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# A proposal for practical and effective biological corridors to connect protected areas in northwest Costa Rica

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## Abstract

Habitat loss and increases in habitat isolation are causing animal population reductions and extirpations in forested areas of the world. This problem extends to protected areas, which, while often well-conserved, can be too small and isolated to maintain species that exist at low densities and require large contiguous areas of habitat (e.g. some large mammals). Costa Rica has been at the forefront of tropical forest conservation and a large proportion of the country's land area is currently under some form of protection. One such area is the northwest portion of Costa Rica, which is an extremely biodiverse region with several noteworthy national and privately-owned protected areas. However, each protected area is an isolated island in a sea of deforestation. Within Costa Rica's existing framework of biological corridors, we propose four sub-corridors as targets for restoration and full protection. These sub-corridors would link five major protected areas in northwest Costa Rica, with all of them linking to larger protected areas in the central portion of the country, while impacting a small number of people who reside within the corridors. After natural or active reforestation of the corridors, the result would be a contiguous protected area of 348,000 ha. The proposed sub-corridors would represent a 3.7% increase in protected area size in the region and only 0.2% of Costa Rica's total land area. Using the jaguar (*Panthera onca*) as a model umbrella species, we estimated that each current isolated protected area could support between 8–104 individuals. Assuming lack of dispersal between protected areas (distance between each ranges from 8.1 to 24.9 km), these population sizes are unlikely to be viable in the long term. However, the combined protected areas, connected by biological sub-corridors, could support about 250 jaguars, a population size with a higher probability of surviving. Our study shows that focusing conservation efforts on a relatively small area of Costa Rica could create a large protected area derived from numerous small isolated preserves.

**Keywords**
biological corridors, conservation, Costa Rica, *Panthera onca*, protected areas

## Introduction

Biological corridors are important conservation tools for maintaining species diversity in places where habitat loss results in small isolated areas of natural landscapes (Taylor et al. 1993, Ewers and Didham 2006, Hilty 2012, Hilty et al. 2012) and may be vitally important for long-term survival of species under the ongoing human-induced climate change (Heller and Zavaleta 2009, Fung et al. 2017). Corridors can help facilitate dispersal (defined as movement of individuals with potential consequences for gene flow across space, Ronce 2007) and subsequently reduce extinction probabilities of some species, especially those that are unlikely to travel across large open spaces (e.g. primates, large terrestrial mammals, Weber and Rabinowitz 1996, Hilty et al. 2006, Crooks and Sanjayan 2006). While not a perfect replacement for large blocks of natural habitat, corridors often allow a number of small populations to effectively function as one large, viable population. Examples of effective corridors include those connecting a network of parks in Bhutan (Wangchuk 2007), the Terai Arc Landscape connecting 14 different protected areas in India and Nepal (Wikramanayake et al. 2004, Harihar and Pandav 2012), the Lower Rio Grande Valley National Wildlife Refuge in south-western United States (US Fish and Wildlife Service 2001) and the European Green Belt, which runs from the Finnish-Russian border all the way through the Balkans (Terry et al. 2006). Biological corridors appear to increase connectivity for a range of taxa, including vertebrates, arthropods and plants (Rosenberg et al. 1997, Bennett 1999, Haddad et al. 2003, Chetkiewicz et al. 2006).

Tropical rainforests continue to undergo rapid deforestation and fragmentation in many parts of the world (Hansen et al. 2010, Achard et al. 2014). However, some countries have slowed deforestation and have even begun to show net positive rates of forest cover (Meyfroidt and Lambin 2011, Keenan et al. 2015). Where deforestation has been largely halted and conservation efforts are strong, the opportunity exists to connect remaining blocks of isolated forest. For example, Costa Rica suffered extremely high rates of deforestation in the latter half of the 20$^{th}$ century, but by the year 2000, reforestation rates were higher than deforestation rates (Keenan et al. 2015). Although the exact amount of Costa Rica's forest cover is debatable, the country has been slowly gaining forest cover (to about 50%, Chacón-Cascante et al. 2012) since the turn of the century (Algeet-Abarquero et al. 2015), indicating that Costa Rica is going through the "forest transition," similar to what has been seen in some countries with highly developed economies (Mather and Needle 1998, Spray and Moran 2006, Jadin et al. 2016). Considering that 27% of Costa Rica is formally protected, much of the country's forest cover exists outside protected areas, forests that are likely necessary to conserve wide-ranging animals. Despite a strong and largely successful track record of forest conservation, many of Costa Rica's protected areas remain small islands of habitat, surrounded by deforested or highly fragmented lands (Sánchez-Azofeifa et al. 2003). These protected areas may lack sufficient area or connectivity to support some species, particularly those with low population densities and/or large home range requirements.

The Mesoamerican Biological Corridor proposal would connect a series of large existing protected areas via biological corridors, allowing connectivity from southern Mexico to Panama (Miller et al. 2001, Independent Evaluation Group 2011, Holland 2012). In part to meet the goals of the Mesoamerican Biological Corridor, Costa Rica's national system of conservation areas (Sistema Nacional de Areas de Conservación, SINAC 2018a) has established a system of biological corridors designed to connect protected areas throughout the country (National Program of Biological Corridors of Costa Rica, SINAC 2006, Fig. 1). However, the corridors established by SINAC are typically quite large (Chacón Cascante et al. 2012) and often include areas with large human populations (e.g. portions of the Paso de las Nubes have > 250 people/km$^2$, CIESIN 2016), extensive deforestation (greater than 50% in some corridors, Sánchez-Azofeifa et al. 2003, Morse et al. 2009, Fagan et al. 2016) and extensive economic activity, in particular agriculture (Fagan et al. 2013). These factors make true functional connectivity difficult or unlikely (i.e. connectivity that allows the successful dispersal of organisms between protected areas that increases the probability of species persistence, Rosenberg et al. 1997, Hess and Fischer 2001). Indeed, the Mesoamerican Corridor project has faced numerous political, social and ecological challenges since its inception (Vega 1994, Kaiser 2001, Miller et al. 2001, Grandia 2007, Mendoza et al. 2013). While Costa Rican efforts, directed at encouraging conservation in the large corridors, such as voluntary reforestation and ecosystem services payments, are likely to have environmental benefits, without coordinated efforts to reduce isolation of forest remnants, these activities are unlikely to produce truly contiguous areas of habitat outside of current protected areas. There have also been efforts (both ongoing projects and proposals) to create smaller biological corridors in Costa Rica that will likely provide direct connectivity between currently protected areas. Examples of these smaller corridors include: Maquenque National Park, which, when fully protected and reforested, would connect Costa Rican and Nicaraguan protected areas (Chassot and Monge-Arias 2012); the Barbilla-Destierro Corridor connecting the Central Volcanic Mountain Range to large protected areas in southern Costa Rica (Gamboa and Salom 2015); and the "Path of the Tapir" connecting protected areas in the south-western part of the country (Newcomer 2002). These corridors would be a fraction of the width of SINAC biological corridors, but would be a contiguous habitat between existing protected areas.

The north-western part of Costa Rica includes several noteworthy state- and privately-owned biological preserves such as Santa Rosa NP, Guanacaste NP, Rincón de la Vieja NP, Arenal NP, Monteverde Cloud Forest Reserve and the Children's Eternal Rainforest. The area is characterised by low elevation terrain punctuated by a series of young volcanic ranges. Habitat diversity is extremely high and includes tropical dry forests, pre-montane forests, cloud forests and tropical wet forests. Currently, pro-

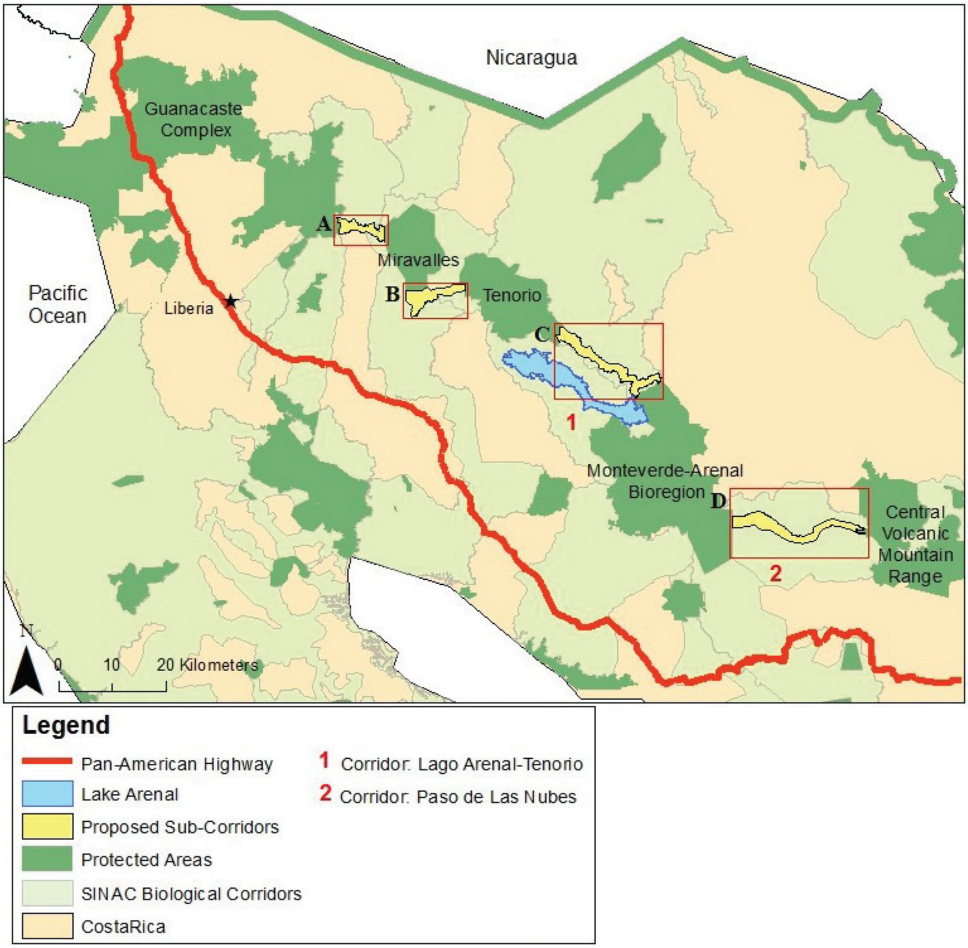


**Figure 1.** Proposed biological sub-corridors within the protected land and Costa Rican government designated biological corridors in north-western Costa Rica. **A** Guanacaste – Miravalles **B** Miravalles – Tenorio **C** Tenorio – Monteverde-Arenal Bioregion **D** Monteverde-Arenal Bioregion – Central Volcanic Mountain Range, 1 = Arenal – Tenorio Biological Corridor (SINAC-designated), 2 = Paso Las Nubes Biological Corridor (SINAC-designated).

