CONSERVATION POLICIES, MAMMAL CORRIDORS, AND LANDSCAPE DYNAMICS WITHIN A COSTA RICAN BIOLOGICAL CORRIDOR

A Dissertation

by

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ABSTRACT

The Payments for Environmental Services (PES) goals, in place in 1997, focus on preservation of biodiversity, scenic beauty, watershed protection, and carbon sequestration, whereas the National Biological Corridor Program (NBCP) focuses on sustainable development to increase connectivity within biological corridors. New legislative actions in 2006 and 2014 have placed spatial bounds on PES funding based on the NBCP official corridors. Due to these conservation policy changes and differing goals, it is important to critically analyze the spatial needs of each policy goal across a heterogeneous biodiversity landscape and a variety of ownerships regimes. In this research I analyzed the efficiency of targeted PES and the NBCP by classifying ASTER 15-meter resolution imagery using object-based classification methods, and compared land cover changes over an initial four-year period of corridor policy enactment. I examined the changes in overall mammal connectivity, and the role of PES properties within the study corridor by mapping connectivity through Circuitscape and least-cost path modeling. Lastly, I used Marxan to model potential reserve networks that aim to meet the specified policy goals of these two conservation programs.

Results indicate a decline in forest over the study time period, along with an increase in urban and pasture land covers. Results from connectivity analyses show PES properties hold a wide variety of species and guild richness, with higher richness in forest protection than reforestation. I established that active PES properties after NBCP played a larger role in connectivity compared to PES properties before. Overall connectivity within the study region has decreased since program enactment. Results from Marxan models indicate that goals within these two programs have differing spatial requirements, especially regarding watershed protection. PES policies targeted within biological corridors must act on present and future drivers of change to accomplish connectivity goals throughout Mesoamerica my results indicate the importance of PES for mammal communities, and the necessity for increased targeting of payments to existing forested corridors, to provide connectivity between protected areas. Multi-goal programs must determine which goals are most important and can strategically select goals with the highest overlap to accomplish the highest returns.

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Thank you to the Applied Biodiversity Science Program for opening my eyes to the world of interdisciplinary research and for providing me with the perfect academic home. I am ever grateful for the conversations about conservation, policy implications for local communities, and how best to support local actors in their conservation goals. Thank you to the Ecology and Evolutionary Biology Program for funding my research in

Costa Rica, and for introducing me to many professors who also conduct watershed research in Costa Rica.

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The Soltis Center in Costa Rica provided me with my home away from home. This could now have been accomplished without the dedication and hard work of the staff at the Soltis Center, who have become my Costa Rica family. Thank you again to Eugenio for your positive attitude and calm reassurances, and for providing the necessary entertainment, including puzzle times and dinners out in La Fortuna. Thank you to Johan, Noylin, and Angie for logistical support, and for helping me with small things while living at the center, including doctor visits, grocery store, and hardware store shops. Thank you to Tarcicio for lending me equipment, such as when I continuously asked for the hammer, and for fixing my flat tires and other mechanical help with my supplies and traps. Thank you to Dona Ana for the wonderful meals and coffee, and cleaning staff for friendship. Thanks to Alberth for being my field guide, for sharing knowledge on all natural things, but especially herps and birds, and most importantly, for being a friend. Lastly, I would like to thank my fellow researchers and students at the Soltis Center, who also became my family abroad. I loved learning about your research and dedication to the country we all cherish.

Thank you to the government agency FONAFIFO for collaborating with me and for providing me with spatial data on PES properties. Thank you to CODEFORSA for welcoming me and partnering with me on this project. Their help was instrumental in connecting me to the PES land owner community. Special thanks to Gilberth Solano for taking me into the field, for sharing your knowledge with me, and for being supportive of my project. The land owners and managers of the Paso de las Nubes Biological Corridor allowed me to work on their properties and opened their homes to me. They hiked the mountainous corridor with me to set camera traps and hair traps, they invited me in for meals with their families, and they shared their knowledge of mammal species.

