Biological Conservation 237 (2019) 41–49

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Conservation in human-dominated landscapes: Lessons from the distribution of the Central American squirrel monkey

Gerardo Ceballos[a,*], Paul R. Ehrlich[b], Jesus Pacheco[a], Natalia Valverde-Zúñiga[a], Gretchen C. Daily[b]

[a] Instituto de Ecología, Universidad Nacional Autónoma de México, Apdo. Postal 70-275, México D.F. 04510, Mexico
[b] Center for Conservation Biology, Department of Biology, Stanford University, Palo Alto, CA 94305-5020, USA

ARTICLE INFO

Keywords:
Squirrel monkey
Area of occupancy
Conservation threats
Costa Rica
Extent of occurrence
Geographic range
Habitat change
Human-dominated landscapes

ABSTRACT

It is becoming increasingly evident that many species can tolerate different degrees of habitat perturbation and that we often underestimate the capacity of some human-modified landscapes to support populations of declining species. We provide new insights into the distribution of the endangered Central American squirrel monkey and habitat changed over the last 20 years. The species has shown an approximate 60% decrease between the historic and the present extent of occurrence, with an area of occupancy of also about 60% of the present extent of occurrence. Despite the large habitat alteration, our results show surprisingly that this endangered monkey can persist in highly perturbed landscapes. This offers opportunities to improve its long-term chances of survival through conservation actions to protect and restore its habitat on the one hand, and to reduce the monkey's direct mortality on the other. Surprisingly we found several troops in 16 localities in a large area along the Rio Coto Brus where the Central American squirrel monkey was previously unrecorded. Some of our observations were made in cloud forests at a record high altitude for this species. We speculate the monkeys are using these highland areas as a corridor between suitable lowland habitats in the Coto Brus and the Rio Sierpe-Osa Peninsula regions. In response, we suggest strategies to help in the monkey's long-term conservation, that can be used as an example for other endangered species.

1. Introduction

Earth is currently experiencing a major loss of biodiversity, one unparalleled in the history of humanity. The sixth mass extinction has already seen the disappearance of thousands of species and billions of populations, and the current high rate of extinction seems doomed to increase (Ceballos et al., 2015, 2017; IUCN, 2019). At least 35 species of mammals have become extinct since 1600, and around 30% of all mammal species are at risk of extinction in one conservative estimate (Ceballos et al., 2015; IUCN, 2019). Primates are particularly vulnerable to human impacts, most are tightly tied to forest habitats that are being fragmented or are disappearing entirely. The rapid loss of tropical forests has already caused the extirpation of many of their populations throughout the world (Oates et al., 2000; Estrada et al., 2017). Many primate species, such as the recently discovered Tapanuli orangutan (*Pongo tapanuliensis*) in lowlands forests of northwestern Sumatra (Nater et al., 2017), the kipunji or highland mangabey (*Rungwecebus kipunji*), a new genus and species from the tropical forest of the Mount Rungwe mountains in Tanzania (Davenport et al., 2008), and the Myanmar snub-nosed monkey (*Rhinopithecus strykeri*) of rainforest in Myanmar and China (Geissmann et al., 2011; Long et al., 2012), have populations of < 1000 individuals. Primates are favorite targets for those hunting for bush-meat, zoo exhibits, pharmaceutical testing, or pets. Many also have low reproductive rates. As result of the impacts of those factors, approximately 60% of the > 500 recognized species are in danger of extinction (Jernvall and Wright, 1998; Cowlishaw, 1999; Wong et al., 2008). Nevertheless, the clear logistic inability to gain the necessary level of understanding for the conservation of the vast majority of billions of endangered species and populations dictates we must try to deal with two fundamental questions. First, how can we deal with the global drivers of biodiversity loss: human overpopulation, overconsumption (especially by the rich)? And second, how through standard and novel approaches, greatly increase efforts to protect refuges for biodiversity, expand them, and modify our impacts on human-dominated landscapes to make them more hospitable to our indispensable fellow creatures?

* Corresponding author.
E-mail addresses: gceballo@ecologia.unam.mx (G. Ceballos), pre@stanford.edu (P.R. Ehrlich), jpacheco@ecologia.unam.mx (J. Pacheco), gdaily@stanford.edu (G.C. Daily).

https://doi.org/10.1016/j.biocon.2019.06.008
Received 3 April 2018; Received in revised form 8 May 2019; Accepted 7 June 2019