tected areas are concentrated in the major volcanic features of the Guanacaste and Tilarán mountain ranges, plus a large area of tropical dry forest (Santa Rosa and Guanacaste National Parks) that stretches to the Pacific Ocean. With the exception of connectivity in the Guanacaste region, where three large national parks are connected either directly (Santa Rosa and Guanacaste) or by a protected corridor (Guanacaste and Rincón de la Vieja), protected areas are relatively small and isolated. For example, the Monteverde-Arenal Bioregion (MAB) is described as connected to its nearest neighbours, Tenorio National Park to the west and Juan Castro Blanco National park to the east, via SINAC's Arenal-Tenorio and Paso Las Nubes Biological Corridors, respectively. On the ground, however, functional connectivity (in terms of ability of forest-dependent organisms to move through these corridors) is less than ideal since the two biological corridors in question are composed mostly of fragments (see results) of forest with little or no formal protection. Recent monitoring of fragmented lands surrounding the MAB indicates that many large mammals found in the parks and preserves are not utilising their habitat outside the protected areas (Zamzow et al. 2018). Therefore, the MAB – which includes Arenal Volcano National Park, the Children's Eternal Rainforest, Monteverde Cloud Forest Biological Reserve, Santa Elena Cloud Forest Reserve and Alberto Manuel Brenes Biological Reserve – remains relatively isolated. This area has extremely high species diversity and endemism and supports a number of endangered species, including jaguar (*Panthera onca*), spider monkey (*Ateles geoffroyi*) and Baird's tapir (*Tapirus bairdii*). Two of the local communities surrounding the MAB, La Fortuna and Monteverde, are major ecotourism destinations (Koens et al. 2009) that generate millions of dollars of tourism revenue and support numerous ecotourism and related jobs (Aylward et al. 1996, Langholz et al. 2000, Stuckey et al. 2014).

The distance between the isolated protected areas in the north-western part of Costa Rica is relatively small (minimum: 8km, maximum: 25 km) and there are areas of natural forest cover (variety of primary and secondary growth, M. Moran and L. Stallcup, personal observation) between these protected areas. Human population density is also relatively low, making for a high potential for creating biological corridors with low impact on human communities.

The goal of this study was to determine if we could identify potential sub-corridors within the larger SINCAC biological corridors that would have parameters that allow for the movement of forest-dependent species. These sub-corridors would meet the minimum size requirement (defined here as having a minimum width of 1000 m, Lees and Peres 2008) to achieve ecological connectivity for organisms unlikely to disperse across deforested or fragmented landscapes, while also having minimum impact on local human populations. We sought to find areas with high levels of current closed-canopy forest cover, as these areas likely retain a considerable amount of biodiversity and it would be relatively cost-effective to achieve complete forest cover through natural regeneration. We assumed that protection of currently forested lands would have less effect on economic activity in the region, since these lands are not currently being utilised for intensive agriculture. By proposing the smallest effective biological sub-corridors and minimising negative impact on current human populations and economic activity, we wanted to increase functional biological connectivity, conservation of natural resources, ecosystem services and benefits to the Costa Rican people. While interested in achieving connectivity of protected areas for the benefit of biodiversity in general, we modelled the current and potential population sizes of the jaguar as an umbrella species following Thornton et al. (2016) to determine if our proposed sub-corridors would be potentially effective in supporting a viable population of this sensitive species. The jaguar is a focal conservation species in Costa Rica (SINAC 2018b) and is declining in parts of the country (Salom-Pérez et al. 2007). It is often considered a valuable proxy for conserving biodiversity (Thornton et al. 2016), in that habitats capable of supporting this top predator species are likely to be able to support many other less sensitive species. In Costa Rica, the jaguar currently exists in several important "jaguar conservation units" that are poorly connected to each other with subsequent limited dispersal opportunities (jaguar conservation unit 154 in our study region, Sanderson et al. 2002).

## Methods

We downloaded boundaries of legally protected terrestrial lands (UNEP-WCMC 2018) and the biological corridor boundaries regulated by the SINAC (Oficina Nacional Forestal 2006). We used the Global Forest Watch database (Hansen et al. 2013, parameters: 30 m × 30 m resolution, images from Landsat 7, GIS layer established in 2000, most recently updated in 2017) to locate forested areas between protected areas in north-western Costa Rica that could provide cover as feasible biological sub-corridors (See Appendix 1 for data sources). Our goals in defining a prospective sub-corridor were to minimise proposed size, minimise overall linear distance (km) between established protected areas, maximise current proportion of forest cover and minimise human population density. We first focused on finding land connecting existing protected areas that was relatively short in distance and maintained at least some forest cover. In all cases, we avoided any dense human population areas (i.e. cities and towns) using visual inspection of satellite data (explained below). When deciding on which route to choose, we ultimately had to make a judgement that considered distance of corridor, amount of forest cover and avoidance of densely populated areas. A limitation to the dataset is that the forest cover maps did not differentiate between native or non-native forest, nor forest quality (except for tree cover proportion).

We then obtained recent satellite views for each of the proposed sub-corridors from Google Earth Pro™. All corridor locations had satellite imagery from the year 2017. We established that the minimum width of any point along the corridor must be at least 1000 m, since this width appears to allow movement of practically all non-flying mammals in the Neotropics (Lees and Peres 2008). Each sub-corridor boundary was adjusted manually (using the Ruler tool in Google Earth) to minimise overlap with human structures and maximise areas of current forest cover (Fig. 2). Once sub-corridor boundaries were constructed, we measured (using visual determination and the Ruler tool) the amount of land that was forest, pasture, developed or other (i.e. barren land, either natural or due to human activity). Developed landscapes were classified as those covered by human-built structures (houses, roads etc.). We counted the number of human structures, other than roads, as a proxy for how many people live in the proposed sub-corridors. If there was some doubt about land cover classification, we used local ground observations (L. Stallcup, personal observations). Proportional land cover was then calculated by dividing the various land use categories by the total corridor area. We also measured the minimum length of each corridor – in other words, the minimal distance an animal would have to travel to move from one current protected area to another via the sub-corridor. Using Arc GIS™, we constructed maps of protected areas,

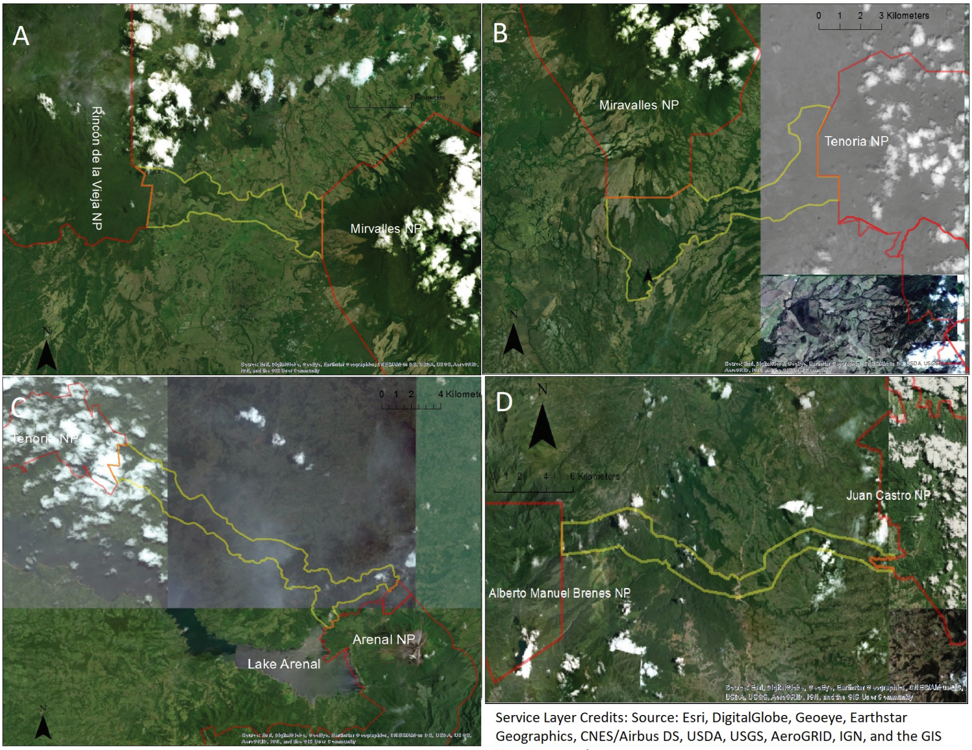


**Figure 2.** Satellite views of the four proposed biological sub-corridors (in yellow) with adjoining protected areas (in red). Dark green areas indicate the presence of forested habitat.

