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TECHNICAL ARTICLE

Corridors in heavily fragmented landscapes: reconnecting populations of critically endangered brown spider monkeys (*Ateles hybridus*) and sympatric terrestrial vertebrates in the lowland rainforests of Central Colombia

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In tropical ecosystems, habitat degradation and fragmentation are some of the most important drivers of biodiversity loss. In Colombia, the Magdalena River basin is home to a megadiverse wildlife community, which has been historically exposed to pervasive habitat loss and fragmentation. Within a long-term project on the conservation of critically endangered brown spider monkeys (*Ateles hybridus*), we signed conservation agreements with local landowners to protect the remaining forests and reconnect them through restoration corridors. We established 10 corridors within a matrix of pastures used for cattle-ranching which reconnect approximately 1,000 ha of forests. We planted trees in 2016/2017 and 2020, established 24 vegetation plots (10 × 10 m) to measure their structure and composition, and compared them with six vegetation plots (50 × 2 m) in forest fragments. We installed camera traps to evaluate the effectiveness of corridors as potential pathways for terrestrial vertebrates in a fragmented landscape. Overall, forest structure differed between young corridors (1 year) and both older corridors (5 years) and forests; older corridors had no structural differences with forest fragments. Throughout this preliminary survey, 21 out of 32 species of vertebrates that have been recorded in forests used the corridors, including apex predators and other large birds and mammals. This study provides initial data supporting the use of corridors as a strategy to reconnect wildlife in isolated forest fragments in heavily fragmented landscapes, as well as the establishment of effective corridors that reconnect forest-dwelling species in relatively short periods of time (<5 years).

Key words: biological corridor, camera trapping, habitat fragmentation, landscape management, sustainable cattle ranching practices

Implications for Practice

- Corridors in lowland forests of Colombia can reach structural complexity similar to the remaining forests in 4–5 years, allowing arboreal vertebrates to move along them.
- Medium and large birds and mammals use corridors as pathways between forest fragments.
- Corridors are an effective strategy to reconnect the isolated forest fragments and recover both structural connectivity and genetic connectivity of wild populations.
- In fragmented landscapes, it is possible to restore corridors for brown spider monkeys (Ateles hybridus) by reducing stressors to natural regeneration processes.
- Corridors may increase wildlife resilience while not compromising the economically productive systems of cattle ranching and agriculturally productive regions.

Introduction

In tropical ecosystems, habitat degradation and fragmentation are some of the most important drivers of biodiversity decline (Taubert et al. 2018; Almond et al. 2020). Recent studies have provided evidence on the effects of habitat fragmentation on biodiversity loss and ecosystem dynamics, threatening the direct, and indirect benefits provided by their ecosystem

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functions (Haddad et al. 2015). The American tropics are being pervasively transformed and fragmented, causing a terrifying vertebrate population decline, with average population losses of approximately 90% since 1970 (Almond et al. 2020). For example, in Northwestern South America, the inter-Andean lowland valleys contain a unique biodiversity—part of the Tumbes-Chocó-Magdalena Biodiversity Hotspot—that is threatened with extinction due to the pervasive transformation of natural habitats into agricultural fields and large-scale cattle ranching. In Colombia, the Magdalena River basin supports over 70% of the country's population and over 85% of these natural habitats have been lost (Correa-Ayram et al. 2020). Most populations of terrestrial vertebrates have been negatively impacted in this region, and especially those extremely sensitive to habitat degradation, such as the endemic and critically endangered (CR) brown spider monkeys (*Ateles hybridus*) and Blue-billed Curassows (*Crax alberti*).

Brown spider monkeys are one of the most threatened primates in the Americas (De Luna & Link 2018). Since 2005, we have been involved in the conservation of some of the last populations of brown spider monkeys and their habitats in Colombia (De Luna & Link 2018). Brown spider monkeys are one of the five species selected to develop a landscape conservation approach that aims to protect the remaining habitats of the middle Magdalena River basin within Proyecto Vida Silvestre (PVS) in Colombia.

Brown spider monkeys prefer undisturbed tropical forests and are directly affected by habitat loss and hunting (De Luna & Link 2018). Their long-life history and large body size make them particularly sensitive to habitat loss. Given that spider monkeys play an important role in tropical forest dynamics through their seed dispersal services, their local extinction may trigger unexpected consequences in forest dynamics (Link & Di Fiore 2006). Finally, spider monkeys are one of the most sensitive terrestrial vertebrates to the effects of hunting and habitat degradation (Michalski & Peres 2005), and their conservation can "embrace" the conservation of most sympatric wildlife. Through the protection of habitats and ecological conditions required by spider monkeys, we can certainly guarantee the conservation of a megadiverse wildlife community in the American tropical lowland rainforests.

Ecological restoration can provide short- and long-term benefits to local wildlife (Hobbs & Norton 1996), by promoting additional habitats for species survival and reproduction, or by increasing the protection of existing habitats (Bennett et al. 2000). Nonetheless, ecological restoration is extremely costly both in financial and physical terms (King 1991; Edwards & Abivardi 1997). Several studies have addressed the financial and logistic benefits and challenges of implementing active versus passive restoration (or a combination of both), and these considerations should be carefully examined based on the particular conditions of each restoration project (see Zahawi et al. 2014; Prach & del Moral 2015; Meli et al. 2017). Thus, selecting priority areas for restoration given their potentiality to recover key ecosystem functions, as well as the feasibility to reach expected results, are key components of restoration planning, and efforts should be directed towards areas where the maximum benefits are likely to be achieved (Orsi et al. 2011). For example, at a local scale, recovering the connectivity of heavily fragmented landscapes through the creation of corridors might increase the long-term survival and viability of local wildlife (Liu et al. 2018).

