdivided into eight 1 m<sup>2</sup> subplots, and on three of them (selected at random) all seedlings between 0.1 and 1 m height were identified and marked individually. Subsequent regular surveys of the same subplots were carried out every 6 months, and on every occasion all new seedlings were identified and marked, and the fate of previously marked seedlings checked. The dataset reported here comprises surveys between July 2009 and October 2016, spanning across 74 months for ITA, VGM, and 73 months for CAR (13 consecutive sampling occasions each), and for 87 months for CBO plots (12 sampling occasions, truncated for logistical reasons between months 48 and 74).

Over the course of the experiment, we followed the fate of a total of 6947 individual seedlings from 166 species. CBO was the region with more species (75), followed by VGM (69), CAR (57) and ITA (50). Seedling communities were characterized by the vast dominance of the palm *Euterpe edulis* (Arecaceae, 41.57% of the seedlings), unmatched by the second most common species, the vine *Phanera microstachya* (Fabaceae, 7.33%). Only 14 dominant species showed more than 1% of the share of the individuals monitored, accounting for 75.9% of the individuals of the entire dataset. The long tail of frequency distribution of abundances in this hyper-diverse community showed that every one of the remaining 152 plant species had less than 1% of the share of the individuals monitored (SI Appendix, Figure S1; Villar et al., 2019).

## 2.3 | Statistical analyses

Different beta diversity coefficients assign different weights to either changes in species composition (e.g. incidence-based coefficients – Jaccard, Sorensen) or to changes in the number of individuals per species (e.g. abundance-based coefficients – Bray–Curtis, Euclidean), and thus may complement each other to inform about the ecological mechanisms driving changes in diversity (Anderson, Ellingsen, & McArdle, 2006; Siqueira, Lacerda, & Saito, 2015). Thus, we estimated beta diversity for every plot-time combination using both incidence-based (Jaccard) and abundance-based (Euclidean) coefficients (the latter after Hellinger transformation) to gain mechanistic insight. We did this by calculating, for every time step and region independently, the distance from every plot to the centroid of the multivariate ordination space formed by all plots within each treatment. Subsequently, we tested if region-specific differences in Euclidean distances to time-varying centroids differed between paired control and enclosure plots by using repeated measures analyses through generalized linear mixed effects models (henceforth GLMMs). Models included Hellinger transformed Euclidean distances as the response variable, and the interaction between treatment and time (continuous). In this way, treatment effects could be detected by the divergence in temporal trajectories between control and enclosure plots (e.g. treatment\*time effects), but not by spurious pre-experimental differences between control and enclosures caused by random selection of experimental plots (e.g. single-term treatment effects in the models). The number of adult *Euterpe edulis* palms around each plot was added as a covariate, because palms fruits are a key resource for frugivores and herbivores in the Atlantic Forest and elsewhere in the Neotropics, and evidence suggests that palm abundance can influence WLP activity (Beck, 2006; Keuroghlian & Eaton, 2009). Indeed, models showed that the abundance of adult *Euterpe edulis* palms was an important covariate for all indices analysed (SI Appendix, Tables S5 and S6). Random effects accounted for effects of plot within plot pair within time (categorical). This random effects specification accounted for the fact that experimental treatment was applied to the same plot within every plot pair repeatedly over time, allowing us to test the time\*treatment interaction of interest in the main effects. We used analogous repeated measures

analyses to test for differences in Jaccard distances to centroid and in seedling abundances.

We also investigated if the trajectories of alpha diversity differed between experimental treatments by calculating Hstar, Dstar and Estar for every plot-time combination and using GLMMs with analogous structure to the ones used in tests of differences in beta-diversity. Hstar (a diversity index), Dstar (equivalent to Hill numbers) and Estar (an index of evenness) are unified indexes of diversity that account for biodiversity indexes profiling similar to Hill numbers, whilst providing measures of alpha diversity amenable to statistical analyses (Mendes, Evangelista, Thomaz, Agostinho, & Gomes, 2008).