SINAC biological corridors and proposed sub-corridors in order to show the locations relative to other geographic features.

We then modelled the potential population size of jaguars, a commonly utilised "umbrella" species, whose presence may indicate a well-functioning ecosystem (Barua 2011, Thornton et al. 2016). The jaguar is a species that appears to have a viable population in some areas of our study (e.g. Guanacaste and Santa Rosa NPs, SINAC 2018b) but is very rare or absent in other protected areas (e.g. MAB, Zamzow et al. 2018). Therefore, if sub-corridor protection were to be initiated, this species could also be monitored in areas where it is currently absent or rare as a measure of whether our proposal was having some conservation success. Based on density estimates of jaguar from literature of published studies of the region (Appendix 2), we calculated the mean population density per 100 $km^2$ (± 2 standard errors of the mean). These values were used as the estimate of the potential carrying capacity of the forested habitat, based on the size of each current contiguous protected area. We then estimated population sizes of jaguars in all current protected areas as if these areas were already connected by the proposed sub-corridors (using area of currently protected areas, plus our proposed sub-corridor areas). In our estimates, we assumed no jaguar mortality other than natural density-dependent population regulation due to carrying capacity of the habitat.

### Limitations and future improvements

Our analysis has limitations worth considering. Except for forest cover proportion, we did not utilise computer software (e.g. Marxan) to choose the best path for our sub-corridors. Instead, once we had located a pathway with the most forest cover that did not cross towns and other settlements, we made individual decisions on corridor shape and path based on local land use, shape of forest blocks, human structures, distance between existing protected areas and existing political frameworks (e.g. existence of current SINAC corridor designations). Our analysis, therefore, does not take into account costs, biodiversity protection or boundary length, as would be incorporated into some programmes (Ball et al. 2009). An important next step would be to determine land ownership patterns and potential interest in conservation amongst land owners within the sub-corridors. Biological monitoring (e.g. camera trap studies) would also be recommended if sub-corridor establishment is commenced to determine before and after use by target animals.

## Results

The four proposed biological sub-corridors in northwest Costa Rica (Fig. 1) represent relatively small areas of the country (about 0.2% of total country area) and are relatively small as compared to the protected areas they will connect (3.7%, Table 1). Each proposed sub-corridor has high percentage forest cover (much of it native, M. Moran and L. Stallcup, personal observations) and low levels of development compared to surrounding landscape (Table 2, Fig. 3). Practically all lands not forested are in pasture, presumably utilised to raise cattle (M. Moran, personal observation).

The sub-corridor we propose to connect the Guanacaste complex (specifically Rincón de la Vieja National Park) to Miravalles National Park, Sub-corridor A, has the most deforested lands and contains the greatest number of human-built structures (Fig. 3A). It should be noted that areas north of proposed Sub-corridor A have a slightly higher proportion of forest cover, but also contain many more human structures (resulting in a judgement call minimising human impact for this recommended route). The corridor proposed to connect Miravalles and Tenorio National Parks, Sub-corridor B, is more than two-thirds forested and contains no visible human structures (Fig. 3B). The area north of Sub-corridor B represents a much shorter distance between protected areas and would be smaller in area, but would also pass directly through the town of Rio Naranjo (population = 1000+, INEC 2015), making it a less desirable route. The corridor connecting Tenorio and the MAB, Sub-corridor C, is also roughly two-thirds forested and contains a minimal number of human structures (Fig. 3C); however, because it connects two more distant protected areas in our study, its area and minimum distance is greater than proposed sub-corridors A and B (Table 2). The other potential locations for sub-corridors in this region between the MAB and Tenorio all have less forest cover, longer distance between protected areas and a greater number of

**Table 1.** Current physical characteristics of proposed biological sub-corridors in northwest Costa Rica that would produce a contiguous protected area from the Guanacaste Region (Santa Rosa NP) to the Central Volcanic Mountain Range. *indicates area covered in recent volcanic activity with sparse, but natural vegetation. †indicates barren land caused by ongoing road construction.

| Corridor | Area (Ha) | Proportion forested | Proportion pasture | Proportion developed | Proportion Other | Length (km) | Human structures |
|---|---|---|---|---|---|---|---|
| Guanacaste–Miravalles | 1,594 | 0.481 | 0.500 | 0.004 | 0.015* | 8.2 | 28 |
| Miravalles–Tenorio | 2,532 | 0.715 | 0.227 | <0.001 | 0.058* | 9.7 | 0 |
| Tenorio–MAB | 3,946 | 0.674 | 0.326 | <0.001 | 0.000 | 18.6 | 12 |
| MAB–CVMT | 4,277 | 0.765 | 0.224 | 0.004 | 0.007† | 24.9 | 19 |
| **Total Corridor Area** | **12,349** | | | | | | |
| **Current Protected Area** | **348,000** | | | | | | |

**Table 2.** Area covered by all proposed corridors, currently protected lands and proportional contributions of these lands relative to current protected areas and Costa Rica as a whole.

| Total corridor area (Ha) | Proportion addition to protected areas (region) | Proportion of Costa Rica |
|---|---|---|
| 12,349 | 0.037 | 0.002 |

human structures. The fourth proposed corridor, Sub-corridor D, would connect the MAB to Juan Castro Blanco National Park, thereby connecting it to the greater Central Volcanic Mountain Range (Fig. 3D). This is the largest and longest sub-corridor. Sub-corridor D falls within the existing SINAC-designated Paso Las Nubes Biological Corridor (Fig. 1), which has a high proportion of forested land in the western portion. However, the eastern section is mostly deforested and passes close to several moderate-sized cities (most notably Ciudad Quesada). However, we were able to locate a route for Sub-corridor D with fewer human structures (Table 2). Regardless of the exact route for this sub-corridor, it is traversed in a north-south direction by the construction of a new highway connecting the cities of Ciudad Quesada and San Ramón, which means that wildlife passageways would need to be included to mitigate road impacts and enable Sub-corridor D to be ecologically functional (Fig. 3D).

The 23 studies that sampled jaguar density in tropical forests of Central America found an average of 7.09 jaguars/100 km$^2$ ± 1.16 (2SE, Appendix 2). Based on this mean value, each current isolated protected area in northwest Costa Rica can support less than 100 individuals (Table 3). The Central Volcanic Mountain Range protected area can support a population of just over 100 jaguars. None of these populations would be considered viable in the long-term (assuming N = 500 as minimum, Thomas 1990) unless there is some dispersal between populations (Rabinowitz and Zeller 2010). By connecting the protected areas in north-western Costa Rica to the Central Volcanic Mountain Range using our biological sub-corridors, the total estimated jaguar population would be more than 250. Assuming a conservative jaguar population estimate, all areas combined could support almost 200 individuals; at the higher range of the estimate, the area could potentially support more than 300 individuals (Table 3).

