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Impact of Collared Peccaries *Dycotiles tajacu* (Artiodactyla: Tayassuidae) on understory vegetation in the tropical rainforest of the Nogal-La Selva Biological Corridor, Costa Rica

Marco Herminio Osorto-Nuñez[1*]; https://orcid.org/0000-0003-2061-4950
Luis Diego Alfaro Alvarado[2]; https://orcid.org/0000-0001-9534-1948
Federico A. Chinchilla Romero[3]; https://orcid.org/0000-0001-5473-4307
Flávio H. Guimarães Rodrigues[4]; https://orcid.org/0000-0002-4797-0085

1. Instituto Internacional de Conservación y Manejo de Vida Silvestre. Universidad Nacional. Facultad de ciencias de la Tierra y el Mar. Campus Omar Dengo, 40101, Provincia de Heredia, Heredia, Costa Rica; marco.osorto.nunez@est.una.ac.cr (*Correspondence)
2. Facultad de Ciencias de la Tierra y el Mar, Escuela de Ciencias Ambientales, Universidad Nacional. Calle 9 y av. 1, 40101, Provincia de Heredia. Heredia, Costa Rica; luis.alfaro.alvarado@una.cr
3. Instituto Monteverde, Puntarenas, Costa Rica; federicoeap@gmail.com
4. Departamento de Genética, Ecologia e Evolução, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Avenida Antônio Carlos 6627, Belo Horizonte, Minas Gerais, Brazil; rodriguesfhg@gmail.com

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ABSTRACT

Introduction: Evidence suggests that herbivores, such as peccaries, shape vegetation structure and diversity through predation, trampling, dispersal, and rooting behavior.

Objective: To evaluate the impact of peccaries (*Dycotiles tajacu*) on the understory vegetation of the tropical rainforest in the Nogal-La Selva Local Biological Corridor, Costa Rica, comparing a site with the absence of peccaries to another with the presence of these animals.

Methodology: From June to November 2021, 20 experimental exclusions and 20 free access plots, each measuring 2 m^2 were used to quantify herbivory, the number of leaf blades, damaged leaves, healthy leaves, sapling height, and fallen biomass at both sites.

Results: A higher sapling density was found in the Nogal Reserve, but a lower sapling diversity, while in La Selva there was a higher sapling diversity, but a lower density of seedlings. Herbivory and sapling height in La Selva exceeded those in Nogal. The exclusion of peccaries reduced seedling damage but did not affect the dynamics of fallen biomass.

Conclusion: For the design, implementation, and evaluation of the effectiveness of biological corridors, it is crucial to consider plant-animal interactions to enhance the flow of ecological processes through functional and structural connectivity, analyzed from interactions such as those presented in this paper.

Key words: Biological Station La Selva; herbivory; sapling height; natural regeneration; Nogal Reserve; *Pecari tajacu*; recruitment.

RESUMEN

Impacto del pecarí de collar, *Dycotiles tajacu* (Artiodactyla: Tayassuidae) en la vegetación del sotobosque del bosque tropical húmedo del Corredor Biológico Local Nogal-La Selva, Costa Rica

Introducción: Existe evidencia que herbívoros, como los saínos, dan forma a la estructura y diversidad de la vegetación a través del comportamiento de depredación, pisoteo, dispersión y enraizamiento.
Objetivo: Evaluar el impacto de los saínos (*Dycotiles tajacu*) en la vegetación del sotobosque del bosque tropical húmedo en el Corredor Biológico Local Nogal-La Selva, Costa Rica, en un sitio con ausencia y en otro con presencia de saínos.
Métodos: De junio a noviembre de 2021 se utilizaron 20 exclusiones experimentales y 20 parcelas de acceso libre de 2 m^2, se cuantifico la herbivoría, número de láminas foliares, hojas dañadas, hojas sanas, altura de brinzales y biomasa caída en ambos sitios.
Resultados: Se encontró una mayor densidad de brinzales en Reserva Nogal pero una menor diversidad, contrario en La Selva donde se encontró una mayor diversidad de brinzales, pero una menor densidad de plántulas. La herbivoría y la altura de brinzales en La Selva fue mayor que en Nogal. La exclusión de los saínos disminuyó el daño a las plántulas, pero no afectó la dinámica de la biomasa caída.
Conclusión: Es necesario contemplar para el diseño, implementación y evaluación de la efectividad de corredores biológicos, las interacciones planta-animal, para potencializar el flujo de procesos ecológicos mediante la conectividad funcional y estructural, analizada a partir de interacciones como las presentadas en este trabajo.

Palabras claves: Estación Biológica La Selva; herbivoría; altura de brinzales; regeneración natural; Reserva Nogal; *Pecari tajacu*; reclutamiento.