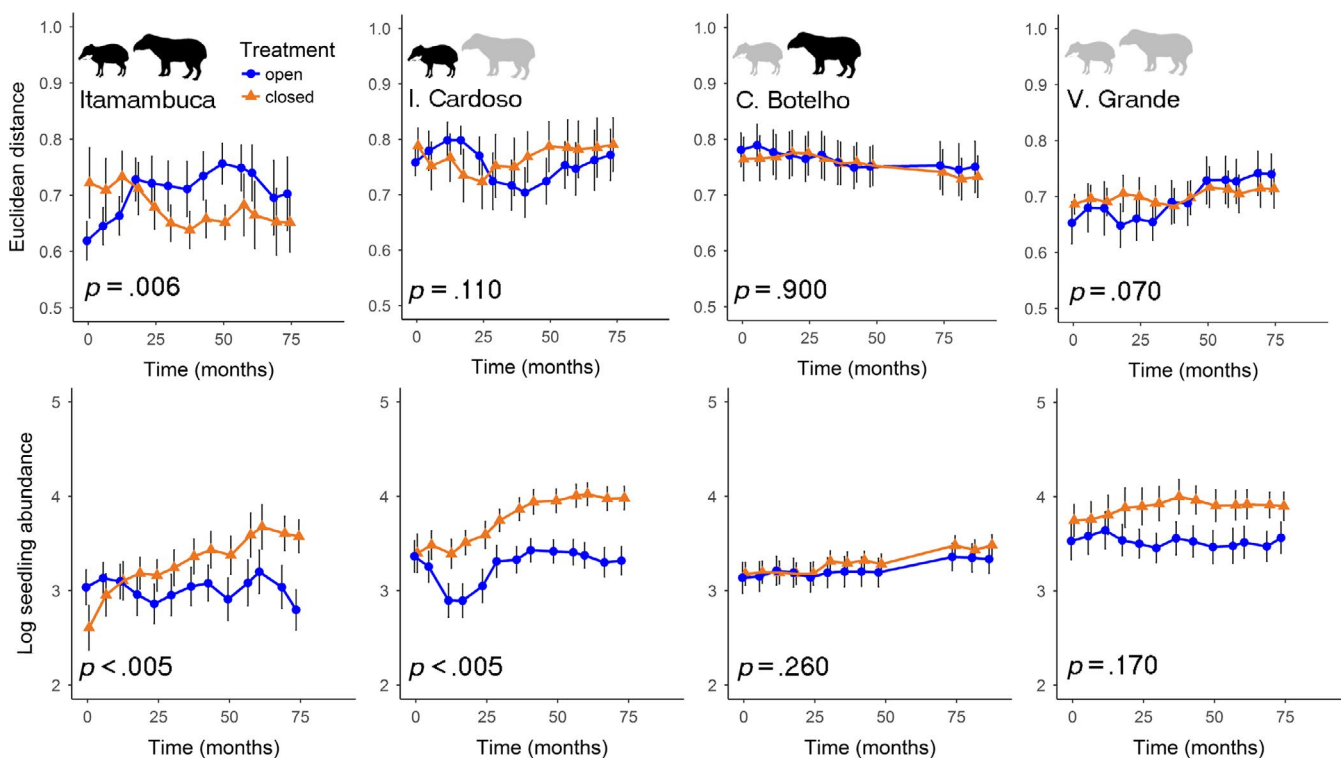
To test the hypothesis that large herbivores affected biodiversity by limiting the abundance of dominant plant species, we further examined differences in beta and alpha diversity and recruitment between treatments for dominant and rare species subsets independently for the region where WLPs and tapirs were present (ITA). This was done in an analogous way to the one described in the previous paragraph. Rare species were defined as those showing up to two individual seedlings across the whole nine enclosure plots at any one time, otherwise were considered as dominant species. Note that this classification does not make any assumption about the abundance of species in open plots (e.g. one species could be rare in enclosures but abundant on controls or vice-versa). We also performed Kendall rank correlation tests to check, for every treatment and site combination independently, whether rank abundances of plant species changed through time relative to the original state. The underlying hypothesis we wanted to check with such tests was that only control plots were temporally

dynamic in terms of ranked vegetation composition. We performed such tests using the full community composition and, in addition, using the dominant species subset (defined as in the previous paragraph). Tests were not performed for rare species because, by definition, rare species show very low abundances at any one time, precluding the use rank correlation tests.