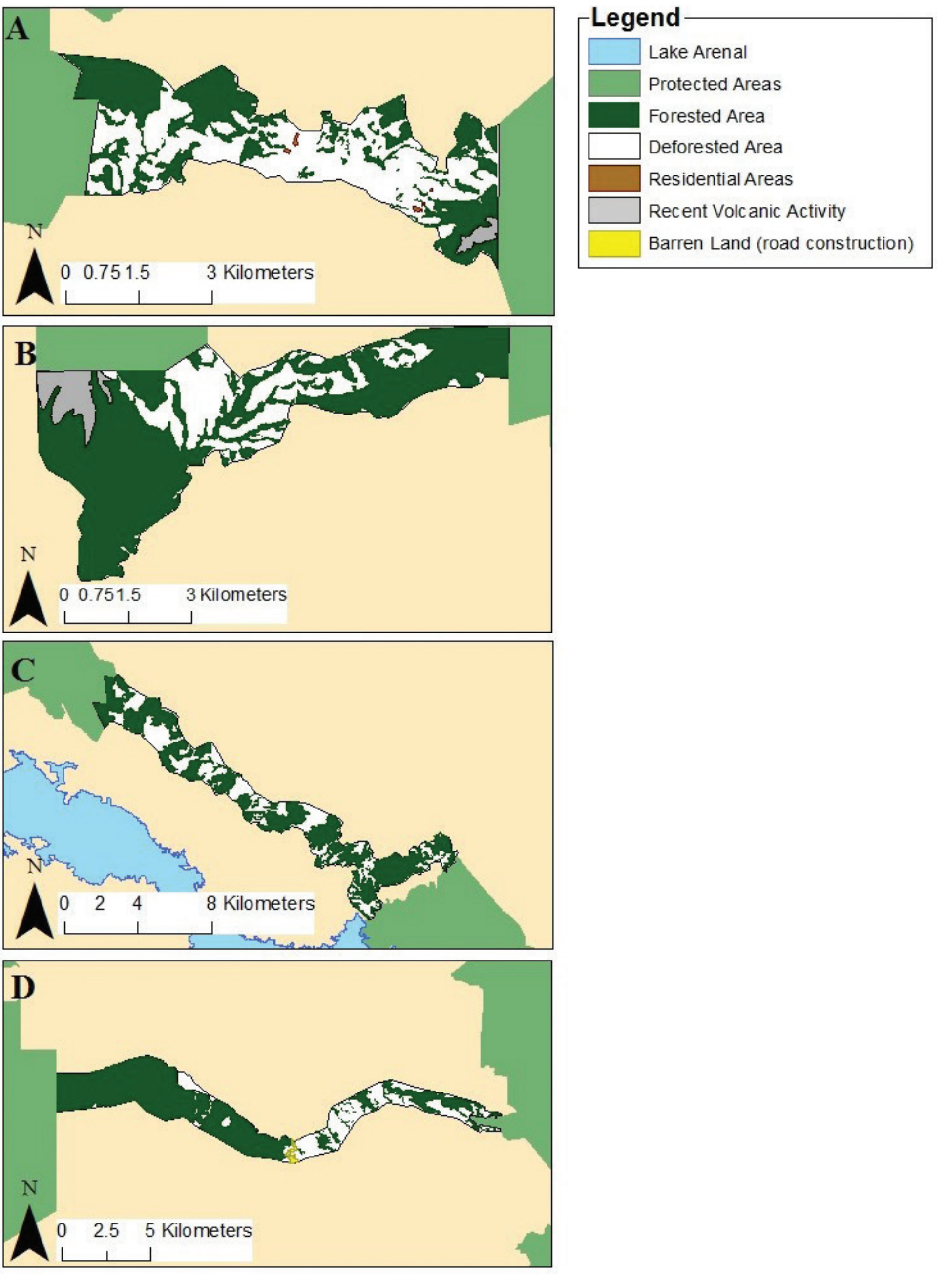


**Figure 3.** Details of land use for each proposed sub-corridor. **A** Guanacaste – Miravalles **B** Miravalles – Tenorio **C** Tenorio – Monteverde-Arenal Bioregion **D** Monteverde-Arenal Bioregion – Central Volcanic Mountain Range.

**Table 3.** Estimated population sizes of jaguar (*Panthera onca*) that could be supported in [1]current contiguous protected areas, [2]proposed contiguous protected areas connected by biological sub-corridors and habitat areas for each location. GC = Guanacaste Complex, M = Miravalles, T = Tenorio, MAB = Monteverde-Arenal Bioregion, CVMR = Central Volcanic Mountain Range, NWCR = Northwest Costa Rica including GC, M, T, MAB and three proposed corridors (Table 1), NWCR & CVMR = All protected areas and proposed corridors from Northwest Costa Rica + Central Volcanic Mountain Range.

| Estimate | GC[1] | M[1] | T[1] | MAB[1] | CVMR[1] | NWCR[2] | NWCR & CVMR[2] |
|---|---|---|---|---|---|---|---|
| Mean | 78 | 8 | 13 | 34 | 104 | 145 | 252 |
| Low | 60 | 6 | 10 | 27 | 80 | 112 | 195 |
| High | 96 | 10 | 16 | 42 | 128 | 179 | 310 |
| Habitat Area (Ha) | 110,241 | 11,670 | 18,492 | 48,500 | 146,794 | 196,975 | 348,049 |

# Discussion

## Overview of four corridors

The four functional sub-corridors proposed in this paper (Fig. 2) represent a preliminary, but potentially feasible, approach to protecting lands that could be useful in connecting populations of terrestrial mammals that are unlikely to travel between the current protected areas. Admittedly, the sub-corridors are relatively small, but human settlement patterns and large agricultural areas make the establishment of larger (in particular wider) contiguous corridors unlikely. However, by facilitating increased connectivity between currently protected areas, including some areas that do have existing jaguar populations (Sanderson et al. 2002, Rabinowitz and Zeller 2010), we create areas of contiguous habitat. This habitat could potentially support species such as the jaguar, which have naturally low population densities and require large areas with limited human activity to sustain viable populations. Some large mammals are missing or rare in isolated protected areas within our study region (Zamzow et al. 2018); often these mammals are species considered important for ecosystem functions, such as prey population regulation (e.g. top predators, Estes et al. 2011) and seed dispersal (e.g. Baird's tapir, Fragoso et al. 2003). Additional benefits of the current proposal include enhanced ecosystem services such as carbon sequestration, water resource protection and increased ecotourism, as has been seen in other parts of the Mesoamerican Biological Corridor (Harvey et al. 2008). These sub-corridors may also allow organisms to disperse more freely in response to climate change, a process that will likely become vitally important in the near future in many regions (Heller and Zavaleta 2009, Fung et al. 2017), including Mesoamerica (Imbach et al. 2013). However, each sub-corridor also has implementation challenges that will require creative solutions, as well as on-the-ground assessment (see Lees and Peres 2008, as an example). Below, we highlight details and challenges of each sub-corridor.

### Sub-Corridor A

This proposed sub-corridor is the smallest and shortest, connecting the relatively large, biodiverse and contiguous reserves of the Guanacaste region (Santa Rosa, Guanacaste and Rincon de la Vieja National Parks) to Miravalles National Park. Presumably, this corridor would increase species richness in the latter since it would connect it to a much larger complex of conserved areas. However, Sub-corridor A also has the lowest level of forest cover (slightly less than 50%) and the greatest number of human structures, including some small developed areas, presumably containing a considerable number of people (Fig. 4A). Areas north and south of the proposed corridor have even larger settlements and less forest cover, so the proposed area seems the only practical option without additional active restoration or rezoning.

### Sub-corridor B

This proposed sub-corridor, which connects Miravalles and Tenorio National Parks, is moderate in size and length, but it is probably the most practical under current land-use conditions. It is more than 75% forested and contains no human dwellings. The only development is a road (Route 6) that passes through the area. While this sub-corridor would be relatively easy to establish (if landowners were willing), it would only connect two relatively small protected areas, Miravalles and Tenorio National Parks. If neither of these conservation areas were connected via biological corridors to other regions, the conservation value, in terms of connecting populations of species that require large habitat areas, would presumably be modest.

### Sub-corridor C

This proposed sub-corridor connects Tenorio with the Monteverde-Arenal Bioregion (MAB). It is relatively large, traverses a long distance, is about two-thirds forested and has relatively few human structures, most of which are located along Route 142 between Lake Arenal and the town of La Fortuna. Many of these developments are associated with ecotourism (Fig. 4B), so it is possible that conservation-minded business owners would be interested in conservation agreements (as has been effectively achieved in other parts of Costa Rica; Pagiola 2002) or other public-private conservation partnerships that could make this sub-corridor more likely. Portions of the land between Tenorio and Arenal Volcano National Parks include part of the watershed that drains to Lake Arenal, a major hydroelectric generating facility (about 15% of total) for Costa Rica, so forest protection and future reforestation in this sub-corridor could improve water quality and reduce sedimentation in Lake Arenal (sensu ecosystem services).

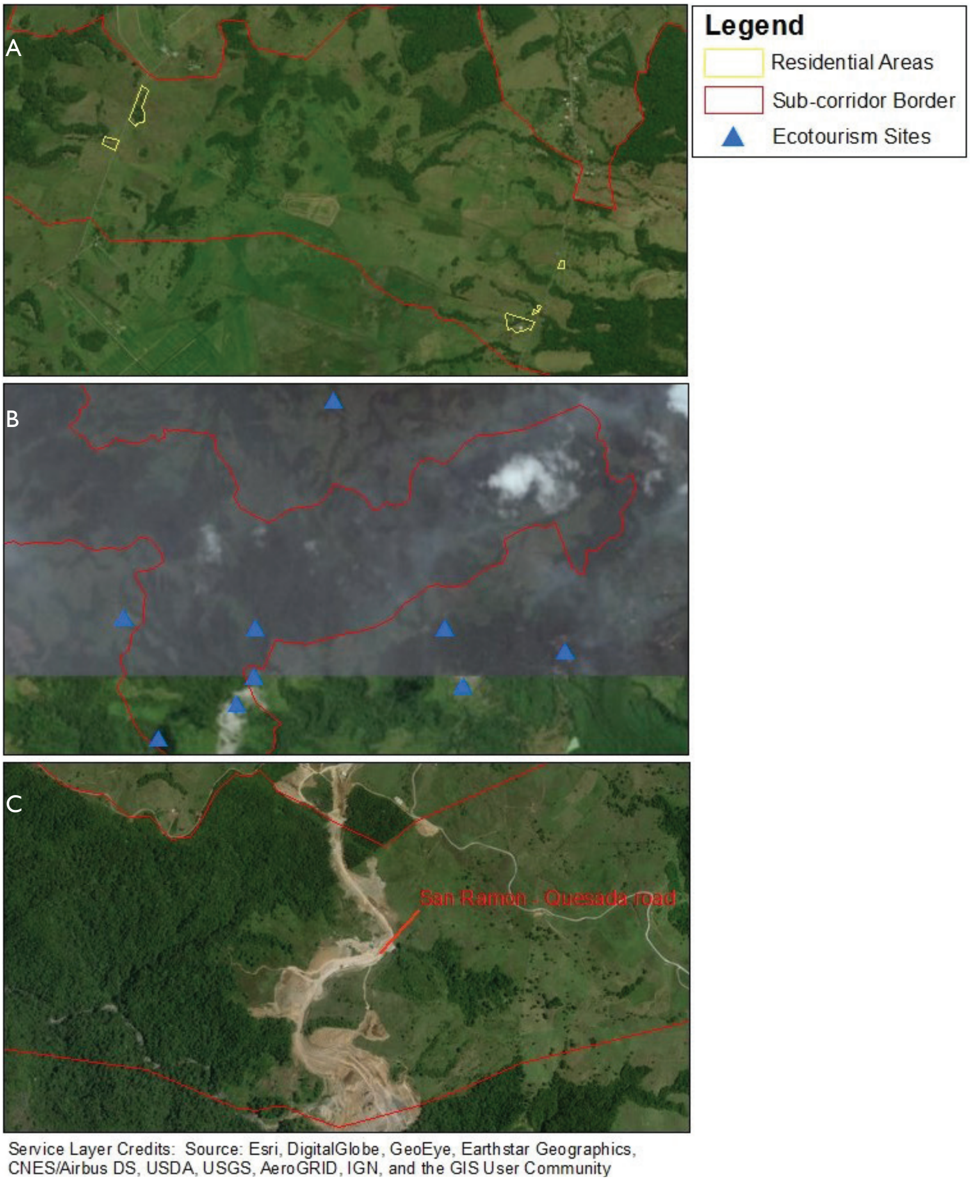


**Figure 4.** Highlighted areas of three biological corridors that have particularly problematic development and infrastructure patterns that would make corridor establishment logistically difficult. **A** Guanacaste – Miravalles **B** Tenorio – Monteverde-Arenal Bioregion **C** Monteverde-Arenal Bioregion – CVMR.