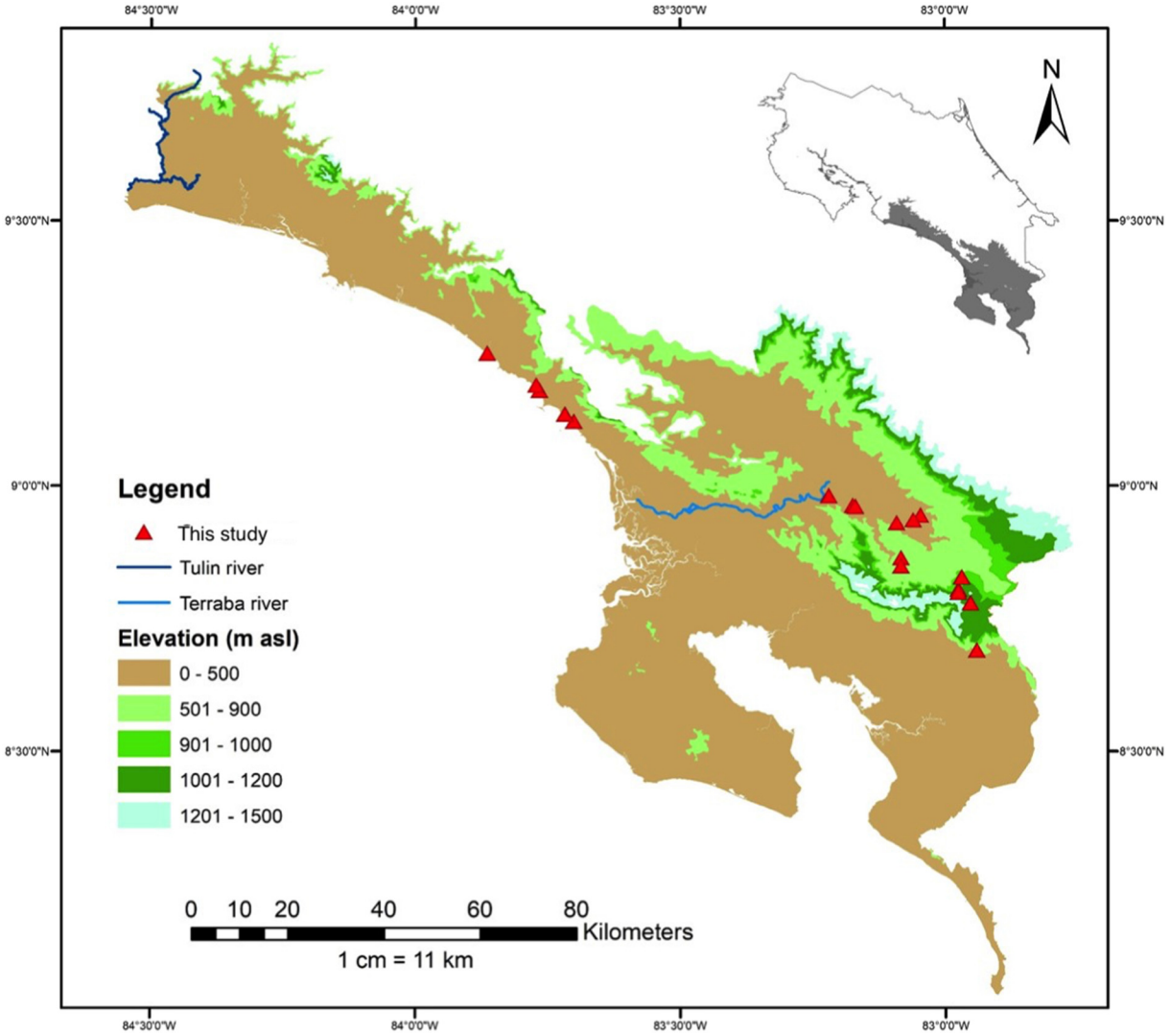

Fig. 1. Observation localities of the Central American squirrel monkey (*Saimiri oerstedii*) reported in this research along the regional altitudinal gradient on the southern end of the Pacific slope, Costa Rica.

Conservation of the endangered mammals, primates in particular, and other vertebrates in general, is increasingly requiring the use of both, traditional and novel methods in response to the diverse and dynamic causes of decline. Setting aside protected areas and biological corridors, encouraging local land owners to maintain habitat through conservation incentives, reintroduction of target species in suitable habitats, and developing economic activities such as ecotourism to incentivize local people to do protect forests, should be methods to promote their long-term conservation (see also Caughley and Gunn, 1996; Goehring et al., 2007). More unusual, sometimes bolder approaches, such as translocations to previously unoccupied suitable habitat, should be more widely tested now.

Primates are particularly important to conserve as they are charismatic, conspicuous, and informative because of their evolutionary relationship to us. Many species, including large ones such as howler monkeys (*Alloutta* spp.), are able to persist in human-dominated landscapes under certain circumstances. Additionally, because many mammal species have relatively extensive geographic ranges, they can serve as "umbrella species," protecting populations of many other less-charismatic organisms. Careful determining of geographic ranges using two broad measurements (sensu Gaston, 2003): the *extent of occurrence*, which is the area defined by the outer limits of the range, and the *area of occupancy*, which is the area used by the species within the extent of occurrence, is important. Understanding an endangered taxon's geographic range is critical to the development and application of effective adaptive management strategies (Holling, 2005; Blair et al., 2013a). The extent of occurrence of a population or species may differ significantly from the area of occupancy because organisms rarely occupy all the habitats or regions within their range (Gaston, 1994; Brown and Lomolino, 1998; Hurlbert and White, 2005; Goehring et al., 2007). Underestimating the area of occupancy of an endangered species may lead to oversight when developing protection strategies for it, thus reducing the chances for long-term conservation of populations or increasing implementation costs (Thomas and Abery, 1995; Caughley and Gunn, 1996). Conversely, assuming that the entire extent of occurrence is fully occupied by a taxon can lead to underestimates of extinction vulnerability, as has previously been observed in many terrestrial mammals (Ceballos and Ehrlich, 2002).

There is abundant evidence of the capacity of mammals and other vertebrates to persist in human – dominated landscapes. For example, in the same area where we studied the squirrel monkeys, our research program on the capacity of agricultural landscapes to support biodiversity has showed that a tropical mixed forest-patch and agriculture landscape can support a substantial sample of the biodiversity of regional undisturbed forest. We found, for example, that within a 23,600 ha study area, the small ribbons of forest weaving through

farmland collectively increased the effective size of a 326-ha local forest reserve up to 16-fold for vertebrates and invertebrates (Daily et al., 2003; Pacheco et al., 2006; Mendenhall et al., 2014). Many species of primates as diverse as orangutans, chimpanzees, gibbons, howler monkeys, lorises, and squirrel monkeys are able to persist in human-dominated landscapes too (Estrada et al., 2017).

Several species of squirrel monkeys are relatively widespread in tropical regions of South America (Rylands et al., 2013; Lynch Alfaro et al., 2015). The Central American squirrel monkey (*Saimiri oerstedii*) has, however, a small historic geographic range disjunct from other species of squirrel monkeys, and restricted to the Pacific lowlands of southern Costa Rica and northern Panama (Reid, 2009; Rylands et al., 2013). It is categorized as an endangered species due to habitat loss, population fragmentation, and hunting (Boinski and Siwt, 1997; Boinski et al., 1998; Sierra et al., 2003; Reid, 2009). It has been almost completely eradicated from Panama (Rylands et al., 2006), and habitat destruction has divided its historic geographic range in Costa Rica into two separate areas (Boinski et al., 1998). It survives in human dominated habitats and because of that can serve as a conservation model.

We discovered a relatively large population of squirrel monkeys in the region of Coto Brus in southern Costa Rica. That prompted us carry out an analysis of the current geographic range of the species. The new information on the distribution of *S. oerstedii* can help improve efforts to restore the habitat and protect this charismatic primate, as well as provide insights for the conservation of other primate species. In this paper, we address the following issues: i) analyze the current extent of occurrence and area of occupancy of the squirrel monkey; ii) document habitat change over the last 20 years; and iii) identify land conservation strategies for preservation of the species.

2. Methods

2.1. Study area

Our study was carried out in the Pacific lowlands of central and southern Costa Rica from the Carara National Park to the Panama border (Fig. 1). We covered all the known geographic range of the species and nearby areas. We conducted most of our fieldwork between February and May 1999, with additional survey periods in March 2001, 2002, 2014 and 2015. We surveyed in an area of approximately 140,000 ha in the Rio Coto Brus region, located just north of the Golfo Dulce in southern Costa Rica. We selected our survey area based on interviews with local people who observed squirrel monkeys in the region. We interviewed informally peasants, ranchers, and hunters who had good knowledge of the local fauna. One of them was hired as our main guide. In the interviews, we showed them pictures of spider, howler, and squirrel monkeys to let them identify the species present. Additionally, we carried out seven, one-day line transects to determine the presence of squirrel monkey troops in different localities in the districts of San Vito, Aguabuena, Limoncito, Pittier, Changuena, Potrero Grande, and Corredor (Table 1). With the exception of the steep, isolated forests adjacent to the study site, we surveyed most of the accessible areas. However, it is likely that some groups of squirrel monkeys were not recorded. Each time squirrel monkeys were observed, their GPS location, altitude, and vegetation type were recorded. During our 2014 and 2015 return visits to previously surveyed localities, we reaffirmed the presence of *S. oerstedii* troops in the Rio Coto Brus region. We also observed *S. oerstedii* in localities around the Marino Ballena National Park during our surveys in the Costa Rican central-south Pacific region.