INTRODUCTION

Herbivory, dispersion, and seed predation by wildlife species are vital processes in forest ecosystems. These processes are a key feature that may significantly influence sapling establishment, growth, composition, and forest recovery (Feng et al., 2021; Genes & Dirzo, 2022; Neuschulz et al., 2016; Norden, 2014; Vallejo-Marín et al., 2006). Herbivory is a crucial ecological process that contributes to the individual adaptation of species (Janzen, 1971). Environmental variables such as temperature fluctuations, humidity, and sunlight also can also impact forest recovery, affecting various trophic levels (Kuprewicz, 2013; Powell et al., 2015; Yong et al., 2011).

Wild mammals play a key role in the conservation of neotropical systems (Curran & Webb, 2000; Hermes et al., 2006), as they affect vegetation community diversity (Dirzo & Miranda, 1991; Ickes et al., 2001; Mendoza & Dirzo, 2007; Terborgh & Wright, 1994), through predation of reproductive and vegetation components, and recovery recruitment (DeMattia et al., 2004). They facilitate modifications in demography and plants composition in the forest (Romero et al., 2016). Some findings suggest that herbivores may become dominant in trophic cascades (Borer et al., 2005). Nevertheless, analyzing the causes of mortality of sapling is vital for understanding the processes that maintain forest species diversity (Paine & Beck, 2007), since, besides herbivory, there are other factors restricting the undergrowth sapling recruitment. These factors include dispersion restriction, environmental filters, biotic and abiotic factors, and the negative density dependence (Ramírez-Mejía & Mendoza, 2010).

Substantial evidence has been encountered, indicating that large herbivores such as peccaries significantly contribute to physical damage and mortality of undergrowth sapling due to their rooting and trampling behaviors while searching for fruits and seeds (Beck, 2005; Queenborough et al., 2012). However, peccaries also contribute to the structure and diversity of ecosystems and vegetation communities since they serve as seed dispensers and predators (Beck, 2005; Beck et al., 2010; Clark & Clark, 1989; Paine & Beck, 2007; Roldán & Simonetti, 2001). Thus, relevance of wild mammals in herbivory, such as peccaries, has been acknowledged; disturbing their densities can have detrimental effects on the forest and organisms that depend on litterfall and dendritic food webs (Beck, 2005; Reider et al., 2013).

On the other hand, peccary populations around La Selva Biological Station have declined or become locally extinct (Kuprewicz, 2013). For instance, there are no reports of peccary presence in the Nogal Private Wildlife Refuge (Nogal) since 2004 by locals or based on monitoring activities conducted by personnel of the reserve. Since 2004, wildlife tracking has been conducted through field observation and camera traps at the site, without sighting any peccaries (pers. comm). In regard to La Selva, studies on the historical and current abundance of peccaries suggest population growth (Kuprewicz, 2013; Michel et al., 2015; Romero et al., 2013). Thus, comprehending the role of this species in natural forest recovery is essential, knowing that there is a possibility of a significant reduction in its population in neotropical areas (Beck, 2005; Gongora et al., 2011; Ontiveros et al., 2021; Reider et al., 2013). This reduction is attributable to rapid deforestation rates and excessive hunting, which may impact in the trophic cascade and the natural recovery (Reider et al., 2013; Stoner et al., 2007).

Overall, recent studies have shown a tendency of increasing peccary populations at La Selva (Romero et al., 2013), leading to the perception that peccaries are the source of negative impact on forest natural recovery (Michel & Sherry, 2012). Based on this, a debate about the management of this species at La Selva has emerged (Romero et al., 2013). Investigations have focused on direct trophic relations with one or more species in trophic cascades (Michel et al., 2014), effects on insectivorous birds and bats (Kalka et al., 2008; Van Bael & Brawn, 2005), interaction and perturbation between palms and peccaries (Avalos et al., 2016; Queenborough et al., 2012), use of natural and anthropized areas (Osorto-Nuñez & Alvarado, 2023) peccaries as important agents that impact litterfall structure, and the abundance of aquatic (anurans), and the terrestrial reptiles (Beck et al., 2010; Reider et al., 2013). However, few investigations have centered on the direct relation of peccaries with recovery dynamics and their influence in the tropical forest at La Selva (Clark & Clark, 1989). Most studies with mammals have been conducted in other natural locations. (DeMattia et al., 2004; Dirzo & Miranda, 1991; Ickes et al., 2001; Mendoza & Dirzo, 2007; Paine & Beck, 2007; Roldán & Simonetti, 2001; Terborgh & Wright, 1994).