We performed model exploration prior to model selection in order to assess for violations of assumptions underpinning linear models (Zuur, Ieno, & Elphick, 2009). Explorations suggested the need to log-transform palm abundance (as explanatory variable) in tests of alpha and Jaccard beta diversity. In addition, they discarded any seasonal signal in the dataset, so we did not include season as a covariate. A Gaussian distribution and the identity link function were used to model the response variables in GLMMs, except in the case of abundances where the Poisson distribution and a log link function were used. We used R (R Core Team, 2017) and packages *vegan* (Oksanen et al., 2017) to calculate Euclidean and Jaccard distances, Hstar, Dstar and Estar; *nlme* and *lme4* (Bates, Maechler, Bolker, & Walker, 2015; Pinheiro, Bates, DebRoy, & Sarkar, 2017) to fit GLMMs, and *Kendall* (McLeod, 2016) for Kendall rank correlation tests. See Villar et al., 2019 for data.

### 3 | RESULTS

Seedling abundance increased substantially over time (e.g. more than doubled) in response to herbivore exclusion in areas where WLPs were present, regardless of the presence of tapirs (Figure 2, Table 1). Such



**FIGURE 2** The effect of experimental defaunation on Euclidean beta-diversity and seedling abundance for every one of the regions with a distinct large mammalian herbivore compositional combination. Figures show means ( $\pm$ SE) for each treatment and time step from the beginning of the experiment and  $p$ -values of the *treatment\*time* interaction denoting region-specific divergence in trajectories between treatments



results validate our assumption about the distinct functional role of these large herbivores as consumers, with WLPs but not tapirs strongly limiting plant recruitment. However, contrary to our predictions, neither alpha nor beta diversity changed in response to herbivore exclusion in areas where either large herbivores species were present in isolation (Tables 1 and 2). These results do not support the hypothesis that high seed and seedling predation by WLPs alone increases alpha diversity and decreases beta diversity, neither they support a homogenizing effect of tapir seed dispersal on plant communities.













Surprisingly, abundance- and incidence-based beta diversity changed only in the area where both herbivore species were present, decreasing over time in the enclosure but not in the control treatment. Both measures of beta diversity showed highly similar qualitative and quantitative results within and across regions (Table 1). However, neither index of alpha diversity measured (Hstar, Dstar or Estar) changed their temporal trajectories in response to herbivore exclusion on this or any other region (Table 2). Thus, the presence of both herbivores on the same region appeared to result in synergic rather than additive effects towards increasing beta diversity of seedling communities, without any changes in alpha diversity at the community level.





A closer look at the region where both WLPs and tapirs were present revealed that changes in beta diversity and seedling abundance resulting from simultaneous experimental exclusion of both herbivores were exclusively driven by changes in the dominant

species set (Figure 3 and Table S2, SI Appendix). The combination of both herbivores on the same region resulted in increased local evenness and beta diversity of dominant species, but decreased alpha diversity of rare species. Beta diversity of dominant species decreased and abundance increased over time on enclosure plots at this region, but not on control plots. Likewise, Estar (evenness) of dominant species decreased over time on enclosures but not on controls, whereas neither Hstar (diversity) nor Dstar (Hill numbers) of dominant species showed a clear trajectory over time or in response to treatment. These results suggest that the combination of both herbivores on the same region limited the recruitment of dominant species, with a subsequent increase in evenness among dominant and subdominant species. Paradoxically, increased evenness did not result in more diverse and homogeneous communities (higher alpha diversity), but rather in more distinct communities (higher beta diversity).

In addition, we found no changes in beta diversity, seedling abundance or Estar over time or in response to experimental treatment for rare species at the region where both WLPs and tapirs were present. In contrast to dominant species, changes in rare species were restricted to Hstar and Dstar, with no net changes over time in control plots, but a substantial increase in enclosures. Thus, results suggest that, in addition to regulate recruitment of dominant species, these herbivores strongly reduced the number of rare species that entered the local community pool.