Here, we present the results of an on-going restoration project aiming to reconnect the isolated forests fragments of the Magdalena River basin in Colombia. As part of our conservation program on brown spider monkeys, we have established 10 corridors in a landscape dedicated to extensive cattle ranching and monitored the restoration process and terrestrial vertebrate presence in five of them. In this study, we aim to provide evidence on the key role of restoration corridors as strategies to recover the structure of local forests to provide connectivity for isolated populations of terrestrial vertebrates. Thus, our main objectives are to: (1) describe the geographic scale of our project aimed to reconnect isolated groups of brown spider monkeys in Colombia; (2) compare the structure and composition of recent corridors (1 year) and older corridors (5 years) with that of reference forests; and (3) evaluate the use of corridors by large terrestrial vertebrates in a heavily fragmented landscape.

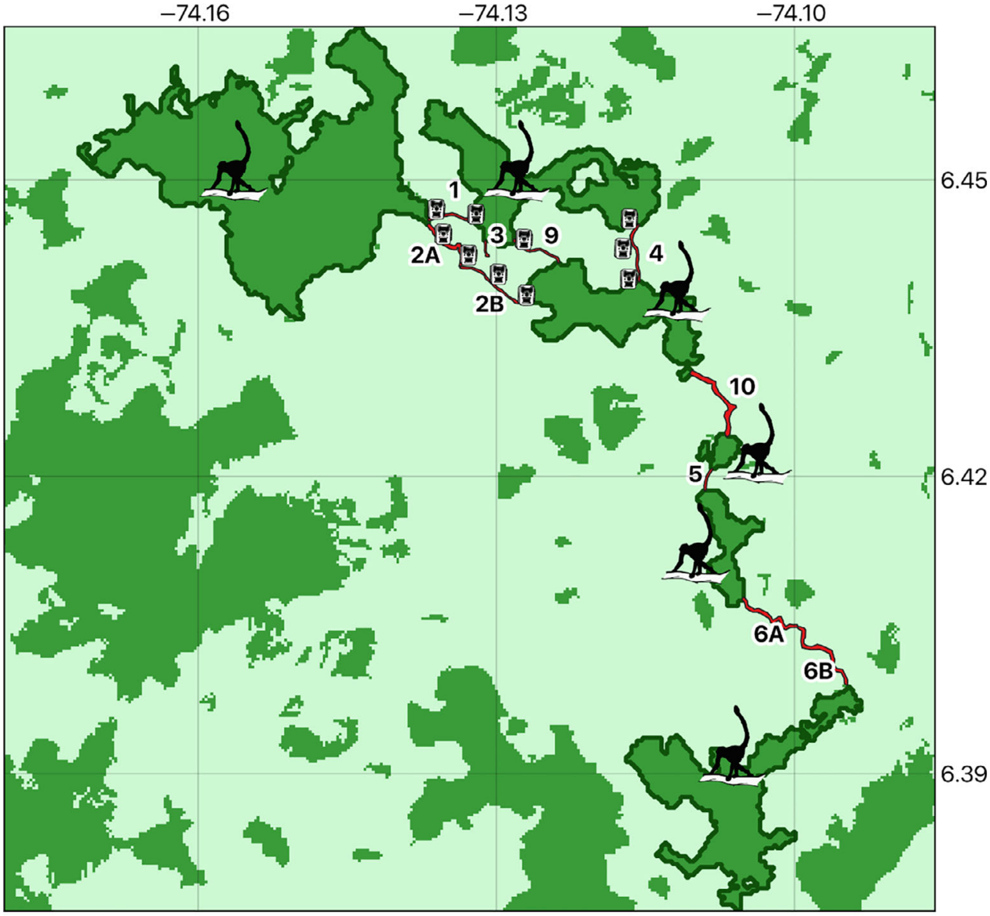
Methods

Study Area

This study takes place in the tropical rainforests of the middle Magdalena River basin; specifically, in the lowland inter-Andean valleys of Central Colombia. The broader region is characterized by pervasive transformation of natural habitats into extensive pastures for cattle ranching and large agroindustries. The study area—Hacienda Lusitania—is a large cattle ranch comprised of a matrix of pastures for cattle ranching, but still holding significant remnants of primary forest fragments and a relatively complete vertebrate community. The area has a bimodal annual precipitation cycle with wet seasons between March and May and between October and December, and an average annual rainfall of 3,500 mm. Hacienda Lusitania has been declared a Privately Protected Area (PPA) (Cat. VI-UICN) in Colombia, and a conservation agreement has been signed to protect the remaining habitats and reconnect isolated forest fragments through corridors.

Habitat Diagnosis and Corridor Planning

Given that fragmentation is directly linked to a severe limitation in dispersal in isolated populations of brown spider monkeys (*Ateles hybridus*), we developed a landscape connectivity model to prioritize—theoretically—the corridors to restore in the specific context of habitat fragmentation in our study area (Supplement S1). The model considered the least-cost paths and the matrix resistance to movement—by brown spider monkeys—through different land covers (see Fig. S1).



Connectivity corridor	Year established	Area (ha)
1	2016	1.1
2A	2017	3.83
2B	2020	1.21
3	2019	0.38
4	2017	1.24
5	2017	0.45
6A	2017	1.8
6B	2021	1.86
9	2020	1.04
10	2021	2

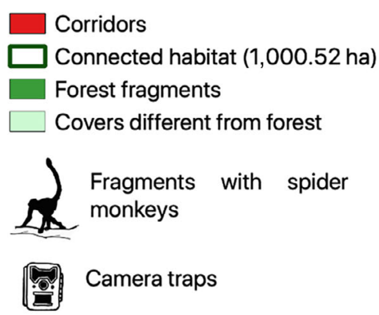


Figure 1. Map of the study area showing the forest fragments with known brown spider monkeys groups and the 10 restoration corridors implemented during this study.

