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Quantifying the effects of deforestation and fragmentation on a range-wide conservation plan for jaguars

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ABSTRACT

The impact of extensive changes in land use and climate on species has led to an increasing focus on large-scale conservation planning. However, these plans are often static conservation prescriptions set against a backdrop of rapidly changing environments, which suggests that large-scale information on threats can improve the functionality of planning efforts. Jaguars (*Panthera onca*) are the focus of a range-wide conservation strategy extending from Mexico to Argentina that consists of jaguar conservation units (JCUs) and modeled corridors. Recent deforestation is a major threat to jaguar populations, but forest loss has not been systematically assessed across the entire jaguar network. In this study, we quantified the amount and rate of deforestation in JCUs and corridors between 2000 and 2012. JCUs lost 37,780 km^2 forest (0.93%) at an increasing rate of 149.2 km^2 yr^{-2}, corridors lost 45,979 km^2 (4.43%) at a decreasing rate of 40.1 km^2 yr^{-2}, and levels of forest fragmentation increased in corridors. Protected sections of JCUs and corridors lost less forest than unprotected sections, suggesting efforts to increase protected status of jaguar conservation areas are warranted. Higher deforestation in corridors indicates difficulties in maintaining connectivity of jaguar populations, and suggests the need for increased engagement with communities within corridor landscapes. Assessment of spatial variability of anthropogenic threats within the jaguar network may improve jaguar conservation by informing network prioritization and function.

1. Introduction

The pervasive impacts of anthropogenic change on species and ecosystems has led to increasing emphasis on developing conservation strategies across broad spatial scales. These conservation plans cross landscapes, regions, and political boundaries, and are often designed to conserve species in the face of global change processes such as large-scale habitat loss, fragmentation, and climate change (Lawler et al., 2010). Such large-scale plans recognize the need to go beyond management of one or a few key areas to consider the wider landscapes and regions that provide connections and conserve ecological processes such as disturbance and connectivity (Guerrero et al., 2015). The development of efforts such as the Yellowstone to Yukon Conservation Initiative (Chester, 2015), growth of organizations that encourage cross-landscape coordination (e.g., Landscape Conservation Cooperatives in the US), and increasing emphasis on landscape or region-wide systematic conservation efforts (e.g., Klein et al., 2009; Pressey and Bottrill, 2009) attest to the new emphasis on ambitious large-scale conservation action.

Once a conservation strategy has been designed, periodic updates are required to assess success and failure and adapt the plan to prioritize conservation action (Pressey, 2004). One key factor in assessing large-scale conservation efforts is an understanding of how ongoing human activities impact the components of a plan (e.g., protected areas), which may be highly variable in intensity and spatial distribution. However, incorporating information on landscape change, or other forms of anthropogenic impacts, into conservation strategy remains difficult at large scales and is often ignored (Heller and Zavaleta, 2009; Pressey et al., 2007). Knowledge of these impacts informs scheduling and

Abbreviations: JCU, jaguar conservation unit; PD, patch density; CLUMPY, clumpiness index.

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prioritizing of conservation actions (Pressey, 2004; Pressey et al., 2007; Visconti et al., 2010). It is therefore important to analyze the effects of anthropogenic pressure on conservation plans to assess their performance and inform priority setting decisions.

Range-wide conservation strategies for single species are one form of large-scale conservation planning (Redford et al., 2011; Sanderson et al., 2008, 2002). Typically, these plans are constructed by identifying priority habitats or sites for conservation across the range of the species, based on some combination of expert opinion, modeling, and ecological literature (e.g., Rabinowitz and Zeller, 2010; Sanderson et al., 2002; Thorbjarnarson et al., 2006; Viña et al., 2010), and often span political and ecological boundaries. When the species is wide-ranging, conservation efforts designed around the needs of that species can serve as an umbrella for many other species (Roberge and Angelstam, 2004; Thornton et al., 2016).

Jaguars (*Panthera onca*) are an ideal candidate for range-wide conservation planning, given declining populations across a large range that encompasses much of Latin America (Sanderson et al., 2002). Major threats to jaguars include habitat loss and fragmentation due to conversion of forest to agriculture (De Angelo et al., 2011; Sanderson et al., 2002), declining prey base (Espinosa, 2012; MacDonald and Loveridge, 2010), and persecution by humans (Azevedo and Murray, 2007; Crawshaw and Quigley, 1991; De Angelo et al., 2013). Identification of major threats to jaguars led to the development of a large-scale conservation plan consisting of core habitat, termed jaguar conservation units (JCUs) (Sanderson et al., 2002), and corridors connecting those JCUs (Rabinowitz and Zeller, 2010). This conservation strategy has been a major driver of conservation action and research across the jaguar's range (e.g., Petracca et al., 2014; Rabinowitz, 2014; Thornton et al., 2016; Zeller et al., 2011). Approximately 34% of JCU's total area is protected (IUCN categories I-VI), while only 11% of the corridor's total area is protected. The goal of large-scale species conservation plans are genetically robust, healthy, representative and resilient populations (Redford et al., 2011). Accomplishing that goal requires assessment of the plan's performance and corresponding actions to address weak points.

The importance of habitat to jaguars and the threat of habitat loss suggest that documenting the extent of habitat change within the species' range can improve conservation efforts by prioritizing targeted conservation actions to maintain populations. Satellite remote sensing is a useful tool for documenting land cover change through deforestation activities (e.g., DeFries et al., 2005; Willis, 2015). The recent development of a global database of forest cover change using Landsat imagery (30-m spatial resolution) (Hansen et al., 2013) provides the opportunity to evaluate changes in forest cover across large areas and at fine spatial resolution. Although jaguars may use habitat other than forest for some activities (Tôrres et al., 2012; Vynne et al., 2011), jaguars generally select more heavily forested landscapes and jaguar population persistence is tied to forest cover (Azevedo and Murray, 2007; Cavalcanti and Gese, 2009; De Angelo et al., 2013, 2011).