2.2. Historical range of S. oerstedii

We determined the historic and present distribution of squirrel monkeys in Costa Rica from reviews of published information, primarily Boinski et al. (1998), Morera-Avila (2000, 2002), Sierra et al. (2003), Solano-Rojas (2007), Blair et al. (2013b), and from our own data. We used the IUCN range data (Wong et al., 2008) to determine the historical extent of occurrence of *S. oerstedii*. All the records used are from forested localities at elevations below 500 masl in an area along the Pacific coast, between the Tulín River in the north to the southern border of Costa Rica in the Burica Peninsula. To calculate the forest area within the historical extent of occurrence, we assumed an 85% forest cover for the year 1900 (Keogh, 1984). The present extent of occurrence was defined as the sum of all forest patches larger than 3 ha within a polygon delimited by the localities where *S. oerstedii* presence has been reported since 1998 until the present day. The forest area was computed from the maps of the National Forest Inventory (SINAC, 2013). Each locality consisted of a 5 km radius around the reported observation points (Boinski et al., 1998; Morera-Avila, 2000, 2002; Sierra et al., 2003; Solano-Rojas, 2007; Blair et al., 2013b, and our own data). The 5 km radius was defined by the daily movement of troops of *S. oerstedii* reported by Baldwin and Baldwin (1972). We excluded those regions where the species have been lost according to Boinski et al. (1998).

We considered two scenarios to calculate the area of occupancy (Gaston, 2003). The *conservative* scenario considered the area of occupancy as the sum of all forest fragments larger than 15 ha within a 5 km radius from each observation point, and the *less conservative* scenario included all forest fragments larger than 5 ha within 5 km radius from each observation point. We used the National Forest Inventory map (SINAC, 2013) to compute the forest area for both scenarios; the selection of both fragment values was based on the minimum area considered as forest (5 ha) by the Costa Rican legislation, and the minimum fragment size (15 ha) required by the species for long term survival (Sáenz and Sáenz, 2008).

2.3. Remote sensing of the change to S. oerstedii habitat

We used the Costa Rica Land Use map of 1992 (MAG, 2008) and the 2012 National Forest Inventory map to identify changes in the location and extent of forest cover of the *S. oerstedii* distribution range. We analyzed the data with ArcGIS 10 (ESRI, 2011) and the Patch Analyst extension (Rempel et al., 2012). The Costa Rican land use map of 1992 was generated from Landsat 5 images and others not specified in the metadata map; the resolution is 30 × 30 m. The 2012 National forest inventory map was generated with RapidEye images, which has finer resolution. We then edited and re-classified both maps to make them comparable for the landscape analysis and defined a patch of habitat as any mature or secondary forest, or mangrove segment larger than 3 ha.

We determined the habitat change that occurred within the present-day extent of occurrence by computing four landscape metrics: area, number of patches, mean patch size, and mean shape index for 1992 and 2012 and for each habitat type (i.e. forest, secondary forest, and mangrove). By area we are referring to the Class Area metric, which indicates the sum of areas of all patches within a coverage class. In this case, the class corresponds to forest area (in the landscape). All data layers were analyzed under the Projected Coordinate System for Costa Rica (CRTM05/WGS84). Using these data and the formula employed by Puyravaud (2003), we estimated the annual rate of change in habitat, number of patches, and mean patch size using the following formula: $= \frac{1}{t2-t1} \times \ln \frac{A2}{A1}$, where A1 and A2 are the forest cover at t1 and t2, respectively; the unit could be per year or percentage per year.

3. Results

3.1. New details on the distribution of S. oerstedii

We found direct and indirect (i.e. interview) evidence of squirrel monkeys in 16 localities along the rivers and forest fragments in the Coto Brus region (Table 1). The majority of localities were below 700 masl, in remnants of tropical lowland and riparian forests surrounded

Table 1
Field observations of the Central American squirrel monkeys (*Saimiri oerstedii*) in Costa Rica. All records are based on observations (O), interviews (I), or photograph (P). Localities in bold represent new, upper altitudinal records for the species.

District	Locality	Coordinates (DD)	Altitude (masl)	Plant association	Type of record
Potrero Grande	Coto Brus river (Minae Reserve)	8.9319444, −83.0922220	300	Lowland forest	O
Potrero Grande	Chocoacos lagoon	8.9644444, −83.1747220	430	Lowland forest	I
Potrero Grande	Las Vueltas	8.9627778, −83.1697220	430	Lowland forest	O
Pittier	Rio Coto Brus (Bonanza I)	8.9463889, −83.0469444	400	Riparian forest	O[a]
Changuena	Rio Limon y Rio Terraba	8.9833333, −83.2200000	300	Riparian forest	I
Limoncito	San Luis (Rio Limon)	8.8661111, −83.0838880	580	Riparian forest	I
San Vito	Quebrada Pavo (San Vito)	8.8297222, −82.9688880	780	Lowland forest	P[b]
San Vito	**Finca Gamboa**	**8.8063889, −82.9750000**	**930**	**Premontane wet forest**	**O**
Aguabuena	**Copal**	**8.7805556, −82.9525000**	**930**	**Premontane wet forest**	**O**
Corredor	Fila de Cal	8.6922222, −82.9408330	800	Lowland forest	I
San Vito	**Finca Gamboa (1.7 km S San Vito)**	**8.8008333, −82.9750000**	**1014**	**Secondary Forest**	**P**
San Vito	**Quebrada Pavo (1 km NE San Vito)**	**8.8297222, −82.9688889**	**960**	**Non-Forest**	**P**
Aguabuena	**Copal**	**8.7805556, −82.9525000**	**1145**	**Secondary Forest**	**O**
Limoncito	Rio Limon (3 km SE San Luis)	8.8505556, −83.0838889	764	Secondary Forest	O
Pittier	Rio Coto Brus (Bonanza II)	8.9463889, −83.0469444	315	Forest	O
Potrero Grande	Rio Coto Brus (3.5 km El Jabillo)	8.9369444, −83.0611111	331	Riparian forest	F
Bahía Ballena	Playa Hermosa	9.1816100, −83.7659000	0	Secondary forest	O
Bahía Ballena	Queb Grande - Ballena	9.1367420, −83.7175400	100	Secondary forest	O
Bahía Ballena	Ballena	9.1233280, −83.7009990	35	Secondary forest	O
Bahía Ballena	Dominical	9.2519444, −83.8641660	23	Non-Forest	O
Bahía Ballena	Rancho Reno	9.1915900, −83.7718800	55	Forest	O
Bahía Ballena	La Cuzinga	9.1367430, −83.7177540	79	Non-Forest	O

[a] Observed by Jorge Pérez.
[b] Photograph provided by Sr. Enrique Laurent from San Vito.

