Jaguar and mammal conservation across agricultural landscapes in Colombia: species ecology and sustainable futures, an interdisciplinary approach

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"There are never victories in conservation. If you want to save a species or a habitat, it's a fight forevermore. You can never turn your back."

George Schaller

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Abstract

As agriculture continues to expand across the tropics there is an urgent need to assess its effects on biodiversity and understand how to reconcile agricultural expansion with conservation and overall sustainable development. Protected areas are not large enough to sustain viable mammal populations, thus it is important to understand how to integrate agricultural regions into conservation strategies. The aims of this thesis were (1) to improve our understanding of jaguars and other medium-large terrestrial mammals across increasing agricultural landscapes; (2) assess the impact of human land uses such as oil palm cultivation on these species; and (3) inform strategies to reconcile biodiversity conservation with other sustainability aspects and regional development in rural areas in Colombia. The methods included field surveys using camera trapping, ecological analysis (e.g. capture-recapture and occupancy models), and scenario and network analysis combined with sustainability assessment.

The findings conclude that there is an effect of agriculture on jaguar populations as densities were lower than in comparable natural areas, however there were resident individuals and breeding, highlighting that modified areas can be important for jaguar long-term survival and connectivity. Wetlands were the only variable explaining jaguar occurrence, while forests impacted puma's occupancy positively and were a predictor of mammal species richness. Conversely, both oil palm and pasture affected several mammal species negatively, and the remaining ones only displayed limited affinity to these land covers, showing that the expansion of oil palm plantations and pastures constitutes a threat for felids and mammals in general. These results suggest that maintaining natural areas such as forests and wetlands across agricultural regions is key to mammal survival, pointing at a land sparing

strategy. Further oil palm expansion, when inevitable, should occur on pastures since they displayed limited to no conservation value for jaguars and other mammals.

Overall, agriculture impacts mammal communities by decreasing their diversity and evenness, while increasing dominance, comparatively to pristine regions. The effect on species richness was not entirely evident, demonstrating that agricultural regions are not necessarily biological deserts. Data also show that jaguars did not affect the occupancy of other felid species and were a positive predictor of mammal species richness, hence conservation strategies focused on this declining keystone species can benefit the wider mammal community, even in modified regions.

This thesis also highlights that rural areas can provide for both people and wildlife if the right conditions are in place. Under the current situation the main agricultural sectors (i.e. cattle ranching and oil palm cultivation) affect wildlife and other aspects of sustainability negatively. Both adopting a stronger regulatory framework with land use planning and applying incentive schemes are improvements, as they would enable to maintain natural habitats that are crucial for jaguar and other species, while improving overall sustainability. Relevant recommendations to reconcile biodiversity conservation with overall sustainable development include the design and adoption of strategic land use planning, making agricultural subsidies conditional to social and environmental standards, consolidating local institutions, designing incentives to foster the implementation of good agricultural practices, favouring small farmers, and creating a demand for certified agricultural commodities. Finally, this research proves that achieving conservation across agricultural regions is inherently complex. Interdisciplinary approaches are needed to study such landscapes and provide solutions that are effective and locally-relevant.

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1. Introduction

1.1 Biodiversity loss and agricultural expansion

Global population is forecast to reach 9.7 billion by 2050 (United Nations, 2015) and Gross Domestic Product (GDP) is projected to increase 1.4% per year until 2050 (Alexandratos & Bruisma, 2012), generating a constant increase of per capita consumption (Tilman et al., 2001; Foley et al., 2005). Both phenomena are causing agricultural expansion and global change (Tilman et al., 2001; Rockstrom et al., 2009; Venter et al. 2016). These drivers act globally and can cause agricultural expansion and cascade effects far from when they are actually occurring (Grau & Aide 2008), which poses further threats to already declining biodiversity. Habitat destruction as a consequence of land-use change is indeed the primary cause of the sixth mass extinction, with rates up to 1000 times higher than pre-humans background levels (Barnosky et al., 2011; Pimm et al., 2014).

Agricultural expansion is a complex issue, being a key driver of both environmental and socio-economic change: it enables hunger reduction and fuels development but comes with a high environmental cost (Foley et al., 2011). Agricultural suitability is undeniably a strong predictor of human footprint and pressure on the natural environment (Venter et al., 2016). As of 2011, croplands and pastures covered 38% of the planet surface, constituting the largest use of land (FAOSTAT 2015). They are also major contributors to climate change (Foley et al., 2005; Rockstrom et al., 2009; Foley et al., 2011), accounting for one-third of global greenhouse gas emission (Harvey & Pilgrim, 2010). Moreover, agriculture is the largest user of freshwater, with 70-80% of water withdrawals being for irrigation, and its intensive use of fertilizers (+700% in the last 40 years) has altered global nutrients cycles and impacted water quality, ecosystems, and even fisheries (Tilman et al., 2001; Canfield et al., 2010).

Last, and perhaps most dramatically, agriculture constitutes a direct cause of biodiversity loss since it is a driver of pollution, and habitat loss, fragmentation, homogenisation, and degradation (Donald 2004; Rockstrom et al., 2009; Maxwell et al. 2016). This has important consequences because biodiversity is crucial for the well-functioning of ecosystems and, consequently, for their provision of ecosystem services (Cardinale et al., 2012). Rocktrom et al. (2009) evidenced that some of these processes, namely biodiversity loss, climate change, and interference with the nitrogen cycle, have already transgressed their critical "planetary boundaries", while global freshwater use, change in land use, and interference with the Phosphorous cycle are quickly approaching the boundaries. This dramatically increases ecosystem vulnerability to further disturbances and their risk of tipping into undesired states.

In addition to direct biodiversity loss, habitat and resources modification affect communities in more complex ways, changing their equilibrium and composition. They can cause species niches to shift and increase their overlap, intensifying competition and extinction risks (Tilman & Lehman, 2001; Ewers & Didham, 2006; Harpole & Tilman, 2007). Intrinsic species traits such as narrow dietary breath, slow life history, restricted environmental conditions, low densities (e.g. top predators), and limited geographic range tend to increase species extinction risk (Purvis et al., 2000). Conversely, those species whose niches have more potential to shift and overlap with the conditions available across modified regions will be favoured (Ewers & Didham, 2006). Large carnivores are generally not amongst such species (Cardillo et al., 2005), and their decline causes further cascade effects. These processes can take time to unfold, leading to extinction debts (Tilmann et al., 1994). By increasing road networks and access, agricultural expansion and habitat loss also act synergistically with other extinction drivers, such as logging, overexploitation of biodiversity, the spread of invasive species, and even disease transmission and competition with domestic animals (Brook et al., 2008).

Overall this alarming evidence suggests that reconciling agricultural production with biodiversity and ecosystems conservation is an ever-increasing challenge (Tscharntke et al., 2012). This is especially true in the tropics, which are a priority for biodiversity and carnivore conservation (Brooks et al., 2006; Di Minin et al., 2016), but are experiencing the fastest land use change and often have dysfunctional governance (Gibbs et al., 2010; Foley et al., 2011; Venter et al., 2016). Tropical forests are the most biodiverse ecosystems on the planet, harbouring more than half of known species (Gaston & Spicer, 2009). They also regulate climate, store carbon, and provide many other ecosystem services (e.g. Bradshaw et al., 2007; Pan et al., 2011). Most of the earth's biodiversity hotspots are in tropical forests since they host species with high level of endemism and threat (Myers et al., 2000; Brooks et al., 2002).

1.2 Oil palm cultivation globally

Amongst agricultural sectors, oil palm *Elaeis guineensis* (Fig. 1.1) cultivation is of particular concern. It covers over 14 million hectares of tropical, high rainfall and lowland areas, which are naturally occupied by biodiversity-rich tropical forests, and it has been steadily increasing since the 1960s (Fitzherbert et al., 2008; Turner et al., 2011). From 2001 to 2014 this crop has increased by 6.5% every year experiencing the largest growth rate together with rapeseed among all crops (FAOSTAT 2015). This is due to its highest yield per ha among all vegetable oils, and to the growing demand for palm oil, especially in Indonesia, India, and China (Fitzherbert et al., 2008). Palm oil and its derivatives are used under several names in a wide spectrum of products from edible oils to ice creams, cosmetics, animal feed, and biofuels (Corley 2009). Most palm oil (84%) is produced in Malaysia and Indonesia where it has caused extensive deforestation, greenhouse gas emissions, and biodiversity loss, but 410–570 million ha of currently forested land across Southeast Asia, Latin America and Central Africa are suitable for oil palm cultivation and could be converted as the demand rises (Fitzhebert et al., 2008; Pacheco, 2012).

Fig. 1.1 Oil palm tree (left) and fruit (right). Photos credit: greenpalm.org

The establishment of oil palm plantations can provide local employment, but it has unfortunately also been responsible for land grabbing, land concentration, and human rights violations (Mignorance, 2006; Ocampo-Valencia, 2009; McCarthy, 2010), as well as dire environmental consequences. This monoculture usually requires pesticides, herbicides, and fertilizers, which cause soil and water pollution (Fitzhebert et al., 2008; Tripathi et al., 2016). Oil palm plantation expansion is also a concern for crucial ecosystem services, such as carbon storage, and water and soil quality; all of which are significantly diminished in these areas (Butler & Laurance, 2009, Danielsen et al., 2009). Overall, the environmental impact of palm oil is highly dependant on the extent of habitat conversion carried out to establish the plantation (Wilcove & Koh, 2010). Furthermore, oil palms start to provide a yield after four years, hence the revenue obtained through deforestation and timber production can help offsetting the costs involved in establishing the plantation, making it a favourable option (Wilcove & Koh, 2010).

Finally, this crop is a severe concern for biodiversity conservation because oil palm areas are considered poor habitats for many taxa, when compared to forests (Maddox et al., 2007; Fitzhebert et al., 2008; Danielsen et al., 2009; Gilroy et al., 2015; Prescott et al., 2016) and even to other crops like cocoa, coffee, and rubber (Peh et al., 2006; Fitzhebert et al., 2008; Edwards et al., 2010). Across all taxa examined by Fitzhebert et al. (2008) a mean of 15% of species found in primary forest was also recorded in oil palm plantations. Mammals are no exceptions, and their richness declines drastically in oil palm areas (Maddox et al., 2007; Yue et al., 2015). Maddox et al., (2007) for example reported that only 10% of the mammal species recorded in the landscape as a whole in Sumatra were regularly detected across oil palm areas, and none of those species had high conservation values. However, we still lack information for many species and this is particularly true in the Neotropics. Only 1% of scientific publications regarding palm oil since 1970 dealt with its effect on biodiversity (Fitzhebert et al., 2008). Therefore it is necessary to gather further information on how this land use affect different species, on how species use agricultural areas with oil palm cultivation, and which strategies are important for their persistence (Fitzherbert et al., 2008; Turner et al., 2008).

1.3 Biodiversity conservation in agricultural landscapes

Protected areas are crucial to conserve the most sensitive species and high quality source habitats, however only 18% of all tropical forests is part of protected areas (Bicknell, 2015), and it is well accepted that biodiversity conservation cannot rely on protected areas alone (Woodroffe & Ginsberg, 1998; Chetkiewicz et al., 2006; Gardner et al., 2009). Furthermore, agricultural regions can be important for species dispersal and host considerable levels of biodiversity (e.g. Daily et al., 2001; Daily et al. 2003; Harvey & Gonzalez Villalobo, 2007; Vandermeer & Perfecto 2007; Cassano et al., 2012). Since such regions are increasing, species survival will depend on sustainable management of these human modified landscapes (Gardner et al., 2009) and their actors (Liu et al., 2007), as well as on the understanding of coupled social–ecological forces acting in these areas, constituting a complex challenge (Harvey et al., 2008; Perfecto & Vandermeer, 2008). Whether it is oil palm or other crops, different strategies have been proposed to achieve biodiversity conservation as well as agricultural production.

First of all reducing per capita consumption (Koh & Lee, 2012), and increasing overall efficiency in food production through improved efficacy in land use and reduction of waste are both essential (Foley et al., 2011). For example, the total area dedicated to meat production, which is made of the croplands used to grow animal feed together with the areas used to raise animals, takes 75% of the world agricultural land (Foley et al., 2011). In addition, it is estimated that a third of the food produced globally is wasted at post-harvest level in developing countries and at retail and consumer levels in developed ones (FAO, 2011).

Other solutions have been proposed with the land sparing vs. land sharing framework (Green et al., 2005). Land sharing implies that biodiversity and agriculture can coexist in the same area through wildlife-friendly practices (Green et al., 2005). On the other hand, land sparing is based on the idea that certain areas can be spared from conversion and retained as natural by maximising yields in others (Green et al., 2005). Farmed areas, regardless of practices adopted, generally host fewer species than pristine habitats, and this is especially true for species with high conservation value (Green et al., 2005, Phalan et al., 2011). However, increasing yields usually entails a greater use of pesticides and fertilizers, which can have spill-over effects on neighbouring areas (Green et al., 2005). Furthermore, even if appropriate policy is guaranteeing set asides, non-cultivated areas could still be converted in the long term, especially in rural areas of tropical countries where law enforcement is often weak (Green et al., 2005; Perfecto & Vandermeer, 2008). Higher profits may also be an incentive for immigration into the area and consequent agricultural expansion (Ewers et al 2009; Angelsen, 2010). Therefore designing and implementing appropriate coupling mechanisms between yield increase and set-asides is imperative (Phalan et al., 2016). It is also important to remember that land sharing vs. land sparing is not always a clear dichotomy and could fail to reflect real world complexity (Tscharntke et al., 2012; Grau et al., 2013). Agro-ecological practices can also lead to improvements in the agricultural production itself, through pest control, pollination services, and better soil quality (Koh, 2008; Foster et al., 2011). This debate is also only starting to take into account important issues such as ecosystem services provision, food security, and social justice (Tscharntke et al., 2012; Law et al., 2016). A land sparing approach may promote land concentration and not guarantee food security even if yields increase due to poverty and access issues (Adams et al., 2004; Perfecto & Vandermeer, 2008; Tscharntke et al., 2012).

Overall, strategies to reconcile production with conservation of natural areas can be designed using both regulatory approaches such as land use planning and legislation, as well as voluntary/incentive-based approaches for implementing best agricultural practices (Lambin et al., 2014). An example of the latter would be certification schemes. Agricultural producers adopting sustainable practices could be incorporated into certification schemes such as the Roundtable of Sustainable Palm Oil and benefit from price premiums, provided there is a demand for green products (Bateman et al., 2010). However, the overall efficacy of certification schemes is still debated (Laurance et al., 2010) and the scale at which certification should be promoted has to be determined carefully, especially if the aim is to conserve wide-ranging species and ecosystem services (Tscharntke et al., 2015).

A major challenge to develop effective conservation strategies in tropical production landscapes is that we still lack data for many species, even across the most-rapidly expanding crops, such as oil palm (Turner et al., 2011; Gardner et al., 2009). Furthermore, while it is imperative to inform policy with scientific knowledge and rigorous data, it is also key for research to address issues and provide solutions that are directly relevant to local stakeholders and policy makers, ultimately enabling science to be proactive (Pretty, 2008). Biodiversity conservation *per se* can be perceived as an externality, hence exploring how landscapes can be designed to achieve multiple sustainability objectives, including biodiversity conservation, should be a priority (Lamb et al., 2005; Tzanopoulos et al. 2011). For this reason, and to achieve a comprehensive understanding of tropical agricultural systems, which are usually complex and characterized by high threats, we need to move towards interdisciplinary research, embracing social sciences methods, participatory approaches, and policy analysis (Knight et al., 2006; Gardner et al., 2009).

1.4 Large carnivore conservation

Amongst all of biodiversity, mammal species in general are a conservation priority in the tropics because their abundance is decreasing due to habitat loss and hunting (Schipper et al., 2008; Visconti et al., 2011). This can lead to important consequences for the ecosystems they inhabit because mammals have an influence on herbivore populations (e.g. predators), carbon storage, nutrient cycling, and seed dispersal, ultimately contributing to sustain healthy forests (Asquith & Mejía-Chang, 2005; Brodie et al., 2009; Jansen et al., 2010; Cavanaugh et al., 2014).

Within mammals, large carnivores are even more of a priority for conservation because they are umbrella, flagship, and keystone species, and are particularly vulnerable to extinction (Cardillo et al., 2005; Estes et al. 2011). Flagship species are charismatic species that help raise awareness and support for conservation efforts;

umbrella species are those requiring such large areas that protecting them will automatically conserve several other species; and lastly, keystone species are species that have impacts on their communities and ecosystems that are much greater than what could be expected from their abundance (Heywood, 1995). By being apex predators, carnivores play a key role in maintaining ecosystem integrity; through limiting populations of herbivorous species, they help maintaining forest structure, which is connected to important ecosystem services such as water regulation (Estes et al. 2011; Ripple et al., 2014). However, large terrestrial carnivores such as tigers (*Panthera tigris*), lions (*Panthera leo*), cheetahs (*Acynox jubatus*), and jaguars (*Panthera onca*), are suffering dramatic declines in both population size and range of distribution (Macdonald et al., 2010). This is because habitat loss and fragmentation, which led to range-wide population declines among many mammalian species (Ceballos & Ehrlich, 2002), constitute an even more severe threat for large carnivores, due to their intrinsic biological traits, such as large area requirements, low densities, and slow population growth rates (Crooks, 2002; Cardillo et al., 2005; Carbone et al., 2007). In addition, their area requirements and the fact that on average 90% of carnivore ranges fall outside protected areas (Di Minin et al., 2016) imply that the latter are not viable for their long-term survival. Instead they have to rely on increasing agricultural and human-dominated landscapes for connectivity and survival, which poses further complications (Woodroffe, 2001; Cardillo et al., 2004; Crooks et al., 2011).

Coexistence between people and carnivores in the same area is challenging since predators can easily generate negative attitudes and be considered problematic animals (Treves & Karanth, 2003; Inskip & Zimmerman, 2009). This is because by preying on livestock they compete for resources with humans causing monetary losses, but also because they are perceived as a threat to human safety (Treves & Karanth, 2003; Sillero-Zubiri et al. 2007; Pooley et al., 2017). Another issue is that local people are often not aware of the ecological role of large predators in the ecosystem and perceive disproportionally high levels of danger (Conforti & De Azevedo, 2003; Marker et al., 2003). As a consequence, carnivores are depleted by retaliatory and preventive killing (Treves & Karanth, 2003). Historical, societal, economic, and cultural dimensions also play a key role in shaping human-carnivore coexistence and/or conflict (Dickman et al., 2014; Sillero et al., 2007; Pooley et al., 2016). All these issues make large carnivores conservation an urgent and complex concern globally, that needs to be tackled interdisciplinary (Pooley et al., 2016).

1.5 Jaguar conservation

The jaguar (Fig. 1.2) is the only living representative of the genus *Panthera* found in the new world; it is the third largest feline overall and the largest cat species existing in America (Nowell & Jackson, 1996). Jaguars, as large carnivores, are umbrella and keystone species (Estes et al., 2011; Thornton et al., 2016) with a strong cultural value dating as far back as pre-Columbian civilizations (Saunders, 1998). The jaguar ranges form Mexico to Argentina with its stronghold in the Amazon basin (Sanderson et al., 2002). However, the latter is considered of low suitability for jaguars compared for example with the Pantanal (Torres et al., 2007).

Jaguars are decreasing in number (Caso et al., 2008), and are estimated to occupy 46% of their historical range (Sanderson et al., 2002). The species is considered Near Threatened due to habitat loss, persecution, and poaching of its prey (Caso et al., 2008). If these threats are not mitigated jaguars overall will be classified as Vulnerable in the near future (Caso et al., 2008), as they already are in Colombia (Rodríguez-Mahecha et al., 2006). Fortunately, the trade in jaguar skins, common in the past, declined drastically after CITES regulations were enforced in the 1970s (Nowell & Jackson, 1996). Hence current persecution of jaguars is due to negative human-jaguar interactions. As for the other large carnivores, jaguars can be considered problematic animals because they prey on livestock and may be perceived as a threat to human safety (Conforti & De Azevedo, 2003; Polisar et al., 2003; Inskip & Zimmermann, 2009; Marchini and Macdonald, 2012). Perceptions of jaguars as a danger generally occur as a consequence of folklore and traditions since attacks on humans are uncommon (Inskip & Zimmermann, 2009).

Fig. 1.2 Jaguar photographed by a camera trap in the study area. Photo credit: V.Boron.

Similarly to other wide-ranging and large-bodies species, the future of the jaguar cannot rely on protected areas alone. Its conservation requires range-wide planning, and a landscape approach in which core protected areas are integrated with human-dominated areas into wider connectivity landscapes (Sanderson et al., 2002). This understanding led to the Jaguar Corridor Initiative, which aims at connecting existing populations of jaguars with suitable habitat and prey base from Mexico to Argentina through corridors (Rabinowitz & Zeller, 2010) (Fig. 1.3). Successful jaguar conservation relies on investigating how jaguars use human-dominated landscapes and on identifying natural and anthropogenic factors that influence their population sizes and habitat use (Foster et al., 2010; Zeller et al., 2011). This will ultimately inform strategies to reconcile socio-economic development with conservation actions for these large cats and the diverse ecosystems they inhabit.

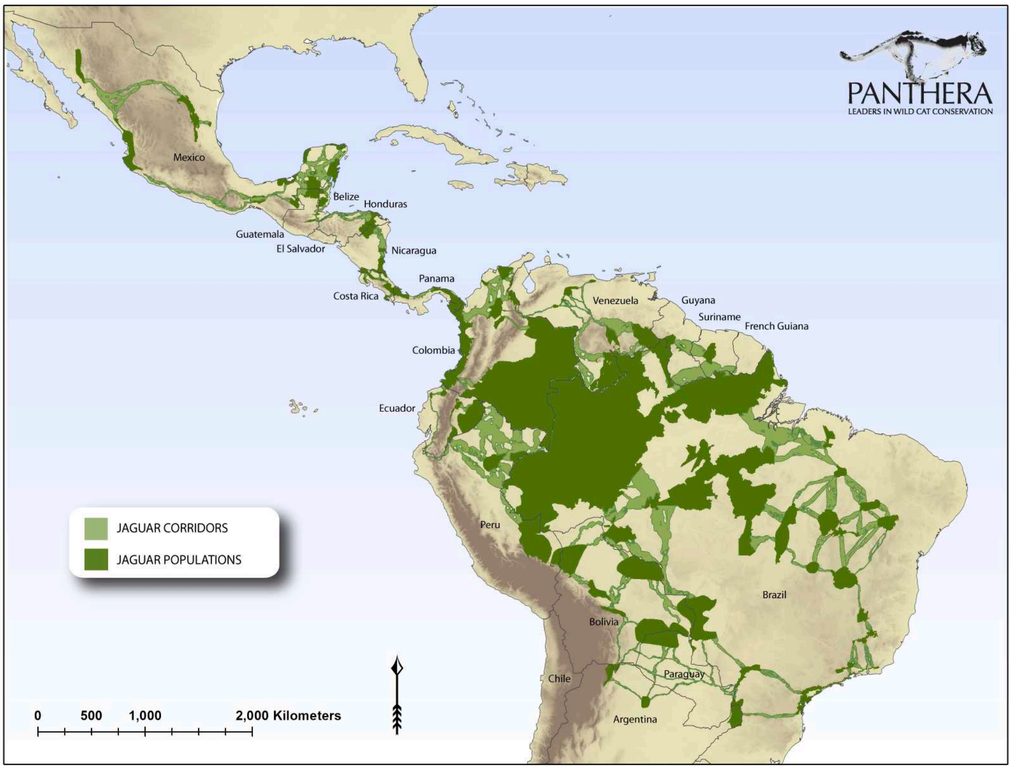

Fig. 1.3 Map of Panthera's Jaguar Corridor Initiative. Source: Panthera (2012).

It is known that jaguars can live in a variety of habitats, from primary and disturbed tropical forests, to scrublands, flooded grasslands, and agricultural landscapes (Nowell & Jackson, 1996; Monroy-Vilchis et al., 2009; Foster et al., 2010). However, they prefer forests over exposed and anthropogenic areas such as pastures and agriculture, and their presence is associated with water (Nowell & Jackson, 1996; Michalski et al., 2006; Monroy-Vilchis et al., 2009; Zeller et al., 2011). Knowledge on jaguar habitat use and population densities across human modified agricultural areas is limited (Foster et al., 2010; De Angelo et al., 2011; De Angelo et al., 2013). For example, only 15% (N = 12) of the jaguar population density estimates available (Tobler & Powell, 2013) come from areas that are entirely unprotected, yet densities are key parameters to monitor population across time and space. Consequently, it is critical to obtain jaguar density estimates and study their habitat use across agricultural areas, including increasing oil palm landscapes, since the latter pose unknown challenges and/or opportunities to jaguar survival.

1.6 The South American context

South America hosts priority conservation areas under all global biodiversity conservation priority templates (Brooks et al. 2006). These include crisis ecoregions, biodiversity hotspots, endemic bird areas, centres of plant diversity, megadiversity countries, global 200 ecoregions, high-biodiversity wilderness areas, frontier forests, and last of the wild (Brooks et al. 2006). The main drivers of habitat conversion in the region have historically been traditional shifting agriculture, illegal crops, and, most importantly, cattle ranching, often supported by government policies and subsidies (Etter et al., 2006; Grau & Aide, 2008).

Extensive cattle ranches are a common land use in South America and constitute a highly inefficient use of land. Such inefficiency in land use has been possible because South America is a large continent with a relatively small population (Grau & Aide, 2008). Both extensive and more intensive forms of cattle ranching can be concerning for biodiversity conservation, ecosystem services, food security, and human rights (Etter et al., 2006; Mc Alpine et al., 2009; Vergara, 2010). Feedlot production requires extensive land to be cultivated for the production of forage crops, which causes habitat conversion (Mc Alpine et al., 2009). On the other hand, extensive grazing also has been accountable of natural ecosystem loss (Grau & Aide, 2008; McAlpine et al., 2009). In addition, both ways of cattle production usually require large areas, potentially fostering land concentration and social conflicts (Vergara, 2010).

Although cattle ranching and other traditional land uses continue to exist and expand in some places, export-oriented commercial agriculture has been increasing and has become the main driver of South American landscape conversion (Pacheco, 2012). This expansion is primarily related to the growing amount of soybean cultivation in Brazil and Argentina, with expansion into Paraguay and Bolivia, as well as the expansion of oil palm in Colombia, and to lesser extent, in Ecuador and Peru (Butler & Laurance, 2009; Pacheco, 2012). The expansion of commercial agriculture and especially of soybean and oil palm cultivation has been shaped by both policy and market conditions: a growing national and global demand for food, and biofuels; growing international trade; an expansion of investments in production technologies, road networks, and processing facilities; land availability; policies affecting demand (e.g. biofuels blending targets) and policies stimulating supply (e.g. cheap credits, tax breaks, price controls, trade incentives) (Grau & Aide, 2008; Pacheco, 2012; Castiblanco et al., 2013).

The outcomes of these transitions are still controversial. On one side this shift has contributed to economic growth and income generation, on the other it has led to loss of natural ecosystems, land concentration, and sharpened social inequalities by favouring industry owners (Mignorance et al., 2006; Pacheco, 2012; Castiblanco et al., 2015). In theory, industrial agriculture has potential to improve land use efficiency: by increasing yields it enables to produce more in less space, thus possibly sparing land for conservation (Green et al., 2005). However, the expansion of commercial crops has happened on both already-cultivated lands and natural ecosystems (Pacheco, 2012). Consequently it has produced negative environmental impacts both locally and globally, mainly through habitat loss and fragmentation, pollution, biodiversity loss, and carbon emissions contributing to climate change (Grau & Aide, 2008; Butler & Laurance 2009; Pacheco, 2012).

1.7 Colombia's biodiversity and its agricultural sector

Colombia is an extremely diverse country: geographically it has six distinct natural regions: the Andes mountain range, the Pacific coastal region, the Caribbean coastal region; the Llanos plains; and the Amazon rainforest region (Federal Research Division, 2010). Colombia is indeed regarded as a "megadiverse" country, covering 0.7% of the planet and hosting 10% of its biodiversity (Rodríguez-Mahecha et al., 2006). It hosts 447 mammal species, and this figure is surpassed only by Indonesia, Peru, Mexico, and Brazil (Rodríguez-Mahecha et al., 2006). Colombia is also particularly important for jaguar connectivity due to its position between Central and South America (Sanderson et al., 2002; Rabinowitz & Zeller, 2010). However, it has been relatively understudied as the armed conflict made many areas unsafe to access. For example, the only jaguar population density estimates available come from the Amazon (Payán, 2009).