Our goal was to examine recent deforestation and fragmentation within jaguar core areas (i.e., JCUs) and corridors using this dataset on forest loss (Hansen et al., 2013). Specifically, we sought to: (1) quantify rates of deforestation and fragmentation in JCUs and modeled corridors between 2000 and 2012; and (2) identify JCUs, corridors, and broader geographic regions with the most deforestation. Given that protected areas are often the backbone of conservation planning and form a key component of the jaguar conservation network, yet are threatened by a variety of processes that may limit their effectiveness (Curran et al., 2004; DeFries et al., 2005; Leverington et al., 2010; Mascia and Pailler, 2011), we also sought to (3) determine intercountry variability in deforestation within protected and unprotected sections of JCUs and corridors. By applying a consistent dataset of recent deforestation across the entire range of the jaguar (from Argentina to Mexico), our analysis is a first step in incorporating anthropogenic threats in range-wide conservation planning for this threatened species.

2. Materials and methods

2.1. Materials

We used an established range-wide conservation network for jaguars in our analysis (Sanderson et al., 2002). This network was developed through consultation with jaguar experts that identified core habitat containing stable jaguar populations, termed jaguar conservation units (JCUs) (Sanderson et al., 2002). These JCUs were defined as areas with a stable prey community that contained a population of at least 50 breeding jaguars, or as areas with fewer than 50 breeding jaguars but with sufficient habitat and prey base such that jaguar populations could increase under favorable conditions (Sanderson et al., 2002). These JCUs were updated in 2006 (Zeller, 2007), and have been further modified to result in the most recent map of JCUs (Fig. 1). Although some local-level refinements to the JCUs have been and will continue to be made (e.g., De Angelo et al., 2013), the JCU network provides a consistent, expert-validated, range-wide model with which to conduct a forest loss comparison.

Evaluation of potential jaguar movement, or dispersal, between JCUs, was missing from the initial range-wide plan. Accordingly, Rabinowitz and Zeller (2010) estimated dispersal corridors between JCUs via least-cost path modeling (Adriaensen et al., 2003). Given a lack of empirical information on how jaguars disperse across landscapes, expert opinion was used to derive the resistance values for the creation of jaguar least-cost corridors. The end result of this analysis was a map representing landscape resistance to jaguar movements and identification of potential least-cost corridors linking JCUs (Fig. 1).

We estimated deforestation in JCUs and jaguar corridors using global maps of forest change between 2000 and 2012 from Hansen et al. (2013). This dataset quantifies recent forest change at high resolution (30 m), which informs habitat loss across large scales. Percent forest cover in 2000, forest loss, loss-year, and forest gain are available online (Hansen et al., 2013). Percent forest cover was defined as canopy cover over 5 m, with loss representing a stand-clearing event (Hansen et al., 2013). The year that the forested pixel was lost is given by an integer value between 1 (lost in 2001) and 12 (lost in 2012). Gain was then defined as the inverse of loss. By defining forest cover as a structural measure, Hansen et al. (2014) acknowledged that their map of forest cover does not differentiate functional forests from agricultural plantations, nor true forest regeneration from agricultural conversion (Tropek et al., 2014). However, in calculating net change in forest cover, we minimize problems related to misclassifications in the initial forest cover layer by focusing on the loss and gain in forest cover. Misclassified regrowth or “gain” could still influence our analysis; however, there was very little forest gain within JCUs and corridors when compared to forest loss.

We generated pixel-level binary layers of forest cover in 2000 (fc_{2000}) and 2012 (fc_{2012}) to analyze forest change and fragmentation. We used a 50% threshold to convert the Hansen et al. (2013) data to a binary map of forest/non-forest. Non-forested pixels that had forest gain were changed to forest for fc_{2012}; similarly, forested pixels that had forest loss were changed to non-forested for the fc_{2012} layer. By incorporating both forest gain and loss into the fc_{2012} dataset, we were able to look at net forest change between 2000 and 2012. We performed a sensitivity analysis by testing a cutoff of 20% forest cover, which was used by Heino et al. (2015) in a global analysis of the same dataset. Our selection of 50% did not qualitatively change the results, with most corridors and JCUs only showing an additional forest loss of 0.10% or less (Appendix A). Moreover, a threshold of 50% cover provides a better indication of functional forest for jaguars, which preferentially move through and select for more heavily forested habitat across their range (Azevedo and Murray, 2007; Cavalcanti and Gese, 2009; Crawshaw and Quigley, 1991; Davis et al., 2011; De Angelo et al., 2011). We included all corridors and JCUs of the jaguar range in our analysis, even those that fall within non-forest biomes (savannas and