## Sub-corridor D

This proposed sub-corridor connecting the MAB to the Central Volcanic Mountain Range has perhaps the highest conservation potential, but is challenging biologically (because of length, Rabinowitz and Zeller 2010), socially and politically. It would be the longest and largest corridor, passing near several large towns, most notably the city of Quesada (population = 44,000). There is also the road construction project (San Carlos-San Ramon Highway) that will bisect any conservation corridor established in this region (Fig. 4C). The western half of Sub-corridor D has a high level of forest cover (almost 100%). Additionally, hydroelectric facilities within the corridor would benefit from increased forest protection. Most important in conservation terms, this corridor would connect two large protected and biodiverse land complexes: the Monteverde-Arenal Bioregion and the Central Volcanic Mountain Range. However, the growing population of the region (Ciudad Quesada has grown 21% since 2000; INEC 2015), along with increasing development that will likely follow the construction of the San Carlos-San Ramon highway, will likely make corridor establishment challenging without mitigation. Large highways are particularly problematic for wildlife, causing direct mortality (from vehicle strikes), dispersal blockage and loss or damage to natural resources (Forman et al. 2003, Clevenger and Wierzchowski 2006, Beckmann et al. 2010). The current land use trajectory suggests maintaining connectivity between protected areas of northwest Costa Rica and the Central Volcanic Mountain Range requires proactive highway planning and mitigation (e.g. wildlife underpasses). Sub-corridor D should be a high priority for research and conservation focus. The implementation of planned mitigation, related to the construction of the San Carlos-San Ramon highway, is currently uncertain (Villalobos Sánchez 2018); however, the land under the long bridge being constructed over the Espino River (of which about 0.25 km will be elevated above ground) within our proposed corridor could act as an effective dispersal pathway. Once construction of the highway is completed, reclamation and restoration of the land disturbed by the bridge construction should be a priority.

## Feasibility

The areas proposed for conservation in this study are very small relative to the size of Costa Rica and less than 5% the size of the current protected areas in the region (stretching from northwest Costa Rica to the Central Volcanic Mountain Range). In addition, the majority of the areas where sub-corridors are proposed already have relatively high proportions of forest cover and would therefore require a small amount of restoration work, such as active native tree planting. Other small corridors in the process of being established in Costa Rica also share these characteristics (Fagan et al. 2016). As has been seen across the country, simply allowing natural regeneration to occur would probably be sufficient to create a forested corridor within a relatively short period of time (e.g. secondary forest within 15 years, Shono et al. 2007). We suggest the proposed sub-corridors could be established with minimal disruption to local human populations and be ecologically effective for a relatively small initial expenditure of resources, once the land is purchased. However, long-term monitoring and management responsibilities would need to be determined prior to any land purchases. Once established, the proposed biological sub-corridors would still require active monitoring and protection, including law enforcement. Unauthorised encroachment, poaching, grazing and resource extraction remain a problem in currently protected areas in Costa Rica, even in places with high levels of enforcement (Hilborn et al. 2006). Protecting the sub-corridors, which in some cases would be located near areas of high human activity, would certainly be a challenge and should be considered as part of a regional protected areas strategy. Additionally, biological monitoring will need to be implemented to determine if the sub-corridors are functioning as intended. In addition to width, corridor qualities such canopy cover, tree height and anthropogenic intrusions affect use by target animals (Rosenberg et al. 1997, Lees and Peres 2008). With the advent of wildlife cameras, monitoring mammals, including secretive ones, is relatively straightforward and cost effective (O'Connell et al. 2010). Monitoring programmes beginning now, while the corridors are still fragmented and extending into the future when corridors become more contiguous, would provide valuable information on effectiveness (perhaps as a model for other regions as well).

One strategy could be the incorporation of these sub-corridors into existing protected areas. All proposed biological corridors would connect directly to existing parks and preserves owned by the Costa Rican government. While requiring additional public resources for purchase and protection, this method would work within the existing framework on land protection. In contrast to direct purchase of land for inclusion into the national system of protected areas, one could consider more creative land conservation methods. For example, targeted ecosystem service payments and/or conservation easements for high priority lands could be employed to promote connectivity in and around the proposed sub-corridors. Costa Rica's current system of environmental service payments, which include carbon emissions offsets, watershed protection, biodiversity maintenance and scenic and recreational enhancement (SINAC 2006), pays landowners to maintain forested lands on private property (Robalino et al. 2011). However, as of this writing, there is a limit of 600 hectares per private property owner (Executive Decree 2017). One alternative would be to lift this size restriction for targeted lands with the highest conservation value or other ecosystem services described above, although this could be controversial as it could benefit those with larger landholdings and presumably those who are wealthier. Discussion with all stakeholders (land owners, industries, conservation groups, government and local communities) will therefore be necessary. In addition to the proposed sub-corridors, there could be targeted reforestation in the vicinity of each sub-corridor, a process that could improve the habitat in the larger region (Mateo-Sánchez et al. 2015). In part, this priority already exists, since Costa Rica is moving in the direction of prioritising corridors and properties within the larger SINAC-designated biological corridors already receive preference for ecosystem service payments (Malavasi and Kellenberg 2002). Finally, the establishment of conservation easements, by which landowners are provided a payment (by a government or non-government conservation group) for maintaining in perpetuity land in its natural state and agreeing to certain management practices, has been effective for protecting lands in many other locations across the globe (Rissman et al. 2007). If combined with good vigilance and enforcement, conservation easements could also be considered for these corridor parcels in Costa Rica, which would offer financial incentives to landowners.

## Conclusions

The current protected areas of northwest Costa Rica are each too small to provide long-term survival to some species, such as the jaguar. While jaguars are present in the region (SINAC 2018b), very few isolated populations are likely to survive long-term (Quigley and Crawshaw 1992). In fact, viable jaguar populations may only occur in only two of the areas of this study: the reserves of the Guanacaste Conservation Area and the Central Volcanic Mountain Range (Sanderson et al. 2002, SINAC 2018b), although our analysis indicates these are also too small to survive in the long-term (Thomas 1990). A recent camera study of the MAB found that jaguars were very rare (and probably non-viable) in that isolated (although relatively large, about 50,000 ha) conservation area (Zamzow et al. 2018). However, if the sub-corridors proposed here were established and protected, they would increase connectivity, presumably increasing the combined population size in all protected areas from the Guanacaste region to the Central Volcanic Mountain Range (jaguar conservation unit 154 in Sanderson et al. 2002). This process would thereby improve long-term viability of jaguar populations (although still with some risk of extinction) and provide additional conservation value to other species that also require large contiguous areas of habitat. Even if these small corridors facilitate limited jaguar use, evidence suggests that even an occasional individual successfully dispersing would improve survivability of the existing isolated populations (Rabinowitz and Zeller 2010). Furthermore, efforts are underway to establish biological corridors across international boundaries; one proposed corridor would connect protected areas near La Selva Biological Station in north-eastern Costa Rica to the Indio Maíz Biological Reserve in south-eastern Nicaragua (Morse et al. 2009), while another would connect the Turrialba region of Costa Rica with the large complex of protected areas in the Talamanca Mountains of Costa Rica and Panama (Cusack and Dixon 2006). If all of these corridors, including our proposed examples, were to be established and subsequently protected, species that occur at low densities, require large territories and which need abundant prey could conceivably roam across almost all of Costa Rica's protected areas (Redondo-Brenes et al. 2010). The proposed corridors would directly connect multiple Central American jaguar conservation units that currently have poor dispersal frequency (Sanderson et al. 2002, Rabinowitz and Zeller 2010). Therefore, species like the jaguar would have a much better chance of survival within Costa Rica, simultaneously ensuring the country's critical role within the Mesoamerican Biological Corridor initiative. Regardless, the chance of survival for sensitive species could be vastly improved in the three-country region (Costa Rica, Panama and Nicaragua) with the addition of the proposed functional biological sub-corridors, supporting the conservation of other key species, as well as ecosystem services in the process.

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## References

Achard F, Beuchle R, Mayaux P, Stibig HJ, Bodart C, Brink A, Carboni S, Desclée B, Donnay F, Eva HD, Lupi A, Raši R, Seliger R, Simonetti D (2014) Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. Global Change Biology 20(8): 2540–2554. https://doi.org/10.1111/gcb.12605

Algeet-Abarquero N, Sánchez-Azofeifa A, Bonatti J, Marchamalo M (2015) Land cover dynamics in Osa Region, Costa Rica: Secondary forest is here to stay. Regional Environmental Change 15(7): 1461–1472. https://doi.org/10.1007/s10113-014-0714-9

Aylward B, Allen K, Echeverría J, Tosi J (1996) Sustainable ecotourism in Costa Rica: The Monteverde cloud forest preserve. Biodiversity and Conservation 5: 315–343. https://doi.org/10.1007/BF00051777

Ball IR, Possingham HP, Watts ME (2009) Marxan and relatives: Software for spatial conservation prioritisation. In: Moilanen A, Wilson KA, Possingham HP (Eds) Spatial Conservation Prioritization: Quantitative Methods and Computational Tools. Oxford University Press, New York, 185–196.