Protected areas cover over 10% of the country's areas (Forero-Medina & Joppa, 2010), while agricultural land has been increasing moderately from the 1960s, reaching 40.4% of the country area in 2013 (World Bank, 2016). Agriculture has historically been the backbone of Colombia's economy, in particular the coffee sector, which has traditionally driven the country's development (Federal Research Division, 2010). Currently the main agricultural sectors are cattle ranching (30% of the total agricultural output), fruits (15.0%), coffee (9.5%), rice (4.9%), flowers (4.2%), and vegetables (4.1%) (Federal Research Division, 2010). Oil palm cultivation is an emerging sector and it is expanding rapidly (Castiblaco et al., 2013). Agriculture still provides almost a fifth of the country employment (World Bank, 2016), and constituted 6.4% of National GDP in 2015 (CIA, 2015). However, its benefits are far from equitably distributed and this is due to land distribution issues. Over 60% of land is owned by 0.4% of landowners (Albertus & Kaplan, 2012) and it is estimated that 40.3% of rural people live below the poverty level (World Bank, 2016).

The increase in overall agricultural area in the country does not imply a balanced increase of all types of agricultural activities and it is mainly due to permanent crops like oil palm (Federal Research Division, 2010). Meanwhile, areas of natural savannahs and forests have been converted to introduced pastures and crops (Etter et al., 2006a). Although there are not actual estimates of forest clearing for Colombia due to a lack of monitoring and availability of cloud-free satellite images, rates are estimated at 310,349 ha/year (0.48%) (IDEAM, 2011). Deforestation occurs predominantly in the lowlands of the Amazon and Pacific regions as well as in the foothills of the Andes in areas that are out of control of the government and have low or no institutional presence (Etter et al., 2006a; Etter et al., 2006b). It is mainly for the establishment of cattle ranches (McAlpine et al., 2009). The patterns of land conversion is usually as follow: clearing, subsistence agriculture or illegal crops, planting of introduced grass to keep the land cleared and then larger areas are cleared for establishing pastures directly. Hence most transfers of public lands to private properties occur precisely as illegal appropriations followed and secured as pastures. Where infrastructure levels and access to markets increase, cattle ranching may become more intensive or be partially replaced by intensive agriculture (e.g. oil palm, citrus, rice, soybean) (Etter et al., 2006a).

1.7.1 Cattle ranching

Extensive cattle ranching is the main agricultural sector in Colombia, accounting for 90% of agricultural land (McAlpine et al., 2009; REDD Desk, 2016) (Fig. 1.4) and 4% of the national GDP (Fedegan & ProExport, 2010; Vergara, 2010). It has played an important role in Colombian society and in shaping the country landscapes. Historically, since the 1500s, it was used to gradually gain control over indigenous land during the colonisation and the search of gold and emeralds, expanding in the Llanos region as well as in the inter-Andean valleys and in the Caribbean (McAlpine et al., 2009). Then, after the 1850s, a high increase in cattle production occurred due to the introduction of wired fencing and exotic grasses, which improve forage quality and impede tree regeneration (McAlpine et al., 2009).

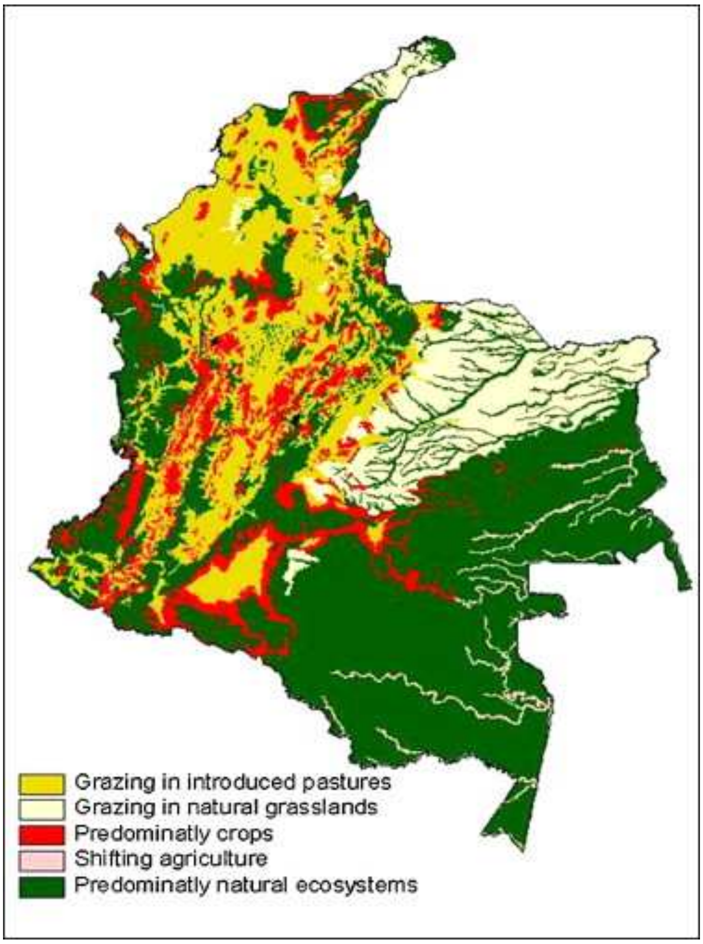

Fig. 1.4 Map of land use in Colombia (McAlpine et al., 2009). Introduced pastures largely coincide with deforested areas (data derived from Etter et al., 2006b).

The number of cattle was close to 25 million in 2014 (FAOSTAT, 2015) with over 30 million heads forecasted for 2019 (MADR, 2013), placing Colombia amongst the top producing countries and the fourth largest producer in South America after Brazil, Argentina, and Mexico (Fedegan & ProExport, 2010). As well as being the main cause of deforestation and ecosystem conversion (Etter et al., 2006a; McAlpine et al., 2009), cattle ranching has also been responsible of generating land inequality and social issues (Yepes, 2001). Finally, it requires low labour force, thus not improving rural employment and development (Yepes, 2001).

1.7.2 Oil palm cultivation

Similarly to the rest of the continent, Colombia has been experiencing a shift towards more commercial agriculture (Pacheco, 2012) and oil palm cultivation is a rapidly growing sector. The country is the world's 4th largest palm oil producer and the leading producer in Latin America (Castiblanco et al., 2013). Production has been increasing since the 1960s (Fig. 1.5).

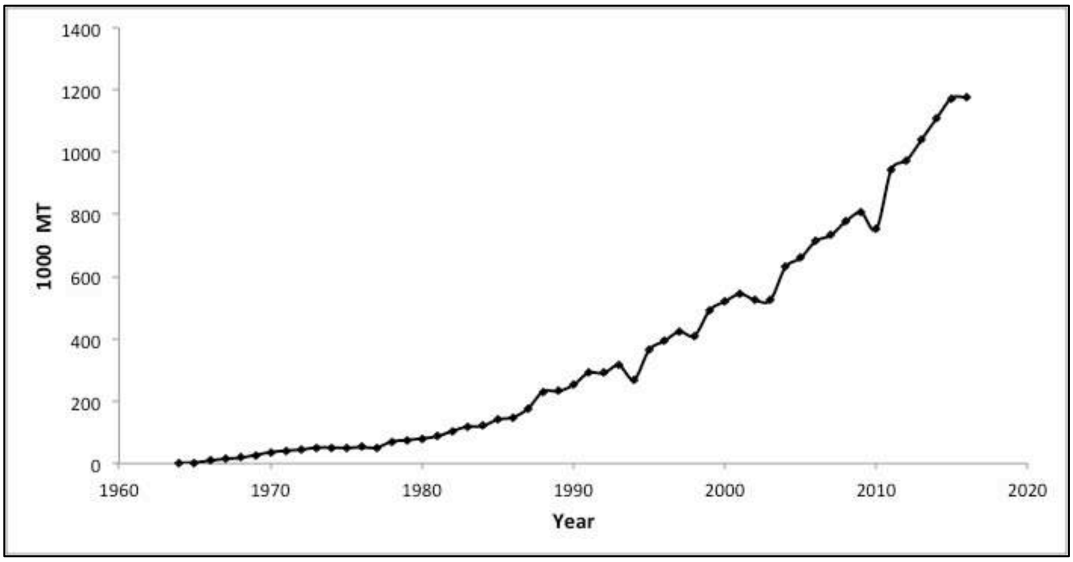

Fig. 1.5 Production of palm oil in Colombia (IndexMundi, 2016). Data: US Department of Agriculture.

Currently a total of 483,733 ha are cultivated (Fedepalma, 2016), making up 10% of crop-cultivated area in the country. A third of the production happens on large plantations (>1000 ha), a third on medium holdings (200 to 1000 ha), and the remaining third on small holdings (<200 ha) (Pacheco, 2012). Palm oil accounts for 90% of the fats produced in Colombia and makes up <1% of total GDP (MADR, 2013). 60% of the overall palm oil produced is consumed in the country, while the remaining 40% is exported (Mignorance, 2006; Pacheco, 2012). At present less than 10% of the total palm oil producing area is certified, which is below the world average of 17% (RSPO, 2016). However, RSPO members are increasing, showing positive momentum.

The palm oil and biodiesel industries have been identified as priority sectors within the national agenda to reach energy independence, increase rural development and employment, and mitigate climate change thanks to a replacement of fossil fuels with biodiesels (Mejía, 2011). The government aims at achieving three million ha of oil palm cultivated land by 2020 (Castiblanco et al., 2013), while Fedepalma, the Colombian plantation owners' association, stated a 2020 vision of a six-fold increase in production of palm oil and a 440% increase of cultivated land (Fedepalma, 2012a). Hence the government has adopted a policy framework aimed at favouring the expansion of oil palm cultivated lands, and at the marketing, promotion, and consumption of biodiesels (Mejía, 2011; Castiblanco et al., 2013). The palm oil sector has access to several incentives and subsidized credit instruments to increase competitiveness (Fedepalma, 2012b). There is also a mandatory 10% biodiesel blend, and by 2020 the target increases to 20% (Castiblanco et al., 2013). Lastly, biodiesel is exempt from the sale tax (Law 939 of 2004), and since 2004 new farms producing selected perennial crops (including palm oil) are exempt from the income tax for 14 years after they start harvesting the crop (Law 939 of 2004 and 1970 of 2005).

From an ecological perspective all these instruments are likely to exacerbate natural ecosystems' loss and fragmentation (Castiblanco et al., 2013). One way to lessen the ecological impact of oil palm plantations, while safeguarding food security and carbon storage would be to establish them on extensive pasture lands (Garcia-Ulloa et al., 2013). However, data on biodiversity responses to this crop is limited and only starting to emerge (Pardo et al., 2015). Gilroy et al. (2015) and Prescott et al. (2016) report that establishing new oil palm plantations on pastures would benefit ants, dung beetles, birds, and herpetofauna. Data on other taxa, including jaguars and mammals in general, is extremely scarce (Boron & Payán, 2013; Pardo & Payan, 2015) and needs to be generated. Another obstacle to the implementation of a sustainable expansion of this crop is the absence of proper spatial planning and/or integration with territorial plans (MADR et al., 2008).

As in other tropical regions, the implications of oil palm expansion in Colombia are not limited to the ecological world. The sector has unfortunately been associated with military groups and human rights violations such as illegal and violent appropriation of land, armed coercion, murders, and displacement (Mignorance, 2006; Segura 2008; Ocampo-Valencia, 2009). Plantations have also become a way for armed groups to control land and eventually entire areas (Segura, 2008). Finally, the expansion of oil palm cultivation is also likely to increase land prices, displacing subsistence crops to more marginal land and thus having an impact on local food prices and food security (Infante & Tobón, 2010). In some cases, oil palm plantations were able to generate employment and build a peaceful development; it happened mainly through the establishment of productive alliances where the company owning the oil palm plantation outsourced the production and gave the land in concession to local farmers (Ocampo-Valencia, 2009; Castiblanco et al., 2015).

1.8 The study region – Middle Magdalena

Data collection took place mostly in the Middle Magdalena region of Colombia, which covers the central area of the inter-Andean Magdalena River valley and encompasses four different Departments: Antioquia, Bolívar, Cesar, and Santander. The region is part of the tropical forest biome and has abundant wetlands (IDEAM et al., 2007). The climate is tropical with average annual temperature of 27°C, and bimodal rainfall, with about 1000-2600 mm annually (IDEAM et al., 2007).

The Middle Magdalena was an appropriate area for this study because it is a modified agricultural region with abundant cattle ranching and increasing oil palm plantations (Etter et al., 2006a; Castiblanco et al., 2013), but still hosts top predators like jaguars and pumas and holds some potential for conservation. A pilot camera trap study recorded a total of 71 species and 23 mammal species (8 orders), of different levels of Global and Regional threat categories (Boron, 2012). Furthermore, the region is also an important genetic corridor for jaguars (Fig. 1.6) and overall, hosting species belonging to the Andean, Caribbean, and Orinoco ecosystems, as well as endangered and endemic species like the brown spider monkey (*Ateles hybridus* ssp. *brunneus*) and the white-footed tamarin (*Sanguinos leucopus*) (Rodriguez-Mahecha et al., 2006; Payán et al., 2013). The majority of the region's natural ecosystems have been converted to cattle ranches and oil palm plantations, whereas the remaining natural areas are at risk of further conversion (Castiblanco et al., 2013).

Its socio-economic context has been traditionally challenging. The area experienced waves of migration, violence, and uneven development as well as a lack of institutions and governance, with the consequent arising of unofficial authorities and armed groups (Molano, 2009; Gómez-Garcia Reyes, 2013). Most land is under private property, there are no national protected areas, and the main economic activities are agriculture and mining (Molano, 2009).

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Fig. 1.6 Location of the study region in relation to the Jaguar Corridor Initiative in Colombia. Map by C.Soto (Panthera Colombia). Darker areas are jaguar populations, whereas lighter areas represent probable corridors linking them.

1.9 Thesis outline and objectives

The pervasive effects of agriculture on biodiversity and ecosystems in Colombia and elsewhere, and the scarcity of information on Neotropical mammals across agricultural and oil palm landscapes, means that robust evidence is needed to guide policy and decision making. At the same time, achieving conservation across tropical agricultural systems is extremely challenging because the latter are complex and involve different stakeholders and interests groups, as well as different scales of action. Hence this thesis aims at (1) improving current understanding of jaguars and other terrestrial mammals across increasing agricultural landscapes; (2) assessing the impact of human land uses such as increasing oil palm and pastures on these species; and (3) informing management and policy recommendations to reconcile biodiversity conservation with other aspects of sustainability and regional development.

The study is interdisciplinary, combining camera trapping and other ecological methods and analyses (Chapters 2-4), with scenario and network analysis, and sustainability assessment (Chapter 5). Results from chapters 2-4 as well as constituting valuable and new ecological knowledge, advise on how to lessen the impact of oil palm and pastures on jaguar and other terrestrial mammal species. Finally, combined with insights from Chapter 5, they guide strategies to reconcile jaguar and mammal conservation with agricultural expansion and regional development.

Chapter 2 uses camera trap data and capture-recapture models to provide the first jaguar density estimates of Colombia outside of the Amazon and in agricultural areas, highlighting the contribution that the latter have for long-term jaguar conservation. This is the only chapter that includes data from another region, the Llanos, which is important for jaguar conservation and host abundant cattle ranching and increasing oil palm plantations.

Chapter 3 looks at how to conserve predators in tropical agricultural landscapes. It combines camera trap data and land cover information from two sites into occupancy modelling to investigate the habitat use of the four felid species recorded in the area: jaguars, pumas, ocelots (*Leopardus pardalis*), and jaguarundis (*Herpailurus yaguaroundi*). It also explores whether there are patterns of spatial overlap or segregation between the cat species.

Chapter 4 is centred on the wider mammal community. It uses camera trapping data and land cover information from two sites to investigate the impacts of agricultural and oil palm expansion on mammal species and communities. The chapter assesses community composition, evenness, and richness. It also investigates determinants of species richness and whether jaguars are a good umbrella species for the wider mammal community. Finally, it uses Canonical Correspondence Analysis to explore intra-community variation and influencing factors in mammal species distribution.

Chapter 5 identifies the current drivers of landscape change in the region and uses a combination of network analysis, scenario analysis, and sustainability assessments to explore how to achieve biodiversity conservation while meeting other sustainability objectives in rural areas in Colombia. It investigates three scenarios: Business and Usual, a regulatory one, and an incentive-based one. It also provides management and policy recommendations at different scales.

Chapter 6 contains the overall thesis discussion, its contributions to conservation science and management, as well as future research directions.

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2. Jaguar densities across human-dominated landscapes in Colombia: the contribution of unprotected areas to long-term conservation

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2.1 Abstract

Large carnivores such as jaguars (*Panthera onca*) are species of conservation concern because they are suffering population declines and are keystone species in their ecosystems. Their large area requirements imply that unprotected and ever-increasing agricultural regions can be important habitats as they allow connectivity and dispersal among core protected areas. Yet information on jaguar densities across unprotected landscapes it is still scarce and crucially needed to assist management and range-wide conservation strategies. Our study provides the first jaguar density estimates of Colombia in agricultural regions which included cattle ranching, the main land use in the country, and oil palm cultivation, an increasing land use across the Neotropics. We used camera trapping across two agricultural landscapes located in the Magdalena River valley and in the Colombian llanos (47-53 stations respectively; >2000 trap nights at both sites) and classic and spatially explicit capture-recapture models with the sex of individuals as a covariate. Density estimates were 2.52±0.46 - 3.15±1.08 adults/100 km^2 in the Magdalena valley, whereas 1.12±0.13 - 2.19±0.99 adults/100 km^2 in the Colombian llanos, depending on analysis used. We suggest that jaguars are able to live across unprotected human-use areas and co-exist with agricultural landscapes including oil-palm plantations if natural areas and riparian habitats persist in the landscape and hunting of both jaguar and prey is limited. In the face of an expanding agriculture across the tropics we recommend land-use planning, adequate incentives, regulations, and good agricultural practices for range-wide jaguar connectivity and survival.

2.2 Introduction

Due to their charisma and functional role in maintaining ecosystem integrity and services (Estes et al., 2011; Ripple et al., 2014) large carnivores such as the big cats have been a focus of conservation research and action (Brodie, 2009). However, despite conservation efforts, their populations are still declining and their range contracting with important ecological consequences (Macdonald et al., 2010; Estes et al., 2011). Habitat loss driven by agricultural expansion is the main cause of biodiversity decline globally (Fahrig, 2003; Foley et al., 2005) and constitutes a severe threat for large carnivores because they occur at low densities, have slow population growth rates, require large areas and sufficient prey (Cardillo et al., 2005; Carbone et al., 2011; Crooks et al., 2011), all of which make them particularly vulnerable to extinction. Their prey requirements also make them susceptible to conflict with humans and retaliatory killing, further increasing their vulnerability (Treves & Karanth, 2003; Inskip & Zimmermann, 2009).

Abundance, density, and distribution estimates are key information for conservation and management strategies, and when they refer to modified areas they can provide valuable information on species tolerance limits (Athreya et al., 2013). Because of large carnivores' cryptic nature and large ranges it is inherently difficult to assess their population status, hindering conservation efforts, particularly across unprotected areas. Spatial requirements of large carnivores imply that most protected areas alone are not viable for their survival (Woodroffe & Ginsberg, 1998; Parks & Harcourt, 2002) and that they have to be integrated with increasing human modified areas into wider connectivity landscapes (Sanderson et al., 2002a, 2002b; Wikramanayake et al., 2004; Crooks & Sanjayan, 2006). There is evidence on the role of unprotected areas for carnivore conservation: species like cheetahs, wolves (*Canis lupus*), pumas (*Puma concolor*), leopards (*Panthera pardus*), and jaguars are able to live in human use landscapes (Mech & Boitani, 2003; Marker et al., 2008; Athreya et al., 2013; Payan et al., 2013).

The jaguar is the only living representative of the genus *Panthera* found in the New World and it is the largest cat existing in the Americas (Nowell & Jackson, 1996). It ranges from Mexico to Argentina and it has been lost from over 50% of its historical range (Sanderson et al., 2002a). Jaguars are keystone species (Estes et al., 2011) and they are considered Near Threatened by the IUCN. They are a species of conservation concern due to habitat loss, poaching of its prey, and retaliatory killing following predation of livestock (Caso et al., 2008).

As for the other large carnivores, protected areas are too few in number for long-term jaguar conservation, which requires a landscape approach with both protected and unprotected lands (Sanderson et al., 2002a; Rabinowitz & Zeller, 2010). However the latter have been neglected, and only 15% (N=12) of the jaguar population density estimates available (Tobler & Powell, 2013) refer to areas that are completely unprotected. Therefore it is crucial to obtain more estimates across such areas as agricultural and oil palm (*Elaeis guineensis*) landscapes. The latter are particularly of concern as a driver of impoverished habitat with unknown survival value for jaguars (Fitzherbert et al., 2008; Boron, 2012; Pacheco, 2012).

Colombia is extremely important for range-wide jaguar conservation and connectivity due to its position between Central and South America (Rabinowitz & Zeller, 2010). In Colombia, jaguars inhabit the Amazon and Llanos regions, the Pacific coast, inter-Andean valleys, and the northern area along the Caribbean coast, yet only two jaguar densities estimate are available and they were both in the Amazon (Payan, 2009). Here we use both SECR and CR models to produce the first jaguar density estimates of Colombia outside the Amazon: across an oil palm landscape in the Magdalena watershed and in an extensive cattle ranch in the llanos ecosystem. These data illustrate the complementary conservation role of unprotected areas to wide ranging large carnivores such as the jaguar.

2.3 Methods

2.3.1 Study areas

We conducted the study at two sites in Colombia (Fig. 2.1). Site-I is located in the central part of the Magdalena River inter-Andean valley (7.3752N -73.8842E to 7.5404N -73.7118E) in the Department of Santander. The region is characterized by humid tropical forests and wetlands (IDEAM et al., 2007), however most has been converted into cattle ranches and oil-palm plantations while the remaining natural habitats are threatened by further agricultural and oil palm conversion (Etter & van Wyngaarden, 2000; Castiblanco et al., 2013). The climate is tropical with mean annual temperature of 27℃ and bimodal rainfall of 2100-2600 mm annually (IDEAM et al., 2007). Land tenure consists mainly of private properties; there are no protected areas; and land cover types comprise secondary forest, shrub, wetlands, pastures, crops, oil-palm plantations, and urban areas.

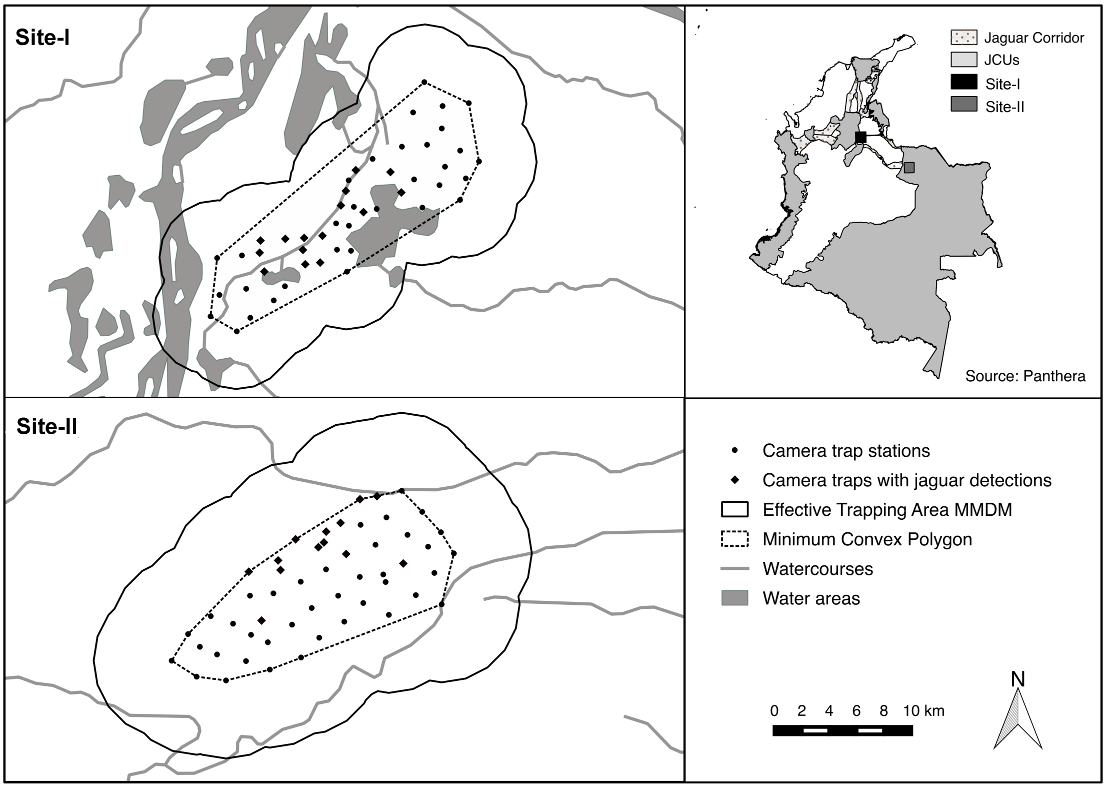

Fig. 2.1 Study areas. Location of the sites in regard to the Jaguar Corridor and Jaguar Conservation Units (JCUs) in Colombia (Sanderson et al., 2002a; Rabinowitz & Zeller, 2010; Panthera, 2012), and map of the study sites with camera locations. Site-1 is part of the Magdalena River valley, while Site-2 is located in the Orinoco River basin. Both sites were surveyed in 2014.

Site-II is located in the Orinoco River basin in the llanos region and in the Department of Casanare (5.9552N -71.4834E to 6.0813N -71.2976E). This area is naturally characterised by seasonally flooded tropical savannahs bisected by riparian forests, and the dominant land use is extensive cattle ranching with introduced grasses (IDEAM et al., 2007). Mean annual temperature is 27°C and average rainfall is between 1000 and 3000 mm with a very marked wet season between April and November (IDEAM et al., 2007). The area is part of the Llanos Amazon Jaguar Conservation Unit (JCU) (Sanderson et al., 2002a) (Fig. 2.1) and hosts most of its biodiversity richness along water bodies (Payán et al., 2011). Land tenure consists mainly of private properties and land cover types include natural and secondary forest, natural and introduced grasslands, and wetlands.

Jaguar prey species have been historically hunted at both sites and hunting still occurs for subsistence and commercial reasons (Rodríguez-Mahecha et al., 2006). Killing of jaguars is rare at Site-I (Boron, 2012) while more frequent at Site-II, although no exact data are available (Garrote, 2012), there has been an estimate based on historical records of killings of 1 individual every 250 km^2 per year (Payan, 2006). Widespread extensive cattle ranching at Site-II favours the occurrence of jaguar predation on livestock and consequent persecution from ranchers (Polisar et al., 2003; Payan et al., 2013).

2.3.2 Camera trapping

Camera trapping surveys were done between April and August 2014 at Site-I and in April-May 2014 at Site-II. We employed a camera design which is recommended for jaguar studies (Silver et al., 2004; Noss et al., 2013; Tobler & Powell, 2013) and meets capture recapture models' assumptions, i.e. the population is closed and all individuals have at least some probability of being captured (Otis et al., 1978; White, 1982). We conducted surveys < 120 days and we placed cameras at a distance of 1.6 ± 0.2 km to meet the assumptions of the models.

We employed paired stations and a block design of 47 stations at Site-I, covering an area of 154.8 km^2 (minimum convex polygon), while a continuous design and 53 stations across 151.3 km^2 at Site-II (Fig. 2.1). We used Cuddeback Attack and Ambush, and Panthera series 3 and 4 cameras and set them at a height of 35 cm.

Paired stations ensure photographs of both flanks of each passing individual for complete identification purposes.

2.3.3 Data processing and capture-recapture analysis

Jaguar individuals were identified from their spot and rosette patterns and sexed by visual inspection of external genitalia. We then produced adult density estimates using both SECR and conventional CR. SECR models were applied to jaguars for the first time by Sollmann et al. (2011) and have the advantage of not requiring arbitrary buffers to estimate the Effective Trapping Areas (ETAs) and hence density values (Efford, 2004; Royle & Young, 2008). They use the individuals' spatial locations to determine their activity centres or home range centres and then estimate the density of home range centres across a polygon which contains the trap grid (Efford, 2004; Royle & Young, 2008). SECR models also assume that home ranges are circular and stable during the survey, individuals activity centres are randomly distributed (as a Poisson process), and the encounter rate of an individual with a trap decreases with increasing distance from the activity centre following a predefined function (Efford, 2004; Royle & Young, 2008).