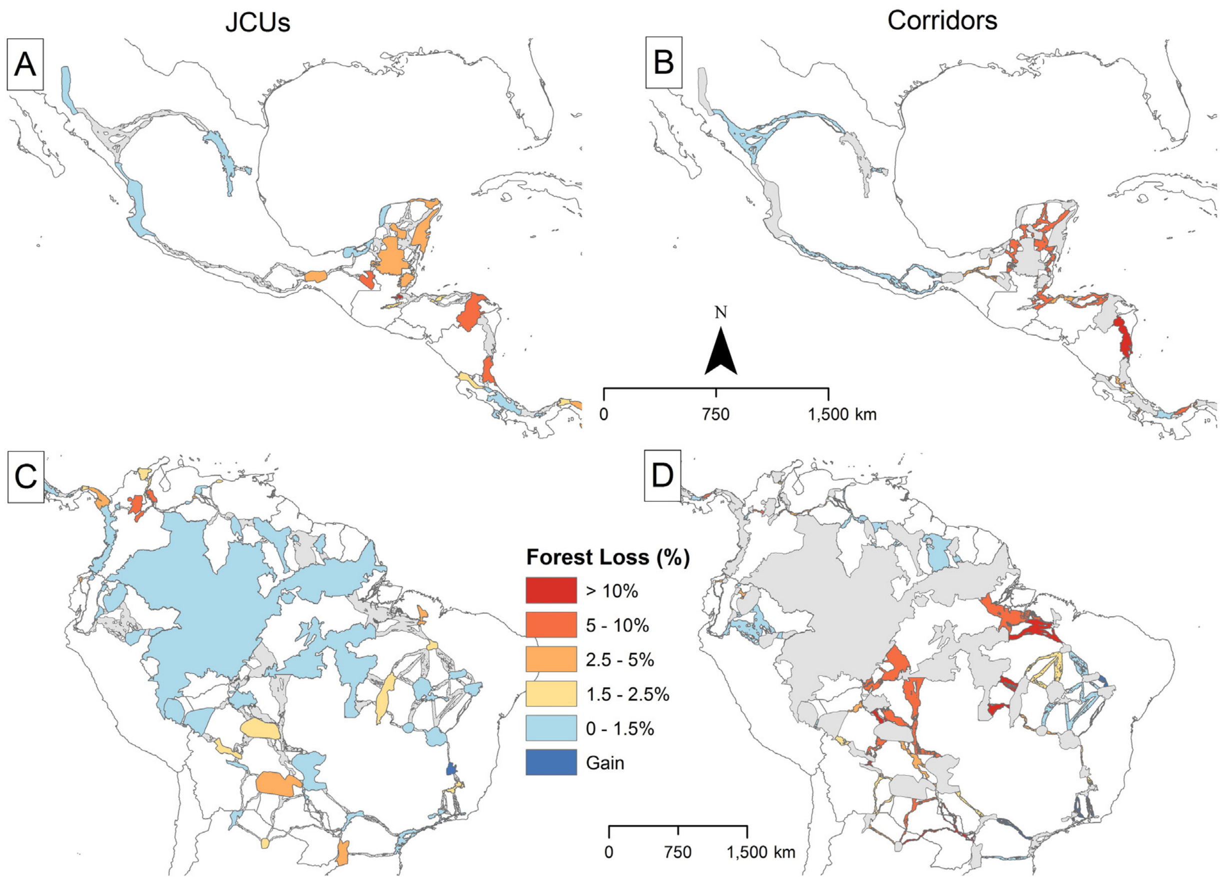

Fig. 1. Percent forest loss (2000−2012) in jaguar conservation units (JCUs) (A, C) and corridors (B, D) in Central America (A, B) and South America (C, D) with warmer colors indicating more deforestation and cooler colors indicating less deforestation. To distinguish between JCUs and corridors, each are grayed out when focusing on the other.

drylands). We determined the majority biome for each JCU and corridor with Climate Change Initiative land cover (CCI-LC) data from the European Space Agency (ESA, 2014). Although forest loss better reflects or represents the impact of anthropogenic disturbance in forested biomes, we included all biomes in the analysis to have a comparable dataset across the range. We note, however, that many corridors and JCUs within non-forested biomes started with relatively low levels of forest cover in 2000.

To examine forest loss and fragmentation within protected and unprotected areas of the jaguar conservation plan, we used a database from the International Union for Conservation of Nature (IUCN) containing polygons for every protected area in Central and South America (IUCN and UNEP-WCMC, 2015). Protected area designations range from a strict nature reserve (Ia) and wilderness areas (Ib) to protected areas with sustainable use of natural resources (VI). For our analysis, we combined all designations (I-VI) into a single category of protected, while all other land was categorized as unprotected.

2.2. Forest change analysis

We calculated forest change between 2000 and 2012 for each JCU and corridor. We calculated change as areal extent (i.e., forest change between 2000 and 2012 [km^2]) and as a percentage of the total land area. To determine change as percentage of the total area, we subtracted the percent of the JCU or corridor that was forest in 2012 from the percent of the JCU or corridor area that was forest in 2000. To assess range-wide trends in deforestation, we determined the slope of the regression line between loss year and forest loss for JCUs and corridors. We used an unequal variance *t*-test to determine whether corridors lost forest at a faster rate than JCUs each year. To assess the effectiveness of designated protected areas for jaguar habitat, JCUs and corridors were pooled at the country level and separated into protected and unprotected sections. Values calculated for each JCU or corridor therefore include total area, fc_{2000}, area change between 2000 and 2012 (km^2), and percent change between 2000 and 2012. Finally, we calculated range-wide trends in forest change for JCUs and corridors over the 12-year period.

2.3. Fragmentation analysis

We used FRAGSTATS 4 (McGarigal and Marks, 1995) to calculate fragmentation metrics for corridors in 2000 and 2012. We did not calculate these metrics for JCUs or the 12 largest corridors (of 83 corridors) due to computer memory limitations in FRAGSTATS 4. Examining fragmentation metrics likely wouldn't improve our understanding of the status of JCUs beyond forest loss metrics as JCUs maintained forest cover in large central blocks. In contrast, fragmentation metrics are more meaningful for corridors, which tend to be narrow, start with less forest cover, lose forest at a higher rate, and are supposed to function as landscape connections. Although omitting the largest corridors from the analysis was not ideal, it is unlikely that this would heavily influence our results. We tested the relationship between corridor size and fragmentation metrics and found no correlation (Pearson's $r < 0.1$).

The two metrics we focused on were patch density (PD) and clumpiness index (CLUMPY). We chose these metrics as indices of changes in fragmentation and connectedness across the landscape, irrespective of corridor size, which varied greatly. PD is the number of patches divided by total landscape area (units are patches per 100 ha), with low PD indicating a more connected landscape and high PD indicating a more fragmented landscape. CLUMPY ranges from −1 to 1, with −1 representing a maximally disaggregated landscape (greater dispersion), 0 having randomly distributed patches, and 1 representing maximally clumped (greater contagion). CLUMPY isolates the configuration component from the area component, thereby giving an effective index of fragmentation that is not confounded by changes in area. We determined if fragmentation metrics significantly changed between 2000 and 2012 with a paired *t*-test.