The Biodiversity Assessment and Monitoring Lab was an integral part to my success at Texas A&M. I feel so fortunate to have been a part of a nurturing and positive lab environment, and my labmates Kelsey, Emma, Jess, Nikki, Jordan, DJ, and Gaby are awesome! I could not have asked for better mentors and friends. I very much enjoyed collaborating with the Central America ABS Team, Katherine, Mike, and Kelsey. Each of us worked on a separate part of conservation research, but our shared experience brought us together to discuss and tackle pressing conservation issues in the region. I especially appreciate how we made sure the others were safe during field work, and provided all forms of advice, from medical advice to food choice decisions (should Pringle consumption continue to go up as you progress through the field season?). I worked with seven dedicated undergraduate students during my dissertation research. Each of them has shown me their motivation and excitement for science and conservation. Thank you to Lili, Becca, and Pablo for work with me in the field, and for enduring those endless rainy days in the jungle with a smile. I could not have asked for three better undergraduate students. They are the reason I was able to complete my field research. Thank you to Becca, Staci, Hailey, and Amanda for help back in the lab with data processing.

My family has always supported my decision to pursue a graduate degree, and has provided moral support along the way. My mom and dad always provided positive motivation necessary to complete my degree, and have shared their love of nature with me, drawing me into the natural world at an early age through hiking the hills of Las Trampas and snorkeling and body surfing the waters of Kauai. And my brother has been a wonderful friend, partner in crime, and confidant in our academic journeys. I miss and love Grandma and Abuelita daily, and am grateful for their never-ending love. And I am so appreciative for grandpa's support and I always remember my summers in my grandparent's cabins and houses in the woods where my brother and I could explore all day long.

When I first arrived at Texas A&M, I could not have envisioned that I would make such amazing lifelong friends. My friends are the reason I was able to stay focused and complete my degree. To my dear friends Kelsey Neam, Emma Gomez, Johanna Harvey, Katherine Dennis, Elizabeth Daut, Alejandra Maldonado, Jess Gilbert, Mike Treglia, Mike Petriello, Carena Van Riper, Kristin and Zach Hurst, and many, many more who are not listed (you know who you are). Friends from afar also provided me with the love, support, and fun travel trips, including Camille Encarnacion, Kaylan Christianer, and Nicole Ystrom. Jesse has supported me during the last few years of my degree. He made College Station my home during our time together. He motivates me to be the best scientist I can be, is a hearty hiking buddy, and is always up for my continual questions about social scientists activities and theories.

NOMENCLATURE

PES	Payment for Environmental (or Ecosystem) Services
NBCP	National Biological Corridor Program
CBPN	Paso de las Nubes Biological Corridor

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CHAPTER I

INTRODUCTION

Conservation research significantly impacts species, ecosystems, and their human inhabitants. Because of this interconnectedness, both social and natural systems must be taken into account when researching conservation policies. Land conversion and deforestation are closely linked to agriculture throughout much of the world, and within Latin America these drivers have resulted in increased isolation of protected areas (DeFries et al. 2005). Deforestation and land conversion are tied to losses in environmental services, and these services are known to benefit human and wildlife populations through mitigation of climate change, stabilization of water resources, and preservation of biodiversity (Foley et al. 2007). Governments and other entities attempt to thwart deforestation and the loss of environmental services through conservation policies, such as neoliberal modeled Payments for Environmental Services (PES) policies (Pagiola 2008; Wunder and Albán 2008). PES is defined as a system where outside benefiters of environmental services pay local communities or landholders to manage their properties to provide those environmental services, either through restoration or protection (Wunder 2005). While many countries in Latin America have experienced forest loss, Costa Rica has seen an increase in forested areas, starting in the 1980s, with 2010 forest coverage totaling ~52% (Aide et al. 2013; FONAFIFO 2012).

Costa Rica is proactive in developing environmental policies to preserve and conserve natural resources. In 1996 Costa Rica established the national PES program, under Costa Rica Forestry Law No. 7575. The goal is to promote watershed stability, biodiversity protection, scenic beauty, and carbon sequestration. This voluntary program solicits applications from landholders with properties that promote conservation, including protection of primary forests, reforestation, or agroforestry; and in return, these registered lands provide environmental services. Jointly aligned with the PES program, the National Biological Corridors Program (NBCP) of Costa Rica was established in 2006 through Executive Order 33106 by the office of the Ministry of Environment, Energy and Telecommunications (MINAE) (National System of Conservation Areas SINAC 2009; Villate et al. 2009). The NBCP aims to strengthen existing protected areas, using spatially targeted PES payments inside of biological corridors to increase forest cover and connectivity, as well as by supporting cooperatives and local groups to enhance stakeholder alliances and sustainable development outside of protected areas (National System of Conservation Areas SINAC 2009; Vargas 2014). Each biological corridor is unique, and contains a multitude of land uses, including areas of urban use, forest, agriculture, and rural development. The corridor program has four main goals: (1) to strengthen the national biological corridor program; (2) to promote the conservation of biodiversity and restore ecological connectivity; (3) to encourage environmentally friendly development within biological corridors; (4) to increase collaborative endeavors with institutions and actors within the biological corridors (National System of Conservation Areas SINAC 2009) (MINAE 2006). Along with biological corridors, other priority areas for targeted PES include the Huetar Norte Forest Program region, areas designated for protection of water resources, areas with a

Social Development Index of less than 40%, and lastly, areas with expiring PES contracts (Wunscher et al. 2006).