Nevertheless, the presence of peccaries and their relationship with the ecosystem should not be considered negative *a priori* because its natural distribution plays a crucial role within the trophic chain or other ecological processes. Therefore, efforts must be channeled to preserve the integrity of mammal communities and research the causes of sapling mortality to better understand the processes that maintain the diversity of forest species. In this way, we can ensure the preservation of fauna and flora and the ecological processes that favor the recovery and maintenance at La Selva. Hence, this study aims to measure the impact of peccaries (*Dycotiles tajacu*) on the understory vegetation of the tropical rainforest at the Nogal-La Selva Biological Corridor, Costa Rica, in a site without peccaries and another location with their presence.

MATERIALS AND METHODS

Study Areas: The study was conducted within the biological corridor at Nogal-La Selva, Heredia, Northwest Costa Rica. The corridor was developed within the *Naturaleza y Communidad* Project located in Nogal (Masis-Aguilar, 2019; Ubieta et al., 2009). It was created through collaborative efforts involving Chiquita Brands, the local community, the Sarapiquí local government, Rainforest Alliance, German Technical Cooperation Agency (GTZ), and the Swiss supermarket chain Migros (Ubieta et al., 2009). Ecological restoration actions took place from 2004 to the present, aiming to connect the Nogal Private Wildlife Refuge (Nogal) with La Selva Biological Station (Masis-Aguilar, 2019). La Selva comprises an area of 1 600 hectares. It is classified as a wet tropical rainforest (Hartshorn, 1983). The average daytime temperatures range from 24.7 to 27.1 °C and receives between 3 800–4 000 mm of rainfall annually (Armstrong et al., 2020; Robinson et al., 2018). The rainfall is slightly lower from January to April (Clark et al., 2013), while higher rainfall occurs from June to July and from November to December (Salazar-Blanco, 2001). La Selva is connected with Braulio Carrillo National Park, featuring primary rainforest, various stages of second growth, and forestry systems (Arroyo-Arce et al., 2013; Oviedo-Pérez, 2008; Raich et al., 2014; Romero et al., 2013). It is located on volcanic origin soil, which provokes an extreme of high fertility of lowlands neotropical forests (Clark et al., 2013) Fig. 1).

Meanwhile, Nogal, owned by Chiquita Brand S.R.L, is in Puerto Viejo district, Sarapiquí, Heredia, North Caribbean region of Costa Rica (10°29'23" N & 83°56'15" W). This reserve adjoins the Río Sucio to the North, forming the Nogal-La Selva ecological corridor (Masis-Aguilar, 2019). There are two areas of 92 hectares of wet rainforest and riverine habitat. The reserve is mainly dominated by second-growth forest and dense scrubland reed (Arundo donax), and it is 7.8 km away from La Selva (Masis-Aguilar, 2019; Rodríguez-Matamoros et al., 2012). The site falls within the tropical rainforest life-zone (Holdridge, 1988) and has a flat topography and elevations ranging from 40 to 51 m.a.s.l. The climate is predominantly warm and humid, with temperatures fluctuating between 26 °C and 28 °C and an annual rainfall of 4 000 mm (Masis-Aguilar, 2019) (refer to Fig. 1).

Design of Exclosures and Control Plots: La Selva served as the control site with the presence of *D. tajacu*, while Nogal Refuge was designated as the exclusion site without