Barua M (2011) Mobilizing metaphors: The popular use of keystone, flagship and umbrella species concepts. Biodiversity and Conservation 20(7): 1427–1440. https://doi.org/10.1007/s10531-011-0035-y

Beckmann JP, Clevenger AP, Huijser MP, Hilty JA (2010) Safe Passages: Highways, Wildlife and Habitat Connectivity. Island Press, Washington.

Bennett AF (1999) Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation. IUCN, Gland and Cambridge, 242 pp.

Chacón-Cascante A, Ibrahim M, Ramos Z, De Clerk F, Vignola R, Robalino J (2012) Costa Rica: National level assessment of the role of economic instruments in the conservation policymix. Policymix. http://repositorio.bibliotecaorton.catie.ac.cr/handle/11554/7741

Chassot O, Monge-Arias G (2012) Connectivity conservation of the Great Green Macaw's landscape in Costa Rica and Nicaragua (1994–2012). Parks 18: 61–69. http://npshistory.com/newsletters/parks/parks-1801.pdf#page=63

Chetkiewicz CLB, St. Clair CC, Boyce MS (2006) Corridors for conservation: Integrating pattern and process. Annual Review of Ecology Evolution and Systematics 37: 317–342. https://doi.org/10.1146/annurev.ecolsys.37.091305.110050

CIESIN (Center for International Earth Science Information Network) (2016) Gridded Population of the World, Version 4 (GPWv4): Data Quality Indicators. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). Columbia University. https://doi.org/10.7927/H49C6VBN

Clevenger AP, Wierzchowski J (2006) Maintaining and restoring connectivity in landscapes fragmented by roads. In: Crooks KR, Sanjayan M (Eds) Connectivity Conservation. Cambridge University Press, Cambridge, 502–535. https://doi.org/10.1017/CBO9780511754821.023

Crooks KR, Sanjayan M (2006) Connectivity conservation (Vol. 14). Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511754821

Cusack D, Dixon L (2006) Community-Based Ecotourism and Sustainability: Cases in Bocas del Toro Province, Panama and Talamanca, Costa Rica. Journal of Sustainable Forestry 22: 157–182. https://doi.org/10.1300/J091v22n01_09

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA (2011) Trophic Downgrading of Planet Earth. Science 333(6040): 301–306. https://doi.org/10.1126/science.1205106

Ewers R, Didham R (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews of the Cambridge Philosophical Society 81(01): 117–142. https://doi.org/10.1017/S1464793105006949

Executive Decree (2017) Decree No. 40596H. Supreme Court of Elections Resolutions, Costa Rica.

Fagan ME, DeFries RS, Sesnie SE, Arroyo JP, Walker W, Soto C, Chazdon RL, Sanchun A (2013) Land cover dynamics following a deforestation ban in northern Costa Rica. Environmental Research Letters. 8: 034017. https://doi.org/10.1088/1748-9326/8/3/034017

Fagan ME, DeFries RS, Sesnie SE, Arroyo-Mora JP, Chazdon RL (2016) Targeted reforestation could reverse declines in connectivity for understory birds in a tropical habitat corridor. Ecological Applications 26(5): 1456–1474. https://doi.org/10.1890/14-2188

Forman RT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France RL, Heanue K, Goldman CR, Jones J (2003) Road ecology: Science and Solutions. Island Press (Washington, DC, USA).

Fragoso J, Silvius KM, Correa JA (2003) Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. Ecology 84(8): 1988–2006. https://doi.org/10.1890/01-0621

Fung E, Imbach P, Corrales L, Vilchez S, Zamora N, Argotty F, Hannah L, Ramos Z (2017) Mapping conservation priorities and connectivity pathways under climate change for tropical ecosystems. Climatic Change 141(1): 77–92. https://doi.org/10.1007/s10584-016-1789-8

Gamboa DA, Salom R (2015) Identificación de sitios de cruce de fauna en la ruta 415, en el Paso del Jaguar, Costa Rica. Infraestructura Vial 17: 5–12. https://revistas.ucr.ac.cr/index.php/vial/article/view/21238/24353

Grandia L (2007) Between Bolivar and bureaucracy: The Mesoamerican biological corridor. Conservation & Society 5: 478–503. http://www.conservationandsociety.org/text.asp?2007/5/4/478/49251

Haddad NM, Bowne DR, Cunningham A, Danielson BJ, Levey DJ, Sargent S, Spira T (2003) Corridor use by diverse taxa. Ecology 84(3): 609–615. https://doi.org/10.1890/0012-9658(2003)084[0609:CUBDT]2.0.CO;2

Hansen MC, Stehman SV, Potapov PV (2010) Quantification of global gross forest cover loss. Proceedings of the National Academy of Sciences of the United States of America 107(19): 8650–8655. https://doi.org/10.1073/pnas.0912668107

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-Resolution Global Maps of 21st-Century Forest Cover Change. Science 342(6160): 850–853. https://doi.org/10.1126/science.1244693

Harihar A, Pandav B (2012) Influence of connectivity, wild prey and disturbance on occupancy of tigers in the human-dominated western Terai Arc Landscape. PLoS One 7(7): e40105. https://doi.org/10.1371/journal.pone.0040105

Harvey CA, Komar O, Chazdon R, Ferguson BG, Finegan B, Griffith DM, Martínez-Ramos MI, Morales H, Nigh R, Soto-Pinto LO, Van Breugel M, Wishnie M (2008) Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. Conservation Biology 22(1): 8–15. https://doi.org/10.1111/j.1523-1739.2007.00863.x

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation 142: 14–32. https://doi.org/10.1016/j.biocon.2008.10.006

Hess GR, Fischer RA (2001) Communicating clearly about conservation corridors. Landscape and urban planning. 55: 195–208. https://doi.org/10.1016/S0169-2046(01)00155-4

Hilborn R, Arcese P, Borner M, Hando J, Hopcraft G, Loibooki M, Mduma S, Sinclair ARE (2006) Effective enforcement in a conservation area. Science 314(5803): 1266–1266. https://doi.org/10.1126/science.1132780

Hilty JA (2012) Climate and conservation: Landscape and seascape science, planning, and action. Island Press, Washington, DC, USA.

Hilty JA, Brooks C, Heaton E, Merenlender AM (2006) Forecasting the effect of land-use change on native and non-native mammalian predator distributions. Biodiversity and Conservation 15: 2853.

Hilty JA, Lidicker WZ, Merenlender AM (2012) Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation. Island Press, Washington, DC, USA.

Holland MB (2012) Mesoamerican Biological Corridor. In: Hilty JA, Chester CC, Cross MS (Eds) Climate and Conservation. Island Press/Center for Resource Economics, Washington DC, 56–66.

Imbach PA, Locatelli B, Molina LG, Ciais P, Leadley PW (2013) Climate change and plant dispersal along corridors in fragmented landscapes of Mesoamerica. Ecology and Evolution 3: 2917–2932. https://doi.org/10.1002/ece3.672

Independent Evaluation Group (2011) Regional Program Review: The Mesoamerican Biological Corridor. World Bank,Washington, DC, 1–108. http://hdl.handle.net/10986/2394

INEC (Instituto Nacional de Estadística y Censos) (2015) Total de nacimientos por grupos de edades del padre, según provincia de residencia de la madre. http://www.inec.go.cr/poblacion/nacimientos

Jadin I, Meyfroidt P, Lambin EF (2016) International trade, and land use intensification and spatial reorganization explain Costa Rica's forest transition. Environmental Research Letters 11(3): 035005. https://doi.org/10.1088/1748-9326/11/3/035005

Kaiser J (2001) Bold corridor project confronts political reality. Science 293(5538): 2196–2199. https://doi.org/10.1126/science.293.5538.2196

Keenan RJ, Reams GA, Achard F, de Freitas JV, Grainger A, Lindquist E (2015) Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. Forest Ecology and Management 352: 9–20. https://doi.org/10.1016/j.foreco.2015.06.014

Koens JF, Dieperink C, Miranda M (2009) Ecotourism as a development strategy: Experiences from Costa Rica. Environment, Development and Sustainability 11(6): 1225–1237. https://doi.org/10.1007/s10668-009-9214-3

Langholz JA, Lassoie JP, Lee D, Chapman D (2000) Economic considerations of privately owned parks. Ecological Economics 33(2): 173–183. https://doi.org/10.1016/S0921-8009(99)00141-X

Lees AC, Peres CA (2008) Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. Conservation Biology 22(2): 439–449. https://doi.org/10.1111/j.1523-1739.2007.00870.x

Malavasi EO, Kellenberg J (2002) Program of payments for ecological services in Costa Rica. In Building Assets for People and Nature: International Expert Meeting on Forest Landscape Restoration, Heredia, Costa Rica (Vol. 27), International Expert Meeting on Forest Landscape Restoration. http://moderncms.ecosystemmarketplace.com/repository/moderncms_documents/lr_ortiz_kellenberg_ext.1.pdf