3. Results

3.1. Forest change analysis

Between 2000 and 2012, deforestation was higher in corridors than JCUs (Fig. 1; Appendix B). JCUs lost 37,780 km^2 of forest and corridors lost 45,979 km^2, representing 0.93% and 4.43% of their total area, respectively. The average JCU lost 522.8 km^2 of forests ($\sigma = 1579.1$ km^2, range: $-13{,}001$–$+2.8$ km^2) or 1.81% ($\sigma = 1.99\%$, range: -11.37%–$+0.03\%$), while the average corridor lost 574.9 km^2 ($\sigma = 1351.1$ km^2, range: -6428–$+161$ km^2) or 3.88% ($\sigma = 4.53\%$, range: -23.18%–$+2.00\%$). Six out of 75 JCUs (8%) lost >5% forest, and only one (1%) surpassed 10% loss. Twenty-three out of 83 corridors (28%) lost >5% of forest cover, and eight of those (10%) surpassed 10% loss. One JCU (1%) and five corridors (6%) in the Atlantic coastal forests of Brazil gained forest cover from 2000 to 2012, while all other JCUs and corridors lost forest over that time frame. See Appendix B for a list of forest change in each JCU and corridor.

The highest deforestation in corridors by area was in South America where the Atlantic Coastal forests of Brazil connect to the Amazon. In particular, Brazil contained the five corridors that lost the most forest (>3000 km^2) (Fig. 1; Appendix B). The heavy deforestation in South American corridors extended to the southern part of the jaguar's range. In Central America, JCUs and corridors from the Yucatan Peninsula in Mexico south through Guatemala, Honduras, and Nicaragua lost the most forest. The two corridors in Central America with the highest deforestation by area were in the Yucatan corridor in Mexico with 1617.9 km^2 (6.77%) and the Bosawas-Cerro Silva corridor in Nicaragua with 1615.7 km^2 (10.58%).

Forest loss within JCUs and corridors demonstrated substantial intercountry variability (Fig. 2). For example, the Yucatan Peninsula showed evenly dispersed deforestation throughout most of the JCUs and corridors, and significant deforestation at the southern edges of JCUs in Guatemala (Fig. 2B). Corridors on both sides of the Honduras–Nicaragua border were heavily deforested, and deforestation in their shared JCU occurs in both countries (Fig. 2C). In Colombia, recent deforestation is expanding from non-forested sections along forest boundaries (Fig. 2D). Across the shared borders between Bolivia, Argentina and Paraguay, large contiguous patches of forest are being clear-cut (note regularly shaped blocks of forest loss), particularly in Paraguay where the corridor to Argentina and surrounding areas have been almost completely deforested (Fig. 2E). Lastly, the group of JCUs and corridors near the Atlantic Coastal forests of Brazil were deforested earlier