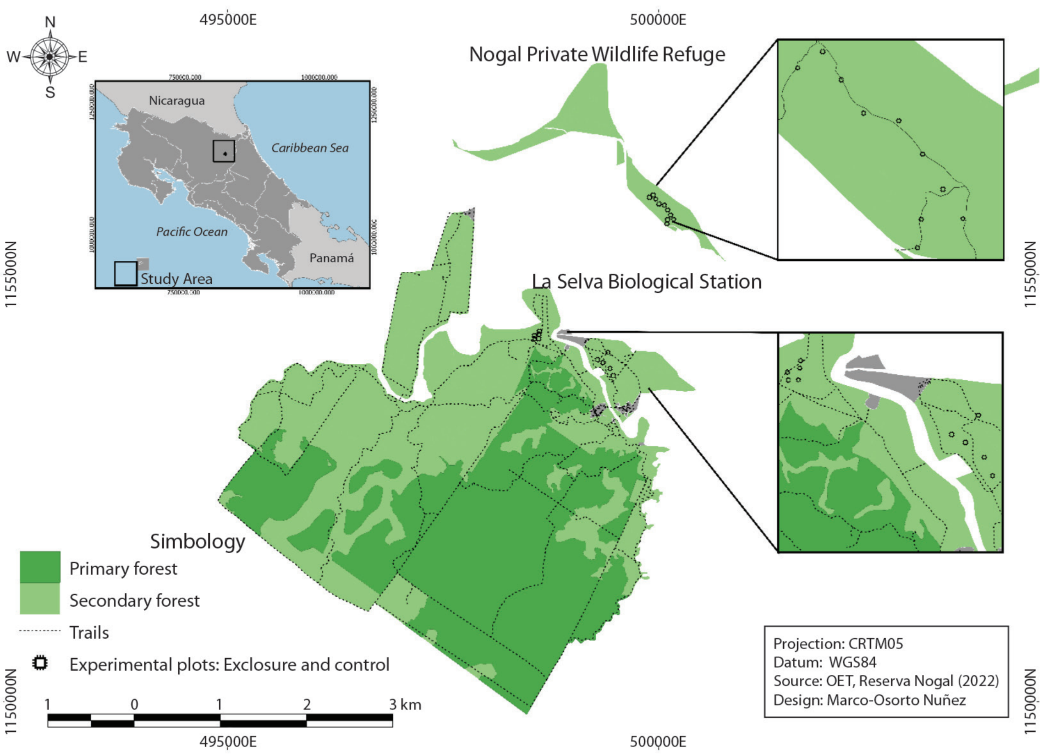

Fig. 1. Location of experimental plots (exclosure and control) at La Selva Biological Station and Nogal Private Wildlife Refuge.

D. tajacu. In both areas, 20 paired plots of 2 x 2 meters were established, consisting of 10 exclosures treatments and 10 control treatments with free access. Sampling periods were conducted from June 9th, 2021, to January 31st, 2022. Before implementing the treatments, several sampling areas were created to select the precise site where plots were located. Polygons were selected in Tres Ríos, Las Vegas, and Arriera-Zompopa trails. Subsequently, random points were created using QGIS 3.10 software, considering 50 meters of separation distance between plots to ensure the rain-induced seed independence from the same parent tree, which is significantly reduced after 50 meters (Ceccon & Hernández, 2009; Cole et al., 2010; Martínez-Ramos & Soto-Castro, 1993) (Fig. 2).

The paired treatments were separated by a 5 m distance as shown in Fig. 3. Exclosure treatments were surrounded by a galvanized metallic mesh extending up to 1.10 m in height, supported by stakes of flat iron rods with corners angled at 40 degrees. Plots had an opening of 15 x 10 cm of wall base to allow the entrance

Fig. 2. Random points and points selected for exclosures and control plots in **A.** Nogal Private Wildlife Reserve and **B.** La Selva Biological Station.

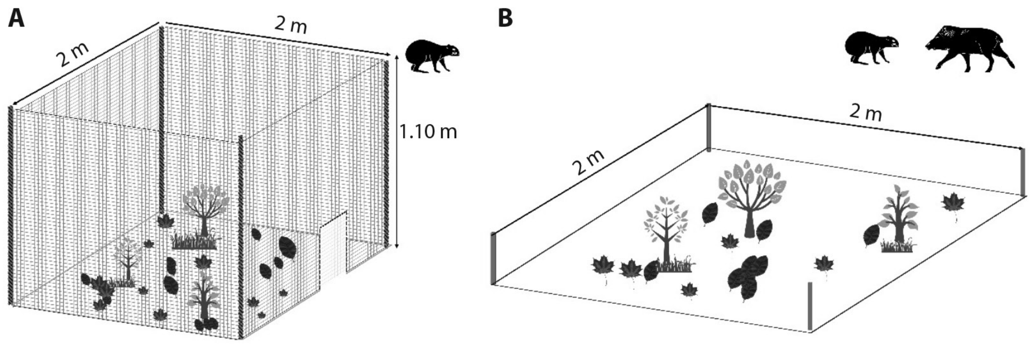

Fig. 3. Diagram of experimental plots conducted at La Selva Biological Station and Nogal Private Wildlife Reserve. **A.** Exclosure plots allowing the entrance of only small mammals. **B.** Control plots located 5 m away from the experimental exclosure, with unrestricted access.

of small mammals and simulate differential extinction of mammals (Galetti et al., 2015; Mendoza & Dirzo, 2007). In the control treatments, plots of 2 m^2 were delimited using a few PVC stakes placed in the corners. Any damage to the trap structures in the exclosure plots was repaired during each visit.

Vegetation Sampling in Exclosure and Control Plots A taxonomy identification was conducted on saplings (0.30–1.50 m height) to determine the most specific taxon possible (genus and species) based on dendrological features. This identification process was carried out with the assistance of botanical experts from La Selva OET and Juvenal Valerio Rodríguez from the Herbarium at Universidad Nacional. Height measurements were recorded for all individuals of forest species in both sites (exclosure and control plots), following Orozco & Brumer (2002).

