

RESEARCH ARTICLE

Nature-based solutions for a changing world

Large wild herbivores slow down the rapid decline of plant diversity in a tropical forest biodiversity hotspot

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Abstract

1. The UN declaration of the Decade of Ecosystem Restoration 2021–2030 emphasizes the need for effective measures to restore ecosystems and safeguard biodiversity. Large herbivores regulate many ecosystem processes and functions; yet, their potential as a nature-based solution to buffer against long-term temporal declines in biodiversity associated with global change and restore diversity in secondary forests remains unknown.
2. By means of an exclusion experiment, we tested experimentally the buffering effects of large wild herbivores to avert against long-term biodiversity collapse in old-growth and secondary tropical forests in the Atlantic Forest of Brazil where sapling abundance and species richness declined c. 20% over the course of 10 years. The experiment comprised 50 large herbivore enclosure-open control plot pairs (25 at the old-growth forest and 25 at the secondary forest), where 2 m² were monitored in every plot during a 10-year period.
3. Large herbivores were able to decelerate diversity declines and compositional change in the species-rich old-growth forest, but only decelerated compositional change in the secondary forest. In contrast, declines in species richness and abundance were unaffected by large herbivores on either forest.
4. The buffering effects of large herbivores were strongly nonlinear and contingent on the initial level of diversity at the patch scale: highly diverse communities suffered the strongest collapse in the absence of large herbivores. Thus, larger buffering effects of large herbivores on the old-growth forest are the logical consequence of large herbivores buffering the many high diversity plant communities found in this forest. Conversely, as the secondary forest held fewer high diversity patches, buffering effects on the secondary forest were weak.
5. *Synthesis and applications.* Our study indicates that large herbivores have moderate yet critical effects on slowing down community change and diversity loss of highly diverse plant communities, thus suggesting that the conservation of (and potentially trophic rewilding with) large herbivores is a fundamental nature-based solution for averting the global collapse of the strongholds of biodiversity. Its buffering effects on biodiversity loss operate at very small spatial scales, are likely

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contingent on successional stage and are most effective in old-growth or high-diversity secondary forests.

KEYWORDS

defaunation, ecosystem services, long-term experiment, nature-based solutions, peccary, rewilding, Tapir, tropical forest

1 | INTRODUCTION

As we enter the UN Decade of Ecosystem Restoration (United Nations, 2019), it is imperative to devise restoration options that avert the long-term decline of global biodiversity. Large herbivores (hereafter LHs) engineer ecosystem processes through trophic and non-trophic pathways (Dirzo et al., 2014; Forbes et al., 2019) and have a pivotal role in the regulation of plant diversity (Bakker et al., 2006; Jia et al., 2018). However, an elusive critical missing piece of evidence pertains to the capacity of LH to buffer against long-term temporal declines in biodiversity common to many of the world's ecosystems. Allegedly, this is one of the most central questions underpinning the functional significance of LH, and a fundamental one for underpinning ecosystem restoration through LH conservation and rewilding in the face of the rapid global decline of biodiversity. It has been proposed that LHs might potentially mitigate the effects of climate change, invasive species and other impacts of global change on ecosystems and biodiversity, yet empirical tests of these hypotheses are still remarkably scarce (Bakker & Svenning, 2018).

The ecological functions of LH in tropical forests are less understood than in other ecosystems where these have been the subject of experimental studies over many decades (Forbes et al., 2019; Villar et al., 2020). Recent experimental manipulations suggest that the LHs affect a number of key ecosystem functions and processes in tropical forests, from beta diversity to nutrient cycling (Galetti et al., 2021; Villar et al., 2020, 2021). Ironically, illegal hunting (Benítez-López et al., 2017) and roadkill (Ascensão et al., 2019; Medici & Abra, 2019; Medici & Desbiez, 2012) among other anthropogenic impacts (Galetti et al., 2021) are decimating populations of tropical forest herbivores at alarming rates so that identifying their ecological functions is becoming as urgent as increasingly challenging.

Tropical rainforests are subjected to unprecedented anthropogenic pressures that compromise their integrity and erode their diversity. Tree loss, widespread defaunation, changes in the functional structure of interactions and the emergence of fire threaten to drive many of such hyper-diverse ecosystems into a nonlinear process of floristic and faunal savannization (Alroy, 2017; Emer et al., 2020; Galetti et al., 2021; Sales et al., 2020; Staal et al., 2020). To halt the ecological meltdown of these hyper-diverse ecosystems, effective conservation and restoration measures are required to preserve the diversity in both old-growth and secondary tropical forests (Rozendaal et al., 2019).