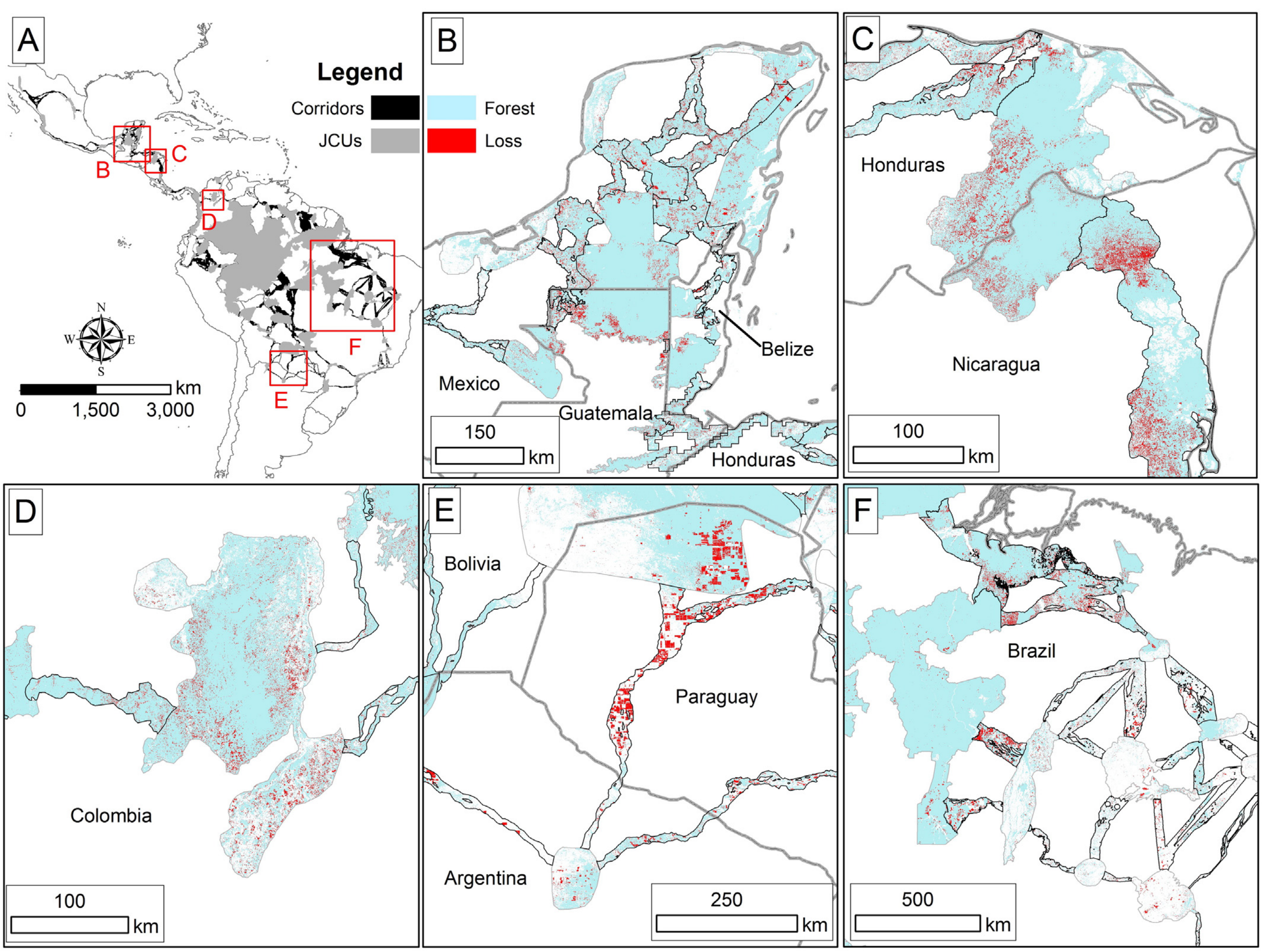

Fig. 2. (A) Central and South America with jaguar conservation units (JCUs; outlined in gray) and corridors (outlined in black), and red boxes indicating the location of close-up forest loss figures. Close-up locations illustrating forest area (cyan) and loss (2000–2012; red) within JCUs and corridors are: (B) Yucatan Peninsula in Mexico, Guatemala, and Belize; (C) Honduras–Nicaragua border; (D) Colombia; (E) borders between Bolivia, Argentina, and Paraguay; and (F) central Brazil and part of the Atlantic Coastal forests.

than 2000 (white areas within JCUs and corridors), and that deforestation subsequently spread westward (Fig. 2F).

In addition to total area lost, we also computed rates of loss. JCUs generally lost around 0.15%–0.25% forest yr^{-1}, while corridors lost 0.3%–0.5% forest yr^{-1} (Fig. 3). Rates of deforestation were higher in corridors than JCUs in all years ($P < 0.05$ in all years; Fig. 3). In terms of forest area lost, JCUs lost an average 3499 km^2 yr^{-1}, while corridors lost 4084 km^2 yr^{-1} (Fig. 3). JCUs showed a slight trend of increasing deforestation ($R^2 = 0.55$, $P = 0.006$) at a rate of 149.2 km^2 yr^{-2}, while corridors on average showed a decreasing trend of 40.1 km^2 yr^{-2} ($R^2 = 0.03$, $P = 0.578$), especially noticeable after 2005 (Fig. 3).

3.2. Fragmentation analysis

In addition to deforestation, most corridors exhibited increased fragmentation based on both metrics examined. Eighty-six percent of corridors showed an increase in PD from 2000 to 2012. Similarly, most corridors (77%) had lower CLUMPY in 2012 than 2000, indicating a shift towards more dispersed or disaggregated patches. When only considering those corridors that fall within the forest biome (excluding savanna and dryland biomes), the results are even more striking, with 93% of corridors increasing in PD and 79% decreasing in CLUMPY. On average, corridors became more highly fragmented with increases in PD for both Central America ($\bar{x} = 0.68$ patches per 100 ha; $P < 0.001$) and South America ($\bar{x} = 0.19$ patches per 100 ha; $P = 0.005$) (Table 1). The change in CLUMPY was more modest, with Central America displaying a larger change ($\bar{x} = 0.03$; $P < 0.001$) than South America ($\bar{x} = 0.01$; $P = 0.33$) (Table 1). Taken together, these results show forest habitat in corridors is becoming more fragmented, particularly in Central America.

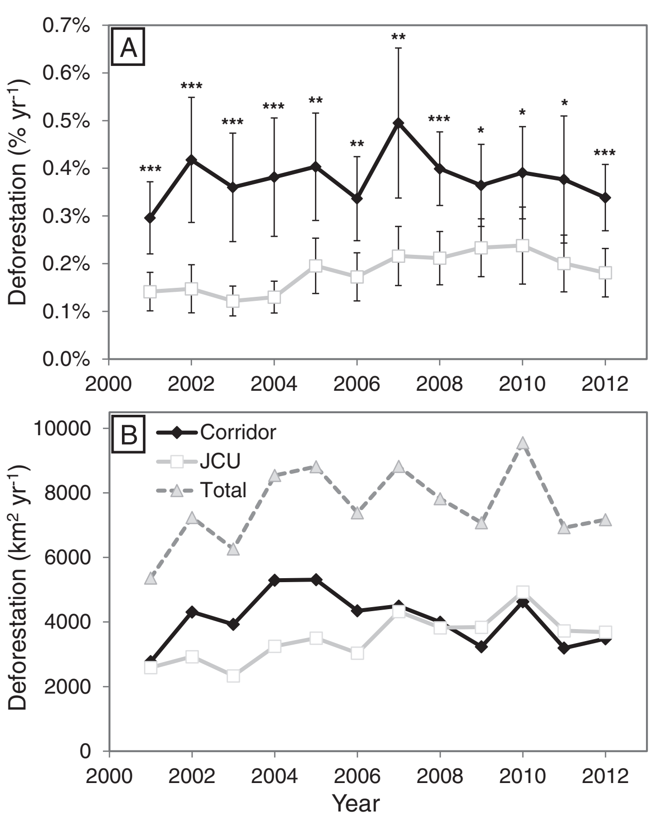

Fig. 3. Average rates of deforestation for jaguar conservation units (JCUs) and corridors between 2000 and 2012. (A) Deforestation was higher in corridors on a percentage basis in every year (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$); error bars represent 95% confidence intervals. (B) On a total area basis, deforestation was similar in corridors and JCUs.