The most commonly used function and the one we also used is the half-normal detection function, which describes the probability of capture (P) of an individual i at a trap j as a function of distance (d) from the activity centre of the individual to the trap as follow: $Pij = g0 \exp(- dij^2/(2\sigma^2))$, where g0 is the probability of capture when the trap is located exactly at the centre of the home range, and sigma (σ) is a spatial parameter related to home range size (Efford, 2004). One model that is most relevant to camera trapping studies is the Bernoulli or binomial encounter model, under which an individual can be recorded at different camera stations during one sampling occasion but only once at each station (Royle et al., 2009; Noss et al., 2013). The models can be fitted in a maximum-likelihood framework (Borchers & Efford, 2008; Efford et al., 2009) or in a Bayesian framework using data augmentation (Royle & Young, 2008; Royle & Gardner, 2011). We chose maximum likelihood because it gives comparable results to the Bayesian framework (Noss et al., 2012; Tobler & Powell, 2013) with quicker computation times and used the package secr in R (Efford, 2015).

We included the exact number of days that each station was active and allowed both parameters g0 and σ to vary with sex of the individuals (Sollmann et al., 2011; Tobler & Powell, 2013; Tobler et al., 2013). We compared four models using the Akaike Information Criterion (AIC) (Burnham & Anderson, 2002): "SECR.0" (null model), "SECR.sex.g0" (g0 varies between males and females), "SECR.sex.σ" (σ varies between males and females), and "SECR.sex" (both g0 and σ vary between males and females). Including individuals sex as a covariate is important because jaguar populations have unequal ranging patterns between sexes, which would affect capture probabilities (White, 1982; Karanth & Nichols, 1998; Silver et al., 2004).

For non-spatial capture recapture analysis we converted the capture histories of each individual into a 1 and 0 matrix and we grouped 6 survey days into one sampling occasion (Sollmann et al., 2011; Noss et al., 2013). We analysed the data with the full likelihood closed captures models in program MARK (White & Burnham, 1999) and compared three models that differ in assumed sources of variation in capture probability (p) using AIC: "Mo" (null model), "Mh" (p varies between individuals), and "Msex" (p varies between males and females). Following, we estimated the effective trapping areas by adding a buffer to the cameras polygon equal to the Mean Maximum Distance Moved (MMDM). The MMDM is calculated by taking the average of the maximum distances between capture locations for all individuals (Karanth & Nichols, 1998). Finally we calculated density as: D=N/ETA. We further included densities estimated with program Capture, the Jacknife estimator and both MMDM and 1/2MMDM in the supporting information (Table 2.4).

2.3.4 Prey capture rates

We calculated capture rates for jaguar prey species at the two sites using the total number of independent capture events of each species divided by the number of trap-nights and expressed as records per 100 trap nights (Carbone et al., 2001; O'Brien et al., 2003). Independent capture events were defined as consecutive photographs of individuals of the same species taken more than 12 hrs apart for gregarious species (i.e. capybaras, *Hydrochoerus* sp.; collared peccaries, *Pecari tajacu*; and white-tailed deer, *Odocoileus virginianus),* and more than 30 min apart for all other species (O'Brien et al., 2003). A species was considered prey if reported in jaguar diet studies (Polisar et al., 2003; Novack et al., 2005; Weckel et al., 2006; Foster et al., 2010). We are aware that capture rates may not reflect real abundance (Carbone et al., 2001; Sollmann et al., 2013) hence we do not report them to make inferences about population sizes but for descriptive purposes.

2.4 Results

We recorded seven females (49 events) and three males (39 events) at Site-I and two females (8 events), three males (57 events), and one adult individual of unknown sex at Site-II (Table 2.1). Four of ten individuals recorded at Site-I have been recorded in the area since 2012. The average number of captures per individual was lower for females than males at both sites: 7 (1-13) vs. 13 (3-26) at Site-I and 4 (3-5) vs. 19 (12-28) at Site-II. Captures of multiple individuals at the same camera stations were common and up to six individuals were recorded at one station in Site-I.

Table 2.1 Parameters and survey features for Site-I and Site-II. N= Number of individuals; MMDM= Mean Maximum Distance Moved.

	Site-I	**Site-II**
Location	Magdalena River valley	Orinoco River basin
Survey period	April-August 2014	April-May 2014
Traps active	47	52
Trap nights	2251	2457
Minimum Convex Camera polygon (km2)	154.8	151.3
N recorded	10	6
MMDM (km)	4.2	5.7
Effective sampled area (km^2)	396.2	537.2

The best CR model for Site-I was Mh (AIC=130.2), but M0 (AIC=130.6) was also strongly supported (ΔAIC<2); whereas for Site-II the best CR model was Msex (AIC=75.4) followed by Mh (AIC=76.6), which also had strong support (ΔAIC<2) (Table 2). Both supported CR models estimated N=10.00 ± 0.00 (SE) and density =

2.52 ± 0.46 (95% CI: 1.63-3.42) (N/100 km^2) at Site-I while N=6.00 ± 0.00 (6.00-6.00) and density = 1.12 ± 0.13 (95% CI: 0.86-1.38) (N/100 km^2) at Site-II.

The best SECR model (AIC=924.2) for Site-I allowed g0 to vary with sex but had a fixed σ (SECR.sex.g0), while for Site-II the best model (AIC=612.5) allowed both parameters to vary with sex (SECR.sex). However, SECR.sex and SECR.sex.g0 also had strong support (ΔAIC<2) for Site-I and Site-II respectively (Table 2.2).

Table 2.2 Model selection parameters for both Capture-Recapture (CR) and Spatially Explicit Capture Recapture (SECR) models at Site-I and Site-II.
AIC=Akaike Information Criterion; ΔAIC = difference in AIC values between each model and the model with the lowest AIC; W= AIC model weights; K= number of model parameters; Dev.=Model Deviances. Mh: capture probability varies between individuals; M0: null model, Msex: capture probability varies between males and females. g0= probability of capture at the home range centre, σ= spatial parameter related to home range size; SECR.sex.g0: g0 varies between males and females; SECR.sex: both g0 andσ vary between males and females; SECR.sex.σ:σ varies between males and females; SECR.0: null model.

Site-I Magdalena River valley						**Site-II Orinoco River basin**					
Model	**AIC**	**ΔAIC**	**W**	**K**	**Dev.**	**Model**	**AIC**	**ΔAIC**	**W**	**K**	**Dev.**
CR Mh	130.2	0	0.55	2	108.4	CR Msex	75.4	0	0.60	2	65.4
CR M0	130.6	0.4	0.45	1	112.7	CR Mh	76.6	1.2	0.33	3	62.2
CR Msex	138.8	8.6	0.00	3	121.6	CR M0	79.7	4.1	0.07	1	69.4
SECR.sex.g0	924.2	0	0.66	5	894.2	SECR.sex	612.5	0	0.66	6	588.5
SECR.sex	925.6	1.4	0.34	5	893.6	SECR.sex.g0	614.0	1.5	0.32	5	592.0
SECR.sex.σ	937.3	13.1	0.00	6	907.3	SECR.sex.σ	619.8	7.3	0.02	5	597.8
SECR.0	953.4	29.2	0.00	4	925.4	SECR.0	628.7	16.2	0.00	4	608.7

Therefore we report density estimates and parameters for both SECR models at both sites (Table 2.3). Under the secr.sex model g0 resulted much lower for females at both sites (0.051 vs. 0.813 at Site-I; 0.009 vs. 0.118 at Site-II), whereas σ was smaller for females at Site-I while for males at Site II (Table 2.3). This led to female home ranges estimates of 42.7 km^2 and 102.1 km^2 at Site-I and Site-II respectively, and to male home range estimates of 52.8 km^2 at Site-I and 38.3 km^2 at Site-II

Table 2.3 Density and parameters estimated by the two best Spatially Explicit Capture Recapture models, i.e. SECR.sex and SECR.sex.g0, at Site-I and Site-II. SE= Standard error; LCI and UCI = lower and upper confidence intervals respectively; CV= Coefficient of Variation; D=Density. Density values are in bold. g0= probability of capture at the home range centre, σ = spatial parameter related to home range size; SECR.sex.g0: g0 varies between males and females; SECR.sex: both g0 and σ vary between males and females; SECR.sex.σ: only σ varies between males and females; SECR.0: null model.

	Site-I Magdalena River valley					**Site-II Orinoco River basin**				
	Value	**SE**	**95% LCI**	**95% UCI**	**CV**	**Value**	**SE**	**95% LCI**	**95% UCI**	**CV**
g0 females SECR.sex	0.051	0.020	0.024	0.106	39%	0.009	0.005	0.003	0.024	56%
g0 males SECR.sex	0.813	0.556	0.003	1.000	68%	0.118	0.025	0.077	0.176	21%
σ females (km) SECR.sex	1.507	0.147	1.245	1.822	10%	2.327	0.693	1.315	4119	30%
σ males (km) SECR.sex	1.674	0.174	1.366	2.051	10%	1.426	0.129	1.195	1.701	9%
D (N/100km^2) SECR.sex	**3.15**	**1.08**	**1.64**	**6.05**	**34%**	**1.88**	**0.87**	**0.79**	**4.48**	**46%**
g0 females SECR.sex.g0	0.046	0.016	0.023	0.088	35%	0.013	0.006	0.006	0.030	46%
g0 males SECR.secr.g0	0.999	0.000	0.999	0.999	0%	0.108	0.022	0.071	0.159	20%
σ (km) SECR.sex.g0	1.617	0.042	1.537	1.701	3%	1533	133	129	1818	9%
D (N/100km^2) SECR.sex.g0	**3.04**	**1.02**	**1.60**	**5.78**	**34%**	**2.19**	**0.99**	**0.93**	**5.13**	**45%**

We recorded 12 prey species at Site-I and 16 at Site-II with Central American agouti (*Dasyprocta punctuata*) and black agouti (*Dasyprocta fuliginosa*) being the most frequently captured species at Site-I and 2 respectively (Table 2.5 in Supporting Information).

2.5 Discussion

It has been recognised that protected areas are inadequate for the long-term conservation of jaguars (Sanderson et al., 2002a; Rabinowitz & Zeller, 2010). Therefore, estimating their population size and density in increasingly modified landscapes helps understanding the extent to which jaguar can persist in human areas and informs conservation planning. We provided the first jaguar density estimates of Colombia outside of the Amazon forest (Payan, 2009) and in agricultural landscapes. Cattle ranching is the primary land use in the country and oil palm cultivation is an emerging land use across the Neotropics (Etter et al., 2006; Pacheco, 2012).

2.5.1 Jaguar densities

Our results at both sites show that unprotected and productive areas with remaining natural habitats can be important for jaguar populations. Protected areas should always be considered core refuges and they can have a direct effect on population size (Payan, 2009), but large-scale landscape connectivity is also essential. National Parks such as Iguazu and Emas can only harbour small jaguar populations if surrounded by matrices of converted habitat and poaching, and jaguar densities were estimated as low as 0.5-0.9 and 0.3 at those parks respectively (Paviolo et al., 2008;

Sollmann et al., 2011).

Jaguar densities tend to be greater in wetter and prey-rich habitats such as lowland tropical forests (Silver et al., 2004; Harmsen, 2006; Tobler et al., 2013) or in the flooded plains of the Pantanal (Soisalo & Cavalcanti, 2006) and lower in drier habitats such as the Gran Chaco (Maffei et al., 2004) and Cerrado (Sollmann et al., 2011) (Table 2.8.3 in Supporting Information). Densities are also affected by the level of human use: they can be high in productive lands such as cattle ranches in the Pantanal (Soisalo & Cavalcanti, 2006), and forestry concessions in the Cerrado (Arispe et al., 2007) and the Amazon (Tobler et al., 2013), but they become low across highly degraded habitats such as Brazilian Atlantic forest (Paviolo et al., 2008) or heavily hunted regions (Quiroga et al., 2013).

Site-I is within the tropical forest biome and has abundant wetlands and seasonal flooded areas (IDEAM et al., 2007), hence it is part of the wetter habitats of the jaguar range. However the SECR density values we obtained at the site (3.0±1.0-3.1±1.1) are lower than similar habitats (Table 2.6 in Supporting Information). Tobler et al. (2013) report an average jaguar density of 4.4 ± 0.7 across the South Western Amazon when using SECR models, while in the Pantanal densities were estimated as high as 6.7 ± 1.1 using a reliable buffer obtained with telemetry (Soisalo & Cavalcanti, 2006). Our lower estimates may have resulted from much of the region being converted to agriculture, including oil palm plantations. However, they are higher than we expected given the extensive habitat conversion. These densities may have resulted from remaining wetlands and existing connectivity with the San Lucas JCU towards the West of the study area as a source for the population (Fig. 2.1). The importance of wetlands for jaguars in the study area is further confirmed by the fact that jaguar were recorded mainly at camera stations situated in wetland habitats and never in oil palm habitats. Connectivity between this area and the Catatumbo and Llanos-Amazon JCUs towards the East and South East (Fig 2.1) is uncertain and should be assessed.

Carnivore densities are highly dependent on the prey base available (Carbone & Gittleman, 2002; Carbone et al., 2011) and levels of hunting of both prey and carnivores themselves (Quiroga et al., 2013). Killing of jaguars at Site-I is rare (Boron, 2012) but larger prey species such as deer, tapirs *(Tapitus terrestris)*, peccaries, giant anteaters (*Mymecophaga tridactyla*), and capybaras on which jaguar depend in other regions (Novack et al., 2005; Weckel et al., 2006; Foster et al., 2010) were absent or infrequent, likely due to both habitat loss and hunting. These species are regularly hunted for subsistence and commercial purposes in Colombia (Rodríguez-Mahecha et al., 2006). It is therefore possible that jaguars complement their terrestrial prey base with aquatic species such as caimans (*Caiman crocodilus*) and turtles (*Podocnemis* and *Trachemys* sp.) as found elsewhere (de Azevedo & Verdade, 2012).

Site-II is part of the Llanos-Amazon JCU (Fig. 2.1), indicating that jaguars at this site are part of a larger population in a connectivity landscape. The llanos' biome, i.e. seasonally flooded grasslands (IDEAM et al., 2007), is similar to the Pantanal but with some important differences. There is more prey biomass in the Pantanal (Schaller, 1983) and flooding is one quarter of the year longer than in the llanos, thus limiting productive human land use. Furthermore, the llanos also were colonized 200 years earlier than the Pantanal and display much higher human density and hunting levels. Finally, jaguar densities in the Pantanal were estimated across ranches without hunting in the past 15 years and with extremely low human density. All these factors could explain the lower jaguar density (1.9±0.9 – 2.2±1.0) we obtained.

Lower jaguar numbers in the llanos could also be due to retaliatory killing following livestock predation. Incidents of jaguar predation on livestock do occur (Payán et al., 2009; Garrote, 2012) however, currently there is a paucity of data regarding human persecution of jaguar. Past systematic hunting of jaguars for the spotted pelt trade could also explain low population numbers (Payán & Trujillo, 2006) but again, that would assume little to no recovery.

Usually more males than females are recorded in camera trap studies because males tend to move more and have larger home ranges (Maffei et al., 2011). This is in accordance to what we obtained at Site-II, however the sex ratio was skewed to females (2.3:1) at Site-I, where we even recorded mating events and cubs. This, in addition to recording resident jaguars (since 2012), suggests that the area is important for jaguar conservation and possibly constitutes a breeding refuge (Maffei et al., 2011).

2.5.2 Methodological considerations and sex specific parameters

Our survey effort (47-53 camera stations) was more comprehensive than most jaguar studies, as only 15% of jaguar studies reviewed by Tobler and Powell (2013) used > 40 camera stations. Density estimates become unbiased and precision increases if the camera polygon is asymmetrical (Sollmann et al., 2012) and encompasses several home ranges (Maffei & Noss, 2008; Tobler & Powell, 2013) which is logistically challenging when sampling wide- ranging species like jaguars. However, even if we assume large home ranges (400 km^2) and low detection probabilities at home range center (g0=0.01) the density bias for polygons like ours, ca. 150 km^2, is less than 10% (Tobler & Powell, 2013).

Jaguar home ranges in wetter habitats vary greatly: some studies (Schaller & Crawshaw Jr, 1980; Rabinowitz & Nottingham, 1986; Ceballos et al., 2002; Crawshaw et al., 2004) estimated home ranges size smaller or comparable to what we obtained at Site-I, while others have reported them much larger (Crawshaw Jr & Quigley, 1991; Cavalcanti & Gese, 2009; Figueroa, 2013; Tobler et al., 2013). At Site-II, female home range was larger than reported by Scognamillo et al. (2003) in the Venezuelan Llanos (53-83 km^2), whereas for males it was the opposite. Female home ranges are usually smaller than those of males' (Crawshaw et al., 2004; Cavalcanti & Gese, 2009; Tobler et al., 2013). We observed the opposite pattern at Site-II and could be an artefact of sample size. SECR models assume circular home ranges, and that may have been violated in our landscapes where jaguars move along watercourses and riparian galleries.

Because of sex-specific detection probabilities and home range sizes, including sex as a covariate reduces the bias in density estimates and produced better SECR models at both sites. However the best CR models at Site-1 did not include sex as a covariate and it could be because CR models do not include spatial behaviour, hence reducing differences between the sexes. Ultimately, with small sample sizes, partitioning the data into sex specific group is a trade-off between bias and precision. We also recommend larger camera polygons than ours to increase the number of individuals captured and achieve more accurate density estimates.

We concur with other authors (Sollmann et al., 2011; Tobler & Powell, 2013; Tobler et al., 2013), and recommend using SECR models over CR ones when estimating densities because they are not biased by arbitrary buffers, are robust even with smaller grids (Sollmann et al., 2012), and can account for larger numbers of individual and site based covariates, producing more reliable estimates and addressing many issues outlined by Foster and Harmsen (2012). Obtaining reliable and comparable estimates is key to avoid biased population statuses, underestimation of threats, and delayed conservation interventions, exposing the species at greater risk of decline. Lastly, we may have under-detected some prey species as all our cameras were placed on roads and trails and might have ignored micro-habitats that are important for certain prey species, however placing cameras on trails is still considered the best option to optimize detection of multiple (forest) mammals at once (Carbone et al., 2001; Rovero et al., 2014; Cusack et al., 2015).

2.5.3 Conclusion

In the case of wide-ranging species such as large carnivores, human-use areas are important habitats for connectivity and dispersal between core protected areas as well as for resident and breeding populations (Linnell et al., 2001; Mech & Boitani, 2003; Athreya et al., 2013). Therefore it is essential to study these species in unprotected and modified areas to understand the limits to their tolerance and survival (Athreya et al., 2013). Our results provide additional evidence on the role of unprotected areas for carnivore conservation, advance current understanding of jaguars in agricultural areas, and provide the first jaguar density estimates in both the llanos ecosystem and in an oil palm landscape. They also indicate that productive areas with extensive cattle ranching and oil palm cultivation can be important for jaguar conservation as long as natural habitats such as wetlands, forests, and riparian galleries persist in the landscape. Natural areas in human-dominated regions are crucial for the survival of landscape species worldwide allowing them to disperse and thrive beyond protected areas (Sanderson et al., 2002a, 2002b; Wikramanayake et al., 2004; Thorbjarnarson et al., 2006).

As agriculture and oil palm cultivation continue to expand across the tropics they need to be integrated into range-wide jaguar conservation strategies. For long-term jaguar conservation it is key to engage landowners, implement land-use plans in both regions to maintain natural habitats in the landscape, and establishing further oil palm plantations in already disturbed areas, as identified by Garcia-Ulloa et al. (2012). Across cattle ranching regions it is also crucial to adopt optimal livestock management practices to ensure low predation and low levels of human-jaguar conflict (Quigley & Crawshaw Jr, 1992; Zimmermann et al., 2005).

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2.8 Supporting Information

Table 2.4 Density results obtained with programme Capture & Mh.
Mh: capture probability varies between individuals. SE= Standard error; LCI and UCI = lower and upper confidence intervals respectively; CV= Coefficient of Variation; N= Number of individuals; p=average capture probability; MMDM=Mean Maximum Distance Moved; ETA=Effective Trapping Area; D=Density.

	Site-I Magdalena River valley					**Site-II Orinoco River basin**				
	Value	**SE**	**95% LCI**	**95% UCI**	**CV**	**Value**	**SE**	**95% LCI**	**95% UCI**	**CV**
N (Mh)	11	1.42	11	18	13%	7	1.38	7	13	20%
p (Mh)	0.34					0.39				
MMDM (km)	4.2					5.7				
ETA MMDM (km^2)	396.2					537.2				
½ MMDM (km)	2.1					2.9				
ETA ½MMDM (km^2)	225.1					308.1				
D Mh MMDM ($N/100km^2$)	**2.77**	0.66	2.77	4.54	24%	**1.30**	0.30	1.30	2.41	23%
D Mh ½MMDM ($N/100km^2$)	**4.88**	1.32	4.88	8.00	27%	**2.27**	0.48	2.27	4.22	21%

Table 2.5 Independent capture events and capture rates of jaguars and their prey species at both sites.

	Site-I		Site-II	
	Capture events	**Capture rates**	**Capture events**	**Capture rates**
Panthera onca	111	4.93	76	3.09
Caiman crocodilus	-	-	5	0.20
Cebus albifrons	40	1.78	-	-
Chelonoidis denticulata	-	-	4	0.16
Cuniculus paca	15	0.67	51	2.08
Dasyprocta fuliginosa	-	-	278	11.31
Dasyprocta punctata	121	5.38	-	-
Dasypus novemcinctus	7	0.31	16	0.65
Didelphis marsupialis	9	0.40	18	0.73
Hydrochoerus hydrochaeris	-	-	238	9.68
Hydrochoerus isthmus	7	0.31	-	-
Iguana iguana	4	0.18	13	0.53
Mazama americana	-	-	52	2.12
Myrmecophaga tridactyla	6	0.27	199	8.10
Odocoileus virginianus	-	-	161	6.55
Pecari tajacu	5	0.22	93	3.79
Philander opossum	-	-	1	0.04
Procyon cancrivorus	60	2.67	1	0.04
Tamandua tetradactyla	6	0.27	33	1.34
Tupinambis sp.	4	0.18	2	0.08

Table 2.6 Jaguar (*Panthera onca*) density estimates (N/100km^2) from camera trap surveys, modified from Tobler and Powell (2013).

Densities are based on the Mh model and a buffer of ½ MMDM, which was the most commonly used method. When available, density estimates based on other methods are also listed. We reported average densities when more estimates were available for the same areas and highlighted rows with density estimates that correspond to exclusively unprotected areas. Mh assumes that capture probability varies across individuals. MMDM=Mean Maximum Distance Moved.

[a] Density estimates based on the Mh MMDM method
[b] Density estimates based on a spatially explicate capture-recapture (SECR) model
[c] Approximate density estimate not based on capture-recapture method
[d] Density estimate based on the Barker robust design model and MMDM

Country	Survey	Density Mh ½ MMDM	Other density estimates	Biome/ Habitat	Protected area	Source
Argentina	Iguazu 2004-2006	1.26 ±0.34	0.49±0.16[a]	Semi deciduous forest	National Park and Forestry Reserve	Paviolo et al. 2008
Argentina	Urugua-i	0.3[c]	0.12[a]	Semi deciduous forest	Provincial Park and Private Reserve	Paviolo et al. 2008
Argentina	Yaboti	0.2[c]	0.11[a]	Semi deciduous forest	Forestry Reserve	Paviolo et al. 2008
Belize	Cockcomb basin	10.50 ±2.13		Broadleaf tropical moist rainforest	Wildlife Sanctuary	Silver et al. 2004; unknown in Maffei et al. 2011; Harmsen 2006
Belize	Chiquibul	7.48±2.74		Deciduous semi-evergreen and seasonal forest	Forest Reserve and National Park	Silver et al. 2004
Belize	Fireburn	5.31±1.76		Tropical moist lowland forests	Private Reserve, Mesoamerican Biological Corridor	Miller 2006

Belize	Gallon Jug 2004-2005	10.05±1.71	Tropical lowland forests	Private reserve	Miller 2005
Belize	Mountain Pine Ridge	3.81	Tropical pine forests	Forest Reserve	M. Kelly unpubl. Data in Maffei et al. 2011
Bolivia	Cerro Cortado I-II Kaa-Iya	5.20±1.42	Xeric Chacoan forest	National Park and Indigenous communal lands	Silver et al. 2004; Maffei et al. 2004
Bolivia	El Encanto	5.66±2.33	Cerrado / tropical dry forests	Certified forestry concession	Arispe et al. 2007
Bolivia	Estacion Isoso I-II, Kaa-Iya 2005-2006	3.54±0.60	Chaco / tropical dry forests (transitional Chaco-Amazon)	National Park	Maffei et al. 2006; Romero-Munoz et al. 2007
Bolivia	Guanaco, Kaa-Iya I-II	2.07±0.28	Chaco / tropical dry forests (grasslands)	National Park and cattle ranches	Cuellar et al. 2004a; Cuellar et al. 2004b
Bolivia	Palmar I-II, Kaa-Iya	1.22±0.06	Chaco / tropical dry forests (transitional Chaco-Chiquitano)	National Park, private reserve, and cattle ranch	Romero-Munoz et al. 2007; Montano et al. 2007
Bolivia	Ravelo I-II, Kaa-Iya	1.92±0.45	Chaco / tropical dry forests (transitional Chaco-Chiquitano)	National Park	Cuellar et al 2003; Maffei et al. 2004
Bolivia	Rios Tuichi and Hondo, Madidi	2.26±0.97	Tropical Andes / tropical moist lowland forest	National Park	Wallace et al. 2003; Silver et al. 2004

Bolivia	San Miguelito	7.61±1.43		Cerrado/ tropical dry forests (Chiquitano dry forest)	Private reserve and cattle ranch	Rumiz et al. 2003; Arispe et al. 2005
Bolivia	Tucavaca I-II, Kaa-Iya	2.83±0.52		Chaco / tropical dry forests (transitional Chaco-Chiquitano)	National Park	Silver et al. 2004;Maffei et al. 2004
Brazil	Emas National Park	2		Cerrado / tropical dry forests	National Park	Silveira 2004
Brazil	Emas National Park	-	0.51±019[a] 0.29±0.10[b]	Cerrado / tropical dry forests	National Park	Sollmann et al. 2011
Brazil	Fazenda Santa Fe	2.59±1.03		Amazon / tropical moist forests – Cerrado / tropical dry forests ecotone	Cattle ranch, State Park	L. Silveira and N.M. Negroes in Maffei et al. 2011
Brazil	Fazenda Sete 2003-2004	11.0±1.2	5.7±0.8[a]	Pantanal / herbaceous lowland grasslands	Cattle ranch	Soisalo and Cavalcanti 2006
Brazil	Moro do Diablo	2.47±0.46		Atlantic / tropical moist lowland forest	National Park	Cullen 2006
Brazil	Serra da Capivara	2.67±1.06	1.28±0.62[a]	Caatinga/xerics	National Park	Silveira et al. 2010
Colombia	Amacayacu	4.2		Amazon / tropical moist lowland forest	National Park and indigenous territory	Payan 2009

Colombia	Calderon river valley	2.5		Amazon / tropical moist lowland forest	National Forestry Reserve and indigenous territory	Payan 2009
Costa Rica	Corcovado	6.98±2.36		Tropical moist lowland forest	National Park	Salom-Perez et al. 2007
Costa Rica	Golfo Dulce / Golfito	2±1.49		Tropical moist lowland forest	Private ranches, Forest Reserve, Wildlife Reserve	Bustamante 2008
Costa Rica	San Cristobal	6.7		Tropical Rainforest, Low Montane Rainforest	Biological; National Park corridor	Rojas 2006
Costa Rica	Talamanca	1.34±0.48				Gutierez and Porras 2008
Costa Rica	Talamanca ZPLT (Coton)	5.42±2.3	2.25[a]	Tropical forest	Protected area	Gonzales-Maya 2007
Ecuador	Yasuni-Waorani	1.38±0.6		Amazon / tropical moist lowland forest	National Park and indigenous territory	S. Espinoza unpubl. Data in Maffei et al. 2011
Ecuador	Yasuni ITT	2.2			National Park	Araguillin et al. 2010
French Guiana	Counami Forest	3.3		Amazon / tropical moist lowland forest	Unprotected	Association Kwata 2009
French Guiana	Montagne de Fer	4.9				Association Kwata 2009
Guatemala	Carmelita-AFISAP	11.28±3.51		Tropical moist lowland forest	Forestry concessions	Moreira et al. 2008a

Guatemala	La Gloria-Lechugal	1.54±0.85		Tropical moist lowland forest	Forestry concession, multiple use zone	Moreira et al. 2007
Guatemala	Mirador, Oeste	1.99±1.57	0.9±0.48[a]			Moreira et al. 2005
Guatemala	Dos Lagunas Rio Azul	11.14±7.45	7.02±6.44[a]	Tropical moist lowland forest	National Park	Moreira et al. 2008b
Guatemala	Tikal	6.63±2.46	3.39[a]	Tropical moist lowland forest	National Park	Garcia et al. 2006
Guatemala	Melchor de Mecos	6.04±1.68	2.91±0.72[a]	Subtropical Humid Forest.	Community concession forest	Moreira et al. 2010
Guatemala	Laguna del Tigre	6.32±1.66	3.73±0.49[a]	Wetlands, lowland forest	National Park, Concession area	Moreira et al. 2009
Honduras	La Mosquitia	5.2[c]		Tropical moist lowland forest	Indigenous territory	Portillo Reyes and Hernandez 2011
Mexico	Sonora	1±1.3[c]		Mexican xerics / tropical thorn scrub	Private Reserve and cattle ranches	Rosas-Rosas 2006
Mexico	San Luis Potosi 2008	3.2±1.9	1.55±1.93[a]	Tropical forest, deciduous and evergreen forest	Unprotected	Avila Najera 2009
Mexico	Quintana Roo	3.88±0.70	1.95±0.45[c]	Tropical forest	Ecological Reserve	Avila Najera et al. 2015
Mexico	Sonora		1.87±0.47 (Barker robust design + MMDM)	Desert scrub, Tropical decisuous forest, grassland	Northern Jaguar Reserve and cattle ranches	Gutierrez Gonzalez et al. 2015

Panama	Darien	3.12	1.70[a]	Tropical moist lowland forest	National Park	Moreno 2006
Peru	Los Amigos 2005-2007	10.11±1.28	4.25±0.95[b]	Tropical Andes / tropical moist lowland forest	Conservation concession	Tobler et al. 2013
Peru	Bahuaja Sonene, Tambopata	8.1±3.6		Tropical Andes / tropical moist lowland forest	National Parks	Tobler et al. 2013
Peru	Espinoza	6.9±1.3	4.9±1.0[b]	Tropical Andes / tropical moist lowland forest	Forestry concessions	Tobler et al. 2013

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3. Conserving predators across tropical agricultural landscapes: habitat use and interactions by four sympatric felids in Colombia.