Within that context, reversing defaunation of tropical forests through LH conservation and rewilding might contribute to restore

lost ecosystem processes and functions (Galetti et al., 2021; Pires et al., 2018; Villar et al., 2020, 2021) and accelerate ecosystem recovery (Root-Bernstein et al., 2017), yet this option is not in the agenda of most ambitious large-scale restoration initiatives (Brancalion et al., 2019; Rodrigues et al., 2009). Indeed, trophic rewilding with LH in particular may help to reverse defaunation and conserve increasingly endangered LH populations, as well as restoring their ecological functions in benefit biodiversity (Svenning, 2016). However, as long as the ecological functions of native LH in tropical forests remain unclear, the consideration of LH conservation and rewilding as a nature-based solution for halting ecological meltdown and restoring biodiversity in tropical forests will remain elusive.

Here we report the first experimental test of the buffering effects of LH against long-term biodiversity collapse in tropical forests, and to our best knowledge, any other forest biome type. We conducted a LH exclosure experiment in old-growth and secondary tropical forests, followed the fate of 7,287 individual saplings and tracked the diversity decline of 100 plant communities in paired open and herbivore exclosure plots during a 10-year period in an isolated forest fragment undergoing rapid ecological meltdown in the highly fragmented Atlantic Forest of Brazil. During the 10-year duration of our study, sapling abundance and species richness declined circa or above a staggering 20%, providing a unique natural experiment to test for the functional significance of LH to avert long-term biodiversity collapse. We experimentally address the effects of LH on buffering precipitous declines in recruitment, diversity and rates of temporal change in community composition in both the old-growth and secondary forest. In doing so, we also explore another important unexplored issue on restoration and trophic rewilding studies: whether large herbivores might differentially affects old-growth versus secondary forests.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted our experiment on Morro do Diabo State Park (MDSP, Figure 1). The park is located in western São Paulo State (22°32'S, 52°18'W) and protects 370 km² of Atlantic Forest, one of the most threatened biomes on earth (Myers et al., 2000). The park includes a mosaic of old-growth and secondary deciduous forest (which account for about two-thirds vs. one-third of the extension of the park, respectively), surrounded by a matrix of cattle ranches and agriculture, mostly sugarcane. Smaller forest fragments (0.02–20 km²) are

scattered around MDSP, adding a total of 127 km² of forest. The park is part of the *plateau forests*, which distinguishes from the coastal Atlantic Forest by having lower annual rainfall and a marked dry season from May to September. The average annual temperature is 22°C, with an annual rainfall of 1,347 mm. Over the past 500 years, the Atlantic Forest has suffered large-scale destruction and fragmentation. In contrast to the eastern part of the biome, the process of deforestation in the plateau is relatively recent (c. 60 years). During the second half of the 20th century, MDSP suffered from increased isolation and fragmentation, as a consequence of the expansion of agriculture and livestock grazing in the region, construction of a major highway and an airport, and occasional small-scale fires. These and other details about the MDSP can be found in de Faria (2006).

2.2 | Experimental design

In July 2004, 50 fenced LH enclosure plots were constructed in the understory of two different areas of MDSP (Figure 1): 25 enclosures in old-growth forest (OGF) and 25 in secondary forest (SF). The exact age of the SF is unknown, but can be dated back to the late 1970s–early 1980s when effective conservation

management in the park started. The disturbance history of the SF includes both hunting and fires, but not cultivation. Control plots, where LH had access, were established 10 m to the right (in reference to the incoming direction from the main path) from the corresponding enclosure, so as to minimize variance within every enclosure-plot pair. Every enclosure-control plot pair was distributed at approximately 50 m distance from each other (Figure 1). The distance to edge of the central plot pair on the SF was 660 m and on the OGF, 2,700 m. Enclosures were designed to exclude the largest LH present at the site (see de Faria (2006) for more details about fauna in MDSP): tapirs (*Tapirus terrestris*), peccaries (*Tayassu pecari*, *Pecari tajacu*) and deer (*Mazama americana*, *Mazama gouazoubira*). The materials used were 1.5 m wooden fence posts and wire mesh (2 × 2 cm). Enclosures were 3 m wide, 6 m long and 1 m tall, and were open on the top. A gap of c. 20 cm was left around the bottom of the physical barrier to allow for the entrance of small terrestrial animals (Figure 1).

Within each enclosure, a central 1 × 4 m sampling area was established and divided into four 1 × 1 m quadrants (Figure 1). The outer 1 m wide buffer zone between the fence and the edge of the sampling area prevented the vegetation in the sampling area from being browsed from the outside and allowed the access to researchers