3.3. Deforestation in protected areas

Collectively, protected sections of JCUs and corridors experienced lower rates of deforestation than unprotected sections (Tables 2 and 3). This pattern is clearest in South America where deforestation occurred at twice the rate in unprotected sections of corridors (−4.85%) compared to protected sections (−2.26%) (Table 3). An example of the effectiveness of protected areas in reducing deforestation is shown in Fig. 4 for two corridors on the border between Brazil and Bolivia. In Corridor 21, there is heavy deforestation on the Brazilian side of the border, except within the protected section of the corridor, and that pattern extends into the protected sections of Corridor 54 in Brazil. However, protected areas did not always reduce deforestation: protected sections of Honduran JCUs lost forest at 2.74 times the rate of unprotected sections (−11.94% vs. −4.36%), and protected sections of Guatemalan corridors lost forest at 1.37 times the rate of unprotected sections (−9.16% vs. −6.67%) (Table 2). Significantly, protected sections of corridors in Central America experienced 1.27 times the rates of loss than protected sections of JCUs (−3.56% vs. −2.80%; Table 2) and 5.14 times the rates of loss in South America (−2.26% vs. −0.44%; Table 3), indicating that the overall higher rates of loss in corridors cannot be solely attributed to lower rates of protection.

We performed individual analyses for each protected area IUCN designation, but no range-wide pattern emerged (Appendix C). While level of protection may be important at a finer scale, not every country utilizes all levels of protection. For example, less than half of Central American and South American countries have any land within JCUs or corridors as a strict nature reserve (IUCN Ia) (Appendix C). Therefore, the relationship between deforestation and protection status is likely confounded by intercountry variability in forest loss.

4. Discussion

4.1. Forest change analysis

Our results demonstrate that jaguar corridors are experiencing high rates of deforestation and fragmentation of forest. Numerous jaguar core areas (JCUs) also experienced substantial forest loss, and JCUs demonstrated accelerating forest loss between 2000 and 2012. These forest loss rates and increased fragmentation of forests were generally higher in Central America and the southern edge of the jaguar range, where JCUs tend to be smaller, which suggests that long-term viability of some core areas for jaguars may be threatened.

Compared to JCUs, forest loss was higher in corridors for both protected and unprotected sites, suggesting that human pressure on remaining forest in corridors is high regardless of protection status. This finding is alarming, considering that maintaining connectivity of jaguar populations across the range is one of the key goals for their conservation (Rabinowitz and Zeller, 2010; Zeller et al., 2013), and that work on determining the functionality of jaguar corridors forms the backbone of much recent research (Cuyckens et al., 2014; Petracca et al., 2014; Rodríguez-Soto et al., 2013; Silveira et al., 2014; Zeller et al., 2011). Given their substantial movement capabilities, jaguars may be able to move across some types of non-forested habitat during dispersal, and therefore minor loss of forest may not always lead to reduced connectivity. However, jaguars are often absent from smaller forest patches (Thornton et al., 2011; Urquiza-Haas et al., 2009), persist better in areas of more forest cover, and are vulnerable to increased human persecution in less forested and more fragmented landscapes (De Angelo et al., 2013), strongly suggesting that forest loss in corridors will be problematic for jaguar connectivity and the persistence of jaguar residents within corridor landscapes. Therefore, these results suggest that increased engagement with communities in key corridors is needed to maintain connectivity for jaguars in the face of rapid land-use change across the jaguar's range. For example, working with communities to minimize human-wildlife conflict, reduce forest loss, or protect private

Table 1
Summary of fragmentation statistics for jaguar corridors in Central America and South America in 2000 and 2012, and the difference between those years (2012−2000). Patch density (PD; patches per 100 ha) measures connectedness of the landscape, and clumpiness index (CLUMPY; −1 to 1) measures the extent to which the landscape is aggregated or clumped. Asterisks represent significance levels from a paired *t*-test (*P < 0.05; **P < 0.01; ***P < 0.001).

	Central America (n = 21)			South America (n = 50)		
	2000	2012	Difference	2000	2012	Difference
PD						
$\bar{x}$	1.86	2.55	0.68***	1.87	2.06	0.19**
$SE_{\bar{x}}$	0.33	0.37	0.16	0.28	0.27	0.06
Min/max	0.09/6.41	0.40/7.24	0.03/3.37	0.00/6.00	0.00/5.89	−1.10/1.72
CLUMPY						
$\bar{x}$	0.73	0.70	−0.03***	0.67	0.69	0.01
$SE_{\bar{x}}$	0.02	0.02	0.01	0.05	0.03	0.01
Min/max	0.49/0.87	0.57/0.87	−0.09/0.08	−0.86/0.94	−0.27/0.93	−0.06/0.60

reserves within corridors may be productive approaches (Hoogesteijn and Hoogesteijn, 2010; Salom-Pérez et al., 2010).

We also documented higher rates of loss in unprotected versus protected sections of corridors and JCUs. This finding confirms other large-scale research regarding the utility of protected areas to buffer against forest loss and other anthropogenic threats (Butsic et al., 2015; Figueroa and Sánchez-Cordero, 2008; Pfaff et al., 2015), particularly in Latin America (Heino et al., 2015). Given differential rates of loss in protected versus unprotected JCUs and corridors, we suggest that efforts should be increased to secure protection for more jaguar habitat, particularly in corridors where only 5% of corridor area is protected in Central America and 12% in South America. For example, Mexico contains 69% of the Central American corridors in terms of total area, with <3% of that area being protected. Further, Mexico is at the current northern edge of jaguar range, providing the only possible link to reestablishing a population in the United States. Based on our results, bringing more forested sections of jaguar corridors under official protection in Mexico would be highly beneficial.