To be submitted:

Boron V., Xofis P., Link A., Payan E., Tzanopoulos J. Conserving predators across tropical agricultural landscapes: habitat use and interactions by four sympatric felids in Colombia.

3.1 Abstract

Given the pervasive spread of habitat loss and degradation across the tropics, there is an urgent need to understand the effects of these threats, as well as species' habitat requirements and distribution within human-modified landscapes, in order to reconcile agricultural expansion with the conservation of endangered and keystone species, like the felids. We combined camera trapping and remote sensing generated data into occupancy modelling to study the habitat use and interactions by four sympatric felids across two agricultural landscapes with different levels of habitat modification in Colombia. The areas include cattle ranching and oil palm cultivation, an emerging land use in the Neotropics. Strong determinants of species occupancy emerged only at one site and were wetlands for jaguars (positive effect); forest and water proximity (positive effect) for pumas; and pasture (negative effect) for pumas, ocelots, and jaguarundis. At this site all felids were recorded on locations that averaged 50-60% natural cover. Furthermore jaguars, pumas, and jaguarundis were never recorded in oil palm areas. Lastly, these four sympatric felids did not display any spatial segregation. To align development with the conservation of top predators it is key to maintain areas of natural habitats across agricultural landscapes and targeting agricultural and oil palm expansion to already-modified areas like pastures, which showed no conservation value. Moreover, habitat conversion beyond 50-60% may be unsustainable for felid populations. Lastly, as there was no spatial segregation between the felids, conservation strategies to simultaneously benefit this guild are possible even in modified landscapes.

3.2 Introduction

Habitat loss and degradation, mainly driven by agricultural expansion, are the main threats to biodiversity worldwide (Foley et al., 2005; Maxwell et al., 2016). Consequently, there is an urgent need to reconcile agricultural expansion with the conservation of endangered and keystone species, such as the felids. This is especially true across tropical countries, which are experiencing considerable land cover change and are a priority for carnivore conservation (Gibbs et al., 2010; Laurance et al., 2014; Di Minin et al., 2016). Wild cats, as other carnivores, exert a key function in maintaining ecosystem integrity: by limiting herbivore population growth, they retain the structure and composition of complex biological communities and ecosystems (Estes et al., 2011; Malhi et al., 2016; Ripple et al., 2014).

Protected areas are crucial to conserve high quality source habitats, however only 9.8% of all tropical forests lies within protected areas (Schmitt et al., 2009) and on average 90% of the geographical distribution of wild carnivores falls outside protected areas (Di Minin et al., 2016), implying that the latter are not able to guarantee their long-term survival. Therefore it is crucial to incorporate increasing agricultural and human modified landscapes into large-scale conservation strategies. This is especially relevant for large predator species such as jaguars (*Panthera onca*) and pumas (*Puma concolor*), which are particularly vulnerable to habitat loss and extinction since they require large areas, live at low population densities, and have slow reproductive rates (Carbone et al. 2011; Cardillo et al. 2005; Crooks 2002).

Populations of all wild felids in Neotropical forests are rapidly declining (IUCN 2015). For example, jaguars - the largest Neotropical cats- have experienced a contraction of their geographical distribution to less than 50% of their historical distribution (Rabinowitz & Zeller, 2010), and are currently considered Near Threatened by the IUCN (Caso et al., 2008). Pumas are listed as Least Concern (Nielsen et al., 2015), however their population estimates are scarce in the Neotropics (Kelly et al., 2008). Both jaguars and pumas are declining in number due to habitat loss, persecution, and poaching of their prey (Caso et al., 2008; Nielsen et al., 2015), yet knowledge about their habitat use across human modified agricultural areas is limited (Foster et al. 2010; De Angelo et al. 2011; De Angelo et al. 2013). Even less is known on the ecology of smaller terrestrial felid species such as ocelots *Leopardus pardalis* and jaguarundis *Herpailurus yaguaorundi* (Least Concern) across agricultural landscapes (Di Bitetti et al., 2006; Kolowski & Alonso, 2010; Giordano, 2015), and both species display decreasing population trends (Caso et al. 2015; Paviolo et al., 2015).

We combine high-resolution land cover maps and camera trapping data into occupancy models to investigate the within home-range habitat use of four sympatric Neotropical felids: jaguars, pumas, ocelots, and jaguarundis (Fig. 3.1) in two agricultural landscapes in Colombia. The areas included cattle ranching, the main land use in the country (Etter et al., 2006), and oil palm plantations, an emerging land use in the Neotropics (Pacheco, 2012). The latter is particularly concerning because it constitutes poor habitat for many species (Fitzherbert et al., 2008; Wilcove and Koh, 2010; Yue et al., 2015) and has an unknown effect on Neotropical felids. Finally we also investigate patterns of spatial co-occurrence or avoidance between the four species to guide management. The data will enable identifying the challenges and opportunities that these ecosystems pose for their survival, and inform strategies to align regional development with conservation actions for these predators and the diverse ecosystems they live in.

Fig. 3.1 Felid species recorded by camera traps at both agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia: Jaguar (a), Puma (b), Ocelot (c), Jaguarundi (d).

3.3 Methods

3.3.1 Study area

We conducted the study at two sites in Colombia: Site-1 (7.3752N -73.8842E to 7.5404N -73.7118E) and Site-2 (5.3450N -72.8471E to 5.4365N -72.7607E) (Fig. 3.2). Both study sites are located in the Department of Santander, in the central part of the Magdalena River valley, in between the Central and Eastern Andes. The straight-line distance between the two sites is 93 km. We chose these two sites because they are both agricultural areas, which include cattle ranching and oil palm plantations, but still host top predators like jaguars and pumas. The region is part of the tropical forest biome and it is rich in wetlands (IDEAM et al., 2007).

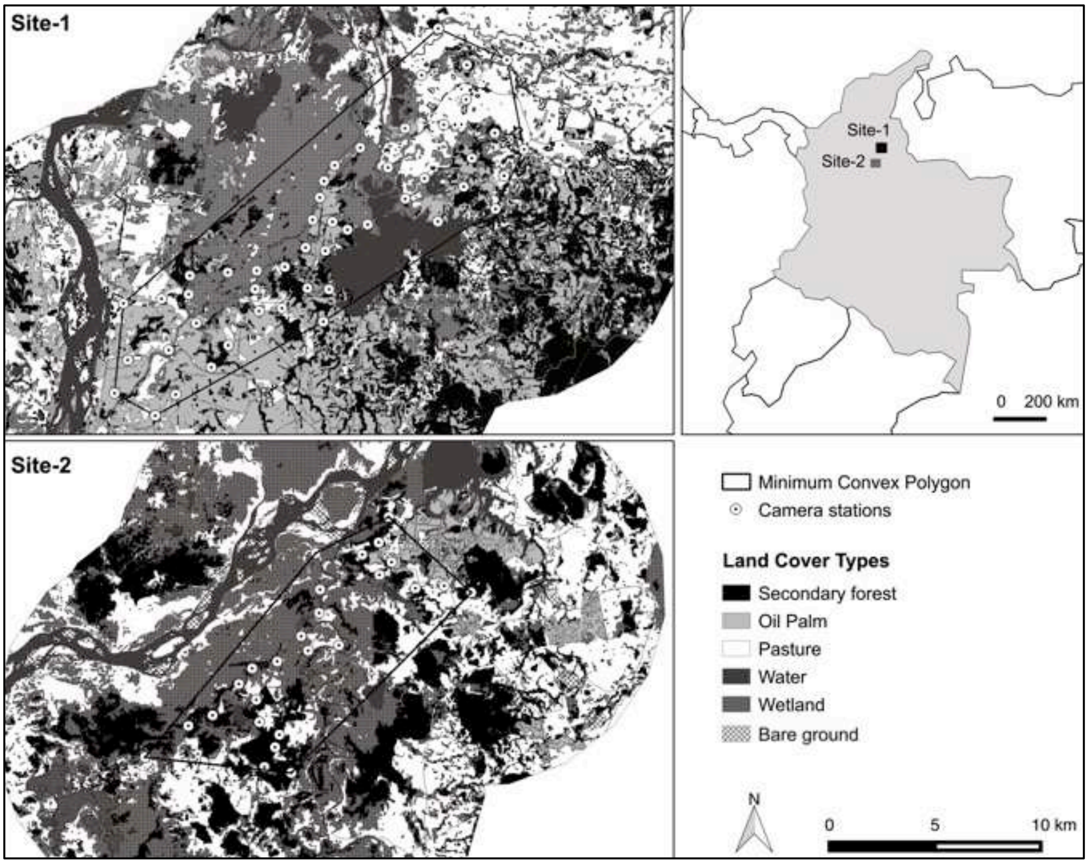

Fig. 3.2 Study maps of the two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia with land cover types and camera trap stations.

It is considered an important genetic corridor for several species including jaguars (Payan-Garrido et al., 2013) and it hosts endangered and endemic species such as the Critically Endangered brown spider monkey (*Ateles hybridus* ssp. *brunneus*) and the Endangered white-footed tamarin (*Sanguinos leucopus*). However, the majority of its historical forest cover has been transformed into cattle ranches and oil-palm plantations, and the remaining natural areas are fragmented and at risk of further conversion (Etter et al., 2006; Castiblanco et al., 2013; Link et al., 2013). Mean annual temperature is 27℃, with 2100-2600 mm of annual precipitation (IDEAM et al., 2007). Land tenure consists principally of private properties and there are no national protected areas. Main land cover types comprise secondary forest, wetlands, pastures, crops, and oil-palm plantations.

3.3.2 Camera trapping

We placed 47 camera stations between April and August 2014 at Site-1 and 26 stations between September and December 2014 at Site-2. The set up followed standardized survey techniques for camera trapping used in previous studies on Neotropical felids (Maffei & Noss, 2008; Davis et al., 2011; Tobler & Powell, 2013). We placed the cameras in a grid at intervals of 1.6±0.3 km (Fig. 2), since this scale of analysis is considered appropriate to investigate within home range habitat use by felids (Davis et al. 2011; Sunarto et al. 2012; Alexander et al. 2015; Everatt et al. 2015; Strampelli 2015). Camera stations were located across all main habitat types of the study areas: forests, wetlands, pastures, and oil palm plantations. We used Cuddeback Attack (model: 1149) and Ambush (model: 1170) camera traps and set them at a height of 35 cm from the forest floor. When possible we placed cameras along roads and established trails to maximise probability of capturing cat species. 60% and 73% of stations were placed on trails at Site-1 and Site-2 respectively and we took these differences into account in the modelling approach. The minimum convex polygon linking the camera stations was 154.8 km^2 at Site-1 and 85.4 km^2 at Site-2.

3.3.3 Occupancy modelling to study habitat use

We used occupancy models in order to investigate the potential effects of different land cover types and variables on species' habitat use and distribution. The latter take into account imperfect detection and use repeated presence-absence surveys (detection histories) at multiple sites to estimate a detection probability (p) and the true proportion of area occupied by a species (ψ) (MacKenzie et al., 2002, 2006). The following assumptions are made: 1) sites are closed to changes in occupancy (i.e. they are either occupied or not by the species for the duration of the survey); 2) species are correctly identified; 3) detections are independent; and 4) heterogeneity in occupancy or detection probability are modeled using covariates (MacKenzie et al., 2006). We conducted our analyses at the scale of the camera trap station rather than at the home range scale. Thus, individuals of all four species were likely to be captured at multiple stations and we were most interested in evaluating habitat use rather than the proportion of study area occupied by each species. Therefore we interpreted ψ as the intensity of use of the various camera stations and modeled both ψ and p using predictor variables (covariates). Under these circumstances assumption 1 can be relaxed and even extensive survey lengths do not represent an issue (MacKenzie et al., 2006). We included in our analyses covariates that have been proposed to explain habitat use (ψ) by felids (Michalski & Peres 2005; Bitetti et al. 2006; Foster et al. 2010; De Angelo et al. 2011; Zeller et al. 2011; Giordano 2015) considering (1) bottom up resources: proportion of the area covered by forests and wetlands around camera stations, distance to water, and amount of prey, as well as (2) top-down anthropogenic pressures: distances to settlements, and the proportion of the area covered by pastures and oil palm plantations around camera stations.

3.3.4 Land cover mapping

We identified land cover types using Object Oriented Image Analysis (OBIA) on three Landsat 8 images, captured on 4/1/2015, 9/3/2015, and 12/7/2015 (downloaded from www.usgs.gov). We increased the spatial resolution of the multispectral image bands by pansharpening, employing the High Pass Filter technique and five as Kernel size. The pansharpened multispectral bands had more than 90% correlation to the original ones in all cases, resulting in limited loss of spectral information. We applied Tasseled Cap Transformation on all images using the coefficients suggested by Liu et al. (2015) for Landsat 8 data, after converting the DN to TOA reflectance values. The classification was further assisted by two vegetation indices, namely: the Normalized Difference Vegetation Index (NDVI) and the Normalized Difference Moisture Index (NDMI). We employed a step-wise Object Based Image Analysis (OBIA, in eCognition Developer 9) for the image classification. In OBIA, spectrally similar adjacent pixels are grouped into meaningful objects, which are then classified into one of the possible classes, using spectral as well as spatial, neighborhood and other characteristics (Bock et al., 2005). For training the classifier and testing the result we collected 343 and 150 ground truth validation points for Site-1 and Site-2 respectively. We used two thirds of the ground-truth dataset for training and one third for testing. Finally we performed an overall accuracy assessment using an error confusion matrix method and calculated classification accuracy and kappa statistics.

3.3.5 Covariates generation

Using the produced land cover maps we extracted the proportion of each land cover type using 800 m buffers around camera stations, and measured the distance of each camera station from water and settlements in ArcMap 10.3. The 800 m radius corresponds to half the average distance between neighboring camera stations (Sollmann et al., 2012). For jaguars and pumas we also considered prey availability. These species have wide dietary breadth but tend to favour larger prey species (Polisar et al. 2003; Foster et al. 2010). Consequently we built two indices: one considering all prey species and another considering only prey species with body mass > 10 kg, which in the study area consisted of capybaras (*Hydrochoerus isthmius*), white-collared peccaries (*Pecari tajacu*), and giant anteaters (*Myrmecophaga tridactyla*). Our index of prey presence was calculated as the sum of the number of days on which a prey species was captured at each camera station, divided by the active trap days at that station (Alexander et al., 2015). We could not test prey availability for ocelots and jaguarundis because they predate also on small prey such as rodents and small reptiles, which are under-detected by our camera trap methodology (Abreua et al., 2008; Giordano, 2015).

As wild felids tend to use roads and trails to facilitate their movement (Schaller & Crawshaw Jr, 1980; Cusack et al., 2015) we included a categorical covariate on p: camera points on roads and established trails were assigned a score of “1” vs. “0” for cameras not located on roads/trails. Both models of camera traps have the same trigger speed (0.25 seconds) and due to high temperatures they were triggered only at distances < 3-4 m. Therefore we did not include camera model as a covariate on p and assumed constant detection probability across habitats. We hypothesized that the proportion of natural habitats, proximity to water, and prey availability would affect cat habitat use positively, whereas proximity to settlements and proportion of anthropogenic land cover types negatively.

3.3.6 Data analysis

We constructed detection histories for each species and each site (camera location) using unambiguously identified species photographs and grouping 14 camera trap nights into one sampling occasion. We then deployed single season single species models in PRESENCE v.10.3 (Hines, 2006). Before running the models we standardized continuous covariates to z scores and tested for collinearity using a cut-off value of r = 0.7 (Dormann et al., 2013). In the first stage we defined a global model for ψ and assessed whether including the covariate on p improved the Akaike Information Criteria adjusted for small sample size (AICc) (Royle & Nichols, 2003). Then to reduce the amount of covariates on ψ and their possible combinations, we tested the effect of each covariate on ψ separately and only retained those covariates that improved the AICc from the null model and had stronger effects on ψ (the 90% confidence intervals of their β coefficients do not overlap 0). Next, we modeled all combinations of the retained covariates. We included a maximum of two covariates per model to avoid over-fitting given the amount of samples (MacKenzie et al., 2006).

We ranked models based on AICc and considered models whose combined weight (w) was > 0.95. We determined whether the influence of a covariate was positive or negative by the sign of the β coefficient (MacKenzie et al., 2006) and employed weighted model averaging to calculate overall estimates of β coefficients (when applicable), ψ, and p (Burnham & Anderson, 2002). We considered covariates to have a robust effect on ψ if the 95% confidence intervals of their β coefficients or averaged β coefficients did not overlap zero (Burnham & Anderson, 2002; Zuur et al., 2010; Everatt et al., 2014). Following, we summed AICc weights for each covariate in the 95% confidence set to evaluate their relative importance. We assessed model fit for the global standard occupancy model by running goodness-of-fit tests using 10,000 bootstrap samples and the overdispersion parameter c-hat calculated in PRESENCE (MacKenzie & Bailey, 2004). We repeated this process for each species.

Finally, to test for species interactions we used two-species single season occupancy models (MacKenzie et al., 2006; Sollmann et al., 2012; Sunarto et al., 2015). If two species, namely A and B, occur independently then the probability of occurrence of both species ψ (A and B) = ψ(A) x ψ(B). Consequently, we determined whether A and B, co-occurred more or less often than expected using ϕ= ψ(A and B)/(ψA x ψB). If ϕ>1 species co-occur more often than expected whereas if ϕ<1, species co-occur less often than expected, provided ϕ's 95% confidence intervals do not overlap 1 (MacKenzie et al., 2006).

3.4 Results

The land cover mapping resulted in the identification of seven types at each site (Table 3.4, Supporting Information). Coverage of natural habitats reached 32% at Site-1 and 53% at Site-2. The overall classification accuracy and kappa statistics were 0.89 and 0.87 indicating an excellent performance of the classifier at both sites. We obtained a sampling effort of 3069 and 1903 trap nights at Site-1 and Site-2 respectively and grouping 14 days into one sampling occasion resulted into 1-58 species detections (Table 3.1). We were able to run occupancy models for all species at Site-1, while only for pumas and ocelots at Site-2. Jaguar detections at Site-1 corresponded to 12 individuals, and ocelot records to 16 and 7 individuals at Site-1 and Site-2 respectively. Pumas and jaguarundis could not be individually identified.

For jaguars the selected models (combined weight of 95%) included the proportion of wetlands (robust positive effect, w=99%) and pastures (negative effect, w=19%) around camera stations as well as the distance to water (negative effect, w=18%)

(Table 3.1 and 3.2). The variables explaining puma occupancy were the proportion of forest (robust positive effect, w=39%) and pasture (robust negative effect, w=46%), distance to water (robust negative effect, w=61%), and availability of prey >10 kg (positive effect, w=24%) at Site-1; whereas distance to settlements (positive effect, w=82%), distance to water (negative effect, w=67%), and proportion of wetland habitats (negative effect, w=26%) at Site-2 (Table 3.1 and 3.2).

Ocelot occupancy was explained by the proportion of pasture (robust negative effect, w=99%) and forest (positive effect, w=26%) at Site-1; whereas the most general model had the strongest support at Site-2 (Table 3.1 and 3.2). Lastly, for jaguarundis the models included the proportion of pasture (robust negative effect, w=90%), wetland (positive effect, w=27%), and forest (positive effect, w=26%) (Table 3.1 and 3.2).

Cameras placed on roads/established trails were more likely to detect jaguars and ocelots (Table 3.2) and including this covariate for p improved models for these species. These cameras were also the only ones to detect jaguarundis. However, for the latter, we could not include it as a covariate on p due to lack of convergence. All felids were recorded on locations that averaged 50-59% natural cover at Site-1, whereas at Site-2 pumas and ocelots were recorded on average at stations with 74% and 58% natural cover respectively (Table 3.5, Supporting Information).

Table 3.1 Model selection results for variables influencing occupancy (ψ) and probability of detection (p) of jaguars, pumas, ocelots, and jaguarundis across two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia. AICc= Akaike's information criterion adjusted for small sample size; ΔAICc difference in AICc between each model and the best one; ML=Model Likelihood; k= no. of parameters, LL= 2log-likelihood (LL); Dist.=Distance; and Settl.=Settlements. We could not perform occupancy modeling for jaguars and jaguarundis at Site-2 due to the low numbers of captures we obtained for these two species, 6 and 1 respectively.

	AICc	ΔAICc	AICc weight	ML	k	LL
Site-1, 47 camera stations						
Jaguar (46 detections, 15 stations)						
ψ(%wetland), p(roads)	173.01	0.00	0.62	1.00	4	164.06
ψ(%wetland, %pasture), p(roads)	175.41	2.40	0.19	0.30	5	163.95
ψ(%wetland, Dist.Water), p(roads)	175.48	2.47	0.18	0.29	5	164.02
Puma (28 detections, 14 stations)						
ψ(%forest, Dist.Water), p(.)	164.55	0.00	0.34	1.00	4	155.6
ψ(%pasture, Dist.Water), p(.)	166.05	1.50	0.15	0.47	4	157.1
ψ(%pasture), p(.)	166.19	1.64	0.14	0.44	3	159.63
ψ(%pasture, prey>10kg), p(.)	166.51	1.96	0.12	0.38	4	157.56
ψ(%prey10, Dist.Water), p(.)	167.16	2.61	0.09	0.27	4	158.21
ψ(%pasture, %forest), p(.)	168.16	3.61	0.05	0.16	4	159.21
ψ(prey>10kg), p(.)	169.05	4.50	0.03	0.11	3	162.49
ψ(Dist.Water), p(.)	169.34	4.79	0.03	0.09	3	162.78
Ocelot (58 detections, 23 stations)						
ψ(%pasture), p(roads)	260.69	0.00	0.71	1.00	4	251.74
ψ(%forest, %pasture), p(roads)	262.72	2.03	0.26	0.36	5	251.26
Jaguarundi (25 detections, 12 stations)						
ψ(%pasture), p(.)	154.11	0.00	0.51	1.00	3	147.55
ψ(%pasture, %wetland), p(.)	156.00	1.89	0.20	0.39	4	147.05
ψ(%forest, %pasture), p(.)	156.06	1.95	0.19	0.38	4	147.11
ψ(%forest, %wetland), p(.)	158.11	4.00	0.07	0.14	4	149.16
Site-2, 26 camera stations						
Puma (12 detections, 7 stations)						
ψ(Dist.Water, Dist.Settl), p(.)	80.55	0.00	0.58	1.00	4	70.65
ψ(Dist.Settl, %wetland), p(.)	82.73	2.18	0.20	0.33	4	72.83
ψ(Dist.Water), p(.)	84.39	3.84	0.09	0.15	3	77.30
ψ(%wetland), p(.)	84.79	4.24	0.07	0.12	3	77.70
ψ(Dist.Settl.), p(.)	86.10	5.55	0.04	0.06	3	79.01
Ocelot (23 detections, 12 stations)						
ψ(.), p(.)	132.05	0.00	0.99	1.00	2	127.53

Table 3.2 Estimates of β coefficient values, their associated standard errors (SE), and summed Akaike weights (W) for covariates that influenced occupancy (ψ) and probability of detection (p) of jaguars, pumas, ocelots and jaguarundis across two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia. Dist.=Distance; Settl.=Settlements. * Denotes covariates with robust impact (β ± 1.96xSE not overlapping 0)

	Jaguar			**Puma**			**Ocelot**			**Jaguarundi**		
	β	SE	W	β	SE	W	β	SE	W	β	SE	W
Site-1 (47 stations)												
ψ.%Wetland	3.06*	1.32	0.99	-	-	-	-	-	-	0.45	0.40	0.27
ψ.%Pasture	-0.31	0.99	0.19	-1.01*	0.51	0.46	-1.20*	0.48	0.98	-1.93*	0.86	0.90
ψ.Dist.Water	-0.15	0.74	0.18	-1.09*	0.54	0.61	-	-	-	-	-	-
ψ.Forest	-	-	-	1.03*	0.48	0.39	0.29	0.43	0.26	0.43	0.39	0.26
ψ.Prey>10kg	-	-	-	0.60	0.37	0.24	-	-	-	-	-	-
p. roads	3.09*	1.10	0.99	-	-	-	0.85	0.44	0.98	-	-	-
Site-2 (26 stations)												
ψ.Dist. Settl.	-	-	-	1.61	0.86	0.82	-	-	-	-	-	-
ψ.Dist. Water	-	-	-	-1.82	0.99	0.67	-	-	-	-	-	-
ψ.%Wetland	-	-	-	-0.09	0.05	0.27	-	-	-	-	-	-

The goodness of fit test for global standard occupancy models for all species indicated no overdispersion, with c values < 1 and p values > 0.05. Species average ψ and p values ranged between 0.27 and 0.67 for ψ; and between 0.24 and 0.35 for p (Table 3.6, Supporting Information). Analyses on species interactions indicate significant co-occurrence (ϕ 95% CI > 1) between jaguars and pumas, pumas and jaguarundis, and ocelots and jaguarundis (Table 3.3).

Table 3.3 Species interaction factors (ϕ) between pairs of cat species across two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia. SE=Standard error, CI=Confidence interval. * denotes significant interactions as the confidence intervals do not overlap 1. We could not assess interactions involving jaguars and jaguarundis at Site-2 due to the low numbers of captures we obtained for these two species.