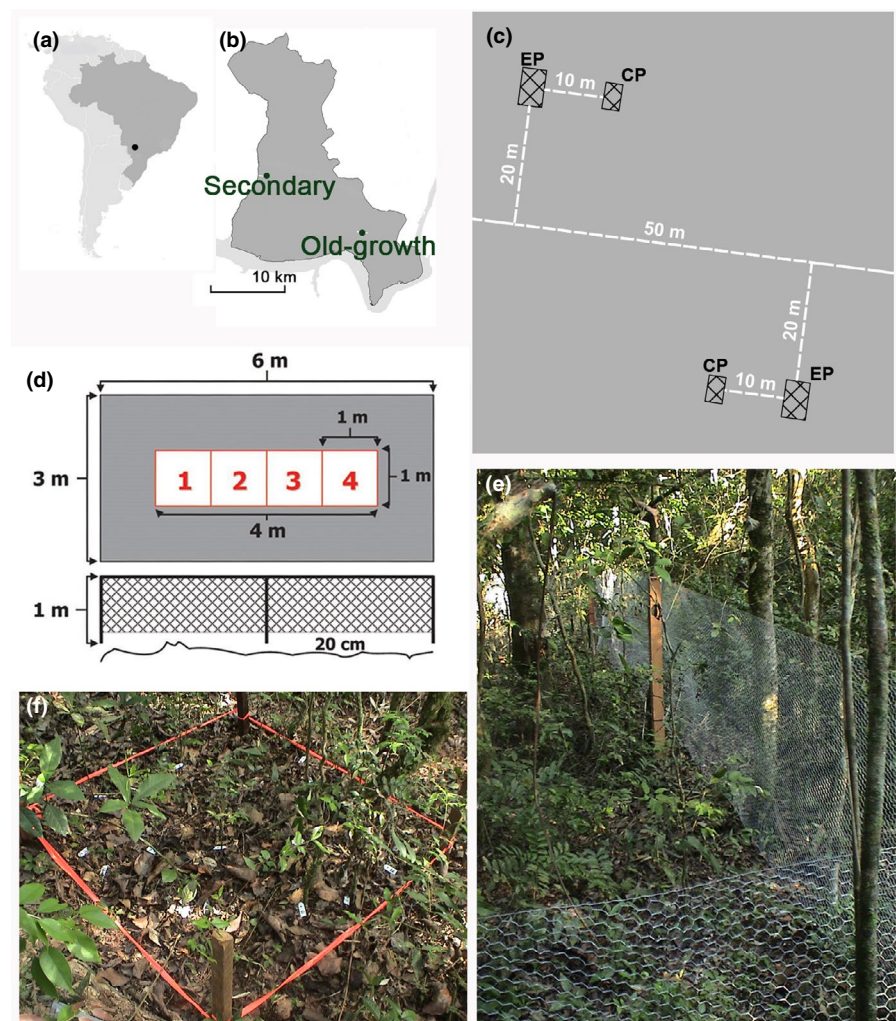


FIGURE 1 Experimental design. (a) Location of Morro do Diabo State Park, where the exclusion experiment was established in (b) old-growth and secondary forests. (c) shows an example of how plot pairs were distributed across the forests (EP = exclusion plots, CP = open control plots) and (d) shows the dimensions of enclosures, with subplots where sampling took place highlighted in red, and the 20 cm vertical gap at the base of the plot so as to allow access for small animals. Examples of enclosures and control plots are shown in (e) and (f), respectively

during sampling. Unfenced control plots were 1 m wide and 4 m long, divided into four 1×1 m quadrants. For each enclosure and control plot, two of the 1×1 m quadrants were randomly chosen to be sampled throughout the study (surveying the four quadrats per plot would have been logistically unattainable). A total of 200 m² was sampled in 100 enclosure and control plots.

In each of the 1×1 m sampling quadrants, all plants higher than 10 cm and diameter ≤ 5 cm were marked with PVC plaques and assigned a reference number and their fate followed through subsequent sampling surveys (Figure 1). New plants emerged during subsequent surveys which also meet the criteria were also incorporated to the monitoring protocol. As in other studies where taxonomic identification of tropical forests saplings is challenging and hereby not feasible for large replicated datasets, plants were separated into morpho-species (e.g. Condit et al., 2002), and always identified by the very same field assistant throughout the experiment, so as to keep consistency. During the first five years of the study (2004–2008), plant measurements were carried out twice a year, in the beginning of the wet season (October) and in the beginning of the dry season (April). During 2009–2012, data collection was carried out once a year. Final measurements took place in 2014, concluding 10 years of data collection (14 measurements).

Hunting is common on the very edges of the park, but very low within its boundaries, so that populations of large herbivores seem to be in good shape. For example, the park is home to roughly about 120 adult tapirs, with an estimated density of 0.30 ind./ha. Unpublished telemetry data on tapirs suggest that large herbivores use homogeneously both old-growth and secondary plots, and, in fact, three enclosures (two on the OGF and one on the SF) were 'destroyed' by tapirs towards the end of the experiment. Cattle are not allowed to roam through the park.