Fig. 2. A Central American squirrel monkey (*Saimiri oerstedii*) crossing a pasture through a fence to reach the Wilson Botanical Garden in the San Vito region in southern Costa Rica. (Photo: Gerardo Ceballos).

by pastures. However, we recorded the presence of *S. oerstedii* at five localities above 900 masl in the premontane wet forests of the Java River near the Las Cruces Reserve, including two above 1000 masl (Figs. 1 and 2, see Daily et al., 2003 and Pacheco et al., 2006 for a description of this region and its mammalian fauna). These are the first reported observations of *S. oerstedii* at this elevation in Costa Rica and the first ones in the Las Cruces forests. We photographed a squirrel monkey troop crossing a pasture to the Wilson Botanical Garden through a cattle fence in Finca Gamboa in 1999 (Fig. 2; Table 1); the local owners of the farm adjacent to the Garden told us they had begun occasionally to observe squirrel monkeys in the region that year. Additionally, we recorded squirrel monkeys in six localities around the Bahía Ballena area (south-central Pacific slope), totaling 22 localities in this study (Table 1).

Based on our reviews and field work, we estimated the historical extent of occurrence of *S. oerstedii* in Costa Rica to be about 550,000 ha (5500 km^2) and the current extent of occurrence about 225,000 ha (2.250 km^2), suggesting a decrease of about 60% between 1900 and

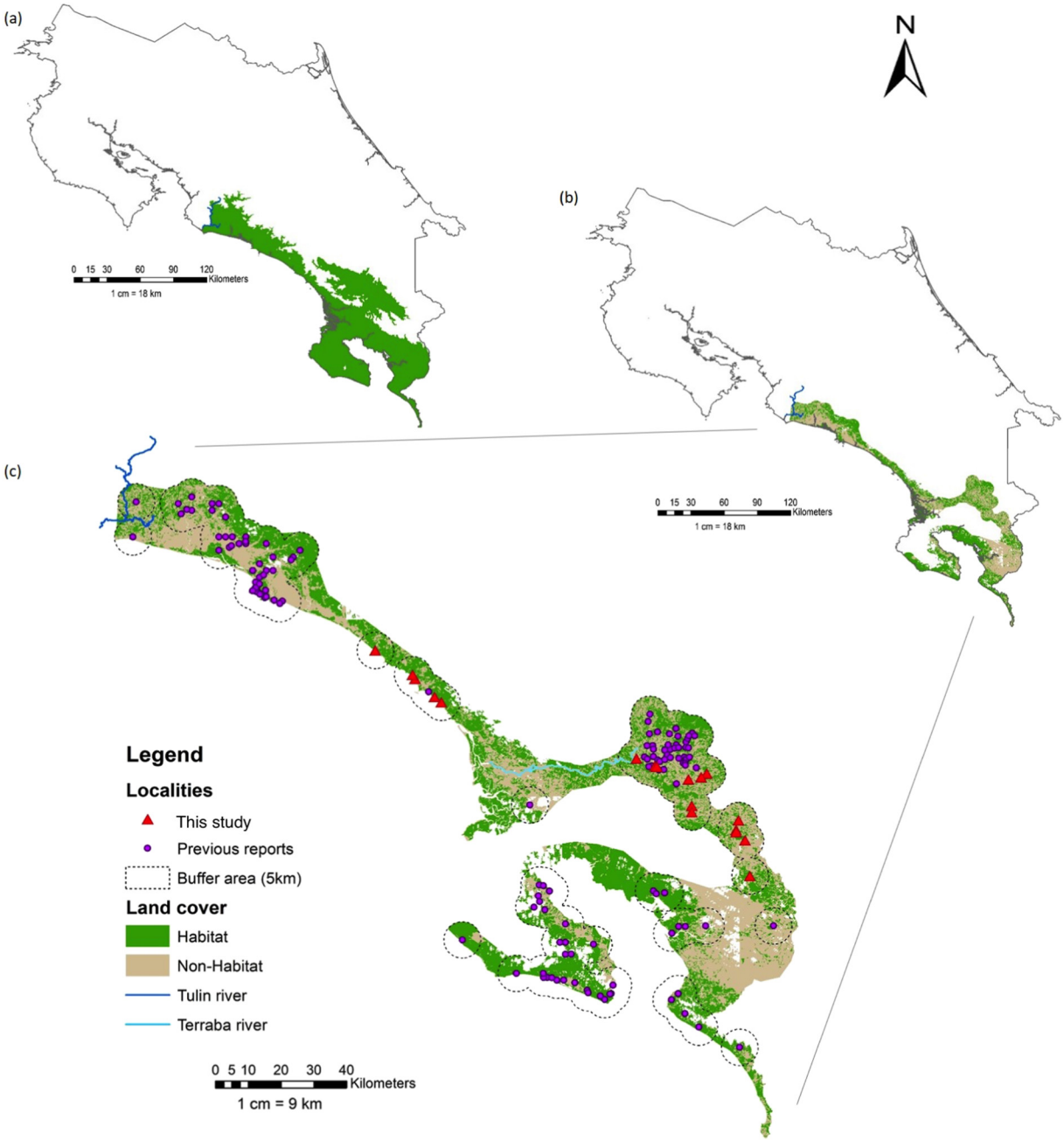

Fig. 3. Central American squirrel monkey (*Saimiri oerstedii*) distribution in Costa Rica: (a) historical extent of occurrence; (b) present extent of occurrence; and (c) present extent of occurrence showing the localities and their buffer areas.

Table 2
Total habitat available in the present area of occupancy of the Central American squirrel monkey (*Saimir oerstedii*) in conservative and less conservative scenarios.

Scenario	Forest (km^2)	Secondary forest (km^2)	Mangrove (km^2)	Total habitat (km^2)
Conservative ($P \geq 0.15\,km^2$)	800	428	53	1281
Less conservative ($P \geq 0.05\,km^2$)	842	490	55	1387

2012 (Fig. 3). We also estimated the present area of occupancy to be 57–62% of the present extent of occurrence, meaning that the species occupies an area of about 128,00–138,700 ha (1280–1387 km^2) in Costa Rica, including mature forest, secondary forest, and mangrove. Mature forest was the dominant forest type in the area of occupancy (Table 2). In relation to the status of habitat protection, the squirrel monkeys are surviving in forest patches in and near the Manuel Antonio, the Marino Ballena, and the Corcovado National Parks. In contrast, the troops present in the Coto Brus - Golfito and Puriscal-Parrita regions are not protected.