Implementation of Corridors at Hacienda Lusitania

Although the connectivity models (described above) identified the most efficient pathways for establishing corridors based on least-cost paths, they did not consider local variables (e.g. water sources or preexisting fencing) or landowner decisions regarding the spatial location of corridors. Thus, we based the initial selection of corridors on the connectivity models and refined these corridors in consultation with local landowners. In 2016, we started a process of establishing connectivity corridors to reconnect forest fragments and isolated groups of brown spider monkeys (Fig. 1). To date, we have established an active restoration process in 10 connectivity corridors at Hacienda Lusitania, and we have monitored the restoration process and terrestrial vertebrate occupancy in five of them (Table 1; Fig. 1). We opted for conducting active restoration—acknowledging their higher costs when compared to passive restoration—given the urgent need to recover structural connectivity and reconnect isolated populations of brown spider monkeys and other terrestrial vertebrates. Thus, by

Table 1. Connectivity corridors at Hacienda Lusitania.

Corridor	*Area (ha)*	*Year*	*Features*
1-Loma	1.1	2016	Divided roughly in half into Terra Firme hills and half in seasonally flooded areas along a small creek. The restoration process in this corridor has not been entirely homogeneous and planted trees have grown faster in the wetland areas. The most abundant trees in this corridor are from *Inga* spp., *Spondias mombin*, *Cedrela odorata*, among other trees. At the onset of the planting of sampling in the corridor, there was a thin line of trees present in part of the corridor, including *Xylopia* spp. trees.
2A-Quebrada Lusitania 2B-Quebrada Lusitania	3.83 1.29	2017 2020	This is one of the longest corridors, and was established along one of the main creeks in the area, reinforcing the existing native tree corridor along the creek. Thus, this corridor mainly increased the width of the earlier corridor and now covers 5.11 ha (3.83 ha from corridor 2A, and 1.29 ha from corridor 2B). All planted areas were previously on pastures without any trees. These two corridors are exposed to flooding frequently (several times a week during the two rainy periods of the year) that drain along the day. Both corridors were planted with several plants species including *Anacardium excelsum*, *S. mombin*, *C. odorata*, *Cariniana pyriformis*, *Jacaranda Hesperia*, *Cordia* sp., and includes a high plant diversity from native plant already present in the corridors. Finally, it is noteworthy that these corridors had an initial structure similar to that of forests, given by the trees present along the creek's borders.
3-Jaguey	0.38	2018	Is a small corridor that was established close to the ranch's house to plant trees that coil attract wildlife. It only encompasses 0.38 ha and was made on top of pastures.
4-Corrales	1.54	2016	Established along the ridge on a hill that connects two forest fragments and encompasses an area of 1.24 ha. This corridor was planted in 2017, and is quite unique as we planted a large number of *Gmelina arborea* saplings—a non-native tree—that grows fast in tropical forests. In this corridor other trees such as *Ceiba pentandra*, *Anacardium excelsum*, and *Cordia* spp. were also planted. The entire corridor was planted on top of open pastures for cattle ranching.
9-El Filo	1.24	2020	Established along a mountain ridge in 2020. The ridge was heavily eroded by the effect of cattle ranching and soils were exposed all over the corridor. A few *Psidium* sp. and *Citrus* sp. trees were inside the corridor, but most of it was covered with pastures or soil. Some of the most abundant trees planted in this corridor are *C. pentandra*, *Albizia saman*, and *Enterolobium cyclocarpum*.

actively planting saplings, we accelerated the initial phases of recruitment of desired tree species by outcompeting grasses and promoting the subsequent arrival of other propagules/seeds passively.

Considering the landscape connectivity model and the areas under conservation agreements, we prioritized six forest fragments that could increase the connectivity for local wildlife. All corridors were isolated to minimize the impact of cattle and allow the regeneration of vegetation to thrive. We planted in the corridors 30 native tree species that we considered provided either structural characteristics that allow terrestrial and arboreal vertebrates to move along them, or that increased food availability (mainly fleshy fruits) to the vertebrate community.

Thus, we selected tree species that have (1) rapid growth, tolerate exposure to direct sunlight, and contribute to recovering forest structure (e.g. *Ceiba pentandra*, *Enterolobium cyclocarpum*, *Genipa americana*, *Hura crepitans*) and/or (2) fruit productivity (*Cassia grandis*, *Garcinia madruno*, *Guazuma ulmifolia*, *Inga spectabilis*) (see Celis & Jose 2011). As mentioned above, this strategy responded to our main goal of rapidly recovering a forest structure that allows brown spider monkeys and wildlife to move between forest fragments.

Our approach to ecological restoration was based on planting mixed native hardwood tree species to enhance diversity, structural complexity, and connectivity along the corridors. Given that forest structure is determinant to the long-term survival of isolated populations of brown spider monkey tree species were selected based on (1) their ability to rapidly and successfully replace open pastures (species with high survival rates, rapid growth, and strong resilience to light exposure), drought, flooding, and degraded soils and (2) the provisioning of food and shelter to target species such as primates and forest-dwelling species (see Table S1).

Overall, corridors were planted with more than 12,000 saplings that were grown in our local greenhouses. We obtained most seeds from local trees within the forest fragments, but also from local persons in the broader area of the middle Magdalena River basin. Prior to planting, we isolated corridors with fencing to reduce direct pressure from cattle. Next, we cleared the existing pastures mechanically and planted individual saplings at an inter-individual distance of 2 m, without a fixed composition design, but still aiming to avoid planting the same species adjacently. Saplings used in the restoration were at least 50 cm tall (between 3 and 6 months old), planted mainly during the rainy seasons and we did not use any fertilizer or hydro retainers in this process. After the saplings were planted, we cleared weeds and grasses from the corridors every 2–3 months until they reached approximately 80 cm, and replaced saplings that had died during the process. Also, we controlled leaf-cutting ants (*Atta* sp.) near corridors when needed. When saplings surpassed maximum grass height, we stopped our active assistance to planted trees and allowed natural processes of growth and the recruitment of new plants to occur. Finally, we maintained fencing throughout the study period to reduce damage to trees and saplings from cattle grazing nearby and mechanically damaging the trees.