2.3 | Statistical analyses

We investigated the buffering potential of LH against long-term plant diversity collapse by examining their effects on sapling abundance, species richness and diversity, temporal diversity, and rate of directional compositional change. We hypothesized that experimental exclusion of LH would lead to a divergence in the trajectories of the time series of those descriptors, characterized by a larger decline on enclosures than on open plots where LH had access. Diversity was characterized through the inverse Simpson index (Chao et al., 2014) and temporal diversity, through mean rank shifts (hereafter *MRS*) and the directional rate of change. *MRS* describe relative changes in species rank abundances between surveys, with larger values indicating larger changes in species dominance between successive surveys (Collins et al., 2008). The rate of compositional change (hereafter *RCCh*) calculates differences in species composition between samples at increasing time intervals (Collins et al., 2000). When values of such differences are regressed against the time lag interval, the slope of the regression line is an indication of the rate and direction of compositional change in the community (e.g. a larger positive

slope indicating larger directional change in composition, see reference for details).

We tested for a divergence between treatments (open vs. LH enclosure) in the trajectories of the time series of every one of those descriptors using generalized linear mixed models (GLMMs). We analysed such divergences for every site (OGF and SF) independently. Abundances, species richness and diversity were modelled as the function of the interaction between treatment and time (years since the beginning of the experiment) as predictors (fixed effects). Initial inspection of data showed that for some parameters and sites, treatments differed in their initial conditions (e.g. the intercept, see Figure 2). However, by focusing on the temporal trajectories, our approach is robust and unaffected by those initial conditions (see e.g. Villar et al., 2020). To account for the nested nature of our experimental design and ensure pairwise interactions between paired plots, we included plot pair and plot within pair as random effects in all GLMMs. In addition, a thorough data exploration indicated that trajectories of *MRS* were nonlinear and showed some signs of seasonality in the OGF (see Figure 2); hence, we modelled *MRS* as the function of the interaction between treatment and a quadratic polynomial time factor plus an additive seasonal component (e.g. *MRS* in transitions from wet to dry season vs. transitions from dry to wet season, dry = June–November, wet = December–May). Finally, differences between treatments in the directional compositional changes in plant communities were assessed by regressing *RCCh* against the time (survey) lag interval and its interaction with treatment as fixed effects.

Additionally, we tested the hypothesis that the effect of LH exclusion on diversity was more severe on forest diversity 'hot patches' (patches within the forest with diversity-rich plant communities) than on diversity 'cold patches' (patches within the forest with diversity-poor plant communities). First, we calculated, for every plot, differences in inverse Simpson (hereafter *DiffSimp*) values between the onset and the end of the experiment. Then we modelled those differences as the function of the interaction between treatment and the log inverse Simpson values at the onset of the experiment (fixed effects). Generalized additive mixed models (GAMMs) were used, as exploration showed clear signs of a curvilinear nonlinearity in the relationship (see Figure 3). Plot pair was included as random effect to ensure pairwise contrasts between paired open and enclosure plots.

For abundances and species richness, we used GLMMs with a Poisson distribution fitted to residuals; for inverse Simpson, *MRS*, *RCCh* (GLMM) and *DiffSimp* (GAMM), we used a Gaussian distribution. Zero-inflated models were used when the distribution showed zero inflation. We report estimates and statistical significance for single terms in the models, and results from likelihood ratio tests of the treatment \times time interaction (linear time for abundances and indices of alpha diversity, linear and quadratic for *MRS*), treatment \times interval interaction for *RCCh* and treatment \times log inverse Simpson for *DiffSimp*. All analyses were performed in R (R Core Team, 2020), using packages 'lme4' and 'GLMMTMB' for GLMMs (Bates et al., 2015; Brooks et al., 2017), 'MGVC' for GAMMs (Wood, 2004) and 'HILLR' to extract diversity values (Li, 2018).