**TABLE 1** Results of repeated measures tests for region-specific differences between control and enclosure plots for beta diversity (Euclidean distance after Hellinger transformation, Jaccard distance) and seedling abundance

Diversity metric	Regional composition	Treat		Time		Treat*time	
		Estimate	<i>p</i>	Estimate	<i>p</i>	Estimate	<i>p</i>
Euclidean		0.0461 (0.0317)	.148	0.0011 (0.0006)	.073	-0.0020 (0.0007)	<.01
		-0.0199 (0.0236)	.401	-0.0004 (0.0004)	.406	0.0009 (0.0006)	.110
		-0.0045 (0.0197)	.821	-0.0004 (0.0004)	.265	-0.0001 (0.0004)	.900
		0.0419 (0.0226)	.065	0.0013 (0.0004)	<.01	-0.0009 (0.0005)	.070
Jaccard		0.0319 (0.0172)	.066	0.0005 (0.0003)	.140	-0.0011 (0.0003)	<.01
		-0.0024 (0.0138)	.860	-0.0002 (0.0002)	.384	0.0004 (0.0003)	.217
		0.0021 (0.0123)	.862	-0.0001 (0.0002)	.678	-0.0001 (0.0003)	.637
		-0.0138 (0.0128)	.283	0.0003 (0.0002)	.228	0.0000 (0.0003)	.882
Log abund.		-0.1466 (0.0795)	.065	0.0003 (0.0021)	.875	0.0113 (0.0017)	<.01
		0.2685 (0.0635)	<.01	0.0033 (0.0016)	.041	0.0059 (0.0014)	<.01
		-0.0104 (0.0565)	.853	0.0024 (0.0013)	.071	0.0013 (0.0012)	.260
		0.2608 (0.0840)	.002	-0.0010 (0.0019)	.600	0.0026 (0.0019)	.170

Note: The table shows estimates and tests results for the main effects of treatment (*Treat*), time and for the interaction between treatment and time (standard errors in brackets). Main *Treat* effects reflect net pre-experimental differences of enclosures from control plots, time effects reflect net temporal trends on open control plots, and their interaction is the “true” experimental effect reflecting net divergent temporal trajectories of enclosures from controls. Regions:  = Itamambuca (both tapir and WLP present);  = Ilha do Cardoso (tapir absent);  = Carlos Botelho (WLP absent);  = Vargem Grande (both tapir and WLP absent).

**TABLE 2** Results of repeated measures tests for region-specific differences between control and enclosure plots for alpha diversity of the complete plant community

Diversity metric	Regional composition	Treat		Time		Treat*time	
		Estimate (SE)	p	Estimate	p	Estimate	p
Hstar		-0.086 (0.092)	.351	-0.003 (0.002)	.103	0.002 (0.002)	.392
		0.127 (0.108)	.242	-0.008 (0.002)	<.01	0.002 (0.003)	.548
		0.053 (0.128)	.682	-0.001 (0.002)	.487	0.000 (0.003)	.879
		0.585 (0.110)	<.01	-0.000 (0.002)	.899	0.003 (0.003)	.209
Dstar		-0.427 (0.304)	.163	-0.010 (0.006)	.138	0.005 (0.007)	.461
		0.748 (0.437)	.089	-0.029 (0.008)	<.01	0.002 (0.010)	.819
		0.153 (0.610)	.802	-0.010 (0.009)	.292	0.002 (0.013)	.869
		2.400 (0.453)	<.01	0.001 (0.008)	.885	0.013 (0.010)	.203
Estar		-0.085 (0.025)	<.01	-0.001 (0.000)	.172	0.000 (0.001)	.436
		-0.061 (0.032)	.052	-0.002 (0.001)	.018	0.000 (0.001)	.692
		-0.069 (0.023)	<.01	-0.000 (0.000)	.351	0.000 (0.000)	.738
		0.043 (0.023)	.060	0.000 (0.000)	.071	0.000 (0.001)	.632