We monitored five corridors to evaluate their structure and composition throughout the restoration process. We also placed 10 camera traps for approximately 65 continuous days in the adjacent forests and within the corridors to verify their use by local wildlife. Thus, we monitored corridors, “1,” “2A,” and “4” that were planted during 2016–2017, and corridors “2B” and “9” that were planted in 2020. Corridors “5,” “6A,” “6B,” and “10” were not monitored in this study (Fig. 1). The complete area devoted to restoration corridors in the area is 14.9 ha, and this study focuses on 9.3 ha of corridors from the five corridors (Table 1).

Vegetation Structure of Corridors and Forest Fragments

We compared the structure and composition of younger (1 year) and older (4–5 year) corridors to that of forest fragments. Since 2017, we established 24 (10 × 10 m) vegetation plots inside corridors. In each plot, we recorded sapling abundance, survival, and measured the height and diameter at breast height (DBH) of planted trees and those already present—or naturally recruited—in the corridors. We sampled 6 (50 × 2 m) vegetation plots within the forest fragments adjacent to corridors and recorded the species richness and composition of the forest community. Tree identification was based on earlier studies on similar forests in the middle Magdalena River basin (Aldana et al. 2008).

Data Analyses

In order to test for differences in plant diversity (composition and abundance) between the corridors and forest fragments, we used a permutational multivariate analysis of variance (PERMANOVA) test. We then used a similarity percentage analysis (SIMPER) to identify the contribution of each species to the existing dissimilarities between sampling sites. For all analyses, we used the Bray–Curtis dissimilarity distances. Finally, in order to test for differences in vegetation structure between corridors and the forest fragments, we compared the mean height of individuals with a DBH greater than or equal to 10 cm between the corridors using a pairwise Kruskal–Wallis test and Dunn’s post hoc tests.

In order to evaluate if corridors were being used by terrestrial medium and large vertebrates at Hacienda Lusitania, we installed 10 Reconyx-Hyperfire cameras within the corridors (Fig. 1). We installed the cameras for a total of 65 days, between 11 June and 15 August 2020, accounting for a 650 night-trap sampling effort. Cameras were set to take photos during the day and at night, and we identified the species in each photograph. We calculated a total beta diversity (β_{sor}) between each of the corridors and the forest fragments using Sorensen’s index (Baselga 2010). The contribution of spatial turnover (β_{sim}) was measured using the Simpson index (Koleff et al. 2003), and beta diversity due to nestedness resultant (β_{nes}) was measured as the difference between β_{sor} and β_{sim} (Baselga 2010). These measures do not overestimate the fraction of total dissimilarity that can be attributable to richness differences and evaluate nesting patterns considering both on paired overlap and matrix filling

Table 2. Species that contribute to the dissimilarity in plant composition between corridors and the forest by 2020. Only species that contributed >1% are included. Values for each corridor and the forests represent the relative abundance of each species.

Taxon	*Cum %*	*%*	*Corridor 1*	*Corridor 2A*	*Corridor 2B*	*Corridor 4*	*Corridor 9*	*Forest*
Gmelina arborea	8.97	8.97	0.00	0.00	0.00	10.00	0.00	0.00
Enterolobium cyclocarpum	16.25	7.28	1.33	0.50	6.75	1.00	8.50	0.00
Albizia saman	22.27	6.02	1.67	0.75	4.25	0.00	7.75	0.00
Ceiba pentandra	28.22	5.95	0.00	0.00	8.00	3.17	2.25	0.00
Cecropia peltata	32.20	3.98	1.50	0.50	5.75	0.00	0.00	0.20
Gliricidia sepium	35.63	3.43	0.00	0.50	2.00	0.00	5.50	0.00
Cedrela odorata	38.79	3.16	1.33	0.50	0.75	0.33	3.50	0.20
Inga spectabilis	41.51	2.72	2.67	0.50	0.00	0.00	0.25	0.00
Isertia haenkeana	43.94	2.43	0.17	3.25	0.00	0.00	0.00	0.20
Ficus sp.	46.11	2.17	0.00	0.00	0.00	0.00	0.00	5.00
Citrus sp.	48.00	1.89	1.33	0.00	0.00	0.33	1.25	0.00
Xylopia sp.	49.87	1.87	0.33	0.50	0.00	0.00	2.00	0.00
Anacardium excelsum	51.63	1.76	0.00	1.00	0.00	1.17	0.00	0.00
Cupania sp.	53.14	1.51	1.00	0.00	0.00	0.83	0.25	0.00
Psidium sp.	54.59	1.45	0.17	0.00	0.00	1.67	0.75	0.00
Cordia gerascanthus	56.00	1.41	0.50	0.50	1.25	0.00	0.00	0.00
Genipa americana	57.36	1.36	1.50	0.00	0.00	0.00	0.25	0.00
Pseudomalmea boyacana	58.70	1.34	0.33	0.00	1.00	0.00	0.25	0.60
Virola flexuosa	59.82	1.12	0.00	0.00	0.00	0.00	0.00	3.40
Vismia baccifera	60.87	1.05	0.33	0.25	1.25	0.00	0.00	0.00

(Baselga 2012). We used R (RStudio Team 2020) for statistical analyses and the Vegan (Oksanen et al. 2013) and Betapart (Baselga 2010) packages. Finally, in order to evaluate a potential relation between vegetation structure and beta diversity, we used a linear regression test between total beta diversity and average height.