Herbivory: Herbivory levels were measured in both treatment sites. The number of leaf sheets of each plant, as well as healthy and damaged leaves were also quantified at both sites. The quantification of herbivory occurred during three periods: the first on July 9th, the second period on September 9th, and the third on November 9th, 2021. The extent of leaf consumption by herbivores was estimated by considering six categories of visual damage in a specific range of consumed leaf area: 0-0 %, 1-6 %, 6-12 %, 12-25 %, 25-50 % and 50-100 % (Dirzo & Dominguez, 1995). The percentage of lost leaf area was calculated using the herbivory index as defined by the following formula:

$$H = (Ci * ni) /N$$

Where **Ci** = mean point of each category.
ni = leaflets in the category of damages;
and **N** = total leaflets rates.

Lastly, every leaf underwent visual analysis to identify browsing signs by mammals, particularly, if leaves were eaten, or partially or entirely removed.

Litter Fall Dynamics: Litter fall was monthly measured by using a PVC sampling frame of 50 cm x 50 cm. Plots were divided into quadrants of equal size, numbered clockwise from one to four. Litter fall was collected from three of the four randomly selected quadrants in the exclosure and control plots (Reider et al., 2013), without using random mechanisms (Chavarria-Bolaños et al., 2012; Reider et al., 2013; Sousa-Neto et al., 2016; Zhu et al., 2019). With this method, there is a possibility of repeating two of the four quadrants in the nesting sampling period and selecting a two-month quadrant of deposited litter fall. Three samples were collected for each treatment every month (n = September 7th, n = October 7th, n = November 6th, and n = December 6th) and placed in paper bags. The collected plant litter material included leaves, part of leaves, flowers, small fruits, seed pods and branches. Branches larger than 20 mm in diameter were excluded as they were considered woody debris (Muller-landau & Wright, 2010). Subsequently, the organic matter samples were weighed in the laboratory. The humid litter fall was dried for 48 hours at 65 °C, and its dry weight was measured.

Fauna Activity within Plots: From July 9th to December 9th, 2021, three camera traps were installed (Bushnell Trophy Cam Hd 12MP model: 119739 and 119736) per site. Cameras were placed only in the control plots because our interest was to observe if medium to large size mammals, such as peccaries, tapirs, and deer, predate or damage saplings. Each camera was mounted on a tree at a height of 50 cm and set to operate for 24 h d^{-1}, in video mode with a minimum delay of 60 seconds after detecting an animal within its sensor reach. Once the cameras were set up, the videos were reviewed within the first 24 hours to change the SD memory card and to check for species recorded at the study site. Subsequently, the cameras were reviewed monthly to replace the SD memory card or check the batteries. For each camera, the study recorded the following data: display, location, camera functioning dates, trap night number, and the number of videos for each species. The cameras remained in each plot for a month, before being moved to the next plot until all plots in La Selva and Nogal were covered.

Data Analysis: The normality of the variables was verified using the Shapiro-Wilk test (Shapiro & Wilk, 1965), and the homogeneity of variance was assessed using the Bartlett test (Bartlett, 1951). Following these tests, a two-way analysis of variance (ANOVA) was conducted to confirm the hypothesis of differences between means of two or more groups (Stahle & Wold, 1989), to ultimately detect potential differences between treatments (exclosure and control). Finally, the study conducted an analysis of between-sites interactions and experimental treatments considering the following variables: rate of herbivory, number of leaf sheets, healthy and damaged leaves, sapling height, and litterfall. This analysis was performed using an analysis of variance to observe if there was evidence of contrasts between each variable in each study site (La Selva and Nogal Reserve).

Fauna Activity within Plots: Species captured on video by the camera traps served as an index of activity in the control plots. All graphs and data were analyzed with Python 3.9 through Google Collaboratory, and geospatial databases were processed using QGIS 3.10. software.

RESULTS

Vegetation Abundance and Diversity: A total of 208 saplings were quantified in the two study sites. In La Selva, 98 individuals represent 33 species from 18 families, and 110 in Nogal Reserve comprising 30 species from 24 families (Table 1). The most numerous families in the Nogal Reserve were Moraceae (n = 30) and Rhamnaceae (n = 8), whereas Rubiaceae (n = 28), Primulaceae (n = 13), and Moraceae (n = 16) were the predominant families in La Selva. In terms of species, *Ardisia nigropunctata* (n = 13), *Sorocea pubivena* (n = 10) and *Psychotria B.* (n = 10) were more numerous in La Selva, and *Sorocea pubivena* (n = 28), and *Colubrina spinosa* (n = 8) were the more common species in Nogal. A dead individual (*Pentaclethra macroloba*) was documented in the Nogal Reserve during this study. Furthermore, during the second sampling period in La Selva, a 30-meter tree fell onto an exclosure plot; consequently, the plot was modified as it was difficult to continue measuring individuals (Table 1).

Sapling Traits and Litterfall: Strong evidence was found for differences in herbivory rates (La Selva only) and the number of

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Table 1
Frequency of plant species found in the plots (exclosure and control) in Nogal Private Wildlife Refuge and La Selva Biological Station.