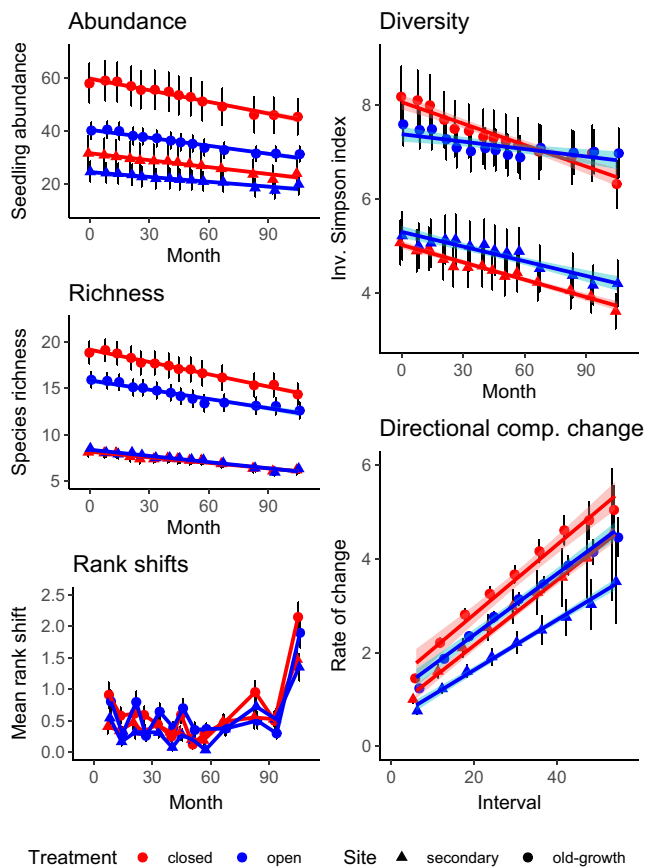


FIGURE 2 Effects of large herbivore exclusion on sapling communities of old-growth and secondary forests during a 10-year period in which sapling abundance and species richness declined c. 20%. Dots and triangles indicate mean values for every survey (except for directional compositional change), vertical bars show the SE, and lines show fitted relationships (see Section 2 for details)

3 | RESULTS

There was a clear long-term collapse in almost all indicators of plant communities in our experiment. Despite clear differences in background levels of abundance, species richness and alpha diversity of tree saplings between the old-growth and secondary forests, there was a long-term decline in all these aspects of plant communities in both forests (Figure 2). This was accompanied by a clear temporal directional change in plant community composition across both forest types (Figure 2).

Initial species richness on open and closed plots of the OGF (mean [SE]) were 15.92 [0.88] and 18.84 [1.22] respectively, for average seedling abundances of 40.16 and 58.08, respectively; on the SF, initial species richness on open and closed plots were 8.52 [0.52] and 8.12 [0.52], respectively, for average seedling abundances of 24.48 and 31.52, respectively. Sapling abundance and species richness declined substantially over the course of the experiment in both forests and treatments: abundance declined by 22.4% in open plots and 21.8% on closed plots of the OGF, and by 19.5% in open plots and 24.4% on closed plots of the SF; species richness

declined by 20.9% in open plots and 23.8% on closed plots of the OGF, and by 25.7% in open plots and 23.5% on closed plots of the SF. However, there was no effect of LH exclusion on the temporal decline of abundances (OGF: $\chi^2(1, N = 686) = 0.013, p = 0.909$; SF: $\chi^2(1, N = 692) = 0.275, p = 0.599$) or species richness (OGF: $\chi^2(1, N = 686) = 0.132, p = 0.717$; SF: $\chi^2(1, N = 692) = 0.158, p = 0.690$) at any of the forests (Figure 2).

Diversity also declined in both forests and treatments during the course of the experiment. On the OGF excluding LH accelerated the decline ($\chi^2(1, N = 686) = 26.584, p < 0.01$), whereas on the SF there were no differences between the trajectories of both treatments ($\chi^2(1, N = 692) = 0.830, p = 0.362$, Figure 2).

The effect of LH on tree sapling diversity strongly dependent on the initial sapling diversity. Forest diversity hot patches benefited the most from the buffering effect of LH (Figure 3). The net effect of LH exclusion on diversity followed a nonlinear trend with the background level of diversity so that diversity declined more severely on forest patches with highly diverse plant communities at the onset of the experiment on the exclusion treatment, while where LH had access, the decline was independent of background diversity (open treatment: estimated degrees of freedom (edf) = 1, $F = 2.16, p = 0.145$; closed treatment: edf = 1.95, $F = 14.62, p < 0.01$).

There was clear directional change in species composition through time in both forests and treatments, as indicated by an increasing rate of directional compositional change (Figure 2). Exclusion of LH accelerated community change in both the OGF ($\chi^2(1, N = 2,232) = 10.941, p < 0.01$) and the SF ($\chi^2(1, N = 2,250) = 6.519, p = 0.01$). Mean rank shifts in species abundances increased non-linearly towards the second half of the experiment in both forests (Figure 2) so that by the end of the experiment rank shifts were approximately three times larger than at the beginning of the experiment. However, there were no differences between the rank shift trajectories of both treatments at any of the forests (OGF: $\chi^2(2, N = 636) = 3.030, p = 0.220$; SF: $\chi^2(2, N = 642) = 0.108, p = 0.948$). In addition, on the OGF, but not on the SF, there was a seasonal effect, with more rank shifts on transitions from dry to wet seasons than from wet to dry seasons (Figure 2; Table 1).

4 | DISCUSSION

To our best knowledge, our study provides the first experimental test on the role of LH in slowing down the long-term collapse of biodiversity. Results suggest that LHs are able to decelerate long-term diversity loss and compositional change in diversity-rich tropical forests undergoing long-term biodiversity collapse. Furthermore, our study indicates that the buffering effects of LH prevent dramatic declines in diversity on forest diversity hot patches so that LH conservation and trophic rewilding could play a key role in preserving biodiversity strongholds even at a very fine spatial scale.