Results

We established 10 corridors (1 in 2016, 4 in 2017, 1 in 2019, 2 in 2020, and 2 in 2021) (Table 1) that connect the forest fragments within Hacienda Lusitania and adjacent neighbors and connect six forest fragments (approximately 992 ha). Overall, the corridors will provide physical, structural, and potentially genetic connectivity to at least six groups of brown spider monkeys that currently live in isolated forest fragments. Through direct observation by our team members, we have consistently recorded the use of 4–5 year corridors by howler monkeys (*Alouatta seniculus*), night monkeys (*Aotus griseimembra*), and white-faced capuchins (*Cebus versicolor*). Brown spider monkeys (*Ateles hybridus*)—our conservation target—have been observed using the two corridors that have been established along major creeks, suggesting they are reaching the structural conditions that allow brown spider monkeys to move between forest fragments.

Floristic Composition and Vegetation Structure in Corridors and Forests

The floristic composition of vegetation plots within the main forest fragments revealed a diverse community of plants in the area. Based on 461 sampled trees (>10 cm in DBH), we identified 165 different species in 121 genera and 48 plant families. The families with higher species richness were Fabaceae (24), Annonaceae (13), Moraceae (12), Rubiaceae (9), Piperaceae (9), and Arecaceae (7), while 21 families only had a single species.

As expected, our sampling on the composition of plots within corridors, revealed statistical differences in the composition and abundance of tree species compared to that of plots in forest fragments ($F = 3.30$; $p < 0.001$) (Figs. S2 & S3). Similarly, we found differences in the composition and abundance of tree species between corridors, except for corridors 2A, 2B, and 9. These differences can be partly attributed to the native species of plants used in the restoration of each corridor (mainly *Enterolobium cyclocarpum*, *Albizia saman*, *Ceiba pentandra*, *Cedrela odorata*, and *Inga spectabilis* y *Anacardium excelsum*) or the non-native species (*Gmelina arborea*) widely used in corridor “4.” Early successional species that have been naturally recruited in the corridors (*Cecropia peltata*, *Isertia haenkeana*), or even preexisting trees that were inside the corridors when they were established (*Citrus* sp., *Xylopia* sp., and *Psidium guajava*) also contributed towards differences between corridors and the forest fragments. Finally, some of the most abundant trees found in forest fragments were still absent from restoration corridors (*Ficus* spp. and *Virola* sp.) (Table 2).

The early regeneration corridors “2B” and “9” were planted in 2020 had a different structure than those planted in 2016/2017 and the forest fragments ($H = 19.67$, $p = 0.001$,

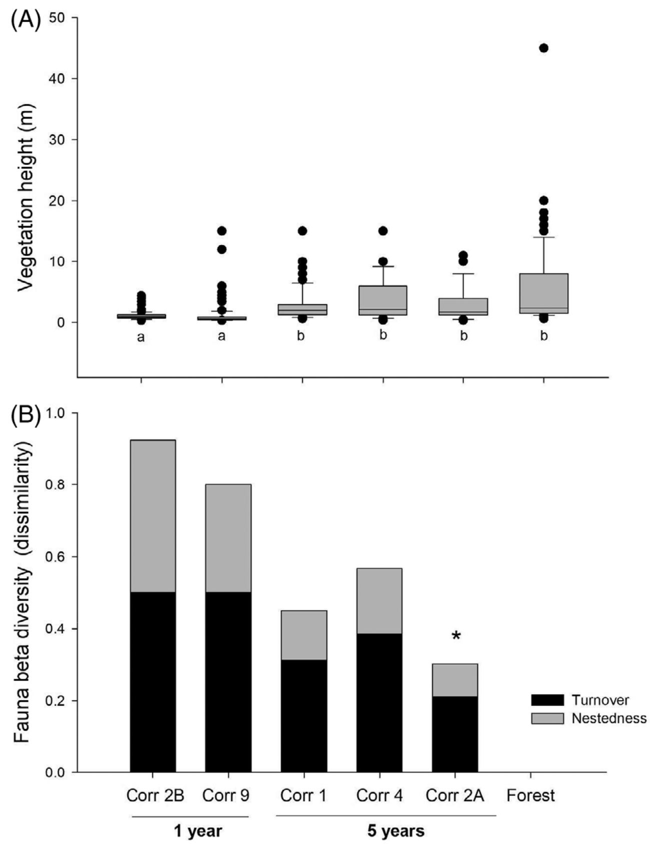


Figure 2. (A) Changes in vegetation cover along corridors measured as the average height of trees with DBH ≥ 10 cm in comparison to reference forest. Letters a and b represent two groups with significant differences among them. (B) Analysis of faunal beta diversity between the corridors and the forests of reference, considering species turnover (black bars) and nestedness (gray bars), calculated from camera trap survey records. Presence of *Ateles hybridus* is depicted with an asterisk.

Fig. 2). Nonetheless, the corridors planted in 2016/2017 did not differ in structure from the main forest fragments, at least when evaluated through the canopy height of trees with DBH > 10 cm ($Z = 2.53$; $p = 0.12$).

Use of Corridors by Terrestrial Vertebrates

The long-term study of the terrestrial medium and large vertebrates of the broader region around Hacienda Lusitania showed that forest fragments bear an almost complete vertebrate community (Link et al. unpublished data). Cameras set up since 2017 in the adjacent forest fragments of the connectivity corridors have detected the presence of at least 32 mammal species (Table 3). The 10 cameras set up within corridors for a period of roughly 2 months, showed that a large proportion of terrestrial vertebrates are indeed using these corridors as movement pathways. We were able to detect 21 species of mammals from seven different orders. Values for beta diversity obtained for mammal diversity between corridors and forests ranged between 0.30 (corridor “2A” implemented in 2017)—indicating a similarity of 70% in the mammals that are using this corridor and

Table 3. Species of mammals recorded and ground-feeding birds along the corridors and forest of reference. Type of record: CT, camera trap; S, sighting. Location: C, corridors; F, forest.