3.2. Habitat change along the present extent of occurrence of S. oerstedii

We found important differences in landscape structure across the years studied (Table 3). The area covered by suitable squirrel monkey habitat did not show drastic changes over the study period, but the

Table 3
Changes in the habitat of the Central American squirrel monkey (*S. oerstedii*) along its present extent of occurrence in Costa Rica from 1992 to 2012.

Land cover by habitat	Year 1992				Year 2012				Annual rate of change (%)		
	Area (km^2)	Number of patches	Mean patch size (km^2)	Mean shape index	Area (km^2)	Number of patches	Mean patch size (km^2)	Mean shape index	Habitat area	Patch size	Mean patch size
Forest	1100	97	11	1.73	1225.34	1978	0.62	4.38	0.54	15.08	−14.54
Secondary forest	856	164	5	1.69	838.96	2588	0.32	4.72	−0.10	13.79	−13.90
Mangrove	213	217	1	1.76	179.34	227	0.79	2.74	−0.87	0.23	−1.10

number of patches was higher and their average size smaller in 2012 than in 1992. The mean shape index over the study period suggests that the patches were not only smaller but more irregular at its end. This pattern of spatial change was consistent across the three habitat categories, but the most significant variation occurred in the mature and secondary forested areas which showed annual rates of change between 13 and 15% in the number of fragments and their mean size. In contrast, the mangrove area showed annual rates of change around 1%, which denote virtually no change in this habitat category during the period of study. Although mean fragment size has decreased, it is still adequate for the survival of *S. oerstedii* troops (Boinski and Siwt, 1997; Sáenz and Sáenz, 2008). Suitable habitat outside the protected areas is, however, more fragmented and isolated from large areas of continuous forest cover, such as in Coto Brus region, rendering them largely unsuitable for troops of squirrel monkeys.

3.3. Land conservation strategies

Based on our results, we suggest conservation strategies to consolidate the squirrel monkey distribution, that include protected areas, biological corridors, environmental payments for land owners of critical unprotected parcels, and introductions into new areas (Fig. 4). It is fundamentally important to expand and improve the connectivity among the Manuel Antonio, Marino Ballena, and Corcovado National Parks. There are biological corridors already established in those regions, such as Paso de las Lapas, Paso de la Danta, Fila Langusiana, and Osa but it is necessary to enhance their protection and functionality. Indigenous reserves could have a critical role as connecting patches among corridors and protected areas, while involving these communities in conservation of charismatic species, and thus potentially generating social benefits. In addition where possible, new protected areas should be created in the Rio Terraba, Rio Coto Brus and the Terraba-Sierpe regions that have squirrel monkey populations; these areas can also act as corridors. It is particularly important to set aside protected areas in the Ciudad Neily valley, where most habitat is gone, and the few remnant native forests are not in any protection category. The federal government conservation payment program in private lands should be expanded to encompass all habitat identified in our study (Fig. 4). Those habitats include indigenous reserves, private ranches, and peasant lands. In addition, it is essential to try novel approaches such as introducing squirrel monkeys into the Carara National Park and the lowlands of the Paso de la Danta Biological Corridor. Such regions are adjacent to the squirrel monkeys' historic geographic range and have very similar habitat to the present areas occupied by the species.

4. Discussion

4.1. New details on the distribution of S. oerstedii

Our observations of *S. oerstedii* at higher elevations than previously reported show that the altitudinal range of the species has been expanding upwards for at least the past two decades. In the Coto Brus region, this range now extends up to ~1200 masl. Although some reports of occurrence identified 800 masl as the upward limit (Morera-Avila, 2000, 2002; Pacheco et al., 2006), historically, and even in recent publications (Sierra et al., 2003; Wong et al., 2008; Blair et al., 2013b), the limit of *S. oerstedii* distribution was stated as being below 500 masl. Our observations of *S. oerstedii* at significantly higher elevations suggest we have identified a relatively large addition to its known extent of occurrence geographic range in a fairly accessible and biologically well-studied region (Daily et al., 2003; Pacheco et al., 2006). Additionally, our information indicates that there may be other localities at high elevations with squirrel monkeys in the vicinity of Las Alturas in the Cordillera de Talamanca, along the Costa Rica - Panama border. Although our findings are novel for this Central American species, squirrel monkeys in South America have frequently established populations at high altitudes. It is likely, considering the South American center of evolution of the group, that *S. orestedii* is pre-adapted to move upward (Lynch Alfaro et al., 2015; Ruiz-García et al., 2015).

The San Vito region has lost most of its natural vegetation due to extensive deforestation that occurred four decades ago (Hughes et al., 2002; Daily et al., 2003). Recent observations of squirrel monkeys at Finca Gamboa and Copal may suggest that as suitable, lower-elevation habitat is destroyed, *S. oerstedii* have been forced to seek new habitat patches at higher elevations. It is, of course, possible that gradual global warming has facilitated this. Deforestation and changes in land use may cause negative impacts to the local fauna, including local extinctions, changes in abundance, and invasion of exotic species (Ceballos and Ehrlich, 2002; Daily et al., 2003). Shifts in range size can be used as an index of the impact of these changes in environmental conditions (Gaston, 1994). At this point, we do not know if *S. oerstedii* will be able to use higher elevation forests in the long term. This may depend on whether climate change actually makes the higher altitude forests more hospitable (Chen et al., 2011).

It is important for conservation purposes to note that a species usually will not occupy its entire extent of occurrence. The area of occupancy of *S. oerstedii* covers a maximum of 60% of its extent of occurrence, which is currently less than half of its historical value despite the addition of the Coto Brus region to the area of geographic distribution. Effective conservation planning requires determining critical areas for *S. oerstedii*. While we believe that *S. oerstedii* occurs at least throughout its entire available habitat, we need to confirm its presence in areas where there are sampling gaps. These areas include the Terraba-Sierpe region, mid-altitude lands near its historic extent of occupancy (800–1500 masl), and the Corcovado and Piedras Blancas National Parks.

4.2. Habitat change along the present extent of occurrence of S. oerstedii

Our research has demonstrated a marked change in the extent of occurrence of *S. oerstedii* since 1992. While the forest patches have maintained their canopy cover, they currently have decreased connectivity, because they are smaller and more irregularly shaped. This in turn has reduced the suitability of the landscape for *S. oerstedii* (Fahrig, 2003; Cushman et al., 2008; Magle et al., 2009). Remaining forests are also not increasing in area or connectivity (Pagiola, 2011; Arriagada et al., 2012; Programa Estado de la Nación, 2014). Despite significant efforts to support local owners to maintain forest cover through programs for environmental services, competing land uses, such as growing crops, cattle ranching, and urban expansion, have had a strong impact