Forest ecosystems are facing unprecedented challenges due to multiple anthropogenic pressures. Our field site is a catalogue

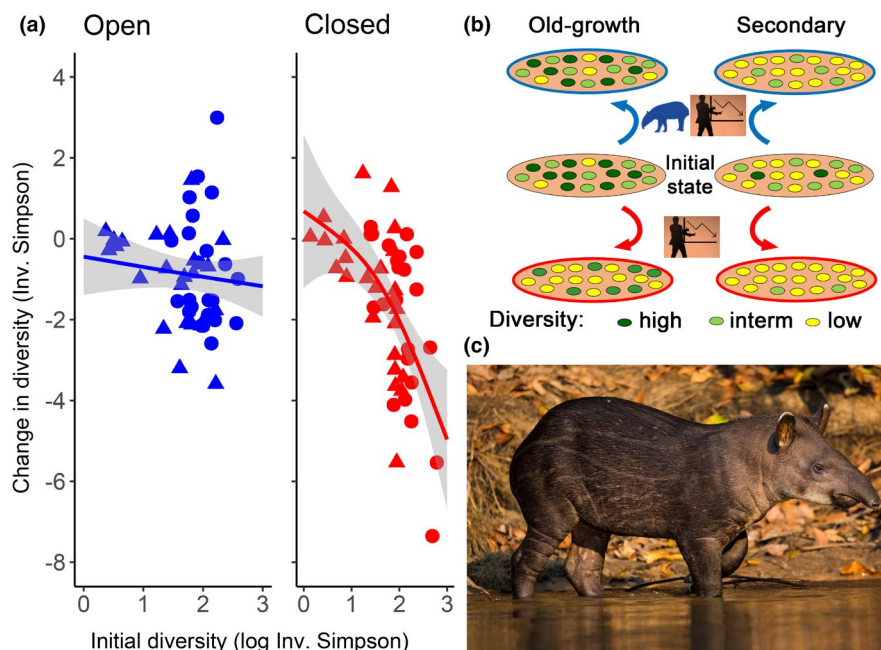


FIGURE 3 (a) Buffering effects of large herbivores are stronger in forest diversity 'hot patches'. Over the 10-year period, diversity decreased strongly nonlinearly with increasing initial diversity at the beginning of the experiment on closed plots, but not on open plots. Circles correspond to old-growth plots, triangles to secondary forest plots and lines are fitted relationships (see Section 2 for details). (b) Conceptual framework showing how large herbivores effects operating at the patch scale can differentially buffer old-growth forests but not secondary forests. In the absence of large herbivores (red arrows), both old-growth and secondary forests lose diversity, but effects are more acute on old-growth forests because they hold a large number of (local) diversity hot patches. In contrast, when large herbivores are present (blue arrows), diversity losses in old-growth forests (but not on secondary forests) are minimized because of their additive buffering effects at the local scale. (c) The lowland tapir *Tapirus terrestris*, the largest wild herbivore at Morro do Diabo State Park and across the Atlantic Forest

of the many challenges experienced by tropical forests. In addition to isolation, hunting on the edges of the park is common. Infrastructure is another major disturbance, including a major highway crossing the park—causing habitat fragmentation and road kill of fauna—and the disturbance legacy of the construction of an already abandoned railway across the park. The use of toxic products and fire in sugarcane plantations in areas adjacent to the park is very common. Myriads of intentional fires originated intentionally so as to clear land for grazing, and others during the construction of the highway. Major fires took place during the second half of the last century, some of which persisted for 20 days through the dry period. Felling for timber extraction has also been a major issue. Similar threats are widespread and ongoing across the Atlantic Forest (Galetti et al., 2021) and many other forests globally. We believe such disturbances might be behind the dramatic decline of sapling recruitment and species richness in the park, reflected in the temporal trajectories of our plots.

Nevertheless, tropical forests require effective conservation and restoration measures to preserve and restore their diversity (Rozendaal et al., 2019). LH conservation and trophic rewilding are increasingly perceived as important tools for restoring forest ecosystems and averting the acute effects of global change on biodiversity on other ecosystems, but such nature-based solutions are not currently perceived as a mainstream conservation option for tropical forest ecosystems by stakeholders and practitioners.

4.1 | Large herbivores preserve the strongholds of diversity

A prominent outcome of our study is the evidence that LHs have a higher and strongly nonlinear buffering effect on safeguarding diversity on forest diversity hot patches than on cold patches: local patches where LH were experimentally removed suffered a larger collapse if their initial levels of diversity were larger (Figure 3), independently of whether they were located in an OGF or SF. However, since OGF are essentially a 'collection' of many highly diverse plant community patches, the buffering effect of LH at small spatial scales add up to a major buffering effect in an OGF. Conversely, as SF holds few highly diverse plant community patches, LH effects were modest. From a fundamental ecology standpoint, these results shed some light into the context dependency of LH effects (Jia et al., 2018; Koerner et al., 2018).