Species				*Common Name*	*Conservation Status*	*Type of Record*	*Site of Record*
Mammalia	Artiodactyla	Tayassuidae	*Pecari tajacu*	Collared peccary	LC	CT	C, F
			Tayassu pecari	White-lipped peccary	VU	CT	F
		Procyonidae	*Procyon cancrivorus*	Crab-eating raccoon	LC	CT	C, F
	Carnivora	Mustelidae	*Eira barbara*	Tayra	LC	CT, S	C, F
			Galictis vittata	Greater grison	LC	CT	C, F
			Lontra longicaudis	Neotropical otter	NT	CT, S	C, F
		Felidae	*Leopardus pardalis*	Ocelot	LC	CT	C, F
			Puma concolor	Cougar	LC	CT	C, F
			Leopardus wiedii	Margay	NT	CT	C, F
			Herpailurus yagouaroundi	Jaguarundi	LC	CT	C, F
			Panthera onca	Jaguar	NT	CT	F
		Canidae	*Cerdocyon thous*	Crab-eating fox	LC	CT	C, F
			Urocyon cinereoargenteus	Gray fox; Gray fox	LC	CT	F
	Cingulata	Dasypodidae	*Cabassous centralis*	Northern naked-tailed armadillo	DD	CT	F
			Dasypus novemcinctus	Nine-banded armadillo	LC	CT	C, F
	Didelphimorphia	Didelphidae	*Didelphis marsupialis*	Common opossum	LC	CT	F
			Metachirus nudicaudatus	Brown four-eyed opossum	LC	CT	C, F
	Perissodactyla	Tapiridae	*Tapirus terrestris*	Lowland tapir	VU	CT	F
	Pilosa	Myrmecophagidae	*Myrmecophaga tridactyla*	Giant anteater	VU	CT	F
			Tamandua mexicana	Northern tamandua	LC	CT	C, F
	Primates	Atelidae	*Alouatta seniculus*	Colombian red howler	LC	S	C, F
			Ateles hybridus	Brown spider monkey	CR	S	C, F
		Cebidae	*Cebus versicolor*	Varied white-fronted capuchin	EN	S	C, F
		Aotidae	*Aotus griseimembra*	Gray-handed night monkey	VU	S	C, F
	Rodentia	Sciuridae	*Microsciurus santanderensis*	Santander dwarf squirrel	DD	CT	F
			Sciurus granatensis	Red-tailed squirrel	LC	CT	C, F
		Caviidae	*Hydrochoerus hydrochaeris*	Capybara	LC	CT	C, F
		Cuniculidae	*Cuniculus paca*	Agouti	LC	CT	C, F
		Echimyidae	*Proechimys chrysaeolus*	Boyacá spiny rat	DD	CT	C, F
		Dasyproctidae	*Dasyprocta fuliginosa*	Black Agouti	LC	CT	F
			Dasyprocta punctata	Central American agouti	LC	CT	F
		Erethizontidae	*Coendou prehensilis*	Brazilian porcupine	LC	CT	F
Aves	Galliformes	Cracidae	*Crax alberti*	Blue-billed Curassow	CR	CT	C, F
			Ortalis columbiana	Colombian Chachalaca	LC	CT,S	C, F
			Penelope purpurascens	Crested Guan	LC	CT	F

the adjacent forests—and 0.92 (corridors "2B" and "9" implemented in 2020) (Fig. 2). Species turnover (referring to species recorded only in corridors but not in forests) accounted for a stronger variation in the beta diversity values than nestedness—the subset of species recorded in both forests and corridors, with values to the former laying between 0.21 and to the later between 0.09 and 0.42. Finally, we found a significant and positive correlation between forest structure—measured as

Figure 3. Sample of some species recorded in the corridors through camera traps. (A) Tayra (*Eira barbara*), (B) agoutis (*Cuniculus paca*), (C) collared peccary (*Pecari tajacu*), (D) Blue-billed Curassows (*Crax alberti*), (E) northern tamandua (*Tamandua mexicana*), (F) cougar (*Puma concolor*), and (G) brown spider monkeys (*Ateles hybridus*) sightings along corridor 2A.