Note: The table shows estimates and tests results for the main effects of treatment (*Treat*), time and for the interaction between treatment and time (standard errors in brackets). Main *Treat* effects reflect net pre-experimental differences of enclosures from control plots, time effects reflect net temporal trends on open control plots, and their interaction is the “true” experimental effect reflecting net divergent temporal trajectories of enclosures from controls. None of the interactions were significant. Regions: = Itamambuca (both tapir and WLP present); = Ilha do Cardoso (tapir absent); = Carlos Botelho (WLP absent); = Vargem Grande (both tapir and WLP absent).

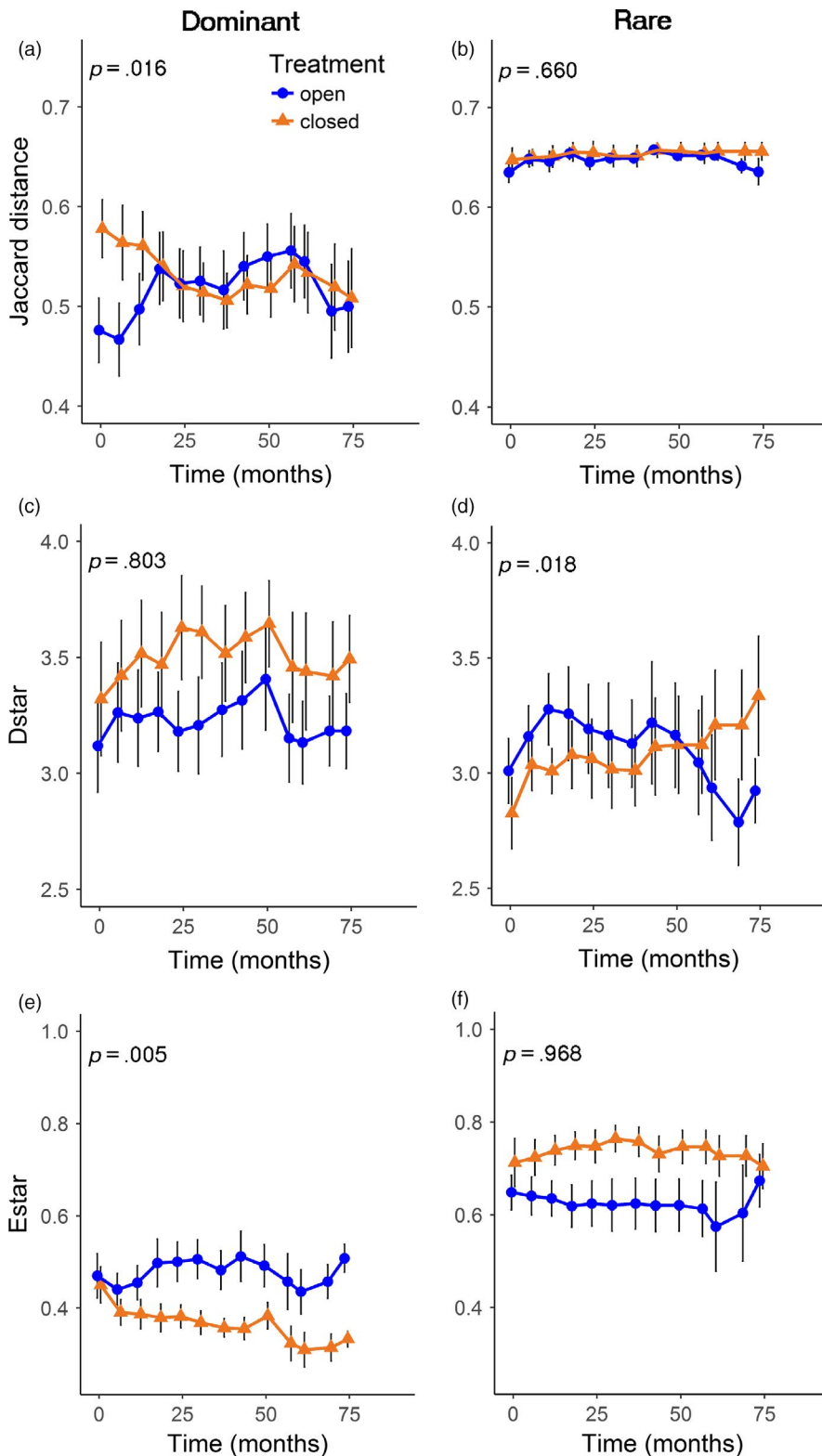
Further results suggested that control plots at the site where both WLPs and tapirs coexist were temporally more dynamic in terms of vegetation composition than plots at any other treatment\*site combination, and supported that this was a result of temporal turnover amongst dominant species. Rank correlation tests applied to every treatment and site combination independently suggested that at the community level (e.g. all species included), rank abundances did not change over time for any of the treatment or regions (SI Appendix, Table S3). However, restricting these tests to the dominant species subset revealed that the simultaneous presence of both herbivores on control plots resulted in changes in rank abundances amongst dominant species through time – for example, by allowing some subdominant species to escalate across the community ladder (ITA, Table S4, SI Appendix). In particular, species such as *Phanera microstachya*, *Asplenium seriale* and *Psychotria nemorosa* increased their share of the community respective to other dominant species such as *Euterpe edulis* (by far the most abundant species, see Table SI and Figure S1, SI Appendix), *Geonoma gamiova*, *Inga marginata* or *Mollinedia schottiana* at certain points in time.