Study sites			
Nogal Private Wildlife Refuge		La Selva Biological Station	
Species	Count	Species	Count
Sorocea pubivena	28	*Ardisia nigropunctata*	13
Colubrina spinosa	8	*Sorocea pubivena*	10
Symphonia globulifera	5	*Psychotria* B.	10
Lauraceae	5	*Virola sebifera*	9
Heisteria macrophylla	5	*Psychotria* A.	8
Guatteria diospyroides	4	*Pentaclethra macroloba*	4
Protium pittieri	4	*Palicourea chiapensis*	3
Virola sebifera	4	*Casearia corymbosa*	3
Hasseltia floribunda	4	*Vochysia guatemalensis*	3
Gloeospermum diversipetalum	4	Dilleniaceae	2
Ardisia nigropunctata	3	*Nectandra reticulata*	2
Annonaceae	2	*Brosimum alicastrum*	2
Tetragastris panamensis	2	*Trophis racemose*	2
Sloanea A.	2	*Perebea angustifolia*	2
Hernandia stenura	2	*Syzygium jambos*	2
Herrania purpurea	2	*Psychotria marginata*	2
Pachira aquatica	2	*Pentagonia monocaulis*	2
Mollinedia pinchotiana	2	*solanaceae*	2
Sorocea sp.	2	*Protium pittieri*	1
Virola koschnyi	2	*Inga sapindoides*	1
Pentagonia sp.	2	*Inga* sp.	1
Spondias mombin	1	*Ocotea cernua*	1
Garcinia sp.	1	*Rhodostemonodaphne kunthiana*	1
Sloanea B.	1	*Theobroma cacao*	1
Inga sp.	1	*Guarea Guidonia*	1
Pentaclethra macroloba	1	*Eugenia selvana*	1
Papilionaceae	1	Piperaceae	1
Piperaceae	1	*Pentagonia* sp.	1
Rubiaceae	1	*Psychotria cyanococca*	1
Chione venosa	1	*Psychotria C.*	1
Salicaceae	1	*Meliosma glabrata*	1
Lunania sp.	1	*Hasseltia floribunda*	1
Allophylus psilospermus	1	*Paullinia* sp.	1
Pouteria sp.	1	*Chrysophyllum cainito*	1
Simarouba glauca	1	*Cestrum schlechtendalii*	1
Cuatresia exiguiflora	1		
Violaceae	1		

damaged leaves between the exclosure and control groups. Moderate evidence was found for number of leaves (La Selva only) and sapling height (La Selva only) between exclosure and control groups. Additionally, strong evidence was found for the effect of this interaction on herbivory, sapling height and litter fall, confirming that these variables depend on the treatment and the site. No interaction effect was found for the number of leaves and the number of damaged leaves. Finally, no evidence of difference was found for the number of healthy leaves in the treatment and interaction effect (Table 2, Fig. 4).