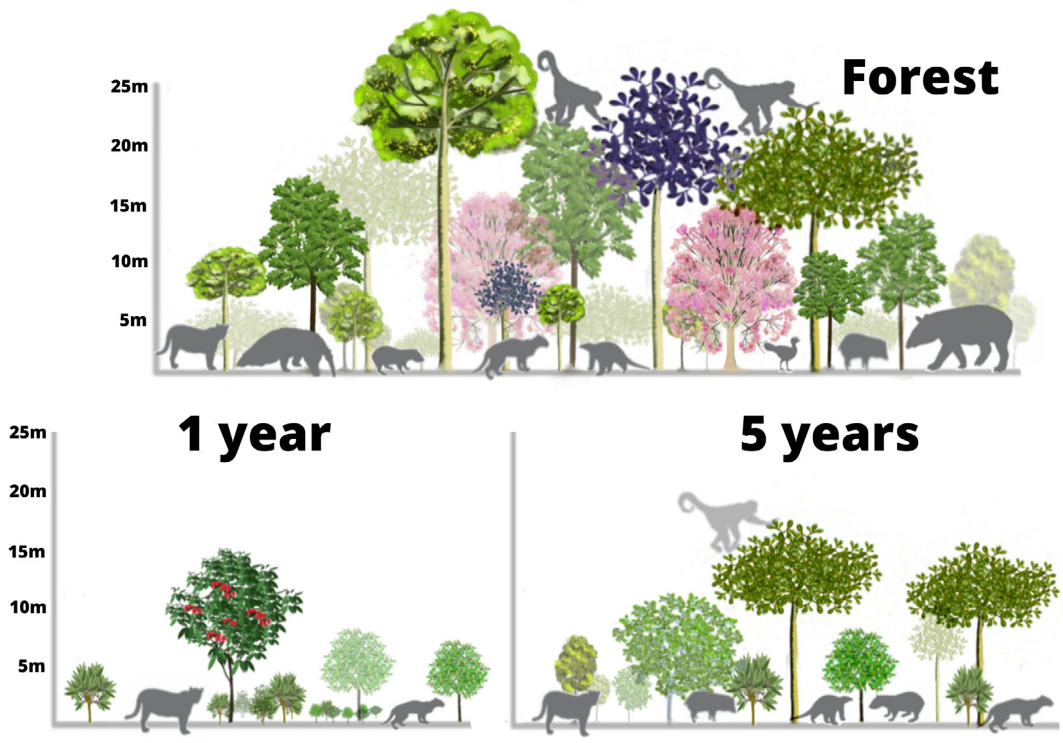


Figure 4. Schematic diagram of young (1 year) and old (5 years) restoration corridors with their associated forest structure (tree height) and the presence of associated terrestrial and arboreal vertebrates at in the lowland inter-Andean forests of Colombia.

average tree height—and a similarity between mammal assemblages in corridors and forests ($r = -0.83$, $p = 0.04$).

Among the species that are found in the forest, this survey provided evidence that the CR Blue-billed Curassows (*Crax alberti*), agoutis (*Cuniculus paca*), and collared peccaries (*Pecari tajacu*), as well as mesopredators, such as ocelots (*Leopardus pardalis*) and tayras (*Eira barbara*) were also detected in older corridors (see Table 3; Fig. 3). The survey also provided evidence of the use of corridors by apex predators, such as pumas (*Puma concolor*), and other uncommon carnivores, such as the jaguarundi (*Herpailurus yagouaroundi*), the greater grison (*Galictis vittata*), and neotropical otters (*Lontra longicaudis*). Overall, during a 2-month sampling period, the 10 cameras recorded more than 65% of the mammal species previously recorded in adjacent forest fragments (see Fig. 4).

Discussion

In this study, we provide evidence on the role of corridors as an effective strategy to reconnect populations of endangered vertebrates and all other sympatric forest-dwelling wildlife in fragmented landscapes. Overall, our project has established 10 corridors which account for approximately 15 ha of on-going restoration, but that aim to reconnect almost 1,000 ha of forests in the study area. This study is not only providing evidence for the rapid (4–5 year) recovery of vegetation structure in tropical rainforest restoration practices, but also, the potentiality of corridors to reestablish physical and genetic connectivity between isolated populations in fragmented landscapes. Future studies should further sample open areas, such as pastures, in order to account or the real additional value of corridors as wildlife pathways compared to open areas.

The notion of "connectivity corridors" has been widely proposed—and used—as a response to the pervasive habitat fragmentation that is taking place all over the planet (Cushman et al. 2013). Nonetheless, the vast majority of studies related to the role of corridors as regional or local strategies to reconnect ecosystems and wildlife have been theoretical and mainly focused on evaluating the best statistical approaches to optimize the design and implementation of such corridors (Rudnick et al. 2012). To the best of our knowledge, most of these studies have focused on the designing of optimized corridors through a wide array of methodological approaches (e.g. least-cost paths, circuit theory, among other methods) (Cushman et al. 2013). Although theoretical approaches to the implementation of corridors might allow decision makers to prioritize areas for the implementation of connectivity projects, they may fail from including structural and social variables that may be important at the implementation stages. For example, our least-cost models provided important evidence on the key areas to implement connectivity between the existing forest fragments, but these proposed corridors had to be locally adjusted to the existing fencing of the cattle ranching at Hacienda Lusitania, to protect water sources, as well as the establishment of corridors in areas under signed conservation agreements. Thus, we acknowledge the great value of connectivity models for planning small and large-scale connectivity projects, but also point out how these should serve as initial models when discussing with stakeholders involved in the design, implementation, monitoring, and stewardship of corridors.

As reviewed by Zahawi and Augspurger (1999), active restoration is often necessary in open grasslands to recover the structure and composition of reference forests. Environmental, ecological, and anthropogenic barriers may reduce the chances of passive restoration to surpass thresholds leading to a static phase of arrested succession (Wieland et al. 2011) often referred to as "at-risk" communities (Briske et al. 2008). Thus, planting of fast growing species that reduce sunlight in the understory (and limit grass growth) or allowing frugivores to perch in restoration areas are some of the activities that can foster more successful restoration processes (Bestelmeyer et al. 2017). These active implementations may allow restoration to surpass key thresholds and may even reverse undesirable transitions (Bestelmeyer et al. 2017).

A key component of successful restoration implementation relies on identifying the local stressors that drive habitat degradation or that prevents it from recovering (Opperman & Merenlender 2020). In the middle Magdalena River basin, an important stressor on plant regeneration is cattle that roam in open pastures, actively feed from grasses and saplings, and mechanically damage regenerating plants. At Lusitania, successional processes responded favorably to the isolation of corridors with fencing—keeping cattle outside of corridors—which largely coincides with earlier results of other studies that have recorded a rapid regeneration of riverine forests once grazing activity is restricted (Opperman & Merenlender 2020).