## 4 | DISCUSSION

Our results indicate that neither top-down regulation of recruitment by a major seed and seedling predator nor potential-assisted

dispersal by a major seed disperser in isolation were sufficient to increase the alpha diversity of rare species, despite demographic control of dominant species. On the contrary, results suggest potential functional complementarity between large generalist mammalian seed and seedling predators and seed dispersers in promoting beta diversity of early-recruiting seedling communities in tropical forests at the landscape scale. Contrary to expectations, higher beta diversity resulted from a strong interaction between large herbivores and dominant plant species assemblages in detriment of rare species, contradicting some of the common assumptions about the effects of large generalist herbivores on the diversity and assembly of their plant resources in tropical forests.

Neither herbivore in isolation appeared to have any noticeable effect on plant diversity patterns. Despite strong demographic control, WLP predation did not suffice to increase local diversity amongst seedling communities as predicted by the Janzen–Connell model. Differences in abundances of WLP and tapirs between regions might have contributed to the patterns observed. However, differences in recruitment between control and enclosure plots in both regions where WLPs were present were of similar magnitude, suggesting similar levels of predation on seedlings by large- and medium-sized mammals. Likewise, the net effects of tapirs on seedling recruitment appear negligible at both sites where they occurred. Thus, it is highly unlikely that differences between such sites might be due to interference from relative abundance differences in the



**FIGURE 3** The effect of experimental defaunation on incidence-based (Jaccard) beta-diversity, alpha diversity (Dstar) and evenness (Estar) for dominant (a, c, e) and rare (b, d, f) species at the region where both tapir and white-lipped peccaries were present (Itamambuca). Figures show means ( $\pm$ SE) for each treatment and time step from the beginning of the experiment and  $p$ -values of the *treatment\*time* interaction denoting region-specific divergence in trajectories between treatments. Results for Jaccard beta-diversity were qualitatively and quantitatively analogous to the ones obtained using Euclidean (abundance-based) distances

two focal herbivore species. Potential confounding effects of background differences in the wider community of mammals between regions are also unlikely, as all regions share a similar large and medium-sized ground-dwelling mammalian composition apart from differences in local extinctions of WLP and tapir (Galetti et al., 2017). Kurten and Carson (2015) proposed that compensatory predation

from mesoconsumers could lead to decreased plant recruitment and diversity when released from larger competitors such as WLPs or tapirs. In our experiment, medium-sized mammal species such as agoutis (*Dasyprocta* spp.), pacas (*Cuniculus paca*), brocket deer (*Mazama* spp.) or collared peccaries (*Pecari tajacu*) were common but, as our results suggest, were nevertheless unable to impose compensatory



herbivory in the absence of WLPs or even tapirs. Small mammals, though abundant and diverse, were able to permeate through the fences, so that interference from this mammal group is also discarded. In summary, our results clearly suggest that differences in the response of plant communities between regions genuinely reflect differences in composition of the two focal species of large herbivores.