	ϕ	SE	95% CI
Site-1 (47 stations)			
Jaguar & Puma	1.93*	0.33	1.38-2.69
Jaguar & Ocelot	0.93	0.27	0.53-1.63
Jaguar & Jaguarundi	0.91	0.58	0.26-3.21
Puma & Ocelot	1.01	0.36	0.50-2.03
Puma & Jaguarundi	2.05*	0.72	1.03-4.07
Ocelot & Jaguarundi	1.47*	0.27	1.02-2.12
Site-2 (26 stations)			
Puma & Ocelot	0.86	0.59	0.22-3.33

3.5 Discussion

As agriculture continues to expand causing habitat loss and degradation across the tropics, there is an urgent need to understand how to achieve conservation of keystone species like the felids across increasingly human dominated landscapes, as the latter are key to ensure their distribution and connectivity beyond protected areas (Karanth & Chellam, 2009; Rabinowitz & Zeller, 2010; Crooks et al., 2011; Boron et al., 2016b). Neotropical felid populations are declining with important ecological consequences (Estes et al., 2011, Galetti & Dirzo, 2013). Our results inform strategies to reconcile development with their conservation and highlight that (1) it is key to maintain wetlands and forests to conserve these cats across agricultural landscapes, (2) loss of natural habitat cover beyond 50-60% may be unsustainable for their conservation, (3) the expansion of oil palm plantations is a growing threat for felids (4) pastures have no conservation value for felids and should be targeted for future agricultural expansion, (5) the four felids did not display any spatial segregation, thus conservation strategies aimed to simultaneously benefit this guild are possible even in modified landscapes.

3.5.1 Factors affecting species habitat use

Wetlands emerged as a key habitat for jaguars and the only variable that influenced their occupancy. Jaguars inhabit a variety of ecosystems but generally prefer forests and water-dominated habitats (Crawshaw Jr & Quigley 1991; Foster et al. 2010; Zeller et al. 2011; De Angelo et al. 2011; De Angelo et al. 2013). The expansion of the cattle ranching and oil palm agro-industries restricted forests to only 12% of Site-1 and increased human disturbance. Consequently, important jaguar prey such as capybaras, peccaries, tapirs (*Tapirus terrestris*), and deer (*Mazama* sp.) (Foster et al., 2010; Polisar et al., 2003), has been depleted due to both habitat loss and hunting (Rodríguez-Mahecha et al., 2006) and indeed exerted no effect on jaguar occupancy. Hence it is likely that jaguars use wetlands to complement their diet with aquatic prey such as caimans (*Caiman crocodilus*) and turtles (*Podocnemis* and *Trachemys* sp.) (Da Silveira et al., 2010), indicating that preserving this habitat is crucial for jaguar survival. Although we did not uncover any significant effect of top-down anthropogenic threats, on average jaguars were recorded across stations with 59% natural habitat cover, which provides an indication of acceptable habitat loss thresholds.

At Site-1 pumas were associated with forest cover while they avoided pastures, suggesting that to conserve the species it is key to maintain forest habitat in modified landscapes. At Site-2 puma occupancy was affected negatively by proximity to settlements, albeit not strongly, and at both sites pumas displayed affiliation with water courses. The puma tends to be considered more habitat generalist than the jaguar (Scognamillo et al., 2003; De Angelo et al., 2011; Sollmann et al., 2012). However, pumas also tend to avoid modified areas and human activity, and prefer forests (Paviolo et al. 2009; Di Bitetti et al. 2010; Foster et al. 2010; De Angelo et al. 2011; Davis et al. 2011), which concurs with our findings. The fact that no variable had a robust effect on pumas occupancy at Site-2 could be due to the lower degree of habitat transformation at this site, showing that species may display stronger habitat selection in more modified landscapes as the value of remaining natural areas for species survival increases. However, it could also be caused by the lower survey effort at this site, and the different time of year.

Ocelots and jaguarundis are generally considered ecologically plastic and more tolerant to habitat loss and degradation than the larger felids (Bitetti et al., 2006; Kolowski and Alonso, 2010; Lyra-Jorge et al., 2008; Michalski et al., 2006). Accordingly, the ocelot was the only cat species recorded in oil palm plantations even if seldomly. There have been previous records of ocelots using oil palm areas (Boron & Payan, 2013; Pardo & Payan, 2015) possibly because the latter have rodent prey and are suitable for hunting due to the open visibility, as found for the leopard cat *Prionailurus bengalensis* (Rajaratnam et al., 2007). However, despite their presumed habitat plasticity, both ocelots and jaguarundis were negatively and strongly affected by pastures at Site-1, which supports earlier findings showing that they favour more natural habitats such as forest and riparian habitats while avoiding human disturbance (Di Bitetti et al., 2008; Giordano, 2015; Massara et al., 2015).

Similarly to pumas, ocelots were more habitat generalists at Site-2, and it could be due to the same reasons (lower degree of habitat transformation of this site, and/or different time of year and survey effort).

3.5.2 Interspecies interactions

Interspecies interactions are stronger between species of similar body mass and overlapping prey preferences, and spatial, temporal, and/or diet segregation can improve co-existence (Donadio & Buskirk, 2006). At the larger scale, puma population sizes seem low where jaguars are abundant and vice versa (Rabinowitz & Nottingham, 1986; de Azevedo & Murray, 2007; Kelly et al., 2008). However, when the two cats are sympatric, their habitat use is similar and segregation tends to be temporal or dietary, rather than spatial (Scognamillo et al. 2003; Harmsen et al. 2009; Foster et al. 2010; Foster et al. 2010b; Di Bitetti et al. 2010). This agrees with our findings of spatial co-occurrence and it is possible that segregation occurs at the diet level with jaguars predating mainly on aquatic prey, while pumas on remaining terrestrial one.

Mesocarnivores like ocelots and jaguarundis may be negatively affected by top predators and succeed when larger predators are rare or absent through phenomena of mesopredator release (Crooks & Soulé, 1999; Moreno et al., 2006; Bianchi et al., 2010). However, ocelots can also thrive in large protected areas with better habitat quality inhabited by top predators (Massara et al., 2015), and both ocelots and jaguarundis can be positively associated with jaguars and/or pumas (Di Bitetti et al., 2010). Accordingly, we found that jaguarundis tend to co-occur with both ocelots and pumas. This co-occurrence could be favoured by temporal segregation as jaguarundis are diurnal, whereas pumas and ocelots mostly crepuscular and nocturnal (Di Bitetti et al., 2010; Harmsen et al., 2011). Overall, the lack of any spatial segregation between species indicates that their distributions can overlap, thus developing conservation strategies to simultaneously benefit this guild is possible even in modified landscapes.

3.5.3 Methodological considerations

We investigated habitat use at a fine scale and within home range. However, habitat selection takes place at a variety of spatial and temporal scales ranging from distribution and home range selection to habitat use within home range (Johnson, 1980; Strampelli, 2015; Sunarto et al., 2012). Therefore extending survey efforts to larger areas and longer periods of time is important, as it would allow exploring different scales and temporal variations. Even more crucial is to continue studying species habitat use across human modified areas to understand their habitat requirements and tolerance limits. Our findings on pumas and ocelots could suggest that species habitat selection may be stronger in such areas, increasing the potential of detecting habitats that are important for them. However, this needs further investigation.

Using OBIA produced highly accurate land cover maps and covariates, nevertheless felids are naturally elusive hence using occupancy modeling to take into account imperfect detection is important to reduce survey bias. Our study also showed that all else being equal, cat species with the exceptions of pumas are more likely to be detected by cameras placed on roads and established trails, thus incorporating this covariate is important to reduce bias. Finally, we are aware that felids are wide-ranging, however our survey design was suitable to study within home range habitat use by felids (Davis et al. 2011; Sunarto et al. 2012; Alexander et al. 2015; Everatt et al. 2015; Strampelli 2015). Our models showed no over dispersion, suggesting that our data was not affected by spatial autocorrelation. Furthermore, the identification of individual jaguars and ocelots shows that adjacent cameras never recorded the same assemblage of individuals.

3.5.4 Conclusion

Unprotected and increasingly human modified areas are crucial for species long-term survival, and especially for wide-ranging carnivores, thus it is important to understand how to achieve conservation there. Pasture is the main land cover in Colombia (Etter et al., 2006) and it had a significantly negative effect for all of pumas, ocelots, and jaguarundis. Therefore our work demonstrated that in order to achieve felid conservation, oil palm expansion, when inevitable, should be targeted to already modified areas such as pastures to minimise the loss of natural habitats (Garcia-Ulloa et al., 2012). Concurring results were documented for other taxa (Gilroy et al., 2014; Prescott et al., 2016). We did not find an effect of oil palm, which could be because it still covers a small proportion of the landscape (19% at Site-1 and 2% at Site-2). Nevertheless jaguars, pumas, and jaguarundis were never detected in oil palm areas and all felids were recorded at points surrounded by an average 50-60% natural habitat cover. Consequently agricultural and oil palm expansion is an emerging threat and may cause unsustainable habitat conversion.

A stronger regulatory framework could facilitate land use planning and incentive-based approaches such as landscape certification and green markets can encourage the preservation of natural areas within productive landscapes (Lambin et al., 2014; Boron et al., 2016a). However, to conserve predator species across human-use areas, habitat preservation needs to be complemented by other actions such as limiting hunting of their prey, and reducing conflict and retaliatory killing (Inskip & Zimmermann, 2009). Finally, these predators did not display any spatial segregation and either overlapped or occurred at random, demonstrating that strategies to simultaneously conserve this guild are feasible also in ever increasing tropical agricultural landscapes.

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3.8 Supporting Information

Table 3.4 Land cover composition of the two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia, extracted using Object Oriented Image Analysis on three Landsat 8 images, and the e-Cognition software.

Land cover types	**Site-1**	**Site-2**
Pasture	35%	36%
Wetlands	20%	34%
Oil palm	19%	2%
Forest	12%	19%
Water	10%	6%
Bare ground	3%	2%
Roads and settlements	<1%	<1%

Table 3.5 Average land cover composition of camera stations detecting each cat species, and of all stations across two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia.
Land cover types were extracted using an 800 m buffer around camera stations. We do not report data for jaguars and jaguarundis at Site-2 due to low numbers of captures we obtained for these two species. SE=Standard error, Tot.=total, Anthr.=anthropogenic.

	Jaguar		**Puma**		**Ocelot**		**Jaguarundi**		**All stations**	
	Value	SE	Value	SE	Value	SE	Value	SE	Value	SE
Site-1 (47 stations)										
Wetland (%)	44.8	6.9	34.5	6.4	31.3	6.1	38.6	7.8	26.3	3.5
Secondary Forest (%)	14.2	3.4	17.4	4.2	18.3	3.2	19.7	4.3	13.4	1.9
Palm Oil (%)	19.0	5.5	24.2	5.8	29.0	5.0	29.2	4.4	26.1	3.3
Pasture (%)	15.9	3.8	17.8	6.1	14.3	3.7	8.3	3.0	25.7	3.6
Water (%)	5.1	3.3	4.6	1.8	5.8	2.7	3.5	2.0	6.0	1.8
Tot. Natural habitat (%)	59.0		51.9		49.6		58.3		39.7	
Tot. Anthr. habitat (%)	34.8		42.1		43.3		37.6		51.8	
Site-2 (26 stations)										
Wetland (%)	-	-	24.7	4.1	33.4	6.9	-	-	38.1	4.2
Secondary Forest (%)	-	-	49.5	6.6	35.8	7.1	-	-	31.2	4.4
Palm Oil (%)	-	-	1.9	1.8	5.9	3.3	-	-	3.1	1.4
Pasture (%)	-	-	21.5	4.0	21.3	2.4	-	-	24.0	2.6
Water (%)	-	-	0.8	0.4	1.3	0.6	-	-	2.3	0.6
Tot. Natural habitat (%)	-		74.2		69.2		-		69.3	
Tot. Anthr. habitat (%)	-		23.4		27.2		-		27.1	

Table 3.6 Model-averaged estimates of probability of site use (ψ), probability of detection (p), and associated standard errors (SE) for jaguars, ocelots, pumas, and jaguarundis across two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia.
We could not perform occupancy modeling for jaguars and jaguarundis at Site-2 due to the low numbers of captures we obtained for these two species.

	ψ	**SE**	**p**	**SE**
Site-1 (47 stations)				
Jaguar	0.42	0.05	0.26	0.04
Ocelot	0.67	0.04	0.32	0.06
Puma	0.31	0.01	0.42	0.06
Jaguarundi	0.27	0.01	0.35	0.06
Site-2 (26 stations)				
Puma	0.33	0.06	0.24	0.07
Ocelot	0.53	0.03	0.35	0.06

4. The consequences of agricultural and oil palm expansion on mammal species and communities in rural landscapes of Colombia.

To be submitted:

Boron V., Xofis P., Quiñones-Guerrero A., Link A., Payan E., Tzanopoulos J. Conserving predators across tropical agricultural landscapes: habitat use and interactions by four sympatric felids in Colombia.

4.1 Abstract

As agricultural and human-modified landscapes are increasing in the tropics, it becomes crucial to understand how they affect mammal species and communities and how to reconcile conservation with development in these areas. We combined land cover information and camera trapping data to investigate the effects of agricultural and oil palm expansion on terrestrial mammal species and communities in rural landscapes in Colombia. We estimated medium-large mammal species diversity, evenness, and richness across two agricultural areas with cattle ranching and oil palm cultivation; explored what environmental variables influence richness; and investigated species associations with environmental variables using Canonical Correspondence Analysis. We also assessed whether jaguars, a declining keystone and flagship species, are a good umbrella species for terrestrial mammal richness. Results highlight that modified and agricultural regions display lower species diversity and evenness, and higher dominance than more pristine sites. Remaining forests had a strong positive effect on species richness and should be conserved. Most mammal species were either affected negatively by oil palm and pasture or showed affinity to only low-intermediate levels of these land cover types, hence retaining natural areas across agricultural landscapes is crucial for mammal conservation. Overall oil palm plantations expansion represent a threat for Neotropical mammals and should be targeted to already modified pastures, which displayed limited conservation value. Finally jaguars were a good umbrella species, thus any conservation effort focused on this species would additionally benefit the wider mammal community. In face of a rapidly expanding agriculture in the tropics, this study provides valuable information to inform land use planning and the design of conservation policies.

4.2 Introduction

Agricultural expansion is driving severe habitat loss and degradation, threatening biodiversity worldwide (Foley et al., 2005; Green et al., 2005; Tscharntke et al., 2012; Maxwell et al., 2016). Consequently reconciling biodiversity conservation with increasing agriculture is an urgent and challenging priority, especially across tropical countries, which are undergoing considerable land cover change and are extremely rich in biodiversity (Gibbs et al., 2010; Laurance et al., 2014). Amongst agricultural sectors, oil palm *Elaeis guineensis* cultivation is particularly concerning because it is an emerging land use in the Neotropics, including Colombia (Butler & Laurance, 2009; Pacheco, 2012; Castiblanco et al., 2013), and it has alarming consequences on biodiversity (Danielsen et al., 2009; Fitzherbert et al., 2008; Yue et al., 2015), yet its impact on Neotropical mammals remains understudied (Boron & Payan, 2013; Pardo & Payan, 2015; Pardo et al., 2015). Colombia is now the 4th largest palm oil producer (Castiblanco et al., 2013), but it is also a megadiverse country, covering 0.7% of the planet and hosting 10% of its known biodiversity (Mittermeier et al., 1997). It displays the greatest mammal diversity (447 species), after Indonesia, Peru, Mexico, and Brazil (Rodríguez-Mahecha et al., 2006).

Mammals in tropical ecosystems are a conservation priority because they are decreasing in abundance due to habitat loss and hunting (Schipper et al., 2008; Visconti et al., 2011) with important consequences for the ecosystems they inhabit. Mammal species play significant roles in ecosystem functioning, as they control herbivore populations, nutrient cycling, and carbon storage; disperse seeds; and ultimately maintain forest structure (Asquith & Mejía-Chang, 2005; Brodie et al., 2009; Jansen et al., 2010; Estes et al., 2011; Cavanaugh et al., 2014). Amongst mammals, large-bodied species like jaguars *Panthera onca* are even more vulnerable to extinction due to their slow population growth rates, and area and diet requirements (Crooks, 2002; Cardillo et al., 2005; Carbone et al., 2011).

Since protected areas are not viable for long-term mammal conservation and agricultural and human-modified landscapes are on the increase there is an urgent need to understand species requirements and how to achieve conservation in these areas (Woodroffe & Ginsberg, 1998; Crooks & Sanjayan, 2006; Karanth & Chellam, 2009; Crooks et al., 2011; Boron et al., 2016b). Data on mammal communities such as richness, eveness, and diversity measures are crucial to perform comparisons across space and time, and understand the impact of anthropogenic factors such as land use and land cover change (Rondinini et al., 2011; Ahumada et al., 2013). Richness indicates the number of species in a community; evenness is a measure on how different the abundances of the species in a community are from each other; and diversity takes into account both (Magurran, 2004). Finally, species may respond differently to disturbance (Crooks, 2002), hence besides community level parameters, it is also essential to study species habitat associations and within community variation.

The main aim of this paper is to investigate how agriculture and oil palm cultivation affect medium-large terrestrial mammal species and communities in rural landscapes in Colombia. More specifically we combine high-resolution land cover maps and camera trapping data, a standardized and increasingly-used survey methods for mammals (Rowcliffe & Carbone, 2008), to a) estimate medium-large mammal species diversity, evenness, and richness across two agricultural landscapes; b) understand what variables influence the latter and test whether jaguars, a declining

(Caso et al. 2008) keystone and flagship species, are a good umbrella species for terrestrial mammal richness; c) investigate intra-community variation and species associations with environmental variables through multivariate analysis. The study areas include cattle ranching, a traditional land use in the Neotropics (Grau & Aide, 2008) and oil palm cultivation.

4.3 Methods

4.3.1 Study area

We conducted the study at two sites in Colombia: Site-1 (7.3752N -73.8842E to 7.5404N -73.7118E) and Site-2 (5.3450N -72.8471E to 5.4365N -72.7607E) (Fig. 4.1). Both sites are situated in the central part of the Magdalena River valley, in between the Central and Eastern Andes, in the Department of Santander, Colombia. The study area is part of the tropical forest biome and it is rich in wetlands (IDEAM et al., 2007). Mean annual temperature is 27℃, and annual precipitation ranges between 2100-2600 mm (IDEAM et al., 2007). Land is primarily private and there are no national protected areas.

The region is considered an important area for several species including jaguars (Payan-Garrido et al., 2013) and it hosts endangered and endemic species like the brown spider monkey (*Ateles hybridus* ssp. *brunneus*) and the white-footed tamarin (*Sanguinos leucopus*). However, most of the region's historical forest cover has been lost due to the expansion of the cattle ranching and oil-palm agro-industries, and the remaining natural areas are at risk of conversion (Etter et al., 2006; Castiblanco et al., 2013; Link et al., 2013).

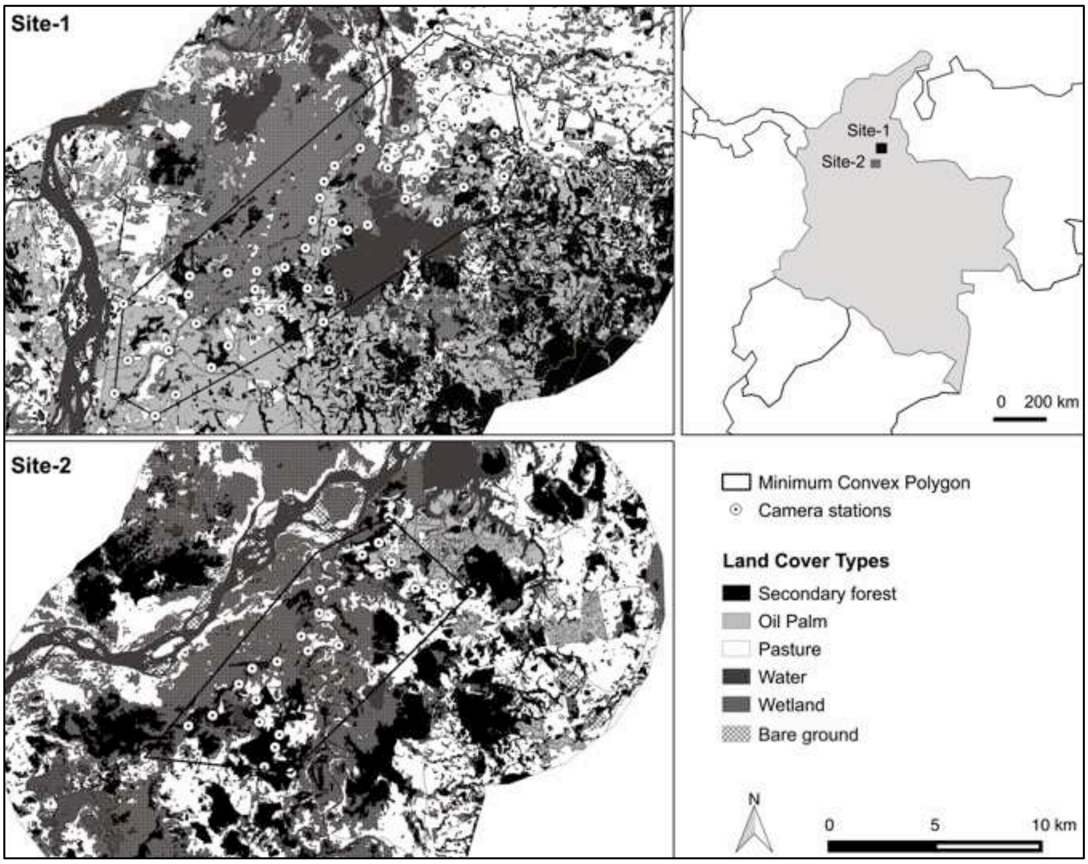

Fig. 4.1 Study map of the two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia with land cover types and camera trap stations.

Site-1 is more modified since coverage of natural habitats reaches only 32%, whereas 53% at Site-2. Main land cover types comprise secondary forest (12% at Site-1, 19% at Site-2), wetlands (20% at Site-1, 34% at Site-2), pastures (35% at Site-1, 36% at Site-2), and oil-palm plantations (19% at Site-1, 2% at Site-2) (Fig. 4.1). The straight-line distance between the two study sites is 93 km. We chose these two sites because they include cattle ranching and oil palm plantations, but still host top predators like jaguars and pumas *Puma concolor* as well as other declining terrestrial mammal species. In addition to habitat loss several mammals are threatened by hunting, which occurs in the region for both subsistence and commercial reasons (Rodríguez-Mahecha et al., 2006).

4.3.2 Camera trapping

We placed 47 camera stations between April and August 2014 at Site-1 and 26 stations between September and December 2014 at Site-2. The minimum convex polygons connecting the camera stations were 154.8 km^2 and 85.4 km^2 at Site-1 and Site-2 respectively. We set-up the cameras following standardized survey techniques for terrestrial mammals, in a grid at intervals of 1.6±0.3 km, and across all main regional land cover types: forests, wetlands, pastures, and oil palm plantations (Ahumada et al., 2011, 2013; Rovero et al., 2014) (Fig. 4.1). When possible, we placed the cameras so that their field of view would be facing a wildlife trail to optimize detection of multiple mammals at once (Cusack et al., 2015). Nineteen (73%) and 28 (60%) stations were placed on trails at Site-1 and Site-2 respectively and we took this into account in our modelling approach. Camera traps are consistently able to detect terrestrial mammals ≥ 0.5 kg, which are commonly referred to as medium-large (Rovero et al., 2010). We deployed Cuddeback Attack (model 1149) and Ambush (model 1170) camera traps and secured them to a tree at a height of 35 cm from the forest floor. Both camera models have the same trigger speed (0.25 seconds) and were triggered only at distances <3-4 m due to the high temperatures of the region.

4.3.3 Species richness, diversity, and evenness

We produced species accumulation curves, Shannon diversity and evenness indices, and the Berger–Parker dominance index (D) from mammal species occurrences and species counts (Magurran, 2004; Ahumada et al., 2011) using EstimateS (Colwell, 2013) for Site-1 and Site-2 separately. Species accumulation curves are useful to compare sites/communities across space and time as they display species richness as a function of increasing sampling effort. The curves reach an asymptote once all detectable species have been recorded and were produced using the rarefaction method with 1000 randomizations (Magurran, 2004; Ahumada et al., 2011).

To control for uneven sampling efforts amongst sites we defined species counts as integer capture rates, and calculated them using the total number of independent capture events of that species divided by the number of trap-nights (TN) and expressed as integer records per 100 trap nights (Carbone et al., 2001; O'Brien et al., 2003). Independent capture events were described as consecutive photographs of individuals of the same species taken more than 12 hrs apart for gregarious species (i.e. capybaras *Hydrochoerus isthmius,* and collared peccaries *Pecari tajacu*) and more than 30 min apart for all other species (O'Brien et al., 2003). We are aware that capture rates may not reflect real abundance, however they still provide more information than just incidence records (Carbone et al., 2001; Sollmann et al., 2013).

4.3.5 Determinants of species richness

We investigated the effect of different environmental variables on species richness using linear mixed-effects models. We performed the analysis at the scale of the camera trap station (Rovero et al., 2014), analysed both sites jointly, and discarded camera traps that had been active for less than 30 days. To account for the fact that not all cameras stations were placed on roads/established trails we included it as a dummy variable. We hypothesized that the proportion of forests and wetlands, canopy cover, and the proximity to water would affect species richness positively, whereas vicinity to settlements and proportion of pasture and oil palm negatively. We further included jaguar capture rates at each station to explore whether jaguars are an umbrella species for mammal richness.

To generate the environmental covariates we used a land cover map we produced with Object Oriented Image Analysis (OBIA) (Bock et al., 2005) in eCognition Developer 9 on three Landsat 8 images, captured on 4/1/2015, 9/3/2015, and 12/7/2015 (downloaded from www.usgs.gov). For more details on the land cover mapping refer to Chapter 3. Following, we extracted the proportion of each land cover type around camera stations in ArcMap 10.3, using a buffer of 800 m, which is half the average distance between neighbouring camera stations (Sollmann et al., 2012). Finally, we measured the distance of each camera station to water and settlements using again ArcMap 10.3. Canopy cover was measured *in situ* using percentages.

We carried out the analysis using R (R Development Core Team, 2013) and maximum likelihood mixed effect models with Poisson error distribution in the lme4 package (Bates et al., 2016). Before running the models we tested for collinearity amongst covariates using a cut-off value of r = 0.7 (Dormann et al., 2013) and rescaled variables to have a mean of 0 and standard deviation of 0.5 (Gelman, 2008). We compared models using the Aikake Information Criteria adjusted for small sample size (AICc) (Burnham & Anderson, 2002). To understand which variables had a robust effect on species richness we estimated the averaged parameter estimates (Betas), their standards errors and confidence intervals through model averaging, using the MuMIn R package (Barton, 2016) and restricting the models set to ΔAICc<4 (Bolker et al., 2009; Tollington et al., 2015). We only retained covariates whose β coefficients sign made sense biologically and considered covariates to have a robust effect on species richness if $\beta \pm 1.96 \times SE$ did not overlap zero (Burnham & Anderson, 2002; Zuur et al., 2010). To assess the relative importance of explanatory variables we report their cumulative weights, obtained summing the Akaike weights across all models that contained the variable. Finally, to ensure that our results were not affected by spatial autocorrelation, we performed Moran's I test in ArcMap 10.3.

4.3.6 Canonical correspondence analysis

To study the effect of different environmental variables on the mammal community, we employed canonical correspondence analysis (CCA), a unimodal constrained ordination method using the CANOCO version 5 software (ter Braak & Šmilauer, 2012; Šmilauer & Lepš, 2014). Species counts were expressed as integer capture rates to control for uneven sampling efforts amongst camera stations. As for species richness, we analysed Site-1 and Site-2 together and discarded camera traps that had been active for less than 30 days. We further eliminated species detected at only one station. Through CCA we constrained species scores to linear combinations of the explanatory variables and maximized the dispersion of these scores (ter Braak, 1986; Jongman et al., 1995). Similarly to richness analysis, we tested the effect of the proportion of forests and wetlands, pasture and oil palm around camera stations (800 m buffer), and the proximity to water and settlements to camera stations. We deployed the forward selection option of Canoco and tested variables' significance by Monte Carlo simulations with 999 permutations (Legendre et al., 2011; ter Braak & Šmilauer, 2012; Šmilauer & Lepš, 2014).

4.4 Results

The total sampling effort resulted in 3069 and 1903 trap nights at Site-1 and Site-2 respectively. We recorded 19 medium-large mammal species at Site-1 and 20 at Site-2 of different global and regional threat categories (Table 4.1). The order Carnivora displayed the highest number of species. Species capture events varied from 1 to 648, with the crab-eating fox (*Cerdocyon thous*) and the Central American agouti (*Dasyprocta punctata*) being the most frequently recorded species at both sites (Table 4.1). Species accumulation curves indicate that we likely recorded all species at Site-1, whereas a larger sampling effort would have enabled to record more species at Site-2 since the curve does not reach an asymptote (Fig. 4.2).