Despite most countries showing less deforestation in protected areas than unprotected, Honduran JCUs and Guatemalan corridors show higher forest loss in protected sections. Moreover, most protected sections of JCUs and corridors in all countries were affected to some extent by deforestation, suggesting that protected area status only slows the rate of deforestation, but does not fully halt habitat loss and fragmentation. Indeed, some protected areas approached or exceeded 5% forest loss, which was approximately equivalent to a global average of forest loss (across all forest including non-protected forest tracts) calculated from the Hansen et al. (2013) dataset (Heino et al., 2015). A full analysis of why certain protected areas were more functional than others is beyond the scope of this paper, but may be related to differential country or site level drivers such as population density, enforcement, or level of development (Butsic et al., 2015; Geldmann et al., 2015; Leverington et al., 2010).

At a regional level, forest loss is quite uneven across the jaguar range; however, some patterns do emerge. Within the core of the range, the Amazon forest and surrounding areas, there is relatively little forest loss. In contrast, heavy deforestation extends from the edges of the jaguar's range to the north, south, and east. Of particular concern is the rapid decline in forest of the jaguar corridors of Central America, where there is already a natural geographic bottleneck and loss of a single corridor could disconnect the entire northern population from South America. Loss of connectivity between jaguar populations in Central and South America could be problematic for maintaining range-wide genetic diversity as well as potentially long-term metapopulation stability (Brown and Kodric-Brown, 1977; Frankham et al., 2002; Soulé and Mills, 1998).

4.2. Limitations

Our use of a global-scale dataset of forest loss and regrowth derived from satellite imagery has some limitations with implications for our results. Some regrowth and areas classified as forest by Hansen et al. (2013) are young regenerating stands or agricultural areas such as palm oil plantations (Tropek et al., 2014), with relatively unknown impacts on jaguar movement or habitat use. Inclusion of such areas as "forest" in our analysis may bias our findings towards lower rates of habitat loss. Refinement of the Hansen et al. (2013) dataset at a smaller, local scale with data from higher-resolution sensors could help alleviate these issues, but would be challenging to implement across the jaguar range. On the other hand, non-forested areas not accounted for in this

Table 2
Country-level analysis of forest change (2000–2012) in protected and unprotected areas of conservation concern for jaguars (*Panthera onca*) in Central America. Protected areas in this table include areas with International Union for the Conservation of Nature (IUCN) designations I-VI. Areas where the designation was not reported are included in the unprotected group. fc_{2000} = forest cover in 2000.

Country	Status	Corridors				JCUs			
		Total area (km^2)	fc_{2000}	Area change (km^2)	Percent change	Total area (km^2)	fc_{2000}	Area change (km^2)	Percent change
Belize	Protected	1007	76.12%	−19.3	−1.91%	6141	97.37%	−125.5	−2.04%
	Unprotected	3602	76.51%	−234.8	−6.52%	1788	94.48%	−66.6	−3.72%
Costa Rica	Protected	375	89.75%	−5.8	−1.56%	9292	93.15%	−48.1	−0.52%
	Unprotected	3144	76.90%	−108.7	−3.46%	8263	79.28%	−184.7	−2.24%
Guatemala	Protected	1874	82.11%	−171.8	−9.16%	11,969	97.04%	−783.4	−6.55%
	Unprotected	4647	66.88%	−309.9	−6.67%	6417	93.53%	−715.9	−11.16%
Honduras	Protected	572	82.57%	−18.5	−3.25%	4105	95.95%	−489.9	−11.94%
	Unprotected	11,133	77.72%	−673.7	−6.05%	14,176	80.94%	−618.3	−4.36%
Mexico	Protected	3162	31.78%	−39.8	−1.26%	27,340	64.89%	−206.5	−0.76%
	Unprotected	105,113	58.69%	−2593.1	−2.47%	113,794	61.78%	−2183.8	−1.92%
Nicaragua	Protected	312	80.43%	−11.6	−3.71%	6674	98.02%	−363.9	−5.45%
	Unprotected	14,220	82.53%	−1539.4	−10.83%	8940	93.30%	−646.3	−7.23%
Panama	Protected	252	95.55%	−2.4	−0.92%	8655	98.25%	−59.8	−0.69%
	Unprotected	6670	91.43%	−202.5	−3.04%	18,965	93.11%	−659.3	−3.48%
Central America totals	Protected	7554	61.03%	−269.2	−3.56%	74,176	84.90%	−2077.1	−2.80%
	Unprotected	148,529	64.94%	−5662.1	−3.81%	172,343	70.80%	−5074.9	−2.94%

Table 3
Country-level analysis of forest change (2000–2012) in protected and unprotected areas of conservation concern for jaguars (*Panthera onca*) in South America. Protected areas in this table include areas with International Union for the Conservation of Nature (IUCN) designations I-VI. Areas where the designation was not reported are included in the unprotected group. fc_{2000} = forest cover in 2000.