From an applied standpoint, such findings indicate that LH conservation and rewilding could be most effective in buffering against strong long-term diversity declines in well-preserved tropical forests with high levels of plant diversity. Since such forests hold abundant and diverse resources for LH (in the case of Neotropics most larger herbivores feed primarily fruits which are more abundant on continuous old-growth forests; Pessoa et al., 2017), these restoration option would disclose a positive feedback between consumer and resource

TABLE 1 Results of statistical analyses on the effects of LH exclusion on the temporal trajectory of different aspects of plant communities at Morro do Diabo State Park. The table shows estimates and significance of individual model terms and also whether the net effects of LH exclusion were positive (+), negative (−) or neutral (Ø). 'C' = closed plots

	Old-growth forest				Secondary forest			
	Estimate	SE	p	Net exclusion effects	Estimate	SE	p	Net exclusion effects
Abundance	Int: 3.614	0.109	<0.01	Ø	Int: 2.928	0.154	<0.01	Ø
	Treat C: 0.298	0.110	<0.01		Treat C: 0.134	0.118	0.255	
	Time: −0.036	0.004	<0.01		Time: −0.037	0.005	<0.01	
	Time × C: 0.000	0.004	0.909		Time × C: −0.003	0.006	0.599	
Richness	Int: 2.726	0.0731	<0.01	Ø	Int: 2.093	0.068	<0.01	Ø
	Treat C: 0.168	0.085	0.048		Treat C: −0.037	0.084	0.656	
	Time: −0.029	0.006	<0.01		Time: −0.035	0.008	<0.01	
	Time × C: −0.003	0.007	0.716		Time × C: 0.004	0.011	0.690	
Diversity	Int: 7.402	0.496	<0.01	−	Int: 5.264	0.448	<0.01	Ø
	Treat C: 0.676	0.596	0.257		Treat C: −0.293	0.448	<0.01	
	Time: −0.074	0.016	<0.01		Time: −0.101	0.012	<0.01	
	Time × C: −0.114	0.022	<0.01		Time × C: −0.016	0.017	0.362	
M. Rank shift	Int: 0.887	0.144	<0.01	Ø	Int: 0.646	0.144	0.010	Ø
	Treat C: 0.245	0.193	0.196		Treat C: 0.031	0.193	<0.01	
	Time: −0.315	0.070	<0.01		Time: −0.276	0.070	0.847	
	Time ² : 0.040	0.007	<0.01		Time ² : 0.039	0.007	<0.01	
	Season Wet: −0.155	0.062	0.012		Season Wet: 0.047	0.062	<0.01	
	Treat C × Time: −0.158	0.098	0.107		Treat C × Time: 0.026	0.098	0.369	
	Treat C × Time ² : 0.020	0.010	0.051		Treat C × Time ² : −0.003	0.144	0.750	
Dir. Rate change	Int: 1.091	0.194	<0.01	+	Int: 0.560	0.400	0.161	+
	Treat C: 0.010	0.110	0.367		Treat C: 0.181	0.182	0.321	
	Time: 0.402	0.018	<0.01		Time: 0.329	0.030	<0.01	
	Time × C: 0.085	0.026	<0.01		Time × C: 0.108	0.042	0.011	

diversity resulting in a win-win option for preserving the trophic interactions, structure and diversity in those hyper-diverse ecosystems while concomitantly facilitating the restoration of the functional processes fostered by LHs (Galetti et al., 2021; Villar et al., 2020, 2021).

Large Neotropical forest herbivores, such as peccaries and tapirs, directly affect understorey plant communities through mutualisms and antagonisms, such as seed and sapling predation, seed dispersal and trampling (Kurten et al., 2015; Villar et al., 2020), and indirectly through a number of other processes (Galetti et al., 2021). In another long-term study, Villar et al. (2020) speculated that the promotion of evenness by large herbivores among dominant species in understorey plant communities might have been the result of the interactive effects of high disturbance (caused by trampling and seed and sapling predation) and simultaneous seed dispersal operating at the patch scale and carried out by different herbivores with complementary ecological functions. It is possible that this might be also the case in our study, though our methodology does not allow to identify the exact mechanisms involved.

While our results indicate no buffering effects of LH on species-poor SF, they nonetheless show that biodiversity strongholds are highly sensitive to disappearance of LH.

It is important to consider that our results are, as always, contingent on our experimental design. For example, our experimental plots were located in one OGF and one SF, hence regional and local conditions and the absence of multi-site replicates might have partially influenced our results. Yet, long-term enclosure experiments like ours are very scarce in tropical forests (Kurten & Carson, 2015; Villar et al., 2020); thus, their outcome provides key evidence for the badly needed understanding of the functional role of large herbivores in tropical forests.