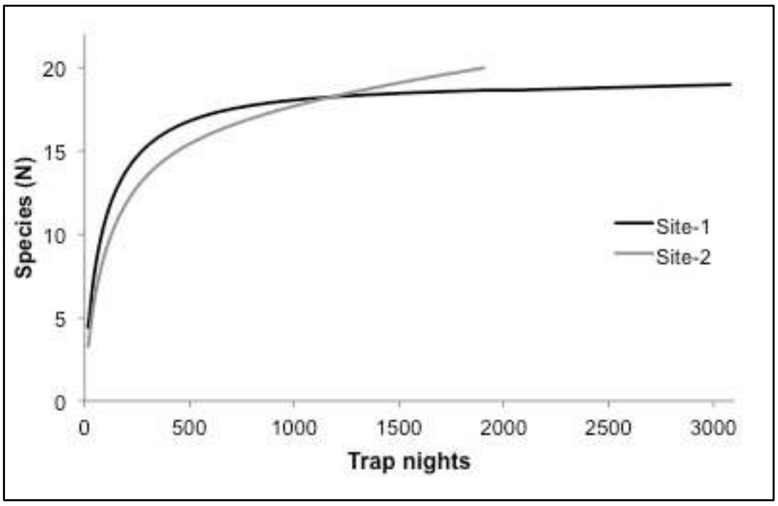

Fig. 4.2 Species accumulation curves across two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia.

Table 4.1 Mammal species recorded across two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley of Colombia, their numbers of capture events (CE), capture rates (CR) in brackets, and IUCN (2015) and Regional Red List (Rodriguez-Mahecha et al. 2006) categories. DD= Data Deficient, LC= Least Concern, NT= Near Threatened, VU= Vulnerable, EN= Endangered.

Scientific name	Common name	IUCN Red List	Regional Red List	Site-1 CE (CR)	Site-2 CE (CR)
Carnivora					
Cerdocyon thous	Crab-eating fox	LC	/	648 (21.11)	121 (6.38)
Eira barbara	Tayra	LC	/	24 (0.78)	14 (0.73)
Galictis victata	Greater grison	LC	/	0	1 (0.05)
Herpailurus yagouaroundi	Jaguarundi	LC	/	42 (1.37)	1 (0.05)
Leopardus pardalis	Ocelot	LC	NT	79 (2.57)	33 (1.73)
Panthera onca	Jaguar	NT	VU	140 (4.56)	7 (0.36)
Procyon cancrivorus	Crab-eating raccoon	LC	/	116 (3.78)	53 (2.78)
Puma concolor	Puma	LC	NT	44 (1.43)	17 (0.89)
Cetartiodactyla					
Pecari tajacu	Collared peccary	LC	/	8 (0.26)	3 (0.16)
Didelphimorphia					
Didelphis marsupialis	Common opossum	LC	/	16 (0.52)	4 (0.21)
Lagomorpha					
Sylvilagus floridanus	Eastern cottontail	LC	/	1 (0.03)	0
Pilosa					
Myrmecophaga tridactyla	Giant anteater	VU	VU	10 (0.33)	2 (0.11)
Tamandua tetradactyla	Northern tamandua	LC	/	7 (0.23)	7 (0.37)
Primates					
Cebus versicolor	Varied capuchin	EN	/	42 (1.37)	11 (0.58)
Alouatta seniculus	Red howler monkey	LC	/	0	1 (0.05)
Rodentia					
Hydrochoerus isthmius	Lesser capybara	DD	/	10 (0.33)	16 (0.84)
Cuniculus paca	Lowland paca	LC	/	23 (0.75)	20 (1.05)
Dasyprocta punctata	Central American agouti	LC	/	179 (5.83)	119 (6.25)
Proechymis chrysaeolus	Spiny rat	DD	/	5 (0.16)	13 (0.68)
Sciurus granatensis	Red-tailed squirrel	LC	/	40 (1.30)	30 (1.58)
Xenarthra					
Dasypus novemcinctus	Nine-banded armadillo	LC	/	17 (0.55)	1 (0.05)
Total N. of species				**19**	**20**

Overall Site-2 displayed moderately higher Shannon diversity (2.23 vs. 2.00) and evenness (0.74 vs. 0.68) and lower dominance (0.21 vs. 0.45) than Site-1. Robust predictors of species richness were the distance from water (negative effect, w=0.90), the proportion of remaining forest (positive effect, w=0.87), and jaguar capture rates (positive effect, w=0.93). The latter indicates that the jaguar is a good umbrella species for other terrestrial mammals. The proportion of pasture also had an effect on richness, albeit not robust (negative effect, w=0.72) (Table 4.2). Model selection results are available in the Supporting Information (Table 4.4). The Morans'I test showed no spatial autocorrelation at either site (Site 1: Index=0.14, Z score=1.75, p=0.08; Site 2: Index=-0.26, Z score=-1.11, p=0.26).

Table 4.2 Estimates of β coefficient values, associated standard errors (SE), lower and upper confidence intervals (LCI and UCI), and summed Akaike weights (W) for covariates that influenced mammal species richness across two agricultural landscapes in the Magdalena river valley of Colombia. Robust explanatory parameters, where 95% confidence intervals do not overlap zero, are in bold.

Variables	**β**	**SE**	**LCI**	**UCI**	**W**
(Intercept)	1.29	0.12	1.06	1.53	
Jaguar capture rates	**0.31**	**0.12**	**0.07**	**0.56**	**0.93**
Distance to water	**0.47**	**0.20**	**-0.86**	**-0.09**	**0.90**
Forest (%)	**0.52**	**0.22**	**0.09**	**0.95**	**0.87**
Pasture (%)	-0.44	0.22	-0.88	0.01	0.72
Oil palm (%)	0.22	0.25	-0.28	0.72	0.41
Wetland (%)	-0.22	0.30	-0.81	0.36	0.28
Canopy cover (%)	-0.10	0.13	-0.37	0.16	0.19

CCA revealed that 18.3% of community variation is explained by the variables we considered (Table 4.3). The proportion of oil palm (p=0.008), pasture (p=0.002), wetland (p=0.003), and the distance from water (p=0.015) were all significant variables in explaining the interspecific differences in distribution of the mammal community and accounted for 15.0% of total variation.

Table 4.3 Results of Canonical Correspondence Analysis on the mammal community across two agricultural landscapes in the Magdalena river valley of Colombia.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.27	0.23	0.16	0.07
Explained variation (cumulative)	6.37	11.80	15.64	17.35
Pseudo-canonical correlation	0.76	0.66	0.58	0.51
Explained fitted variation	34.82	64.49	85.47	94.82

Jaguars and capybaras showed strong relationships with wetland habitats and were negatively affected by pastures, oil palm, and distance to water. Jaguarundis *Herpailurus yagouaroundi*, ocelots *Leopardus pardalis*, and giant anteaters *Myrmecophaga tridactyla* were favoured by intermediate availability of wetlands. Jaguarundis were also negatively affected by pastures and distance to water, whereas ocelots and giant anteaters favoured low levels of pasture, but were negatively associated with oil palm, and were found at small and medium distances to water (Fig. 4.3).

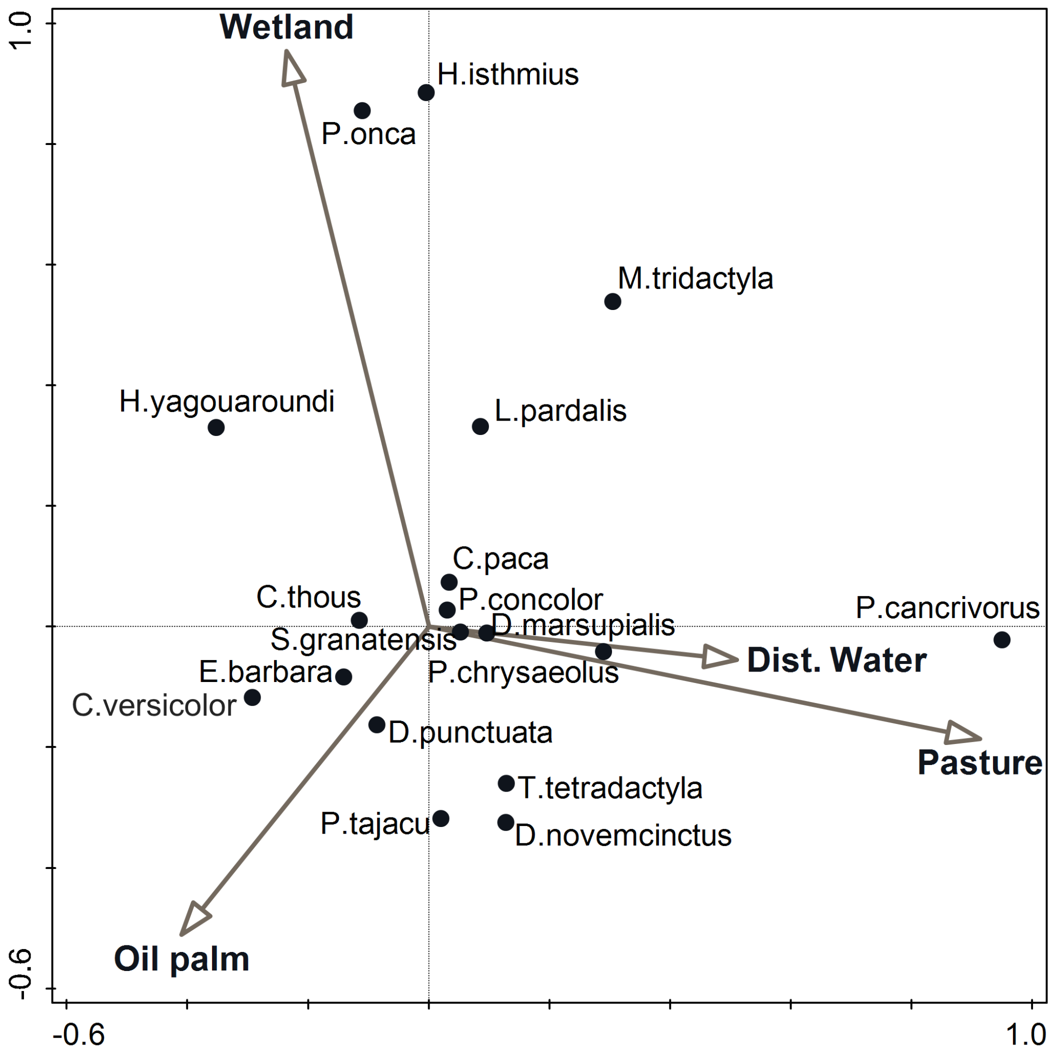

Fig. 4.3 Results of Canonical Correspondence Analysis on the mammal community across two agricultural landscapes in the Magdalena river valley of Colombia. The relative importance of the significant environmental variables is revealed by their vectors' length.

Species like agoutis, collared peccaries, varied capuchins *Cebus versicolor*, tayras *Eira barbara*, crab-eating foxes, lesser anteaters *Tamandua tetradactyla,* and armadillos *Dasypus novemcintus* showed affiliation to low-intermediate levels of oil palm. All these species with the exception of the crab-eating fox were also negatively associated with wetlands. Furthermore crab-eating foxes, tayras, agoutis, and varied capuchins were negatively associated with pastures and distance to water, while peccaries, lesser anteaters, and armadillos favoured low-intermediate levels of pastures and preferred small to medium distances from water (Fig. 4.3).

A group of species, namely the common opossum *Didelpphis marsupialis,* the red-tailed squirrel *Sciurus granatensis*, the paca *Cuniculus paca*, and the puma showed limited affiliation or aversion to any of the variables. Finally, crab-eating raccoons *Procyon cancrivorus* and spiny rats *Proechymis chrysaeolus* displayed high and medium affinity to pasture respectively, and aversion to oil palm and wetlands. Overall, all species with the exception of crab-eating raccoons were either negatively associated to oil palm and pasture or displayed affinity to only low to intermediate levels of these land cover types (Fig. 4.3).

4.5 Discussion

As agricultural and human-modified landscapes are on the increase in the tropics it becomes crucial to understand how they affect species and communities and how to achieve conservation in these areas. Mammals are a key component of tropical forests yet they are declining (Schipper et al., 2008; Visconti et al., 2011). By combining land cover information and camera trapping data we produced the first systematic study on Neotropical mammals across agricultural landscapes with oil palm cultivation. Our results highlight that: modified landscapes display lower species diversity and evenness, and higher dominance than more pristine sites; remaining forest areas across modified landscapes have a robust and positive effect on species richness and should therefore be conserved; preserving natural areas across agricultural regions is crucial also because most species were either negatively affected by oil palm and pasture or only displayed limited affinity to these land covers; new oil palm plantations should be targeted to already modified pastures, which displayed limited conservation value. Lastly, our study demonstrated that jaguars are a good umbrella species for other terrestrial mammals.

4.5.1 Species richness and community structure

The number of terrestrial mammal species we recorded in these two agricultural landscapes with 1900 TN survey effort, was 19 at Site-1 and 20 at Site-2, which is comparable to other sites in the Amazon in Colombia (19 sp.; 1793 TN) (Payan, 2009) and Brazil (21 sp; 1969 TN) (Ahumada et al., 2011); while higher than at the Volcan Barva Transect in Costa Rica (15 sp.; 1619 TN), which is situated in a highly fragmented landscape (Ahumada et al., 2011). However, we recorded less Near Threatened, Vulnerable and Endangered species than other studies (e.g. Tobler et al. 2008; Payan et al., 2009; Ahumada et al. 2011) and our species list mainly contains common species included in the Least Concern category.

If we consider larger sampling efforts (3000-4000 TN) the mammal species recorded across highly modified landscapes, such as our Site-1 (19 sp.) or an oil palm landscape in the Colombian Llanos (16 sp.) (Pardo & Payan, 2015), become fewer than in pristine areas such as the Peruvian Amazon (28 sp.) (Tobler et al., 2008). Since the species accumulation curve at Site-2 did not reach the asymptote, it is likely that with larger sampling effort we would have detected more species, confirming that less modified sites tend to host more species. While a sampling effort of 1800 TN is considered enough to detect >70% of species present in the landscape (Rovero et al., 2010), we recommend larger sampling efforts to perform robust comparisons.

These results indicate that agricultural landscapes with remaining natural habitat cover still hold some potential for medium-large mammal conservation (Daily et al., 2003; Cassano et al., 2012; Magioli et al., 2016) but maintaining forest areas is crucial since the proportion of forest surrounding camera points emerged as a significant predictor of species richness. Similarly, Magioli et al. (2016) conclude that maintaining connectivity in agricultural region is crucial to preserve functional mammal communities, while Prescott et al. (2016) highlighted the importance of retaining forests across Neotropical agricultural landscapes as they increase phylogenetic richness in bird communities. Jaguar capture frequency at camera stations also had a significant and positive effect on species richness, demonstrating that this large predator is a good umbrella species for other terrestrial mammals. This is in contrast to what reported by Caro et al. (2004) and it could be because the area the authors surveyed did not encompass sufficient habitat heterogeneity to detect differences in species richness and/or jaguar use. Our data complements what reported by Thornton et al. (2016), which show that the jaguar network of populations and corridors overlaps with larger amounts of interior and high-quality habitat than random networks, benefiting other terrestrial mammals.

Site-1 is more modified than Site-2 and displayed lower species diversity (2.0 vs. 2.2) and evenness (0.68 vs. 0.74) while higher dominance (0.45 vs. 0.21). Furthermore, both our sites displayed lower diversity and evenness, and much higher dominance than the values reported by (Ahumada et al., 2011) for each mammal community across the tropics (Diversity: 2.3-3.1; Evenness: 0.84-0.93; Dominance: 0.08-0.18). This is not surprising considering that both our study areas show high capture rates of a few very common species such as the crab-eating fox and the Central American agouti, which are resilient and adaptable to habitat degradation (Maffei & Taber, 2003; Naughton-Treves et al., 2003; Bogoni et al., 2016). These results confirm that habitat loss changes mammal communities, decreasing diversity and increasing dominance (Ahumada et al., 2011; Bogoni et al., 2016). The effect on species richness was not clearly evident and it could be because generalist species spread and/or colonise modified landscapes, as suitable niches become available (Ewers & Disham, 2006; Bogoni et al., 2016)

Keystone species and top predators like jaguars and pumas were recorded across both study areas, however, their prey community seems impoverished as all of armadillos, pacas, peccaries (*Pecari tajacu*), capybaras (*Hydrochoerus isthmius*), and deer (*Mazama* sp.) were absent or rare at both sites. Therefore it is likely that puma survival depends on smaller prey such as widespread agoutis, while jaguars rely on aquatic prey like caimans (*Caiman crocodilus*) and turtles (*Podocnemis* and *Trachemys* sp.) (Da Silveira et al., 2010).

4.5.2 Intra-community variation

The proportion of oil palm, pasture, wetland, and the distance from water were all significant variables in explaining the interspecific differences in distribution within the mammal community. Oil palm seems to represent a more concerning threat for some species than others. For example, jaguars, ocelots and important prey such as capybaras, pacas and giant anteaters were negatively affected by oil palm, while pumas and jaguarundis only showed minimum aversion to this crop. There have been previous records of jaguars, ocelots, and jaguarundis using certain oil palm areas but this was specific to a particular plantation where oil palm areas are interspersed in forest and wetland areas (Boron & Payan, 2013). Pardo and Payan (2015) examined a larger plantation and found concurring results: jaguars were absent, and pumas, and ocelots were rare. Conversely, mesopredators like tayras and crab-eating foxes, as well as other species like agoutis, collared peccaries, and varied capuchins showed affiliation to low-intermediate levels of this crop. Mesocarnivores and omnivores are generally considered more tolerant to oil palm and disturbance than larger carnivores due to their plasticity in habitat and resource use (Crooks, 2002; Cardillo et al, 2005; Rajaratnam et al., 2007; Bigoni et al., 2016).

Overall, oil palm should at best be limited to low-intermediate levels, proving that this expanding crop is an emerging threat for Neotropical mammals. Similar findings were documented in South East Asia, where oil palm plantations have been responsible for landscape homogenization and represent poor habitats for the majority of species (Fitzherbert et al., 2008; Danielsen et al., 2009; Yue et al., 2015). To lessen the impact of this crop and retain Neotropical medium-large mammals, its presence in the landscape should be limited and combined with natural habitats, such as forests and wetlands. For felid species natural habitat cover needs to extend on 50-60% of the landscape (Chapter 3) and further studies should assess these thresholds for all remaining mammals species to identify optimum levels of habitat conversion, and guide land use planning.

Only the crab-eating raccoon, a medium-bodied omnivore, showed affiliation for pasture, whereas all other mammal species were either negatively affected by pasture or tolerated low to medium levels of this land cover type. Similarly to what we documented for oil palm, these results suggest that in order to conserve mammals it is crucial to limit pastures to low-intermediate levels and highlight that pastures have limited conservation value for medium-large Neotropical mammals, as found for other taxa (Gilroy et al., 2015; Prescott et al., 2016). Finally, wetlands were extremely important for jaguars and capybaras while ocelots, jaguarundis, and giant anteaters showed moderate affinity for this habitat. Jaguars' association with wetlands is in line with results from Chapter 3 and previous evidence (Soisalo & Cavalcanti, 2006; Caso et al., 2008). The conservation of this top predator in the study region will ultimately depend on the preservation of these wetlands and the aquatic prey they host.

4.5.3 Conclusion

Unprotected and increasingly human modified areas are vital for species long-term survival and connectivity, thus it is important to identify suitable conservation strategies. Our results show that habitat loss changes medium-large mammal communities reducing diversity and increasing dominance. These effects may not have entirely unfolded yet and lead to extinction debts (Tilman et al., 1994). Species responded to disturbance differently: some were more vulnerable to agriculture and strongly connected to natural habitats (e.g. jaguars); others were extremely common and more resistant to disturbance (e.g. crab-eating foxes, crab-eating raccoons, Central American agouti). Such generalist species will persist longer in modified landscapes (Ewers & Didham, 2006; Bogoni et al., 2016). Findings also highlight that it is crucial to maintain forests since they had a significant impact on species richness. Furthermore, it is imperative to conserve natural habitat cover across agricultural and oil palm landscapes, as the majority of mammals were either negatively affected by oil palm and pasture or showed low to intermediate affiliation for these land cover types.

As oil palm expansion continues across the tropics, including Colombia, it is crucial to minimize its impact. In order to reconcile regional development with medium-large mammal conservation, a valuable solution is for the crop to expand on pastures, as we attested that they hold limited value for terrestrial mammals. This confirms what found for other taxa (Gilroy et al., 2015; Prescott et al., 2016). Establishing new oil palm plantations on pastures would additionally enable to maximise food security, carbon storage, and natural habitat cover (Garcia-Ulloa et al., 2012). Both, a stronger regulatory framework, including land use planning and adequate monitoring and enforcement, as well as incentives could help retain vital natural habitats and achieve mixed landscapes (Lambin et al., 2014; Boron et al., 2016a). In addition, to accomplish mammal conservation across human dominated landscapes, habitat preservation needs to be complemented with hunting limitations. Finally, we proved that jaguars are good umbrella species, thus any conservation effort focused on this species on would additionally benefit the wider medium-large mammal community, even in modified landscapes.

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4.8 Supporting Information

Table 4.4 Model selection results for variables influencing mammal species richness across two agricultural landscapes (Site-1 and Site-2) in the Magdalena river valley. AICc= Akaike's information criterion adjusted for small sample size; ΔAICc difference in AICc between each model and the best one; and logLik= log-Likelihood. 1= Canopy cover (%); 2=Distance water; 3= Forest (%); 4= Jaguar capture rates, 5= Oil palm (%); 6= Pasture (%); 7=Wetland (%).

Model	logLik	AICc	ΔAICc	AICc Weight	Deviance
2346	-156.43	326.28	0	0.17	312.86
2345	-156.65	326.73	0.45	0.14	313.31
23467	-155.7	327.33	1.04	0.1	311.4
23456	-155.85	327.64	1.36	0.09	311.71
12346	-156.09	328.12	1.83	0.07	312.19
12345	-156.38	328.69	2.41	0.05	312.76
23457	-156.51	328.95	2.67	0.05	313.02
234	-159.07	329.14	2.85	0.04	318.14
123467	-155.39	329.3	3.02	0.04	310.78
236	-159.25	329.49	3.21	0.03	318.49
6	-161.57	329.52	3.24	0.03	323.14
346	-159.26	329.53	3.24	0.03	318.53
24567	-156.85	329.63	3.34	0.03	313.7
46	-160.52	329.7	3.41	0.03	321.04
123456	-155.63	329.8	3.51	0.03	311.27
2467	-158.24	329.9	3.62	0.03	316.48
234567	-155.69	329.91	3.62	0.03	311.38

5. Achieving sustainable development in rural areas in Colombia: future scenarios for biodiversity conservation under land use change.

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5.1 Abstract

Agricultural expansion is a complex land use change phenomenon with deep environmental and socio-economic consequences, especially across tropical countries where most of this expansion is occurring. Here we use scenario and network analysis combined with sustainability assessment to understand the drivers of landscape change and their effects on sustainable development in Colombia's rural areas, using the Central Magdalena region as a case study, and ultimately informing strategies to reconcile agricultural expansion with biodiversity conservation and rural development. Using this approach we investigated three environmental and agricultural policy scenarios: the Business as Usual scenario, enforcing a stronger regulatory framework, and adopting incentives. Our analysis show that the Business as Usual scenario is not supported by stakeholders and negatively affects most sustainability objectives with the predominant agricultural sectors in the region (cattle ranching and oil palm) not improving social inequality, and threatening biodiversity, natural resources, and food security. Both alternative scenarios improve overall sustainability, including biodiversity. Therefore to reconcile agricultural expansion, biodiversity and sustainable development, it is important to adopt a stronger regulatory and enforcement framework at different administrative levels, as well as incentive schemes focusing on small holders. Our study also shows that history cannot be ignored when thinking about the future and sustainability especially in areas with legacies of strong inequalities caused by armed conflict. Finally, we suggest that combining scenario analysis, network analysis, and sustainability assessment is a useful methodology for studying land use changes holistically, exploring complex systems at different scales, and informing locally-relevant strategies and recommendations, ultimately enabling science to be proactive.

5.2 Introduction

With an increasing human population and consumption reconciling agricultural expansion with biodiversity conservation and sustainable development is an ever increasing challenge, especially in the tropics where most of this expansion is occurring (Foley et al., 2005; Gibbs et al., 2010; Tscharntke et al., 2012). Increasing agriculture is a complex land use change phenomenon, being a key driver of both environmental and socio-economic change: it increases food production and stimulates economic development, but it comes at a high environmental cost, particularly in areas with weak and dysfunctional governance such as the tropics (Foley et al., 2005, 2011; Gibbs et al., 2010). Agricultural expansion leads to habitat loss and fragmentation, which in turn are the main causes of biodiversity decline worldwide (Fahrig, 2003; Green et al., 2005). It also accounts for one-third of global greenhouse gas emissions, thus contributing to climate change and is the largest user of freshwater (Foley et al., 2005; Rockström et al., 2009); while its intensive use of fertilizers (+700% in the last 40 years) has altered global nutrients cycles and impacted water quality, ecosystems, and fisheries (Tilman et al., 2001; Rockström et al., 2009). Since agriculture is expanding, both biodiversity conservation and sustainable development will ultimately depend on understanding the different forces (socio-political and economic) acting in these systems and on strategies to achieve integrated landscape management where environmental and socio-economic objectives can be met in the same region (Harvey et al., 2008; Perfecto & Vandermeer, 2008; Gardner et al., 2009; Grau et al., 2013).

Historically traditional shifting agriculture, illegal crops, and extensive cattle ranching, have been the main drivers of deforestation and habitat conversion in

South America, including Colombia (Etter et al. 2006; Grau & Aide 2008). However new land uses are now causing landscape conversion, driven by export-oriented industrial agricultural policies and strong market conditions (Grau & Aide 2008, Pacheco 2012). This is primarily related to the expansion of soybean cultivation in Brazil, Argentina, Paraguay and Bolivia, as well as the expansion of oil palm in Colombia, and to lesser extent, in Ecuador and Peru (Pacheco, 2012). The expansion of oil palm has led to the conversion of natural ecosystems, landscape homogenisation, pollution, biodiversity loss, and carbon emissions both across the tropics and in Colombia (Fitzherbert et al., 2008; Danielsen et al., 2009; Turner et al., 2011; Wicke et al., 2011; Pacheco, 2012; Castiblanco et al., 2013; Savilaakso et al., 2014). While the sector can contribute to countries' economic growth and income generation, it can also exacerbate problems associated with social inequalities and concentrate land ownership by favouring industry owners (Mingorance, 2006; McCarthy, 2010; Vermeulen & Cotula, 2010; Castiblanco et al., 2015).

In Colombia extensive cattle ranches still occupy as much as 70% of the agricultural land (Etter et al. 2006a; McAlpine et al. 2009). However oil palm cultivation has been expanding since the 1970s supported by the National government with tax exemptions, subsidised credits, and mandatory consumption through biodiesel blends (Castiblanco et al., 2013), turning the country in the 4th largest oil palm producer worldwide. Such land use changes can impact sustainability in multiple ways; hence it is challenging to design strategies to ensure both biodiversity conservation and socio-economic development across regions where complex land use transitions are occurring.

Scenario analysis combined with sustainability assessment can be a great tool for strategy development and for providing future recommendations because it is a way of investigating future pathways as well as the consequences of different policies within complex systems (Alcamo & Henrichs, 2008; Spangenberg, 2007, Tzanopoulos et al., 2011). To guide sustainable development, assessment of future scenarios should include all dimensions of sustainability, i.e. environmental, social, and economic aspects, as well as the relations between them (Pope et al., 2004; Reidsma et al., 2011). Strategy development also requires understanding of the drivers of change acting on a system and their impact, which can be achieved with Network Analysis (Wasserman & Faust, 1994).

Here we deploy scenario and network analysis combined with sustainability assessment to understand the drivers of change and their effects on sustainability under different environmental and agricultural policy scenarios in the Magdalena region of Colombia, ultimately informing strategies to achieve biodiversity conservation while fostering sustainable development across an agricultural area. This is particularly timely in the country considering it aims to achieve a sustainable and green growth (DNP, 2014) and it is undertaking a peace process, which will open new investment and development opportunities. Finally, our study will demonstrate how combining scenario analysis, network analysis and sustainability assessment is a useful methodology to understand systems in which multiple drivers interact at different scales affecting different aspects of sustainability, to study complex phenomena such as land use changes in a holistic way, and to inform locally-relevant strategies and recommendations.