Mateo-Sánchez MC, Balkenhol N, Cushman S, Pérez T, Domínguez A, Saura S (2015) Estimating effective landscape distances and movement corridors: Comparison of habitat and genetic data. Ecosphere 6(4): 1–16. https://doi.org/10.1890/ES14-00387.1

Mather AS, Needle CL (1998) The forest transition: A theoretical basis. Area 30(2): 117–124. https://doi.org/10.1111/j.1475-4762.1998.tb00055.x

Mendoza E, Fuller TL, Thomassen HA, Buermann W, Ramírez-Mejía D, Smith TB (2013) A preliminary assessment of the effectiveness of the Mesoamerican Biological Corridor for protecting potential Baird's tapir (*Tapirus bairdii*) habitat in southern Mexico. Integrative Zoology 8(1): 35–47. https://doi.org/10.1111/1749-4877.12005

Meyfroidt P, Lambin EF (2011) Global forest transition: Prospects for an end to deforestation. Annual Review of Environment and Resources 36(1): 343–371. https://doi.org/10.1146/annurev-environ-090710-143732

Miller K, Chang E, Johnson N (2001) Defining common ground for the Mesoamerican Biological Corridor. World Resources Institute, Washington, DC, 1–55. http://www.bio-nica.info/Biblioteca/Miller2001.pdf

Morse WC, Schedlbauer JL, Sesnie SE, Finegan B, Harvey CA, Hollenhorst SJ, Kavanagh KL, Stoian D, Wulfhorst JD (2009) Consequences of environmental service payments for forest retention and recruitment in a Costa Rican biological corridor. Ecology and Society 14(1): 23. https://doi.org/10.5751/ES-02688-140123

Newcomer Q (2002) Path of the Tapir: Integrating biological corridors, ecosystem management, and socioeconomic development in Costa Rica. Endangered Species Update 19: 186–193. https://deepblue.lib.umich.edu/bitstream/handle/2027.42/91254/ESUjulyaugust2002.pdf?sequence=1#page=122

O'Connell AF, Nichols JD, Karanth KU (2010) Camera Traps in Animal Ecology: Methods and Analyses. Springer Science & Business Media, Berlin, Germany.

Oficina Nacional Forestal (2006) Corredores Biológicos. http://www.onfcr.org/psa/capas-de-prioridades

Pagiola S (2002) Paying for water services in Central America: learning from Costa Rica. In: Pagiola S, Bishop J, Landell-Mills N (Eds) Selling forest environmental services: Market-based mechanisms for conservation and development. Earthscan Publications Limited, New York, 37–62.

Quigley HB, Crawshaw Jr PG (1992) A conservation plan for the jaguar *Panthera onca* in the Pantanal region of Brazil. Biological Conservation 61(3): 149–157. https://doi.org/10.1016/0006-3207(92)91111-5

Rabinowitz A, Zeller KA (2010) A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. Biological Conservation 143(4): 939–945. https://doi.org/10.1016/j.biocon.2010.01.002

Redondo-Brenes A, Chiu A, Snow S (2010) Small-Scale Restoration Efforts Using Mixed-Tree Plantations in the Path of the Tapir Biological Corridor, Costa Rica. Tropical Resources Bulletin 29: 27–32. http://costarica.jsd.claremont.edu/pdf/FCRE%20Pubs/Redondo,%20Chiu,%20and%20Snow%202010.pdf

Rissman AR, Lozier L, Comendant T, Kareiva P, Kiesecker JM, Shaw MR, Merenlender AM (2007) Conservation easements: Biodiversity protection and private use. Conservation Biology 21(3): 709–718. https://doi.org/10.1111/j.1523-1739.2007.00660.x

Robalino J, Pfaff A, Villalobos L (2011) Assessing the Impact of Institutional Design of Payments for Environmental Services: The Costa Rican Experience. In: Rapide B, De Clerk F, Le Coq JF, Beer J (Eds) Ecosystem Services from Agriculture and Agroforesty: Measurement and Payment. Earthscan Ltd., London, 305–318.

Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. AnnualReview of Ecology, Evolution, and Systematics 38: 231–253. https://doi.org/10.1146/annurev.ecolsys.38.091206.095611

Rosenberg DK, Noon BR, Meslow EC (1997) Biological corridors: Form, function, and efficacy. Bioscience 47(10): 677–687. https://doi.org/10.2307/1313208

Salom-Pérez R, Carrillo E, Sáenz JC, Mora JM (2007) Critical condition of the jaguar (*Panthera onca*) population in Corcovado National Park, Costa Rica. Oryx. 41: 51–6. https://doi.org/10.1017/S0030605307001615

Sánchez-Azofeifa GA, Daily GC, Pfaff AS, Busch C (2003) Integrity and isolation of Costa Rica's national parks and biological reserves: Examining the dynamics of land-cover change. Biological Conservation 109(1): 123–135. https://doi.org/10.1016/S0006-3207(02)00145-3

Sanderson EW, Redford KH, Chetkiewicz CL, Medellin RA, Rabinowitz AR, Robinson JG, Taber AB (2002) Planning to save a species: The jaguar as a model. Conservation Biology 16(1): 58–72. https://doi.org/10.1046/j.1523-1739.2002.00352.x

Shono K, Cadaweng EA, Durst PB (2007) Application of assisted natural regeneration to restore degraded tropical forestlands. Restoration Ecology 15(4): 620–626. https://doi.org/10.1111/j.1526-100X.2007.00274.x

SINAC (2018a) Sistema Nacional de Áreas de Conservación Costa Rica: National Program of Biological Corridors of Costa Rica. http://www.sinac.go.cr/EN-US/correbiolo/Pages/default.aspx

SINAC (Sistema Nacional de Áreas de Conservación de Costa Rica) (2006) National Biological Corridor Program. Executive Decree of Costa Rica Republic No. 33106-MINAE. http://www.sinac.go.cr/EN-US/correbiolo/Pages/default.aspx

SINAC (Sistema Nacional de Áreas de Conservación de Costa Rica) (2018b) Estado de conservación del jaguar (*Panthera onca*) en costa rica a través de la integración de datos de registro de la especie y modelaje del habitat idóneo. Proyecto MAPCOBIO-SINAC-JICA-Santo Domingo de Heredia, Costa Rica. http://www.sinac.go.cr/ES/partciudygober/Monitoreo%20Ambiental/Estado%20de%20la%20Conservacion%20del%20Jaguar.pdf

Spray SL, Moran MD (2006) Tropical deforestation. Rowman & Littlefield, Lanham, 1–193.

Stuckey JD, Camacho FC, Vargas GL, Stuckey SA, Vargas JL (2014) Agriculture in Monteverde, Moving Toward Sustainability. In: Nadkarni NM, Wheelwright NT (Eds) Monteverde: ecology and conservation of a tropical cloud forest. Oxford University Press, New York, 389–417.

Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. Oikos 68(3): 571–573. https://doi.org/10.2307/3544927

Terry A, Ullrich K, Riecken U (2006) The green belt of Europe: from vision to reality. IUCN, Gland, Switzerland and Cambridge, UK, 1–214.

Thomas CD (1990) What do real population dynamics tell us about minimum viable population sizes? Conservation Biology 4(3): 324–327. https://doi.org/10.1111/j.1523-1739.1990.tb00295.x

Thornton D, Zeller K, Rondinini C, Boitani L, Crooks K, Burdett C, Rabinowitz A, Quigley H (2016) Assessing the umbrella value of a range-wide conservation network for jaguars (*Panthera onca*). Ecological Applications 26(4): 1112–1124. https://doi.org/10.1890/15-0602

UNEP-WCMC (2018) Protected Area Profile for Costa Rica from the World Database of Protected Areas, January 2018. www.protectedplanet.net

US Fish and Wildlife Service (2001) Lower Rio Grande Valley National Wildlife Refuge. https://www.fws.gov/refuge/lower_rio_grande_valley/

Vega A (1994) Corredores conservacionistas en la Region centroamericana: Memorias de una conferencia regional auspiciada por el proyecto Paseo pantera, Heredia (Costa Rica) Sep 17–20, 1993. Tropical Research and Development, Florida (EUA).

Villalobos Sánchez HV (2018) Estudio técnico para determinar rutas de conectividad en el Corredor Biológica Paso Las Nubes. CBPN, Ciudad Quesada, Costa Rica.