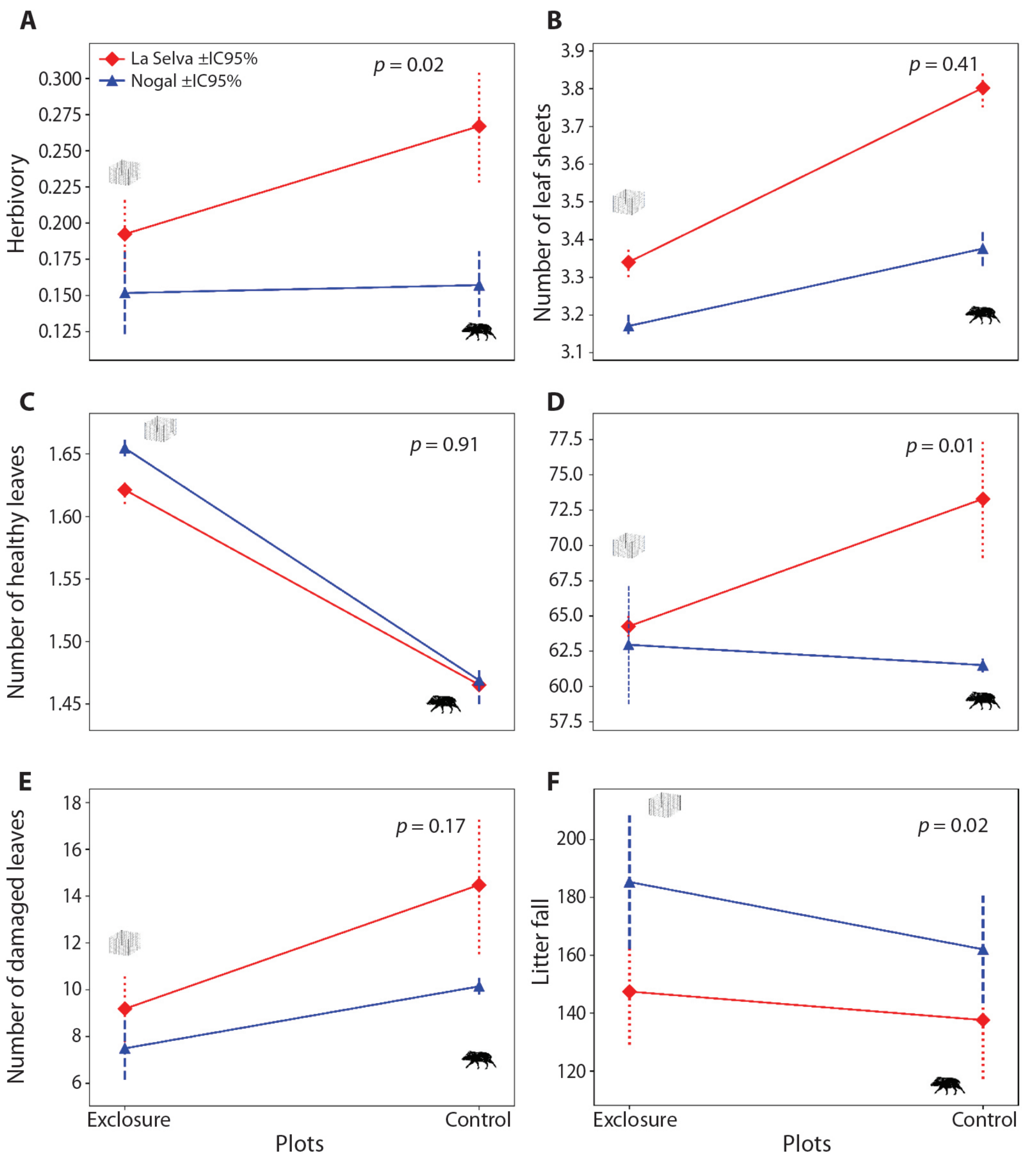

Fig. 4. Effects of the two-way interaction between treatment factors (exclosure and control) and the study sites La Selva Biological Station and Nogal Private Wildlife Refuge, Costa Rica, for the following variables: **A.** Herbivory, **B.** Number of leaf sheets, **C.** Number of healthy leaves, **D.** Sapling height, **E.** Number of damaged leaves and **F.** Litterfall.

Table 2
Statistics summary for variables between exclosure and control plots at La Selva Biological Station and Nogal Private Wildlife Refuge, Sarapiquí, Costa Rica.

Variable	Mean		Anova *p*
	Exclosure	Control	
Herbivory rates			
La Selva	0.1923	0.1516	0.002
Nogal	0.1516	0.1571	0.773
Number of leaf sheets			
La Selva	13.22	20.06	0.01
Nogal	14.69	14.19	0.84
Number of damaged leaves			
La Selva	9.17	14.47	0.002
Nogal	7.49	10.14	0.007
Healthy leaves			
La Selva	3.97	5.56	0.21
Nogal	7.18	4.05	0.10
Sapling height			
La Selva	63.74	72.55	0.006
Nogal	62.95	61.51	0.632
Litter fall			
La Selva	147.48	137.62	0.479
Nogal	185.33	162.06	0.124

Fauna Activity within Plots: A total of 152 trap days were recorded in the control plots. Omnivorous and frugivorous mammals were the predominant guilds captured on video in both study sites; for instance, 120 captures involving 16 species were documented in La Selva; while in Nogal Reserve, 88 captures of 13 species were recorded. *Dycotiles tajacu* accounted for only 12 % (n = 14) of the video captures in the control plots, ranking as the fourth most frequently recorded species. In contrast, agouti was the species with the most captures on video (37 %, n = 44). No traces, direct sighting reports, or fecal evidence of *T. bairdii* and *O. virginianus* were found near the plots in La Selva during the period of this study. In Nogal Reserve, the most frequently captured species on video was *Nasua narica* (n = 36), representing 42 % of the captures, followed by *Cuniculus paca* which accounted for 17 % (n = 15). No captures of *Dycotiles tajacu* were reported on this site.