Since the isolated effect of tapir browsing on seedling demography was negligible on the region with no WLPs, the synergic contribution of tapirs to the patterns observed when in combination with WLPs cannot be a result of tapir's antagonist effects. A more intuitive explanation concurrent with detailed knowledge of tapir's natural history involves its seed dispersal function (O'Farrill et al., 2013). Given tapir's solitary habit, large-scale movements, broad diet and large latrines (Fragoso, Silviu, & Correa, 2003; O'Farrill et al., 2013; Pires, Guimarães, Galetti, & Jordano, 2018), it is likely that this generalist seed disperser might contribute towards the maintenance of higher compositional beta diversity by simultaneous stochastic long-distance aggregated seed dispersal events and localized disturbance (Fragoso et al., 2003). If that were the case, our study would indicate that the mutualistic effect of assisted dispersal by tapirs does not suffice for successful colonization of new patches, and that the strong antagonistic consumer effects of the WLP are also needed to provide new opportunities for successful colonization by dispersers into new patches, and vice versa.

As a generalist consumer, the WLP might limit recruitment of seedlings through predation of abundant fruits and seedlings. Our results support this prediction, showing that decreases in recruitment in open plots were exclusively linked to reductions in the number of recruits from dominant species. It is possible that assisted generalist dispersal by tapirs can aid to increase recruitment of regionally abundant species successfully away from mother trees by allowing potential recruits to escape from the high levels of predation and parasitism from specialized enemies under parent trees. In turn, the antagonistic effect of generalist predation might limit landscape-scale recruitment of common species, hence generating new opportunities for successful colonization by dispersers into new patches. Despite several studies have suggested that seed dispersal by large herbivores might be a relevant process contributing towards tropical forest diversity, our experiment provides the first large-scale experimental evidence suggesting that only when in combination with predation this might be the case. In grassland ecosystems, for example, manipulative studies suggest that disturbance is a far more critical mechanism regulating diversity structure than dispersal (Catano, Dickson, & Myers, 2017; Myers & Harms, 2009). However, our results challenge the current view that the impact of large herbivores on tropical forest diversity results exclusively from antagonistic effects.

Despite the well-defined functional roles of WLPs and tapirs as consumers, other non-mutually exclusive mechanisms might contribute to generate synergic effects. Given the large size of tapirs and the large number of individual peccaries found in herds, for example, these large herbivores might differentially redistribute

substantial amounts of limiting soil nutrients among their feeding patches (Malhi et al., 2016; Ripple et al., 2015). It is also possible that the mechanical disturbance from large herbivores influences the physical structure of the soil, vegetation cover on the understory, soil biochemistry, microorganism communities and nutrient cycling, as reported in grassland ecosystems (Frank, McNaughton, & Tracy, 1998). Ultimately, these mechanisms might influence competitive relationships among plant species and affect the outcome of community assembly (Augustine & McNaughton, 1998; Borer et al., 2014; McNaughton, 1985). However, the relevance of these mechanisms is still cryptic and still needs to be evaluated experimentally on tropical forests.