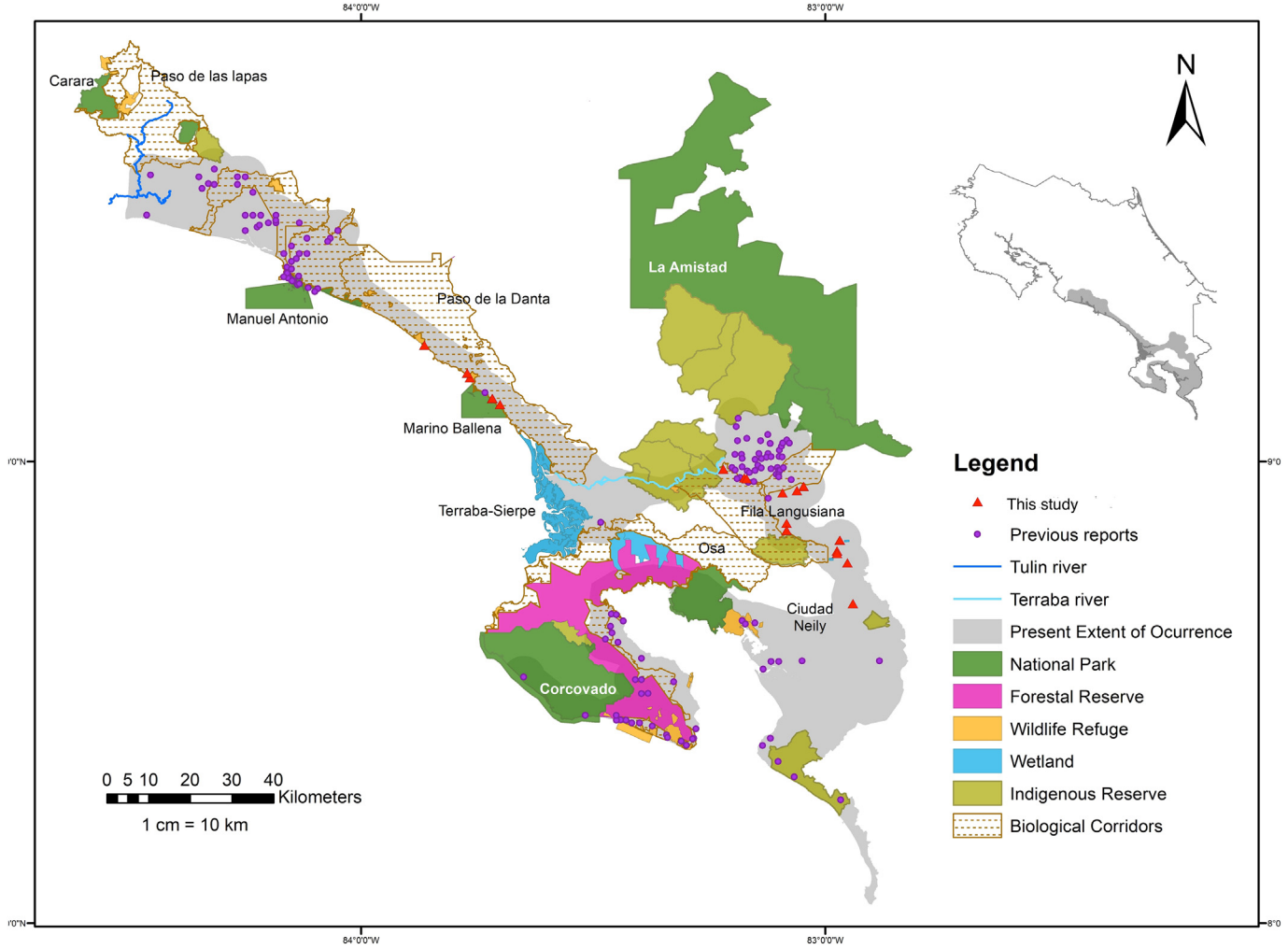

Fig. 4. Priority areas for conservation of the Central American squirrel monkey (*Saimiri oerstedii*) in Costa Rica. Although there are no records in the region where the Carara National Park is located, the habitat is practically the same where the species is found, so it can be introduced to have a larger protected population.

in land used by *S. oerstedii*. So, in addition to environmental services incentives, constant vigilance is required to ensure the survival of the species. Furthermore, tourism, concentrated along the coastal and lowland areas, places additional pressure on primate populations in the fragmented habitats there (Wong, 2002; Picón-Cruz and Baltodano-Zúñiga, 2006; Baltodano, 2007; Calvo-Alvarado et al., 2009).

Primate populations can persist in fragmented landscapes if the remnant patches provide sufficient resources, are allowed to regenerate, and maintain good connectivity to larger patches (Estrada et al., 2006; Sáenz and Sáenz, 2008). We have demonstrated that the squirrel monkey's extent of occurrence is likely expanding. This, together with the ability of its populations to survive in highly fragmented habitat, offers new possibilities for ensuring long-term preservation.

4.3. S. oerstedii as a conservation model

The results of our research illustrate a basic challenge facing conservation biology, providing sufficiently detailed information to make required conservation decisions for endangered and threatened species. Additionally, our research highlights several important, take-home conservation messages which may offer guidance for reducing the threats to other species. First, even very conspicuous organisms such as the Central American squirrel monkey, which are under tremendous pressure from habitat destruction, persecution as pests and capture as pets for trade, may attain relatively stable populations in a highly-fragmented, human-dominated landscape, if properly protected. Other primates that are good examples of such flexibility are orangutans, howler monkeys, and lorises (Estrada et al., 2017). Second, the benefits of protecting habitat to maintain stable *S. oerstedii* populations in Coto Brus will also benefit many other populations of vertebrates and other organisms (Daily et al., 2003; Pacheco et al., 2006; Mendenhall et al., 2014). Third, expanding and enhancing protected areas, and promoting benefits for local owners of unprotected habitat will also help populations of many other species. Four, as our squirrel monkey study has shown, critical information for conservation can now be acquired relatively simply and inexpensively in light of the powerful satellite technologies now increasingly available. But, of course, such effort will likely remain logistically impossible for the vast majority of populations and species.

It is easy to underestimate the capacity of some human-modified landscapes to support vulnerable faunal populations. Our research shows that the population of a threatened primate species and a wide range of other associated mammal species, can survive in an area significantly modified by agriculture, primarily because of the presence of remnant forest patches of suitable size and connectivity. Patches of secondary and riparian forests serve as buffers that increase landscape connectivity are critical for the conservation of many threatened species (Marsh, 2013; Newbold et al., 2015). An improved protection status of this landscape, framed on coherent and ecologically-based policies, is essential to ensuring that its ecological functionality is not further compromised (Baltodano, 2007). This concept reinforces the

view that key contributions of conservation biologists are the development and application of techniques used to accurately diagnose a landscape's capacity to maintain wildlife populations (Daily et al., 2003), and recommending actions that will enhance this capacity.