DISCUSSION

Floristic Composition: Peccaries affect the recruitment of individuals in the natural understory regeneration in La Selva, since in Nogal *S. pubivena* (consumed by peccaries) accounts for 25.45 % of the individuals (Table 1). In addition, individuals belonging to the Moraceae family were more abundant in Nogal than in La Selva. The species of this family are one of the most important in the diet of peccaries according to the meta-analysis conducted by Beck (2005) and the one found by Osorto-Nuñez et al. (2023) in La Selva, Costa Rica. Defaunated understories tend to have a higher plant density and lower diversity compared to forests with a higher degree of conservation (Dirzo & Miranda, 1991). The defaunation of vertebrates, especially mammals, can alter those ecological mechanisms allowing the coexistence of thousands of plants in tropical forests (Wright, 2003). This is considered as an indirect effect for the impoverishment of floristic diversity (Dirzo & Miranda, 1991; Kurten, 2013; Leigh et al., 1993; Terborgh, 1992; Terborgh & Wright, 1994).

The absence of wild mammals may negatively affect certain plant species while benefiting others (Kurten, 2013). In areas where peccary populations have decreased, there is a top-down effect on (Michel et al., 2014) plant-animal interaction. This is because seed predators and herbivores limit the abundance of slow- to moderate-growing forest species that form the upper layers in a natural forest (Camargo-Sanabria et al., 2015; Kurten, 2013; Wright, 2003). However, there are other biotic and abiotic factors that hinder regeneration recruitment such as temperature variation, humidity, light, wind, water availability, soil properties, diseases, energy or nutrient reserves, and storms, among others (Augspurger, 1984; Bullied et al., 2012; Cano & Stevenson, 2009; Kéfi et al., 2012; Leigh et al., 1993; Osunkoya et al., 1993; Paine & Beck, 2007; Ramírez-Mejía & Mendoza, 2010). If there is a selective behavior in the consumption of vegetation by herbivorous mammals, its absence could allow certain species to be freed from herbivory, favoring the dominance of these species in the ecosystem (Roldán & Simonetti, 2001); this could be the case of *S. pubivena* in Nogal.

Herbivory: Sounders of peccaries, when they are abundant, such as those found in La Selva, influence natural regeneration through herbivory, given the differences observed with Nogal (Fig. 2 A), herbivore exclusions reduce foliar herbivory (Pearson et al., 2003), and populations of medium and large mammals have substantial effects on regeneration (Belovsky & Slade, 2000; Medinaceli et al., 2004). According to the camera records in the plots, the most abundant species was *D. punctata*, which coincides with (Kuprewicz, 2013), who in turn points to the peccary as the other most abundant mammal species. This combination of agouti and peccary may contribute to higher herbivory rates in La Selva compared to Nogal. According to the sampling data, the most abundant species in Nogal was *N. narica,* which primarily feeds on fruits and insects and, therefore, it would not have a significant impact on herbivory rates (Valenzuela, 1998). It is worth noting that the agouti is a predator and seed disperser, but it does not eat or trample vegetation (Kuprewicz, 2013).

The growth in height of saplings contrasts with the studies by Osunkoya et al. (1993) and Wahungu et al. (2002). These researchers found that seedlings in excluded areas grew at a faster rate than those in unprotected areas. However, this could be related to the total number of leaves and branches since there was evidence of disparity in the number of leaf laminae biased toward the open access plots and is a covariate related to seedling size (Arteaga, 2006; Grossnickle & MacDonald, 2018; Seiwa & Kikuzawa, 1991). The peccary trampling could affect the height of saplings, but the differences in height in La Selva compared to Nogal (Fig 2B) indicate that there was a compensation as a positive plant response to herbivory, since the damaged seedlings alter their resource allocation, physiology, and phenology in order to reduce the impact of the damage in their growth and reproduction in relation to the less damaged plants (Hawkes & Sullivan, 2001; Maschinski & Whitham, 1989; McNaughton, 1983).

In the short term, mammals alter the condition of plant species that are part of their diet and influence other components of food webs, which can affect insect herbivores (Firn et al., 2017; Vandegehuchte et al., 2017) by reducing the amount of food resources (Teichman et al., 2013). Thus, the exclusion of mammals could lead to positive effects for herbivorous insects (Vandegehuchte et al., 2017). However, in the long term, mammals such as peccaries can modify the vegetation composition, including the relative abundance of preferred plants, which in turn may affect herbivore insects associated with these plants (Beck, 2005; Huntly, 1991; Kurten, 2013; Rumiz, 2010).

In the context of biological corridors, the analysis of ecological dynamics becomes highly relevant given the particularities of a landscape that is confronted with changing conditions at a faster rate compared to areas of absolute protection, such as national parks. This study conducted in two key areas of the Nogal - La Selva biological corridor shows the complexity that governs plant-animal interactions, taking the *D. tajacu*'s influence on the regeneration of species as an example at the sapling level in lowland tropical rainforests. Therefore, the design, implementation, and evaluation of the effectiveness of biological corridors should consider this type of complexities in order to maximize the success of biodiversity conservation, ecosystem services to human communities, and the flow of ecological processes through functional and structural connectivity, the latter being analyzed from interactions such as those presented in this study.

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