Wangchuk S (2007) Maintaining ecological resilience by linking protected areas through biological corridors in Bhutan. Tropical Ecology 48: 176–187. http://www.tropecol.com/pdf/open/PDF_48_2/05%20Wangchuk.pdf

Weber W, Rabinowitz A (1996) A global perspective on large carnivore conservation. Conservation Biology 10(4): 1046–1054. https://doi.org/10.1046/j.1523-1739.1996.10041046.x

Wikramanayake E, McKnight M, Dinerstein E, Joshi A, Gurung B, Smith D (2004) Designing a conservation landscape for tigers in human-dominated environments. Conservation Biology 18: 839–844. https://doi.org/10.1111/j.1523-1739.2004.00145.x

Zamzow BK, Nieman SJ, Davis CN, Garro Cruz M, Monroe A, Stallcup L, Moran MD (2018) Status of large terrestrial vertebrates in the Monteverde-Arenal Bioregion, Northwestern Costa Rica. Tropical Conservation Science 11: 1940082918809617. https://doi.org/10.1177/1940082918809617

## Appendix 1

Sources for GIS data utilised for corridor construction.

| Data Description | Source | Link | Year |
|---|---|---|---|
| Protected areas of Costa Rica | Protected Planet | https://www.protectedplanet.net/country/CR | 2017 |
| Biological Corridors of Costa Rica | Sistema Nacional de Áreas de Conservación de Costa Rica (SINAC) | http://www.onfcr.org/psa/capas-de-prioridades | 2016 |
| Forest Cover | Global Forest Watch | https://beta-gfw.opendata.arcgis.com/items/7876b225f8034a0ebba79fad4afb80ad | 2017 |
| Human Population Estimates | Center for International Earth Science Information Network | http://beta.sedac.ciesin.columbia.edu/data/set/gpw-v4-population-density/data-download | 2015 |
| Administrative Roads of Costa Rica | MapCruzin | https://mapcruzin.com/free-costa-rica-country-city-place-gis-shapefiles.htm | 2018 |
| Costa Rica and Nicaragua Boundaries | Diva-GIS | http://www.diva-gis.org/datadown | 2001 |

## Appendix 2

Data sources for the estimation of jaguar (*Panthera onca*) densities in Central American habitats.

| Density (N/100 km$^2$) | Habitat | Location | Source |
|---|---|---|---|
| 8.80 | Moist Tropical Rainforest | Cockscomb, Belize | Silver 2004 |
| 7.48 | Moist Tropical Rainforest | Chiquibul, Belize | Silver 2004 |
| 5.40 | Tropical Dry Forest | Jalisco, Mexico | Núñez-Pérez 2011 |
| 8.80 | Moist Tropical Rainforest | Cockscomb, Belize | Harmsen 2006 |
| 4.82 | Moist Tropical Rainforest | Cockscomb, Belize | Harmsen 2006 |
| 18.29 | Moist Tropical Rainforest | Cockscomb, Belize | Harmsen 2006 |
| 11.45 | Moist Tropical Rainforest | Cockscomb, Belize | Harmsen 2006 |
| 5.30 | Tropical Dry Forest | Fireburn, Belize | Miller 2005 |
| 11.28 | Moist Tropical Rainforest | Gallon Jug, Belize | Miller 2005 |
| 8.82 | Moist Tropical Rainforest | Gallon Jug, Belize | Miller 2006 |
| 6.98 | Moist Tropical Rainforest | Corcovado, Costa Rica | Salom-Pérez et al. 2007 |
| 2.00 | Moist Tropical Rainforest | Golfo Dulce, Costa Rica | Bustamante 2008 |
| 6.70 | Moist Tropical Rainforest | Guanacaste, Costa Rica | Rojas 2006 |
| 1.34 | Moist Tropical Rainforest | Talamanca, Costa Rica | Gutierrez and Porras 2008 |
| 5.42 | Moist Tropical Rainforest | Talamanca, Costa Rica | González-Maya 2007 |
| 11.28 | Moist Tropical Rainforest | Carmelita, Guatemala | Moreira et al. 2008a |
| 1.54 | Moist Tropical Rainforest | La Gloria, Guatemala | Moreira et al. 2007 |
| 1.99 | Moist Tropical Rainforest | Mirador, Guatemala | Moreira et al. 2005 |
| 11.14 | Moist Tropical Rainforest | Dos Lagunas, Guatemala | Moreira et al. 2008b |
| 6.63 | Moist Tropical Rainforest | Tikal, Guatemala | García et al. 2006 |
| 6.04 | Moist Tropical Rainforest | Mechor de Mecos, Guatemala | Moreira et al. 2010 |
| 6.32 | Moist Tropical Rainforest | Laguna del Tigre, Guatemala | Moreira et al. 2009 |
| 5.20 | Moist Tropical Rainforest | La Mosquitia, Honduras | Portillo-Reyes and Hernández 2011 |
| Mean (per 100 km$^2$) | 7.09 | | |
| Standard Error | 0.81 | | |

## Literature cited (Appendix 2)

Bustamante A (2008) Densidad y uso de hábitat por los felinos en la parte sureste del área de amortiguamiento del Parque Nacional Corcovado, Península de Osa, Costa Rica. MS Thesis. Universidad Nacional de Costa Rica (Heredia).

García R, McNab RB, Shoender JS, Radachowsky J, Moreira J, Estrada C, Méndez V, Juárez D, Dubón T, Córdova M, Córdova F, Oliva F, Tut G, Tut K, González E, Muñoz E, Morales L, Flores L (2006) Los jaguares del corazón del Parque Nacional Tikal, Petén, Guatemala. Wildlife Conservation Society-Programa para Guatemala, Guatemala. https://guatemala.wcs.org/DesktopModules/Bring2mind/DMX/Download.aspx?EntryId=9601&PortalId=115&DownloadMethod=attachment

González-Maya JF (2007) Densidad, uso de hábitat y presas del jaguar (*Panthera onca*) y el conflicto con humanos en la región de Talamanca, Costa Rica. MS Thesis. Centro Agronomico Tropical de Investigación y Enseñanza, Costa Rica (Turrialba).

Gutierrez DC, Porras JC (2008) Ecología Poblacional de Jaguar (*Panthera onca*) y Puma (*Puma concolor*) y Dieta de Jaguar, en el Sector Pacífico de la Cordillera de Talamanca. Costa Rica. Trabajo de grado. Universidad Latina.

Harmsen BJ (2006) The use of camera traps for estimating abundance and studying the ecology of Jaguars. PhD Thesis. University of Southampton (Southampton). http://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.439502

Miller CM (2005) Jaguar density in Gallon Jug Estate, Belize. Wildlife Conservation Society (WCS) Belize: http://eprints.uberibz.org/759/1/Miller_GJE_Jaguar_Density_2005(3).pdf

Miller CM (2006) Jaguar density in Fireburn, Belize. Report for Wildlife Conservation Society and Belize Forest Department: http://eprints.uberibz.org/7/1/Fireburn_Jaguar_Density_2005.pdf

Moreira J, García R, McNab RB, Ruano G, Ponce G, Mérida M, Tut K, Díaz P, González E, Córdova M, Centeno E, López C, Vanegas A, Vanegas Y, Córdova F, Kay J, Polanco G, Barnes M (2005) Abundancia de jaguares y presas asociadas al fototrampeo en el sector oeste del Parque Nacional Mirador - Río Azul, Reserva de Biosfera Maya. Wildlife Conservation Society-Programa para Guatemala, Guatemala.

Moreira J, McNab RB, Thornton D, García R, Méndez V, Vanegas A, Ical G, Zepeda E, Senturión R, García I, Cruz J, Asij G, Ponce G, Radachowsky J, Córdova M (2007) Abundancia de jaguares en La Gloria-El Lechugal, Zona de Usos Múltiples, Reserva de la Biosfera Maya, Petén, Guatemala. Wildlife Conservation Society-Programa para Guatemala, Guatemala.

Moreira J, McNab RB, García R, Méndez V, Barnes M, Ponce G, Vanegas A, Ical G, Zepeda E, García I, Córdova M (2008a) Densidad de jaguares dentro de la Concesión Comunitaria de Carmelita y de la Asociación Forestal Integral San Andrés Petén, Guatemala. Wildlife Conservation Society - Jaguar Conservation Program, Guatemala.

Moreira J, McNab RB, García R, Méndez V, Ponce-Santizo G, Córdova M, Tun S, Caal T, Corado J (2008b) Densidad de jaguars en el Biotopo Protegido dos Lagunas, Parque Nacional Mirador Rio Azul, Petén, Guatemala. Wildlife Conservation Society – Jaguar Conservation Program, Guatemala.

Moreira J, McNab R, García R, Ponce G, Mérida M, Méndez V, Córdova M, Ruano G, Tut K, Tut H, Córdova F, Muñoz E, González E, Cholom J, Xol A (2009) Abundancia y densidad de jaguares en el Parque Nacional Laguna del Tigre-Corredor Biológico Central, Reserva de la Biosfera Maya. Wildlife Conservation Society-Programa para Guatemala, Guatemala.

Moreira J, García R, McNab R, Santizo GP, Mérida M, Méndez V, Ruano G, Córdova M, Córdova F, López Y, Castellanos E, Lima R, Burgos M (2010) Abundancia de jaguares y evaluación de presas asociadas al fototrampeo en las Concesiones Comunitarias del Bloque de Melchor de Mencos, Reserva de la Biosfera Maya, Petén, Guatemala. Wildlife Conservation Society-Programa para Guatemala, Guatemala.

Núñez-Pérez R (2011) Estimating jaguar population density using camera-traps: a comparison with radio-telemetry estimates. Journal of Zoology 285: 39–45. https://doi.org/10.1111/j.1469-7998.2011.00812.x

Portillo-Reyes HO, Hernández J (2011) Densidad del jaguar (*Panthera onca*) en honduras: primer estudio con trampas-cámara en la Mosquitia Hondureña. Revista Latinoamericana de Conservación. Revista Latinoamericana de Conservación 2: 45–50. http://www.academia.edu/download/30271571/Portillo-Reyes_Hernandez_RLC2(1)_45-50.pdf

Rojas RA (2006) El jaguar (*Panthera onca*) en el sector San Cristobal del Área de Conservación Guanacaste-Costa Rica: densidad, abundancia de presas y depredación de ganado. MSc Thesis. Universidad Nacional, Costa Rica (Heredia).

Salom-Pérez R, Carrillo E, Sáenz JC, Mora JM (2007) Critical condition of the jaguar *Panthera onca* population in Corcovado National Park, Costa Rica. Oryx 41: https://doi.org/10.1017/S0030605307001615

Silver SC, Ostro LET, Marsh LK, Maffei L, Noss AJ, Kelly MJ, Wallace RB, Gómez H, Ayala G (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. Oryx 38: 148–154. https://doi.org/10.1017/S0030605304000286