5.3 Methods

5.3.1 Study area

The study took place in the Middle Magdalena region of Colombia, which covers the central area of the inter-Andean Magdalena River valley, in the Department of Santander and in the municipalities of Sabana de Torres and Puerto Wilches, extending over 3000 km^2 (Fig.5.1).

Fig. 5.1 Map of the study region.

The region is part of the rainforest biome; it is naturally characterized by humid tropical forests and wetlands and has a tropical climate with mean annual temperature of 27℃ and bimodal rainfall of 2100-2600 mm annually (IDEAM et al., 2007). It hosts endangered and endemic species and it is considered an important genetic corridor as well as an important site for migratory bird species (Hernández-Camacho et al., 1992). However, the majority of its natural ecosystem has been converted into cattle ranches and oil palm plantations while the remaining natural habitats are threatened by further agricultural conversion (Castiblanco et al., 2013; Etter et al., 2006). Extensive and low productivity cattle ranching and increasing oil palm plantations are the dominant land uses in the region, which has the second largest amount of suitable land for oil-palm conversion in the country (Etter et al. 2006a; Molano 2009; Castiblanco et al. 2013). Other economic activities are gold mining and oil extraction (Molano, 2009).

The economic and social context has been characterised by violence, uneven development, and lack of government presence and institutions, which led to a coercive context of powerful elites, unofficial authorities, and poor participation (Molano, 2009). Poverty is still widespread with all municipalities except Barrancabermeja displaying unmet basic needs indexes greater than 60% (PDPMM-CINEP, 2007). Peace arrived in the region less than ten years ago but land inequality and power imbalance persist, making sustainable rural development challenging to achieve (Molano, 2009).

5.3.2 Data collection and analysis

We used an integrated methodology that combines scenario analysis and sustainability assessment (Pope et al. 2004; Sheate et al. 2008; Partidário et al. 2009) with network analysis (Tzanopoulos et al., 2011) to investigate the drivers of change in the region, their effect on sustainability under different scenarios, and to define management and policy recommendations for sustainable development (Fig. 5.2). Scenario analysis is often used in environmental research topics such as land use and biodiversity (Sala, 2000; Berkel & Verburg, 2012) and combined with sustainability assessment can help policy makers to understand the impact of potential policies or management plans (Westhoek et al., 2006). Such assessments can be conducted against a baseline to verify how acceptable the impacts of a proposal would be or against a series of aspirational objectives (Pope et al. 2004). We used the latter because it focuses on positive change, instead of merely minimizing any negative effects (Pope et al. 2004).

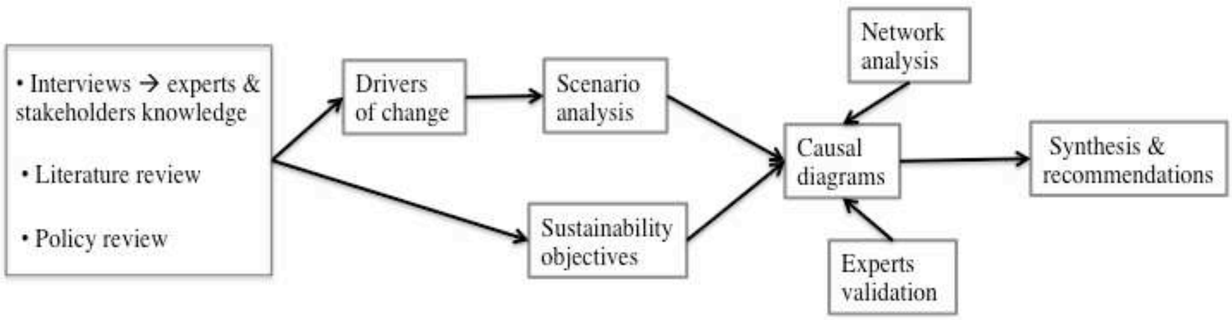

Fig. 5.2 Diagram of the methodological framework employed.

We further integrated network analysis to understand the relationships between drivers, impacts, and sustainability, and to inform management and policy recommendations to reconcile agricultural expansion and rural development with biodiversity conservation in the region. Network analysis is based on graph theory and focuses on the causal relationships (links) among different entities (nodes) (Wasserman & Faust, 1994). It is particularly helpful to explore real world systems in which drivers do not act in isolation and may have multiple consequences, and to identify which entities are key within such systems (de Nooy & Mrvar, 2005).

The research involved a number of stages. First, we conducted a literature review on the region and on Colombian agricultural policy to understand the changes that have occurred in the area and its social, economic, and environmental issues. We then interviewed experts and stakeholders (N=42) to understand further the drivers of change acting in the area and their impact on sustainability, to explore potential future scenarios and interviewees' views on them, and to identify important sustainability objectives. Through the interviews we also wanted to incorporate local knowledge, explore trade-offs, and consider different perspectives of landscape change and views for the future, as recommended by previous studies (Mitchley et al., 2006; Sheate et al., 2008). In order to achieve a comprehensive portrait of the region we ensured that different administrative levels and stakeholder groups were represented in the interviewees sample including: farmers and landowners (N=10), of which three were large holders (>1000 ha), and seven were medium and small holders (<1000 ha); researchers/experts within ecology, agriculture, and social sciences (N=13); conservation practitioners/NGOs representatives (N=12); politicians and/or authorities (N=11). The interviews were semi-structured and the questions dealt with the main drivers of landscape change in the region in the last 40 years and their impact; objectives that would be important to achieve in the area; visions of the future; and potential solutions to reconcile agricultural expansion and rural development with biodiversity conservation. Through both processes (interviews and literature review) we identified the main drivers of change acting in the system at different scales and their consequences. We then developed a list of sustainability objectives under which the different scenarios would be assessed, incorporating the following aspects: biodiversity conservation, natural resource management, and socio-economic development. The objectives were informed by a review of policy documents, including the National Development Plan for Colombia (DNP, 2014), and by the interviews to ensure their relevance at the local level.

In the following stage we conceptualised the scenarios. Because the focus of the study is how to achieve biodiversity conservation across agricultural landscapes the scenarios were centred on that. We formulated the scenarios with a 25 year time horizon and based them on the knowledge gathered during the interviews, an extensive literature review on conservation in tropical agricultural regions, current agricultural policies, and desired future states for biodiversity in the region. We considered both peer-reviewed articles as well as reports and policy documents that focused on: tropical agriculture; Colombia's land use, policy trends and consequences, history and armed conflict; sustainability; and strategies to achieve biodiversity conservation in agricultural landscapes. We investigated three alternative scenarios and their implications for overall sustainability: the business as usual scenario (BAU), an incentive based one (INC) and a regulatory one (REG). Both incentive-based conservation approaches vs. regulatory ones are established strategies to achieve conservation outcomes in agricultural landscapes (Harvey et al., 2008; McAlpine et al., 2009; Phalan et al., 2011; Kumaraswamy & Kunte, 2013; Arima et al., 2014; Lambin et al., 2014). Under the INC scenario, the national government increases spending on the environment and provides incentives to landowners to maintain natural habitats and establishing food security crops areas through changes in fiscal policies. Also, we designed the incentives to be even more advantageous and easily available for small farmers. Under the REG scenario increased monitoring and enforcement would ensure that current environmental legislation is enforced and adequate land use plans are developed through a participatory approach. In addition the agricultural sector would be required to perform Environmental Impact Assessments (EIAs), and the current agricultural subsidies would become conditional to maintaining existing natural habitats and meeting social standards (e.g. no land grabbing or displacement).

Following this, we produced network diagrams depicting the causal relationships between drivers of change and their impacts on the previously identified objectives under the three scenarios. We then explored the scenarios, the sustainability objectives, and the diagrams with experts (an ecologist, two social scientists, a land-use planning researcher, and two conservation practitioners), five of which were part of the 42 interviewees at the initial stage. In these network graphs the drivers of change, their consequences, and the sustainability objectives are the nodes, while the causal relationships between them are represented with arrows. The assessment of stakeholders/experts views on each scenario was carried out through discussion on potential scenarios and ways forward during the initial stage interviews and at a later stage through the experts input on the conceptualised scenarios and network graphs. We further investigated these graphs with network analysis and the Pajek software (de Nooy & Mrvar, 2005). This enabled us to identify the central nodes in the graphs, which correspond to the entities that have a primary effect on the system and therefore on the sustainability objectives. We treated the network as an undirected one and used degree centrality. The latter consists of assigning to each node/entity a value that corresponds to the number of lines that are connected to it. We then define as key entities the four nodes with the highest degree centrality (de Nooy & Mrvar, 2005). Finally, we developed a comparison matrix from the network graphs validated by the experts to summarize the positive or negative effects of the three scenarios on each sustainability objective, reporting the driver(s) directly responsible for those effects. Both understanding what entities have a central role in this system and the comparison matrix particularly informed on which measures/strategies should be adopted to achieve the sustainability objectives.

5.4 Results

5.4.1 Business as Usual Scenario: drivers of change and effects on sustainability

This scenario describes the process and drivers of change that have been occurring in the region for the last 40 years and projects them and their consequences in the future (25 years). The causal relationships between the drivers of change (D1-D6), their impact, and the sustainability objectives (Obj. 1-18) (Table 5.1) are represented in Fig. 5.3 and explained here. The drivers, their impacts, and their effects on sustainability under the different scenarios are also listed in Table 5.2.

Table 5.1 Sustainability objectives for the study area.

Study Area Objectives	
Rural-economic development	
Obj. 1	Develop a tourism sector
Obj. 2	Improve infrastructures
Obj. 3	Increase employment and income
Obj. 4	Increase small holders potential and competitiveness
Obj. 5	Increase sustainable farming practices
Obj. 6	Increase municipalities income
Social development	
Obj. 7	Achieve better healthcare, education, and housing conditions
Obj. 8	Improve security and human rights
Obj. 9	Improve social equity
Obj. 10	Maintain food security and farming cultural heritage
Institutional capacity	
Obj. 11	Strengthen institutions and law enforcement
Obj. 12	Increase local participation into policy and decision making
Obj. 13	Encourage and increase small farmers alliances/cooperatives
Biodiversity and natural resources	
Obj. 14	Conserve native habitats and connectivity
Obj. 15	Maintain ecosystem services provision
Obj. 16	Conserve species richness and diversity
Obj. 17	Maintain ecosystem resilience to climate change and natural disasters
Obj. 18	Increase environmental awareness and connections between people and biodiversity

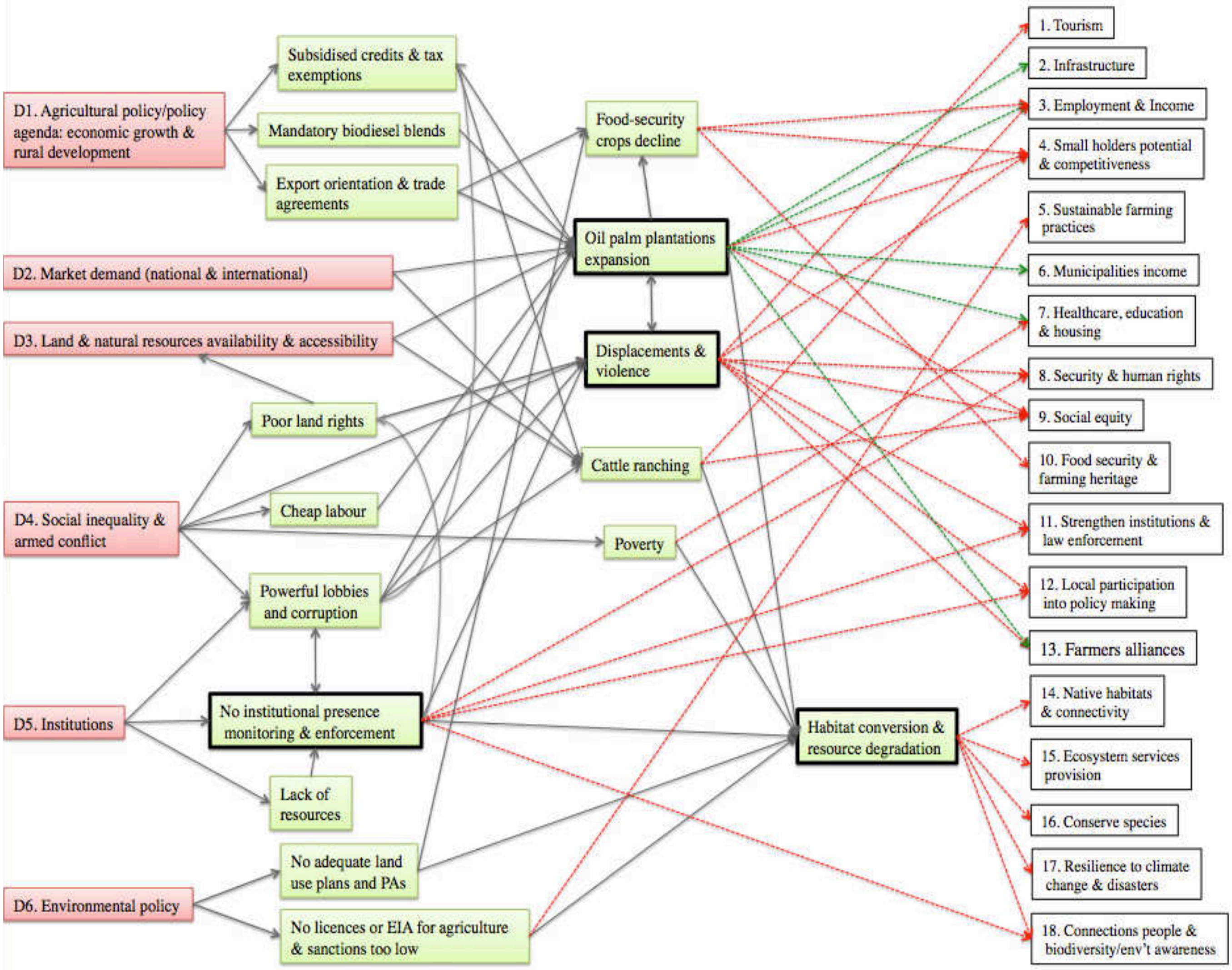

Fig. 5.3 Network graph representing the causal relationships between the drivers of change (D1-D6), their consequences and their positive (green dotted lines) and negative (red dotted lines) effect on the sustainability objectives (1-18) under the BAU scenario. Thicker boxes represent central nodes in the graph.

Table 5.2 A comparison matrix of the drivers and/or their impacts and their positive (+) or negative (-) effect on the sustainability objectives under the tree scenarios (Obj. 1-18).

Obj.	BAU Scenario	Regulatory Scenario	Incentives Scenario
Rural-economic development			
Obj. 1	(-) Displacements & violence	(-) Displacements & violence	(-) Displacements & violence
Obj. 2	(+) Oil palm expansion	(+) Oil palm expansion	(+) Oil palm expansion
Obj. 3	(+) Oil palm expansion	(+) Oil palm expansion	(+) Oil palm expansion
	(-) Cattle ranching	(-) Cattle ranching	(-) Cattle ranching
	(-) Food security crops decline	(+) Food security crops area	(+) Food security crops area
			(+) Small holders credit access
Obj. 4	(-) Displacements & violence	(-) Displacements & violence	(-) Displacements & violence
	(-) Oil palm expansion	(-) Oil palm expansion	(-) Oil palm expansion
	(-) Food security crops decline	(+) Food security crops area	(+) Food security crops area
			(+) Small holders credit access
Obj. 5	(-) No licenses/EIA for agriculture	(+) Licenses/EIA/Sanctions for agriculture	(-) No licenses/EIA for agriculture
		(+) Conditions on subsidies	(+) Incentives for natural habitats and food security
Obj. 6	(+) Oil palm expansion	(+) Oil palm expansion	(+) Oil palm expansion
Social development			
Obj. 7	(-) Poverty	(-) Poverty	(-) Poverty
	(+) Oil palm expansion	(+) Oil palm expansion	(+) Oil palm expansion
Obj. 8	(-) Displacements & violence	(-) Displacements & violence	(-) Displacements & violence
	(-) No institutional presence	(+) Institutional presence	(-) No institutional presence
Obj. 9	(-) Displacements & violence	(-) Displacements & violence	(-) Displacements & violence
	(-) Cattle ranching	(-) Cattle ranching	(-) Cattle ranching
	(-) Oil palm expansion	(-) Oil palm expansion	(-) Oil palm expansion
			(+) Small holders credit access

Obj. 10	(-) Oil palm expansion	(-) Oil palm expansion	(-) Oil palm expansion
	(-) Food security crops decline	(+) Food security crops areas	(+) Food security crops areas
	(-) No land use plans		
Institutional capacity			
Obj. 11	(-) No institutional presence	(+) Institutional presence	(-) No institutional presence
	(-) Displacements & violence	(-) Displacements & violence	(-) Displacements & violence
Obj. 12	(-) No institutional presence	(+) Institutional presence	(-) No institutional presence
	(-) Displacements & violence	(-) Displacements & violence	(-) Displacements & violence
		(+) Adequate land use planning	
Obj. 13	(+) Oil palm expansion	(+) Oil palm expansion	(+) Oil palm expansion
	(-) No institutional presence	(+) Institutional presence	(-) No institutional presence
			(+) Small holders credit access
Biodiversity & natural resources			
Obj. 14	(-) Habitat conversion & resource degradation	(-) Habitat conversion & resource degradation	(-) Habitat conversion & resource degradation
		(+) Secure natural areas	(+) Natural habitats
Obj. 15	(-) Habitat conversion & resource degradation	(-) Habitat conversion & resource degradation	(-) Habitat conversion & resource degradation
		(+) Secure natural areas	(+) Natural habitats
Obj. 16	(-) Habitat conversion & resource degradation	(-) Habitat conversion & resource degradation	(-) Habitat conversion & resource degradation
		(+) Secure natural areas	(+) Natural habitats
Obj. 17	(-) Habitat conversion & resource degradation	(-) Habitat conversion & resource degradation	(-) Habitat conversion & resource degradation
		(+) Secure natural areas	(+) Natural habitats
Obj. 18	(-) No institutional presence	(+) Institutional presence	(-) No institutional presence
	(-) Habitat conversion & resource degradation	(-) Habitat conversion & resource degradation	(-) Habitat conversion & resource degradation
		(+) Secure natural areas	(+) Natural habitats

The region has two predominant agricultural sectors: cattle ranching and oil palm cultivation, which are supported by the agricultural policy (D1), national and international market demand (D2), and land and natural resource availability (D3). They also have benefitted from social inequalities, the armed conflict (D4) and lack of institutions (D5) through very powerful supporting lobbies. These trends are expected to continue in the years to follow, as well as the sectors' environmental and socio-economic consequences.

Cattle ranching negatively affects the environmental sustainability objectives (Obj. 14-18), social equity (Obj. 3), and does not generate employment (Obj. 9) because of its high inefficiency and its low labour force requirements (Vergara, 2010). Rates of natural habitat conversion for cattle ranching are estimated at 150,000-250,000 ha/year for forest and 50,000 ha/year for savannahs at the national level (Etter et al. 2006). The sector has played an important role in the Colombian society and in shaping the country landscapes since the 1500s, when it was used to gradually gain control over indigenous land during the colonisation (McAlpine et al., 2009). Nowadays the industry is still responsible of land appropriation through habitat clearing later secured by the planting of introduced grasses and used as pasture (Etter et al. 2006).

Oil palm cultivation has been expanding in the area favoured by national policy (D1) through subsidized credit, mandatory biodiesel blends (20% by 2020), and tax exemptions such as the biodiesel sale tax or producers income tax (Law 939 of 2004 and 1970 of 2005) and there are no signs of policy shifting. Although at the national level the oil palm industry only represents 2.6% of the agricultural GDP (MADR, 2013) when it is present in an area, such as our study region, it has important effects. Oil palm plantations cause habitat and biodiversity loss and affect soil quality and water resources through the use pesticides, fertilisers and the draining of water bodies (Obj. 14-18). They also cause forced displacements, violation of human rights, loss of traditional farming practices and local food security, thus negatively affecting Obj. 4, 9, and 10. All these effects are expected to continue into the future. Although not all palm plantations establishment happened through violence and forced displacement, different authors documented the connections between oil palm plantations, armed groups, and violence (Mingorance 2006; Ocampo-Valencia 2009; Segura 2008; Castiblanco et al. 2015). A decrease in food security in the region happened as a consequence of both oil palm expansion, which increase land prices and displaces subsistence crops to more marginal lands, and trade agreements affecting the small farm economy (Salamanca et al. 2009; Infante & Tobón 2010).

On the development side, oil palm plantations increase infrastructure (Obj. 2), employment (Obj. 3) and can achieve lower rates of unmet basic needs and higher municipalities income (Obj. 6 and 7), as also reported by Castiblanco et al. (2015). However, interviewees' views on the quality of employment provided by the sector were not always positive: because of the lack of labour unions as a consequence of violence in the region (Molano, 2009) contracts are often temporary, with few workers' benefits and rights. Oil palm plantations also have a positive effect on the establishment of farmers "productive alliances" (Obj. 13) where the company owning the plantation outsources the production to local farmers, but there is scepticism of how beneficial they really are for farmers because companies retain control over the fruit price (Ocampo-Valencia, 2009). Overall the oil palm sector tends to negatively affect social equity (Obj. 9) because of the differences between farmers earnings and the income generated at the industrialization and commercialization stage (Castiblanco et al., 2015) and it is generally a mean of land concentration because large holders are more likely to access credits and can afford the 4-year wait until the first yield. There seem to be no signs of changes in these trends in the future.

Social inequality and the resulting armed conflict (D4) have long been part of Colombian history with over 60% of land owned by 0.4% of landowners (Albertus & Kaplan, 2012). Land grabbing and forced displacement are also severe issues and affected almost 5 million people in the country from 1985 to 2008 (Fensuagro, 2012). Even if violence and displacement ceased in the region in the last 10 years their numerous consequences are still present. They foster powerful lobbies and corruption and negatively affect tourism (Obj. 1), security and human rights (Obj. 8), social equity (Obj. 9), institutions and law enforcement (Obj. 11), local participation into policy making (Obj. 12), and farmers' alliances (Obj. 13). Displacements can also have positive and negative effects on natural habitat cover (Sánchez-Cuervo & Aide, 2013).

This regional and national context is further aggravated by the lack of institutions (D5), monitoring and enforcement. Because of power imbalance and corruption, politically powerful groups such as large oil palm growers and cattle ranchers blocked most large-scale reforms and have been key factors in influencing agricultural policies by means of providing statistical support, lobbying, and allowing public officials to be part of their board of directors (Albertus & Kaplan, 2012). The same power dynamics apply to the environmental sector: authorities lack resources and power to actually make a difference, while excessive bureaucracy and corruption hinder they credibility and efficiency.

Finally, the environmental policy (D6) is insufficient or not applied, thus failing to protect habitats and biodiversity. Municipalities are required to have land use plans, but these are often out dated, not integrated at different scales and administrative levels, and not applied. Furthermore no Environmental Impact Assessment (EIA) is required for the agricultural sector, sanctions are too low, and not all Departments require companies to have environmental management plans. Overall, if current policies and drivers of change persist, all trends described are also expected to continue into the future. It is also possible that if the system was to reach unknown thresholds and tipping points it could precipitate into unforeseen environmental states.

5.4.1.1 Stakeholders' views

Stakeholders generally held negative views on this scenario as it is producing more negative than positive effects on sustainability. Some of the issues they raised were that the BAU is not improving land and social inequality issues, while it is threatening key natural resources such as biodiversity and water. They claimed that national policy agendas and trade agreements were beneficial for strongly profitable land uses (e.g. oil palm cultivation) at the expenses of small-scale producers, ultimately worsening their condition and exacerbating social inequality. They also reported that institutional weakness and corruption has hindered significant socio-economic improvements.

5.4.2 Incentives based scenario: drivers of change and effects on sustainability

In the INC scenario, the national government increases its spending on the environment and provides incentives to landowners to maintain natural habitats and establishing food security crops areas with a focus on small farmers alliances/cooperatives. Under this scenario many of the causal links remain the same but we would expect an increase in food security crops production, persistence of some natural habitats in the landscape, and increased credit accessibility for small holders and farmers alliances (Fig. 5.4). This in turn would impact positively several sustainability objectives: employment and income (Obj. 3), smallholder potential and competitiveness (Obj. 4), social equity (Obj. 9), food security and farming heritage (Obj. 10), the establishment of farmers alliances (Obj. 13), and the environmental ones (Obj. 14-18) (Fig. 5.4). Overall this scenario would represent an improvement to the BAU since more sustainability objectives are positively affected (Table 5.2).

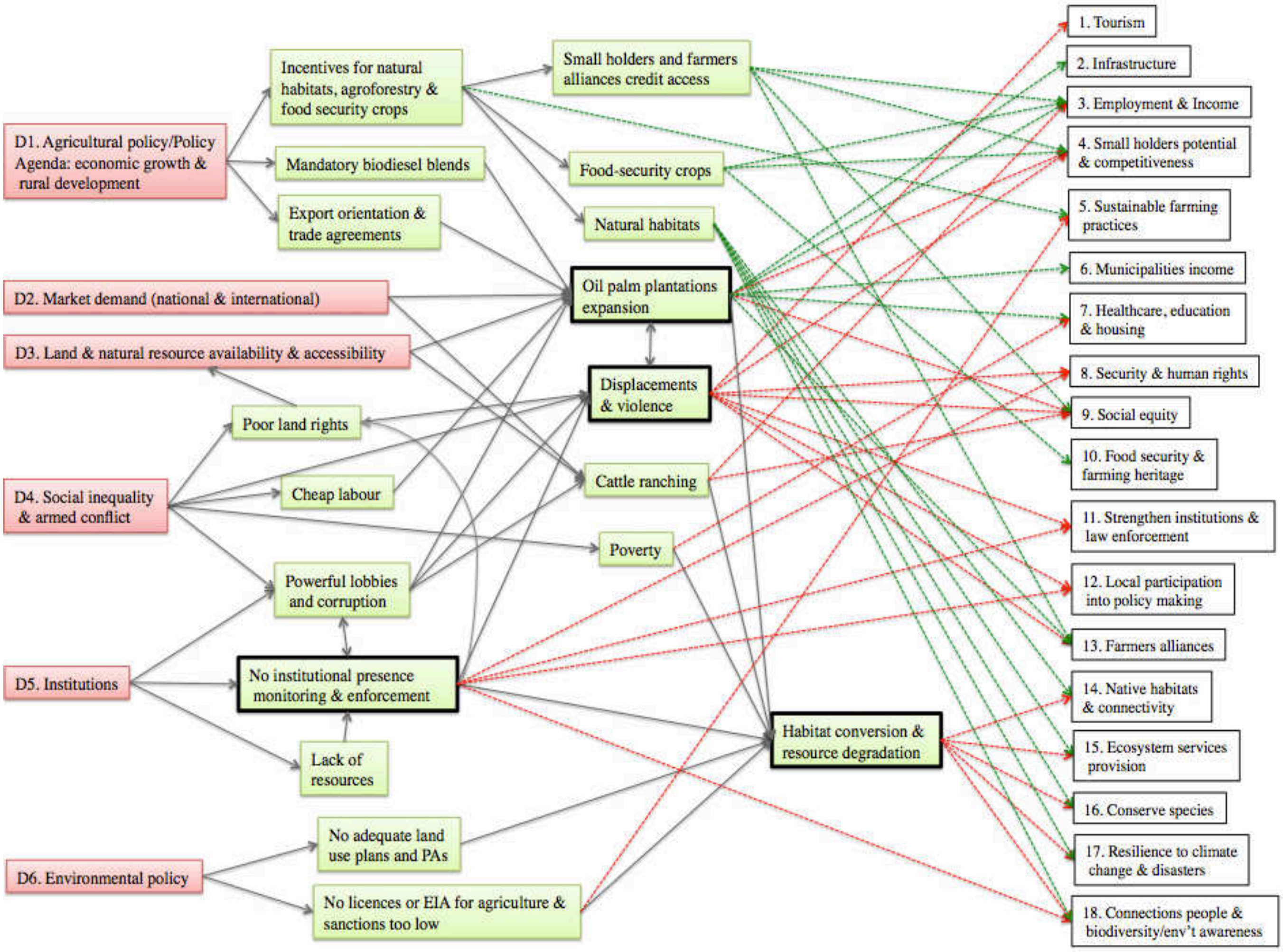

Fig. 5.4 Network graph representing the causal relationships between the drivers of change (D1-D6), their consequences and their positive (green dotted lines) and negative (red dotted lines) effect on the sustainability objectives (1-18) under the INC scenario. Thicker boxes represent central nodes in the graph.