Country	Status	Corridors				JCUs			
		Total area (km^2)	fc_{2000}	Area change (km^2)	Percent change	Total area (km^2)	fc_{2000}	Area change (km^2)	Percent change
Argentina	Protected	8	62.48%	−0.2	−3.35%	5923	87.88%	−30.6	−0.52%
	Unprotected	9240	44.74%	−430.8	−4.66%	28,657	69.47%	−945.0	−3.30%
Brazil	Protected	58,726	67.44%	−1978.8	−3.37%	902,583	89.17%	−3611.8	−0.40%
	Unprotected	488,637	65.00%	−30,637.2	−6.27%	1,549,950	86.79%	−7856.4	−0.51%
Bolivia	Protected	11,651	97.15%	−149.9	−1.29%	116,625	79.22%	−890.2	−0.76%
	Unprotected	57,618	90.37%	−2431.8	−4.22%	103,578	76.83%	−1727.6	−1.67%
Colombia	Protected	878	97.49%	−9.3	−1.06%	51,405	94.68%	−561.4	−1.09%
	Unprotected	7081	80.11%	−219.7	−3.10%	652,023	79.60%	−10,987.0	−1.69%
Ecuador	Protected	908	93.61%	−14.4	−1.59%	22,997	98.87%	−74.1	−0.32%
	Unprotected	14,373	88.82%	−360.6	−2.51%	41,935	98.74%	−193.5	−0.46%
French Guiana	Protected	–	–	–	–	194	96.20%	−1.1	−0.56%
	Unprotected	–	–	–	–	3	99.17%	0.0	−1.74%
Guyana	Protected	2230	99.71%	−1.3	−0.06%	4534	99.82%	−3.6	−0.08%
	Unprotected	55,482	99.29%	−55.5	−0.10%	8023	88.17%	−32.3	−0.40%
Paraguay	Protected	803	94.14%	−3.8	−0.47%	7557	66.44%	−77.1	−1.02%
	Unprotected	27,563	44.33%	−3112.7	−11.29%	32,108	57.99%	−2277.2	−7.09%
Peru	Protected	8541	99.22%	−7.0	−0.08%	75,784	98.62%	−173.2	−0.23%
	Unprotected	73,112	97.91%	−220.8	−0.30%	53,769	96.25%	−661.8	−1.23%
Suriname	Protected	18	100.00%	0.0	−0.02%	11,680	99.76%	−6.7	−0.06%
	Unprotected	24,792	99.31%	−10.9	−0.04%	4935	98.99%	−3.9	−0.08%
Venezuela	Protected	20,121	95.39%	−186.9	−0.93%	108,630	89.34%	−321.9	−0.30%
	Unprotected	19,813	55.77%	−216.0	−1.09%	18,504	56.71%	−191.8	−1.04%
South America totals	Protected	103,884	80.19%	−2351.6	−2.26%	1,307,912	89.23%	−5751.7	−0.44%
	Unprotected	777,711	72.88%	−37,696.0	−4.85%	2,493,485	84.14%	−24,876.5	−1.00%

study may be suitable habitat for jaguars. Savanna and shrubland habitat that is otherwise unaffected by humans can be used by jaguars (Tôrres et al., 2012; Vynne et al., 2011). However, Sanderson et al. (2002) categorized most savanna, grasslands, and shrublands as serving low to medium probability of sustaining jaguar populations long-term, and thus these areas may only be suitable for dispersal. We also do not consider potential impacts to habitat that can occur without deforestation, such as overhunting of prey species, which may impact jaguar movement and survival. However, our analysis provides a first step in developing an understanding of the most important driver of jaguar decline–deforestation–and how that relates to a range-wide conservation plan.

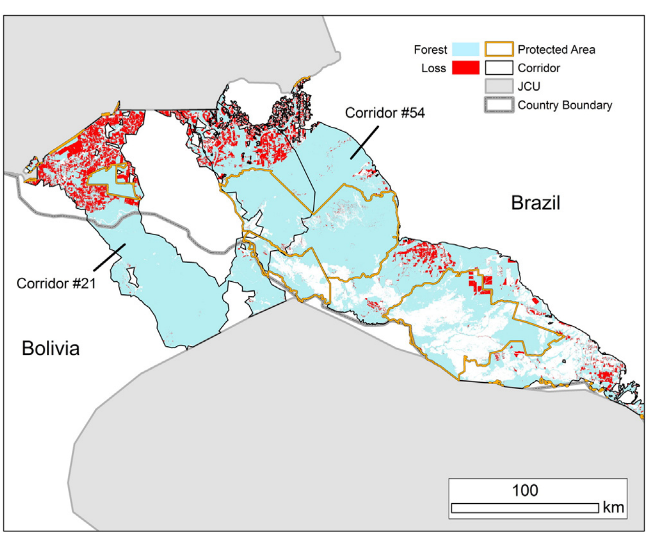

Fig. 4. An example of the effectiveness of protected areas in reducing deforestation in two corridors on the border between Brazil and Bolivia. In Corridor 21 (left) there is heavy deforestation on the Brazilian side of the border, except within the protected section of the corridor (orange boundary). The pattern extends into Corridor 54 (right), where protected sections of the corridor contain relatively little deforestation compared to unprotected sections.

Another potential concern with our analysis is that jaguars may utilize additional corridors for dispersal not accounted for in this analysis. It is important for conservation prioritization plans to account for this, particularly in rapidly changing environments such as the Neotropics. Mapping alternative corridors should be explored in future research, for example via circuit theory (McRae et al., 2008), which identifies multiple potential dispersal pathways. More than one forested route between JCUs may be viable for jaguars, but least-cost corridors (such as the ones used in the design of the jaguar network) will only identify the single "best" corridor, and therefore may underrepresent connectivity. If alternative corridors are present that are not experiencing rapid deforestation, overall network connectivity may be relatively unaffected, but in Central America, where the options for connectivity are already limited, alternative pathways are unlikely.

4.3. Implications for conservation planning

Our results generally align with the Zeller et al. (2013) prioritization of conservation areas, who found that Mexico, Central America, and the very southern and eastern areas of jaguar range were the highest priority for maintaining a range-wide conservation network based on graph theory indices. The addition of land-use change to identify priority areas bolsters the case for the importance of these areas, indicating which corridors and JCUs are most affected by deforestation, and therefore most urgently in need of conservation action. Systematic conservation planning literature suggests that accounting for anthropogenic threats such as habitat loss in the planning process can result in more effective conservation prioritization (Moilanen and Cabeza, 2007; Pressey et al., 2007; Visconti et al., 2010). For example, given that not all sites can be protected or managed at the same time, information on threats can be used to aid in deciding which sites receive attention first (Pressey et al., 2007). Our results clarify which areas are under greatest threat from habitat loss, and therefore where conservation intervention should be considered or alternative corridors advanced. More broadly, our study demonstrates the utility of combining spatially explicit information about protected areas and habitat change when considering strategies for conserving species. Given the rapid pace of landscape and climate change in many parts of the world, this approach may be important for assessing the functionality of a wide variety of large-scale conservation plans and keeping them current in a changing world.

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Supplementary data

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