Although there are successful examples of passive restoration that suggest that early successional stages may not need active stimuli once stressors are eliminated (see Sampaio et al. 2007 for deciduous forests in Brazil) and may prove to be more cost effective, this approach may lead to static successional stages if such stressors remain (Hopkins 1983; but see Zahawi et al. 2014). For example, areas planted with a large number of native trees ($n = 79$ species) were still dominated by pioneer species after a decade of implementation of restoration and had a low species richness and density in late-successional trees (de Souza & Batista 2004). Passive regeneration should be implemented whenever possible as it offers the possibility of rapid regeneration with a lower financial cost and the possibility of scaling regional restoration and connectivity projects.

Prior to working towards recovering the composition and diversity of corridors (similar to existing forest fragments), the first aim of corridors was to achieve structural connectivity to allow brown spider monkeys—the largest arboreal vertebrates in the area—to move between forest fragments. Five-year corridors have reached a similar tree height structure similar to that of adjacent forests, although the floristic composition is still quite different. These results were expected as the early successional process had the potential to recover the forest's structure while still having a limited set of species. Suganuma and Durigan (2015) also documented that restoration processes lead to structural similarities to those of reference forests where recovering the composition of a mature forest can take up to 70 years.

Forests at Hacienda Lusitania are well conserved although some of the most important hardwoods were selectively logged decades ago. Currently, these forests have more than 100 plant species, with a continuous canopy and several keystone trees including hardwoods, such as *Cariniana pyriformis*, *Isidodendron tripterocarpum*, and *Aniba perutilis*. Even though there are clear differences between forest fragments and the corridors, especially those established more recently, in only 5 years corridors have reached a structural connectivity that allows primates and other arboreal vertebrates to move along them. This structural connectivity has been attained through fast-growing trees and those particularly resistant to drought and open environments that can rapidly reach heights of 20–30 m (e.g. *Enterolobium cyclocarpum*, *Ceiba pentandra*, and *A. saman)* (Griscom et al. 2005; Celis & Jose 2011), as well as other species that can bear fruit in the near future for brown spider monkeys and the frugivore community at Lusitania (e.g. *Inga spectabilis*, *Genipa americana*, and *Spondias mombin*).

The positive results from this pioneer experience in reconnecting forests in fragmented landscapes are part of an integral strategy in which we have been able to minimize or control key stressors. The process of (1) signing/reaching conservation agreements; (2) identifying potential corridors; (3) isolating the areas for restoration; and (4) the planting and monitoring of saplings, can most probably be implemented at larger scales. Nonetheless, we caution that the establishment of corridors can have detrimental effects on wildlife if activities, such as hunting and wildlife trafficking are in place, as animals are more vulnerable due to restricted movements in the thin corridors.

At Lusitania, a large proportion of the terrestrial vertebrates found in local rainforests and wetlands actually used the corridors. Even with a relatively small sampling effort (650 camera nights) at 10 different locations within the corridors, we were able to record 23 out of 35 terrestrial vertebrates present in the area. Interestingly, we recorded frugivores, omnivores, mesocarnivores, and even apex predators in the corridors, suggesting they may be used by most medium and large animals. Further studies should focus on the positive or negative effects of corridors as they may enhance connectivity between forest fragments or provide additional resources, but they may also increase predation risk or intraspecific contest competition. Future studies with robust methodological designs will help to further understand if corridors are used more, and more often, than open pastures by local wildlife in areas with pervasive deforestation.

Although our restoration project was based on an initial strategy to connect isolated populations of the CR brown spider monkey (*Ateles hybridus*), the overall purpose of the project was to increase both physical and genetic connectivity for local wildlife that may improve the resilience of extant populations within the heavily disturbed matrix of lowland ecosystems in Central Colombia. Thus, selecting spider monkeys as umbrella species for the conservation of the megadiverse forest-dwelling wildlife in the inter-Andean rainforests of Colombia will encompass the conservation of a rich biological community.

Given that several considerations have emerged in the use of single umbrella species as landscape conservation strategies, several authors have proposed the combination of conservation strategies directed towards "surrogate" species that may encompass a more complete conservation approach (Ward et al. 2020). Thus, not only will it be important to expand the geographical scale of our corridors focused on brown spider monkeys, but connectivity strategies should encompass surrogate species with complementary ecological requirements. As part of Proyecto Vida Silvestre in the middle Magdalena River basin, we have joined forces with other local non-profit organizations (NGOs) to jointly protect brown spider monkeys, Blue-billed Curassows (*Crax alberti*), American manatees (*Trichechus manatus*), spotted catfish (*Pseudoplatystoma magdaleniatum*), and carreto trees (*Aspidosperma polyneuron*) within a landscape conservation approach for the wetlands and forests of Central Colombia. Moving forward, our next two challenges for increasing connectivity in the Magdalena River basin will include: (1) exploring the role of natural (passive) regeneration for the establishment of corridors, as it conveys a relatively cost-effective strategy compared to active regeneration, and (2) including a holistic connectivity strategy for a set of surrogate species that can increase ecosystem resilience within large cattle ranching and agricultural landscapes in the Tumbes-Chocó-Magdalena global biodiversity hotspot.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Connectivity model based on least-cost paths with potential connectivity corridors (in red) at Hacienda Lusitania, in Central Colombia.

Figure S2. Changes in vegetation structure in corridors at Hacienda Lusitania.

Figure S3. Comparison between (A) corridor 2b before sowing (April 2020), (B) corridor with saplings (May 2020), (C) corridor 5 months later (October 2020), and (D) current state of corridor. (April 2020).

Table S1. Main characteristics of tree species most frequently used in restoration of corridors in the lowland pastures at Hacienda Lusitania, Colombia.

Supplement S1. Habitat diagnosis and corridor planning.

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