This study of squirrel money conservation illustrates another extremely important point about global conservation of biodiversity. A very large amount of effort by many investigators has been required to illuminate the situation of *S. oerstedii*, even though it is a relatively large, attractive, and easily-observed animal. This tells us that there is no hope of attaining similar understanding of the many millions of species and billions of populations of most organisms. That's why modern conservation biology recognizes that the global level of biodiversity, the status of humanity's life-support system, is strongly linked with a wide range of human disturbances, such as habitat destruction, climate disruption and toxification (Ceballos et al., 2015). Finding ways to deal with the rapid increase of the global human population and its unrelenting efforts to expand consumption by the rich and middle class are among the greatest conservation challenges in a world addicted to mindless economic growth. On the positive side, our study shows that despite these trends, there can be great value in efforts to preserve protected areas, establish new ones, and enhance the quality of human-dominated landscapes from the viewpoint of their non-human occupants.

Acknowledgments

We extend our deepest appreciation to Jorge Perez for sharing with us his love of, and intimate knowledge of, the mammals from the Coto Brus region; he told us for the first time about the presence of squirrel monkeys in this region. Mr. Enrique Laurent from San Vito generously gave us some of his squirrel monkey photos and reported the localities where he took them around San Vito. We also like to thank Gerardo Suzan and Randy Figueroa for their help with field work and Josiane Segar for providing comments on an early draft of the manuscript. Our appreciation to the Jardin Botanico Wilson of the OTS for providing all kind of logistic support, especially to Emilce Ramirez and Rodrigo Quiroz. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

References

Arriagada, R.A., Ferraro, P.J., Sills, E.O., Pattanayak, S.K., Cordero-Sancho, S., 2012. Do payments for environmental services affect forest cover? A farm-level evaluation from Costa Rica. Land Econ. 88, 382–399.
Baldwin, J.D., Baldwin, J., 1972. The ecology and behavior of squirrel monkeys (Saimiri oerstedii) in a natural forest in Western Panama. Folia Primatol. 18, 161–184.
Baltodano, J., 2007. Bosque, cobertura y uso forestal. In: Informe Final. Programa Estado de la Nación, San José, Costa Rica, pp. 43.
Blair, M.E., Bynum, N., Sterling, E.J., 2013a. Determining conservation status and contributing to in situ conservation action. In: Sterling, E.J., Bynum, N., Blair, M.E. (Eds.), Primate Ecology and Conservation: A Handbook of Techniques, 1st ed. Oxford University Press, Oxford.
Blair, M.E., Gutierrez-Espeleta, G.A., Melnick, D.J., 2013b. Subspecies of the central American squirrel monkey (*Saimiri oerstedii*) as units for conservation. Int. J. Primatol. 34, 86–98.
Boinski, S., Siwt, L., 1997. Uncertain conservation status of squirrel monkeys in Costa Rica, Saimiri oerstedii oerstedii and Saimiri oerstedii citrinellus. Folia Primatol. 68, 181–193.
Boinski, S., Jack, K., Lamarsh, C., Coltrane, J.A., 1998. Squirrel monkeys in Costa Rica: drifting to extinction. Oryx 32, 45–58.
Brown, J.H., Lomolino, M.V., 1998. Biogeography, 2nd ed. Sinauer Associates, Sunderland, Mass.
Calvo-Alvarado, J., Mclennan, B., Sánchez-Azofeifa, G.A., Garvin, T., 2009. Deforestation and forest restoration in Guanacaste, Costa Rica: putting conservation policies in context. For. Ecol. Manag. 258, 931–940.
Caughley, G., Gunn, A., 1996. Conservation Biology in Theory and Practice. Blackwell Science, Cambridge, Massachusetts, U.S.A.
Ceballos, G., Ehrlich, P.R., 2002. Mammal population losses and the extinction crisis. Science (New York, N.Y.) 296, 904–907.
Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253.
Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc. Natl. Acad. Sci. 114, E6089–E6096.
Chen, I.-C., Hill, J.K., Ohlemuller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026.
Cowlishaw, G., 1999. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. Conserv. Biol. 13, 1183–1193.
Cushman, S.A., Mcgarigal, K., Neel, M.C., 2008. Parsimony in landscape metrics: strength, universality, and consistency. Ecol. Indic. 8, 691–703.
Daily, G.C., Ceballos, G., Pacheco, J., Suzán, G., Sánchez-Azofeifa, A., 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conserv. Biol. 17, 1814–1826.
Davenport, T.R.B., De Luca, D.W., Jones, T., Mpunga, N.E., Machaga, S.J., Kitegile, A., Phillipps, G.P., 2008. The critically endangered kipunji Rungwecebus kipunji of southern Tanzania: first census and conservation status assessment. Oryx 42.
ESRI, 2011. ArcGIS Desktop: Release 10. (Redlands, CA).
Estrada, A., Garber, P.A., Pavelka, M.S.M., 2006. Introduction: Population responses to disturbance. In: Estrada, A., Garber, P.A., Pavelka, M.S., Luecke, L. (Eds.), New Perspectives in the Study of Mesoamerican Primates Distribution, Ecology, Behavior, and Conservation, 1st edition. Springer, New York, pp. 116–120.
Estrada, A., Garber, P.A., Rylands, A.B., Roos, C., Fernandez-Duque, E., Di Fiore, A., et al., 2017. Impending extinction crisis of the world's primates: why primates matter. Sci. Adv. 3, e1600946.
Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.
Gaston, K.J., 1994. Measuring geographic range sizes. Ecography 17, 198–205.
Gaston, K.J., 2003. The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford.
Geissmann, T., Lwin, N., Aung, S.S., Aung, T.N., Aung, Z.M., Hla, T.H., et al., 2011. A new species of snub-nosed monkey, genus Rhinopithecus Milne-Edwards, 1872 (Primates, Colobinae), from northern Kachin state, northeastern Myanmar. Am. J. Primatol. 73, 96–107.
Goehring, D.M., Daily, G.C., Dasgupta, S., Ehrlich, P.R., 2007. Range occupancy and endangerment: a test with a butterfly community. Am. Midl. Nat. 157, 106–120.
Holling, C.S. (Ed.), 2005. Adaptive environmental assessment and management. Blackburn Press, Caldwell, NJ Reprint of the 1978 ed.
Hughes, J.B., Daily, G.C., Ehrlich, P.R., 2002. Conservation of tropical forest birds in countryside habitats. Ecol. Lett. 5, 121–129.
Hurlbert, A.H., White, E.P., 2005. Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications: range map- vs. survey-based species richness. Ecol. Lett. 8, 319–327.
IUCN, 2019. The IUCN Red List of Threatened Species. Version 2019-1. https://www.iucnredlist.org.
Jernvall, J., Wright, P.C., 1998. Diversity components of impending primate extinctions. Proc. Natl. Acad. Sci. 95, 11279–11283.
Keogh, R.M., 1984. Changes in the forest cover of Costa Rica through history. Turrialba 34, 325–331.
Long, Y., Momberg, F., Ma, J., Wang, Y., Luo, Y., Li, H., et al., 2012. Rhinopithecus strykeri found in China!: Rhinopithecus strykeri in China. Am. J. Primatol. 74, 871–873.
Lynch Alfaro, J.W., Boubli, J.P., Paim, F.P., Ribas, C.C., da Silva, M.N.F., Messias, M.R., et al., 2015. Biogeography of squirrel monkeys (genus Saimiri): south-central Amazon origin and rapid pan-Amazonian diversification of a lowland primate. Mol. Phylogenet. Evol. 82, 436–454.
Magle, S.B., Theobald, D.M., Crooks, K.R., 2009. A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. Landsc. Ecol. 24, 267–280.
Marsh, L.K., 2013. Because conservation counts: primates and fragmentation. In: Marsh, L.K., Chapman, C.A. (Eds.), Primates in Fragments: Complexity and Resilience, 1st edition. Springer-Verlag New York, New York, pp. 3–11.
Mendenhall, C.D., Frishkoff, L.O., Santos-Barrera, G., Pacheco, J., Mesfun, E., Quijano, F.M., et al., 2014. Countryside biogeography of Neotropical reptiles and amphibians. Ecology 95, 856–870.
Ministerio de Agricultura y Ganadería (MAG), 2008. Atlas Digital de Costa Rica. Uso de la Tierra en Costa Rica en 1992. Laboratorio de Sistemas de Información Geográfica, Escuela de Ingeniería Forestal, ITCR, Cartago, Costa Rica.
Morera-Avila, R., 2000. Análisis Situacional del Mono Titi en el Área de Amortiguamiento del Parque Internacional La Amistad Pacífico 'Una Estrategia para su Conservación'. Área de Conservación La Amistad-Pacífico (ACLAP), Parque Internacional La Amistad (PILA), Instituto Nacional de Biodiversidad (INBio), San José, Costa Rica, pp. 18.
Morera-Avila, R., 2002. Análisis Situacional del Mono Titi en el Área de Amortiguamiento del Parque Internacional La Amistad. In: 'Una Estrategia para su Conservación' (Segunda Etapa). Convenio Instituto Nacional de Biodiversidad - Sistema de Áreas de Conservación (Área de Conservación La Amistad-Pacífico), San José, Costa Rica, pp. 25.
Nater, A., Mattle-Greminger, M.P., Nurcahyo, A., Nowak, M.G., De Manuel, M., Desai, T., et al., 2017. Morphometric, behavioral, and genomic evidence for a new orangutan species. Curr. Biol. 27, 3487–3498 (e10).
Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., et al., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50.
Oates, J.F., Abedi-Lartey, M., Mcgraw, W.S., Struhsaker, T.T., Whitesides, G.H., 2000. Extinction of a west African red Colobus monkey. Conserv. Biol. 14, 1526–1532.
Pacheco, J., Ceballos, G., Daily, G.C., Ehrlich, P.R., Suzán, G., Rodríguez-Herrera, B., Marcé, E., 2006. Diversidad,historia natural y conservación de los mamíferos de San Vito de Coto Brus, Costa Rica. Rev. Biol. Trop. 54, 219–240.
Pagiola, S., 2011. Using Payments for Environmental Services (PES) to Implement Reduced Emissions From Deforestation and Forest Degradation (REDD). World Bank