4.2 | Large herbivores partially buffer against directional compositional change

Many ecosystems around the world are going through rapid compositional changes (Dornelas et al., 2014). Our study indicates that

LH partially buffer against temporal compositional changes in both diversity-rich old-growth and diversity-poor secondary forests. Despite rank shifts increased nonlinearly in both forest types and treatments, directional rate of change in composition increased more rapidly on plots where LHs were excluded. LH increase evenness in plant communities in a variety of ecosystem types (Jia et al., 2018), suppressing temporal bursts of dominance that prevent a few opportunistic species from monopolizing communities (Koerner et al., 2018; Mortensen et al., 2017). In that context, our combined results from MRS and temporal change in composition indicate that LHs slow down compositional change by delaying the process of incorporation of foreign dominant species into the community, promoting rank shifts within the existing community of plant species pool.

In the Atlantic Forest, a previous study also suggests that large herbivores' promotion of evenness and beta diversity is linked to rank shifts within the pre-existing subset of dominant and subdominant plant species (Villar et al., 2020). Indeed, wild LHs have been shown to protect plant communities against invasive species, though empirical evidence is still scarce and inconclusive (Derham et al., 2018; Guyton et al., 2020). Our results contribute to this body of work, indicating that LH conservation and rewilding could slow down compositional change by filtering out the arrival of new species into communities. In the context of tropical forests, it is also noteworthy that the combined effects of climate change and land use are contributing to tree loss, forest functional changes and the emergence of fire, leading to a process of increasing faunal and floristic savannization (Alroy, 2017; Emer et al., 2020; Sales et al., 2020; Staal et al., 2020). LH might contribute to decelerate such process by decelerating compositional change and filtering against invasive species and life-forms typical of savanna-like forests.

4.3 | Successional stage may limit LH buffering effects on secondary forests

The diversity of secondary tropical forests is related to their successional stage (Rozendaal et al., 2019). Despite its immediate geographical contiguity, the number of species per plot on the secondary forest in our experiment was about half of that on the old-growth forest, suggesting a relatively early successional stage. Our results indicate that at such early stage of succession and relatively low background levels of plant diversity, LH has limited buffering against diversity loss, and long-term regional environmental change jeopardizes the recovery potential of such early-stage secondary forests and their transition into more mature and diverse forests.

It is possible that early-stage secondary forests might benefit from proximity to old-growth forests in other aspects. Old-growth forests might provide a diverse source of plant propagules and communities of herbivores that facilitate the dispersal process (García et al., 2020; Paolucci et al., 2019; Pires et al., 2018;

Wandrag et al., 2017). Furthermore, contiguity to old-growth forests might also facilitate the recolonization of secondary forests by LH communities as early as 20 years from anthropogenic disturbance, provided LH communities are not locally extinct on such old-growth forests (Arévalo-Sandi et al., 2018). While such considerations are critical, our experimental exclusion experiment addresses more readily the effects of defaunation so that the impact of rewilding on the successional trajectory of secondary forests should be addressed in future 'truly' experimental rewilding studies. Yet, on light of our results, we suggest that for LH buffering to be most effective, LH conservation and rewilding on secondary forests should target forests with relatively high levels of species richness, though this conclusion needs to be experimentally ascertained.

Large herbivores conservation and rewilding, particularly for tropical forests, is nontrivial and is bound to pose important challenges. Many large Neotropical herbivores, such as tapirs and peccaries, are highly threatened and locally extinct across large tracts of their distribution. The lowland tapir, for example, is categorized as 'Vulnerable' across its entire distribution by the IUCN, and the white-lipped peccary is considered 'Critically Endangered' for the Atlantic Forest by the IUCN, and can only be found in about a dozen sites across the entire whole 1,315,460 km² span of Atlantic Forest ecoregion. Hence, it could be argued that actively rewilding Neotropical forests with large herbivores might be de facto the most effective solution for improving the conservation status of many large herbivore species in tropical forests. Yet, a route for effective rewilding of these herbivores, must necessarily include (a) effective landscape management, enforcement and conservation measures aiming to increase their local population densities and facilitate their dispersal and movement between forest remnants and population strongholds; (b) reintroductions and translocations into the many large tracts of diversity rich old-growth forests that are currently devoid of these LH (due to overhunting, roadkill and other drivers of defaunation; Galetti et al., 2021), but that fall within their distributional range. These and other practicalities are beyond the scope of this manuscript. However, based on our results, we suggest that LH conservation and rewilding should start with old-growth forests and then move on to secondary forests with high levels of diversity.

5 | CONCLUSIONS

There is a long road ahead for identifying the most efficient nature-based solutions so as to preserve and restore ecosystem structure, processes and functions in face of the unprecedented challenges posed by global change. Our results indicate that LHs have moderate yet critical effects in averting the long-term collapse of biodiversity and compositional change in the strongholds of biodiversity, and that plant diversity in old-growth forests and diversity-rich secondary forests might benefit mostly from conservation and trophic rewilding with LH.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

E.P.M. designed the research; E.P.M. and team collected the data; E.P.M., N.V. conceived the manuscript; N.V. analysed the data and drafted the manuscript; E.P.M. and N.V. contributed towards the final version of the manuscript. Both authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.5mkkw76z> (Villar & Medici, 2021).

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