5.4.2.1 Stakeholders' views

Stakeholders and experts viewed this scenario more positively than the current situation but they felt that even if adequate incentives could achieve some positive and localised changes, without a strong enforcement framework and coordination between different authorities it would be unlikely to achieve long term changes at the scale needed.

5.4.3 Regulatory based scenario: drivers of change and effects on sustainability

In the REG scenario increased monitoring and enforcement ensures that adequate land use plans are developed and enforced together with environmental law. Also, the agricultural sector is required to perform EIAs, and the current agricultural subsidies become conditional to social and environmental standards. Even with a much stronger regulatory framework in place is unrealistic to think that no habitat conversion and resource use and degradation would occur in the system, hence those entities persist. However because of institutional strengthening and law enforcement and the new conditions on the subsidies to the agricultural sector oil palm plantation should not cause displacements (Fig. 5.5). Institutional presence, monitoring, and enforcement would also have a positive effect on security and human rights (Obj. 8), while adequate and participatory land use plans would help biodiversity and natural resources conservation (Obj. 14-18), increase participation in policy making (Obj. 12), and improve food security (Obj. 10). Having food security crops areas can also help income generation and small farmers (Obj. 3 and 4). In addition, the introduction of EIAs, adequate sanctions, and new conditions on agricultural subsidies would contribute to secure natural areas. This would have a positive effect on the biodiversity and natural resources sustainability objectives (Obj. 14-18) as well as on achieving sustainable farming practices (Obj. 5). This scenario seems to deliver positive effects on more sustainability objectives than the incentive one (Table 5.2), however it is highly dependant on institutional presence and high level of enforcement, which are hindered by the powerful lobbies and corruption still present in the system as a consequence of armed conflict and social inequality.

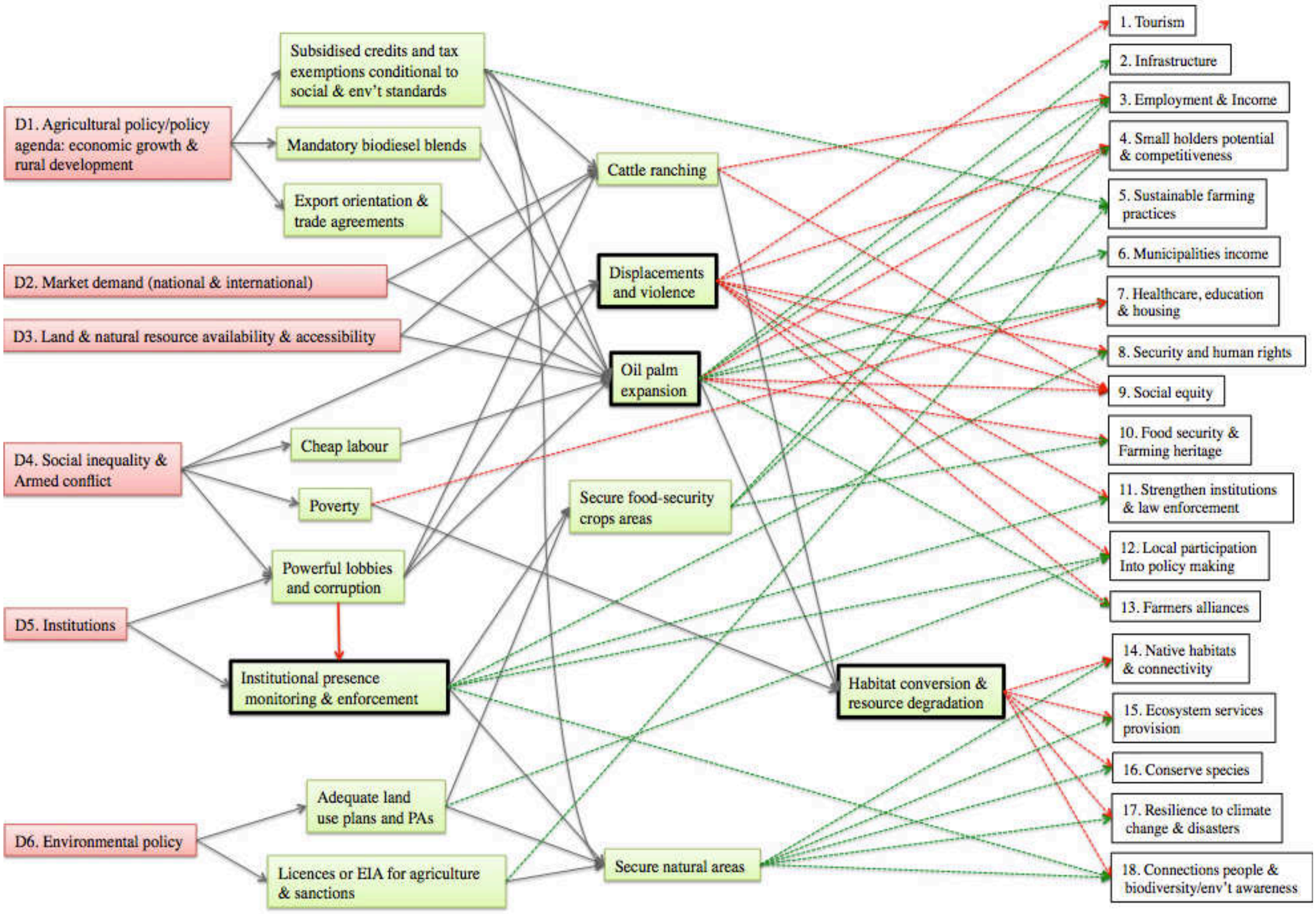

Fig. 5.5 Network graph representing the causal relationships between the drivers of change (D1-D6), their consequences and their positive (green dotted lines) and negative (red dotted lines) effect on the sustainability objectives (1-18) under the REG scenario. Thicker boxes represent central nodes in the graph.

5.4.3.1 Stakeholders' views

Stakeholders and experts preferred this scenario to the INC and BAU ones as they considered that a robust regulatory framework is necessary to achieve desired changes. They expressed that empowering institutions and increasing enforcement is key to improve sustainability in the region and also stressed that coordination between authorities and institutions at different levels is imperative.

5.4.4 Key nodes and identification of management priorities

The sustainability objectives tend to be affected by multiple drivers and their interactions, resulting in a complex network. For example, in the BAU scenario the achievement of species conservation is directly affected by habitat conversion and resource degradation, which in turn are directly and/or indirectly affected by agricultural policy, market demand, institutions, environmental policy, and even the armed conflict. Therefore we used Network analysis to identify the key factors in the achievement of the sustainability objectives under each scenario. The analysis showed that under all scenarios key entities in the system are *oil palm plantation expansion* and *displacements and violence*, followed by the *lack of institutional presence and enforcement*, and *habitat conversion and resource degradation*. This suggests that to achieve a sustainable development of the area we should focus on policies applying to the oil palm sector, improving both its environmental and social standards, as well as addressing violence and displacements or their consequences. Also, halting resource degradation and habitat conversion is key since it underpins the achievement of all sustainability objectives related to biodiversity conservation and natural resources (Obj. 14-18). Finally it is imperative to increase institutional presence, monitoring and enforcement because it directly and/or indirectly affects many sustainability objectives. Changes in different drivers (e.g. agricultural policy, market demand, environmental policy) may not improve significantly the sustainable development of the area unless institutions and monitoring improve.

5.5 Discussion

Given an increasing human population and per capita consumption, reconciling agricultural expansion with biodiversity conservation and overall sustainable development is a challenging but crucial priority, especially in biodiversity-rich tropical countries such as Colombia. Our analysis showed that agricultural expansion is indeed a complex land use change phenomenon and it does have direct and/or indirect impacts on all aspects of sustainability: environmental, social, and economic. It is therefore important to focus on the agricultural sector to achieve a sustainable development in the region. To understand such complex land use problems it is crucial to understand the system in which they occur, integrating different disciplines and scales (Grau et al., 2013; Nesheim et al., 2014) while unravelling the causal relationships between drivers and impacts; and our methodology enabled us to do so. The exploration of the BAU scenario showed that most sustainability aspects are impacted negatively. Current national policy agendas, trade agreements, and agricultural subsidies are only beneficial to certain land uses (such as oil palm cultivation) and to large holders preferentially thus failing to achieve significant socio-economic development and securing a more sustainable future, as also described by the World Bank (2008) .

Cattle ranching and the expansion of oil palm plantations in the region are damaging ecosystems, biodiversity and natural resources as found elsewhere (Fitzherbert et al., 2008; Danielsen et al., 2009; Koh & Wilcove, 2009; McAlpine et al., 2009) and are not improving social inequality issues. Land and income concentration in turn exacerbate corruption, weaken already frail institutions, and slow long-term socio-economic development (Molano, 2009; Castiblanco et al., 2015). The impacts of oil palm cultivation on rural development described in our study region are aligned to the national level and to other regions, i.e. Indonesia (McCarthy, 2010), Brazil (Martinelli et al., 2010), and Africa (Vermeulen & Cotula, 2010). On the contrary, oil palm plantations can benefit small holders but authorities, farmers' alliances, and clear land rights played a key role for this to happen in Colombia and elsewhere (Molano, 2009; Rist et al., 2010).

The analysis of the two alternative scenarios show that both a stronger regulatory framework or different incentives within the agricultural policy could improve sustainable development in the region and are preferable to the current situation. Adopting the regulatory scenario would deliver more objectives but it is also more vulnerable to existing corruption. Both regulatory and incentive based approaches to conservation of biodiversity in agricultural landscapes have been explored in other countries by previous literature, which confirms that the former are generally more effective and bring greater additionality but are also more costly and more prone to leakage and weak governance (Harvey et al., 2008; Phalan et al., 2013; Lambin et al., 2014). On the other hand, voluntary approaches do not necessarily deliver sustainable land use at the scale needed since they are not adopted by all producers within a region or country and can have negative consequences if dropped by future governments or policy changes (Phalan et al., 2013; Lambin et al., 2014).

In order to provide policy recommendations, informed by network and scenario analysis, it is key to focus on the central entities identified by the network analysis and on the administrative levels of the various drivers of change. The national agricultural policy and policy agenda (D1) is an exogenous driver controlled both by the national government and international trends such as globalisation of markets

(Hazell & Wood, 2008). Similarly market demand (D2) is both an exogenous and endogenous driver as the demand is local, national and international. The same also applies for social inequality and armed conflict (D4), institutions (D5), and environmental policy (D6) since they are not confined to the study area and may be partially or totally governed at higher administrative levels. Therefore to address the key entities in the graph (i.e. oil palm plantation expansion, displacements and violence, lack of institutional presence and monitoring, habitat conversion and resource degradation) it is key to coordinate policy and decision making at different levels.

Habitat conversion and resource degradation were identified as important entities because they underpin all environmental sustainability objectives. However, providing policy recommendations exclusively aimed at reducing habitat and resource loss might not be highly effective because it would not address the drivers behind them. Therefore the focus of policy recommendations is on the other key entities emerged.

At the *international level* in the developed world reducing consumption, waste, and requiring certified products may help reducing oil palm expansion or making it more sustainable (Koh & Lee, 2012). At the *national level*, as shown by the scenario analysis a stronger regulatory framework is needed. Strict environmental and social criteria should be put in place to gain access to the current subsidies within the agricultural sector, as well as requiring EIAs and increasing sanctions. Stronger regulatory framework have been suggested as successful for biodiversity conservation in productive landscapes elsewhere (Arima et al., 2014; Lambin et al., 2014; Verburg et al., 2014). At the same time new incentives and subsidies to other land uses that are not oil palm should be adopted, and the government could request that all palm oil used in biodiesel blends in the country is certified. Certification and traceability should become prerequisites for the Colombian oil palm industry to keep a share of the international markets while continuing to increase its importance in national ones. However the level at which certification should be promoted has to be determined carefully (Tscharntke et al., 2015) and a strong national and international consumer demand for Certified Sustainable Palm Oil must be created first, as it can be key driver of increased sustainability in agricultural production systems (Ruviaro et al., 2014).

At the *regional* and *local* levels good land use plan should be developed though a participatory approach, integrated at the different scales, and enforced; while oil palm expansion should be directed on already modified pasture lands as identified by Garcia-Ulloa et al. (2012). This would minimise its environmental impact and would ensure that remaining natural habitats in the region and important wetlands are conserved and can serve as refuges for biodiversity, including threatened and iconic species such as jaguars (*Panthera onca*) and West Indian manatees *(Trichecus manatus manatus)*. In addition, to address the consequences of past displacements and violence in the region and of low institutional presence, local and regional authorities, including environmental ones, should be strengthened and restructured to decrease corruption levels.

Stronger institutions, enforcement and coordination at *all administrative levels* are crucial to achieve a more sustainable development (Nesheim et al., 2014). Also, more participatory approaches to decision making and more engagement and knowledge exchange between the different sectors and stakeholders would be highly beneficial, as highlighted by previous research (Pretty, 2008; Reed, 2008; Tzanopoulos et al., 2011). Finally, governments at the national and local level should promote further agricultural (including oil palm) development via individual smallholdings rather than large agribusiness. Policies should focus on small farmer development, competitiveness and access to markets. The need to re-orient rural policies in favour of small farmers to achieve sustainable agricultural landscapes has been highlighted before since it would decrease poverty, increase well-being and social equity, safeguard food security, maintain higher levels of biodiversity, and even improve resilience to climate change (Pretty, 2008; Tscharntke et al., 2012; Pokorny et al., 2013).

5.5.1 Conclusion

To achieve biodiversity conservation and sustainable development in the area and similar rural areas in the tropics it is imperative to coordinate policy and decision making at different administrative levels. It is optimal to adopt a mixed policy approach encompassing both a stronger regulatory and enforcement framework as well as incentive schemes. It is also key to advance and enforce good land use planning if we are to conserve remaining habitats, biodiversity and ecosystem services. While to maintain food security and achieve social equity and long-term growth policies should be re-oriented to favour small farmers. Lastly institutions at all administrative levels need be strengthened and restructured to decrease corruption. Our analysis has also shown that history cannot be ignored when thinking about the future, especially in areas of armed conflicts that have lead to strong inequalities. Changes in agricultural policies alone are not enough to achieve sustainable development if the deep social and economic impacts of such conflicts (and resulting social structures) are not addressed by other social restructuring policies.

Finally, combining scenario analysis, network analysis and sustainability assessment can provide a useful methodological tool to study complex land use change issues holistically and integrate knowledge from different disciplines, enabling to explore systems with different drivers and desired outcomes from different perspectives (environmental, social and economic) and at different scales. It also allows formulating management and policy recommendations that are locally relevant thanks to stakeholders and experts consultations, ultimately enabling science to be proactive.

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6. Discussion

6.1 Thesis main contributions to conservation science

Agricultural expansion is an important driver of global change and species decline (Rockström et al., 2009; Maxwell et al., 2016; Venter et al., 2016). Its pervasive effects are particularly concerning in megadiverse tropical countries such as Colombia (Mittermeier et al., 1997; Gibbs et al., 2010) and on large carnivores like jaguars, due to their life history traits (Cardillo et al., 2005; Carbone et al., 2011). The main aims of this thesis were to improve current understanding of jaguars and other terrestrial mammals across increasing agricultural landscapes and assess the impact of human land uses such as oil palm cultivation on these species, in order to inform better conservation and management actions. This is relevant because there is a scarcity of information on Neotropical mammals across agricultural and especially oil palm landscapes, which are increasing in Latin America (Pacheco, 2012). However, biodiversity conservation is only part of the picture, hence this thesis also aims to inform strategies to reconcile biodiversity conservation with other aspects of sustainability and regional development in rural areas of Colombia.

Chapter 2 provided the first jaguar population estimates for Colombia outside of the Amazon forest and across agricultural areas with oil palm plantations, specifying a baseline to assess future population changes, and enabling comparisons with other sites. More importantly, the data conclude that there is a negative effect of agriculture on jaguar populations as densities were lower than in comparable natural areas (Soisalo & Cavalcanti, 2006; Tobler & Powell, 2013; Tobler et al., 2013), equal to only 2-3 individuals/100km^2. However, these values are still higher than those reported for other regions across the jaguar range (Tobler & Powell, 2013) and there were resident individuals and breeding. The findings highlight that unprotected areas can be important for large carnivore long-term survival and connectivity and should therefore be included in their conservation strategies, complementing protected areas (Sanderson et al., 2002; Rabinowitz & Zeller, 2010).

Chapter 3 and 4 conclude that maintaining wetlands and forests is critical to conserve jaguar and other mammal species across agricultural landscapes. Wetlands were an extremely strong factor explaining jaguar occurrence, while forests had a positive effect on puma occupancy, reinforcing the importance of such habitats for the survival of these large felids (Soisalo & Cavalcanti, 2006; De Angelo et al., 2011). Forests were also a predictor of mammal species richness. Furthermore the data showed that widespread loss of natural habitat cover beyond 50-60% may be unsustainable for felid conservation. Both oil palm and pasture exerted a negative effect on several mammal species, whereas the remaining species could only tolerate low/intermediate levels of these land cover types. Consequently, the expansion of oil palm plantations and pastures emerged as a growing threat for felids and the wider mammal community, similarly to other Neotropical taxa (Gilroy et al., 2015; Prescott et al., 2016).

The results also show that habitat modification has an effect on mammal communities by lowering species diversity and evenness, while increasing dominance (Ahumada et al., 2011), whereas the impact on species richness is not clear. Lastly, data from these chapters show that jaguars did not have a negative effect on the occupancy of the other felid species and were a significant predictor of mammal species richness, complementing what Thornton et al. (2016) reported on the jaguar network of populations and corridors being effective at protecting core habitat for sympatric mammals.

Chapter 5 highlights that rural areas can provide for both people and wildlife if the right conditions exist. The research reveals that under the current situation (the Business As Usual scenario) main agricultural sectors such as cattle ranching and oil palm cultivation are affecting wildlife and several other aspects of sustainability negatively. They are not improving social inequality issues and food security, but are instead creating unstable employment and threatening biodiversity, natural resources, and cultural heritage. Both alternative scenarios (a stronger regulatory framework with land use planning and the adoption of incentives) represent improvements, since they would allow maintaining natural habitats that are key for jaguars and other species survival, while improving overall sustainability, which is in line with current understanding (Lambin et al., 2014). Network analysis proved that to achieve sustainable development it is key to focus on the oil palm sector, address the legacies of the armed conflict, and reinforce institutions.

The chapter also showed that history cannot be ignored when thinking about the future and sustainability, and enabled formulation of policy and management recommendations at different scales. These include the design and adoption of strategic land use planning, targeted and efficiently implemented regulations to make agricultural subsidies conditional to social and environmental standards, strengthening institutions, and designing incentives to foster the implementation of best agricultural practices. While to guarantee food security and social equity policies should favour small farmers. Strengthening and restructuring institutions at different administrative levels is needed also to decrease existing corruption. Finally, creating a demand for certified agricultural commodities at both the national and international level is also crucial.

6.2 Wider context and management implications

Agricultural expansion and related habitat loss and modification are extremely concerning threats to biodiversity because they affect species and communities in multiple ways and this research provided further evidence on these changes. In addition to direct effects of biodiversity loss, habitat and resources modification can cause species niches to shift and increasingly overlap, increasing competition and extinction risks (Tilman & Lehman, 2001; Ewers & Didham, 2006; Harpole & Tilman, 2007). Those species whose niches overlap more with the newly available conditions in agricultural regions will be favoured and survive longer (Ewers & Didham, 2006; Harpole & Tilman, 2007). Species like crab-eating foxes, Central American agoutis, and crab-eating racoons were indeed extremely common in the study area and more tolerant to agriculture than other species (Fig. 4.3). However, large carnivores are generally not amongst such species (Cardillo et al., 2005), and this thesis confirmed it.

The decrease of apex predators is not just concerning *per se* since it additionally leads to phenomena of mesopredator release (Crooks & Soulé, 1999) and important cascade effects (Estes et al., 2011). All these processes can drastically change communities, although some of these effects may take time to manifest and lead to extinction debts (Tilman et al., 1994). This research's findings of mammal communities with decreased diversity and evenness, and higher dominance are in line with the theories mentioned and may represent the beginning of these processes.

Overall, the biodiversity and socio-economic consequences of oil palm plantations and cattle ranching that I documented for the study area are comparable to other regions (Fitzherbert et al., 2008; McAlpine et al., 2009; Martinelli et al., 2010; McCarthy, 2010; Vermeulen & Cotula, 2010; Castiblanco et al., 2015; Gilroy et al., 2015; Yue et al., 2015; Prescott et al., 2016) and this thesis provided insights on how to decrease them. Regulatory approaches to conservation are generally more effective but suffer from leakage and weak governance, which are not uncommon in the tropics (Harvey et al., 2008; Phalan et al., 2013; Lambin et al., 2014). On the other hand, voluntary approaches may not deliver sustainable land use at a wide scale and can have negative consequences if ceased (Phalan et al., 2013; Lambin et al., 2014). As this research shows, to achieve sustainable development and the persistence of natural areas across agricultural regions on which the survival of threatened and iconic species like the jaguar depends of, a policy mix that combines both regulatory and voluntary approaches is needed. In addition, creating green markets and a demand for sustainably produced commodities can be a driver of increased sustainability in agricultural regions (Ruviaro et al., 2014).

Land use planning is particularly important to conserve remaining natural habitats, biodiversity, and ecosystem services. It should be holistic, including protected areas and human-use areas. As agriculture and oil palm cultivation are on the increase, they need to be integrated into conservation strategies and land use planning. Furthermore this research proved, that agricultural landscapes are not biological deserts and can be important for jaguar and mammal conservation. At the regional and local levels land use plan should be developed though a participatory approach, integrated at different scales, and enforced.

The findings of this thesis also help informing land use planning in Colombia. The data reveals how important it is for mammals that natural areas remain in the landscape, pointing to a land sparing approach (Green et al., 2005). The latter is generally considered more effective for conservation (Phalan et al., 2011) and can deliver multiple stakeholder targets and ecosystem services (Law et al., 2016). Preserving forests in Colombian agricultural landscapes would additionally benefit ants, dungbettles, birds, and herpetofauna (Gilroy et al., 2015; Prescott et al., 2016). If the landscape homogenously becomes more than 50-60% modified, it will threaten felid species and further studies should assess such values for other species. The results also highlight that pastures displayed no conservation value for felids and other mammal species, hence they could be targeted for future oil palm expansion. This is in line with data reported for other taxa (Gilroy et al., 2015; Prescott et al., 2016) and would additionally benefit carbon storage, natural habitat cover, and food security (Garcia-Ulloa et al., 2012).

Although outside the scope of this thesis it is important to note that to achieve mammal conservation across human-use areas, habitat preservation needs to be combined with regulations on poaching. Similarly, to conserve jaguars, adopting best livestock management practices, and conserving their natural prey is crucial because it minimizes jaguar predation on livestock and human-jaguar conflict (Polisar et al., 2003; Inskip & Zimmermann, 2009; Cavalcanti et al., 2010). The latter is particularly relevant considering that the majority of Colombia' s agricultural land is under cattle ranching (Etter et al., 2006). Finally, this research proved that jaguars are a good umbrella species, thus conservation strategies focused on this charismatic and declining keystone species can benefit the wider mammal community, even in modified areas.

6.3 Methodological insights

To advance our understanding of species ecology across anthropogenic areas and assess the effects of human activities it is vital to obtain land cover data accurately and time-efficiently, which can be challenging in the tropics. Object Based Image Analysis (Bock et al., 2005) is a very promising way forward, as it produced very accurate maps with reasonable time investment while using freely available satellite images.

Obtaining reliable species density estimates is also crucial in order to perform comparisons and avoid biased assessment of population status. The latter could lead to underestimating threats and delaying conservation actions, making species even more vulnerable to extinction. Using spatially explicit capture-recapture methods (Borchers & Efford, 2008; Royle et al., 2009) and including individuals' sex as a covariate tended to produce better models, highlighting their potential to improve population estimates, especially for species with different ranging behaviour between sexes like jaguars and other felids.

Most felids are inherently difficult to study as they are cryptic in nature and wide ranging. Since camera trap surveys are especially costly for such species, in addition to optimising the number of sampling occasions and cameras needed to obtain cost-efficiency (Gálvez et al., 2016), it is advisable to place cameras on trails where possible. Entirely random placement of cameras may not deliver sufficient data and may ultimately not be worth the effort. Placing the majority of camera traps on trails was extremely valuable in this work to increase the probability of detection of three out of four felid species, all else being equal. At the same time, I was able to detect many other mammal species. This is in line with previous research, which emphasizes that placing cameras on trails is recommended to detect the majority of the mammal community, including carnivores (Cusack et al., 2015). A mix of camera placement strategies in the same study (e.g. on trails vs. not) could be a favourable option to ensure records of species that do not favour trails and it does not constitute an issue since such differences can be incorporated into the modelling process to avoid bias.

This thesis also highlights that studying land use change and sustainability is highly complex, as many drivers of landscape change take place simultaneously creating intertwined consequences, and involving different stakeholders and scales of action. Network analysis (Wasserman & Faust, 1994) proved to be a successful tool to interpret and explore these complex systems. Furthermore, the combination of scenario analysis, network analysis, and sustainability assessment can be a useful methodological approach to investigate land use change issues holistically, allowing to consider different scales and desired outcomes. By consulting stakeholders and experts this method also enables science to be proactive and devise locally-relevant management and policy recommendations. Finally, this work demonstrates that achieving conservation and sustainable development across tropical agricultural systems is extremely challenging because of their inherent complexity, hence the need for interdisciplinary research is at the highest.

6.4 Future research directions and final remarks

A limitation of this study was that to assess the impact of different land uses in the most rigorous way possible, it would be necessary to have large continuous blocks of natural habitats as control, and large areas of oil palm and cattle ranching, none of which was available, as different land covers were mixed in the landscape. Future research should be carried out under these conditions and should incorporate other land uses such as soy, coffee, cocoa, rubber, and pine and eucalyptus plantations. Similarly, repeated surveys before and after conversion would be extremely valuable to assess impact robustly, while subsequent surveys in post conversion areas would enable to explore phenomena of extinction debts (Tilman et al., 1994).

More jaguar density estimates are needed across the range and different land uses to build range-wide population estimates, while finer scale connectivity studies should be carried out to identify critical corridors at the regional scale. In the meantime further studies should quantify the habitat requirements and potential habitat loss thresholds of priority species across the biodiversity spectrum to identify optimum levels of habitat conversion, ultimately informing land use planning.

In lucrative agricultural sectors such as oil palm, research should identify and possibly value ecosystem services and yield benefits provided by sustainable practices. Landscape certification schemes should also be piloted and explored, as they work at a scale that is more appropriate for conserving wide ranging species like jaguars and for safeguarding vital ecosystem services. On the demand side, it would be valuable to understand further what are the best ways to raise awareness and generate a demand for certified products.

The open question remains of how conservation can compete with the cash revenue generated by production systems. Current evidence suggests a mixed approach, including green markets and price premiums, ecotourism, sustainable use of land as opposed to no use, national government funding, payment for ecosystem services schemes, non-governmental organizations' funds, and Reducing Emissions from Deforestation and forest Degradation mechanisms (Koh & Wilcove, 2007; Venter et al., 2009; Wilcove & Koh, 2010; Abram et al., 2014). Furthermore, identifying which mechanisms and policies can couple higher production with biodiversity and habitat preservation should be a priority, exploring the synergies between biodiversity, carbon, and food security (Phalan et al., 2016).

This thesis combined methods and analysis from different disciplines to generate new ecological knowledge and management and policy recommendations across tropical agricultural landscapes, including increasing oil palm areas. Achieving biodiversity conservation in the face of rapidly expanding agricultural areas is one of the greatest challenges conservation is facing (Tscharntke et al., 2012), but in a time of needed conservation optimism, it is not impossible. As protected areas only cover 18% of tropical forests (Bicknell, 2015) and 10% of Colombia's area (Forero-Medina & Joppa, 2010), the integration of unprotected and agricultural regions into conservation strategies and land use planning is key, in the Neotropics and elsewhere. Understanding how species use these human-dominated landscapes and how to better design them to deliver multiple objectives is equally important. Finally, jaguars and other mammal species can co-exist with agriculture if the appropriate conditions are in place. Following this thesis' recommendations there is potential to achieve sustainable agricultural landscapes that are able to provide for both biodiversity and people.

6.5 References

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