Group, Washington DC, USA.
Picón-Cruz, J.C., Baltodano-Zúñiga, V.J., 2006. Planificación turística en zonas costeras de Costa Rica. Algunas referencias a Playa Tamarindo (Santa Cruz, Guanacaste). Inter Sedes 3, 149–170.
Programa Estado de la Nación, 2014. Vigésimo Informe Estado de la Nación en Desarrollo Humano Sostenible. Programa Estado de la Nación, San José, Costa Rica.
Puyravaud, J.-P., 2003. Standardizing the calculation of the annual rate of deforestation. For. Ecol. Manag. 593–596.
Reid, F., 2009. A Field Guide to the Mammals of Central America and Southeast México II. Oxford University Press, New York, E.E.U.U.
Rempel, R.S., Kaukinen, D., Carr, A.P., 2012. Patch Analyst and Patch Grid. Thunder Bay, Ontario.
Ruiz-García, M., Luengas-Villamil, K., Leguizamon, N., De Thoisy, B., Gálvez, H., 2015. Molecular phylogenetics and phylogeography of all the Saimiri taxa (Cebidae, Primates) inferred from mt COI and COII gene sequences. Primates 56, 145–161.
Rylands, A.B., Groves, C.P., Mittermeier, R.A., Cortés-Ortiz, L., Hines, J.J.H., 2006. Taxonomy and distributions of Mesoamerican primates. In: Estrada, A., Garber, P.A., Pavelka, M.S.M., Luecke, L. (Eds.), New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation. Springer US, Boston, MA, pp. 29–79.
Rylands, A.B., Mittermeier, R.A., Bezerra, B.M., Paim, F.P., Queiroz, H.L., 2013. Species accounts of Cebidae. In: Mittermeier, R.A., Rylands, A.B., Wilson, D.E. (Eds.), Handbook of the Mammals of the World, Volume 3: Primates. Lynx Edicions: Conservation International: IUCN, Barcelona.
Sáenz, J.C., Sáenz, P., 2008. Influencia de las variables de hábitat y paisaje sobre la presencia-ausencia del mono tití y del mono carablanca en un área fragmentada del Pacífico Central de Costa Rica. In: Evaluación y conservación de biodiversidad en paisajes fragmentados de Mesoamérica. INBio, Heredia, Costa Rica 620p.
Sierra, C., Jiménez, I., Altrichter, M., Fernandez, M., Gómez, G., González, J.A., et al., 2003. New data on the distribution and abundance of Saimiri oerstedii citrinellus. Primate Conservation 19, 5–9.
Sistema Nacional de Áreas de Conservación (SINAC), 2013. Tipos de Bosque del Inventario Nacional Forestal. Cobertura Costa Rica 2012.
Solano-Rojas, D., 2007. Evaluación del Paisaje, Habitat y Poblacion del Mono Titi (Cebidae: Samiri oerstedii oerstedii) en la Peninsula de Osa. Tesis de Grado, Maestría en Vida Silvestre y Conservacion, Instituto Internacional de Conservacion y Manejo de Vida Silvestre, Universidad Nacional, Heredia, Costa Rica.
Thomas, C., Abery, J.C., 1995. Estimating rates of butterfly decline from distribution maps: the effect of scale. Biol. Conserv. 73, 59–65.
Wong, G., 2002. Mono tití en peligro de extinción. Ambientico 107, 3.
Wong, G., Cuarón, A.D., Rodríguez-Luna, E., De Grammont, P.C., 2008. *Saimiri oerstedii*. The IUCN Red List of Threatened Species 2008. The IUCN Red List of Threatened Species. www.iucnredlist.org, Accessed date: 26 May 2016.