Costa Rica ranks in the top 20 most biodiverse countries with 0.03% of the earth's land surface holding 4% of the world's species (INBio 2015). Biological corridors and connectivity are integral components to the overall protection of biodiversity, reducing extinction rates from restricted gene flow due to fragmentation and decreasing the impact of stochastic disturbances acting on isolated populations (DeClerck et al. 2010; Hodgson et al. 2011). The Costa Rican biological corridors are embedded within the multinational Mesoamerican biological corridor, which was created in 1998 and runs through eight countries from Mexico to Panama (Miller et al. 2001). Costa Rica has 47 proposed biological corridors and in 2010 had 24 active biological corridors, each facing unique conservation challenges (DeClerck et al. 2010). Many of the Costa Rica biological corridors are composed of agricultural matrices, encompassing all forms of land use from private farms to government hydroelectric projects. Extensive human habitation, with its variety of land uses, causes heterogeneous patterns of human pressures within these corridor matrices.

The Paso de las Nubes Biological Corridor (CBPN) is a critical connection point for the eastern and western transects of the greater Mesoamerican corridor within Costa Rica, and is important for national protected area connectivity. Located northwest of the capitol of San José, this corridor serves as the northern-most corridor connection for protected areas on either side of the continental divide, and is the main corridor linking the threatened northwestern dry forests to the eastern slopes. The CBPN encompasses a large altitudinal gradient, ranging from 300 to 2100 meters above sea level, making the CBPN well-suited for the protection and persistence of biodiversity in the face of a changing climate (Becker et al. 2007; Loarie et al. 2009). Lastly, this biological corridor and neighboring protected areas serve as the headwaters for more than five major rivers that provide drinking water for cities throughout central Costa Rica.

The NBCP utilizes the conservation strategy of land sharing to foster connectivity. Land-sharing studies have shown the importance of remnant forests contained in a permeable agricultural matrix (Daily et al. 2003; Horner-Devine et al. 2003; Perfecto and Vandermeer 2010). This matrix is composed of agricultural production areas, human settlements, agroforestry, and remnant forests, and these matrices can function as habitat or as a corridor system linking distant protected areas (Baum et al. 2004; Nagendra et al. 2013; Perfecto and Vandermeer 2002). The existence of Costa Rican protected areas has been shown to decrease deforestation in areas directly outside of protected area boundaries, further aiding in connectivity and enriching the agricultural matrix (Andam et al. 2008). Along with connectivity, the agricultural matrix can provide environmental services to local human populations, and these services are rewarded through the PES program (Jauker et al. 2009). The maintenance of biological corridors within the agricultural matrix is essential for effective management of protected areas, biodiversity, and environmental services.

Within the matrix, some wildlife species are able to persist and travel, but many forest dependent species cannot cross large stretches of open lands between protected areas (Daily et al. 2003; Tabarelli et al. 2010). Within Costa Rica, the majority of large-bodied forest dependent mammal species are nationally endangered due to loss of habitat and hunting (INBio 2015). Within the Mesoamerican corridor, Costa Rica has the highest percentage of land held within protected areas (35%), but even with large areas under protection, connectivity is key for the utility of protected areas for wildlife species (DeClerck et al. 2010). The CBPN is essential for the movement of species requiring large home ranges or long dispersal distances. Male jaguars (*Panthera onca*) have a home range between 40-83 km^2, while male puma (*Puma concolor*) require a home range of 200-800 km^2, and male ranges rarely overlap (Rabinowitz and Jr 1986; Reid 1998; Soisalo and Cavalcanti 2006). Even small carnivores such as the jaguarundi (*Puma yaguarondi*) require home ranges of up to 20 km^2 (Michalski et al. 2006). Neighboring protected areas do not have sufficient area to cover the home range of one individual male puma. Thus, the CBPN acts as a buffer zone to the extensive adjacent protected areas of Juan Castro Blanco National Park (145 km^2), Alberto Manuel Brenes Biological Reserve (78 km^2) and Monteverde Cloud Forest Reserve (260 km^2), further extending essential habitat for wildlife species.