A further insight into consumers' effects on the community assembly of resources is provided by the strong link detected between large tropical herbivores and dominant plant species. The combination of WLPs and tapirs on the same region increased evenness amongst the dominant plant community on the open plots. Such increase was accompanied by temporal changes in rank abundance that contributed to higher beta diversity, suggesting that large herbivores eased some subdominant species to "climb up" along the dominant community "ladder". Equivalent regulating effects in dominance by herbivores have been reported for grassland ecosystems (Borer et al., 2014; Mortensen et al., 2017). However, unlike in those systems, higher evenness in our experiment was insufficient to lead to higher alpha diversity (Hstar or Dstar) amongst dominant species. Furthermore, results indicate a strong reduction of alpha diversity amongst rare species in the presence of both species. This suggests that these large herbivores might facilitate internal shifts in dominance amongst abundant species in net detriment of rare species, which showed higher alpha diversity at experimentally defaunated plots. Thus, it appears that these functionally complementary large herbivores pose a strong selection filter on rare species, reducing community size of rare species at the local scale whilst promoting stochastic distribution of the most dominant species at the landscape scale. Whether this results from increased spatial flows among patches or other mechanisms would need further evaluation. Nevertheless, because large herbivores have substantial differential impacts on the demography of dominant and rare species, they might have a substantial role in community assembly and contribute towards the increased level of density dependence in rare species reported elsewhere (Comita, Muller-Landau, Aguilar, & Hubbell, 2010).

Tropical forests are hyper-diverse ecosystems where overlapping antagonism and mutualisms between consumers and resources are ubiquitous. Despite some limitations common to large-scale experiments in challenging locations, our multi-region replicated experiment along functional gradients of defaunation unveils some directional patterns that do not fit within mainstream perceptions on the functional role of large herbivores in tropical forests. An increasing body of experimental evidence suggests that the isolated role of large herbivore predation on the regulation of diversity in tropical forests is yet uncertain and might vary with the wider community composition of herbivores (Clark et al., 2012;

Kurten & Carson, 2015; Kurten et al., 2015; Paine et al., 2016). A synergic role of mutualists and antagonists in the regulation of tropical forest diversity is an understated possibility that requires more attention. Rather than homogenize plant communities, functional complementarity between generalist consumers might in fact reinforce the regulation of diversity through spatiotemporal feedbacks and provide larger spatial insurance and compositional turnover over space and time (Shanafelt et al., 2015; Wilcox et al., 2017). Indeed, the patterns observed in our study resemble predictions from meta-ecosystem models that link high rates of herbivore movement to spatially heterogeneous equilibria and increased ecosystem function (Marleau et al., 2014), suggesting that functional complementarity amongst tropical forest consumers might be critical for ecosystem dynamics. Our results contrast with studies in grassland ecosystems, where both herbivory and dispersal are thought to increase alpha diversity but not net beta diversity in herbaceous communities (Catano et al., 2017; Myers & Harms, 2009), suggesting a homogenizing role of large herbivores in such systems. We propose that future studies should aim to evaluate how interactions between predation and assisted dispersal regulate the spatiotemporal structure of diversity and ecosystem function and dynamics in forest ecosystems, and investigate whether the result from those interactions differs between grassland and forest ecosystems.

## ACKNOWLEDGEMENTS

We thank the Fundação de Amparo a Pesquisa do Estado de São Paulo (BIOTA/FAPESP – grant 2014/01986-0; grant 2013/50424-1) for financial support. N. Villar received a FAPESP Postdoctoral Fellowship (2015/11521-7). G.B., C.R.B. and L.H. received a fellowship from CAPES. M.G. receives a fellowship from CNPq. We thank the Instituto Florestal and Fundação Florestal do Estado de São Paulo for allowing our research in nature reserves. We also acknowledge all the hard work from students, technicians, nature reserve personnel and other collaborators that contributed to make this research possible. We thank Sergio Nazareth for maintaining the plots and the field team in high mood.

## AUTHORS' CONTRIBUTIONS

M.G. and V.Z. designed the experiment; M.G., N.V., T.S., V.Z. and P.J. conceived the manuscript; V.Z., F.F., G.S., L.H. and C.R.B. collected the data; N.V. and T.S. analysed the data; N.V. wrote the first draft; N.V., T.S., V.Z., F.F., P.J. and M.G. contributed towards the final version of the manuscript.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.88d5v17> (Villar et al., 2019).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Villar N, Siqueira T, Zipparro V, et al. The cryptic regulation of diversity by functionally complementary large tropical forest herbivores. *J Ecol.* 2019;00:1–12. <https://doi.org/10.1111/1365-2745.13257>