Ecological connectivity is deemed vital for both biodiversity and ecosystem services by the Convention on Biological Diversity (CBD), as defined in Aichi Target 11. The CBD describes ecological connectivity as an essential component of protected area management, and connectivity bolsters the effectiveness of protected area networks. The CBD further specifies that connectivity should be met through employing ecosystem approaches to efficiently enhance critical ecological processes and functions

(Convention on Biological Diversity 2011). Landscape and economic diversity are inherent properties of biological corridors, which can increase ecosystem resilience when properly managed, further benefiting biodiversity and conservation (Schippers et al. 2015). Management of landscape features and patterns of economic activity within corridors, however, requires collaboration with local landowners to enhance connectivity while also providing appropriate economic incentives.

Corridor designs can take many forms, including linear features along the landscape, lattice shaped networks, or stepping-stones (Saura et al. 2014; Townsend and Masters 2015). Now many corridor spatial designs also take into account the potential future impacts of climate change (Williams et al. 2005), with inclusion of latitudinal gradients and elevation bands to create a lattice network of connectivity built along rivers and streams, allowing for elevational movement of species and providing refuge to non-vagile species within specific elevational levels (Townsend and Masters 2015). Environmental connectivity has several definitions, including landscape connectivity, habitat connectivity, ecological connectivity, and evolutionary processes connectivity (Lindenmayer and Fischer 2006) (Worboys et al. 2010). Habitat connectivity is defined as an anthropogenic view of vegetation patterns, while habitat connectivity is connections of habitat patches for species (Lindenmayer and Fischer 2006). Ecological connectivity deals with larger ecosystem and hydrologic processes, and evolutionary connectivity focuses on genetic flow throughout populations (Lindenmayer and Fischer 2006).

And when enacting connectivity plans, there are several considerations, including configuration, and population sources and sinks. Patches, while beneficial, can act as population sinks for species dispersing out of ideal habitat areas and into areas that do not hold the required resources. Sinks can also place wildlife in direct contact and competition with humans, causing potential conflict (Kilpatrick et al. 2009; Marshall 2010). The size of the patch can also dictate the utility of the patches for particular species, with smaller or spatially narrow patches providing less habitat and resources compared to larger patches (Forman 1995) (Levin and Paine 1974).

Costa Rica uses a neoliberal conservation tool, PES, to increase connectivity in the National Biological Corridor system, as stated above in outcomes and goals of the SINAC strategic plan (National System of Conservation Areas SINAC 2009). All PES participants within biological corridors are given an increase probability of application selection (MINAE 2014). Property location within the biological corridors, however, is not a separate factor for selection within this program; the level of spatial specificity is at the level of the biological corridor. Nevertheless, the configuration of patches and the matrix in which they are embedded is essential to determine the degree of connectivity and the potential utility for wildlife (Baum et al. 2004).

To tie landscape connectivity and land use changes together, conservation planning is the ideal tool to use to understand future conservation actions and outcomes. Conservation planning has become an indispensable step in the examination and enactment of conservation policies. Planning provides spatial targets based on social and biological variables. There is a growing literature of studies conducting conservation landscape scenario modeling, with integration of biodiversity measures and social management land cover costs (Reyers et al. 2012) (Cowling et al. 2008) (De Groot et al. 2010) (Nelson et al. 2009) (Tallis and Polasky 2009). Conservation planning has been used widely in the marine field to determine overlapping sustainable fishing regions and priority no-take zones (Klein et al. 2009) (Mazor et al. 2014); and this method has recently also been used extensively on terrestrial ecosystems (Levin et al. 2013) (Chan et al. 2006). Conservation planning allows for a cost-benefit analysis of a series of scenarios, and projects the resulting options onto the landscape, in a spatially explicit form with detailed costs for each reserve scenario.

Conservation planning can now take into account both private and public lands to provide an optimal solution across various ownership and land use management (Ball et al. 2009). Conservation planning studies have illuminated the level of overlap between ecosystem service oriented goals and biodiversity oriented goals, permitting researchers to understand how to meet both needs within a study system (Chan et al. 2006). The focus of conservation programs has changed from solely protected areas to creating more permeable landscapes and healthy ecosystems. Because of these larger and more complex goals, conservation planning has become a necessary tool to understand trade-offs and relationships among costs within ecosystems. Taking into account biodiversity held within private lands increases the biodiversity value of the landscape and provides a more representative measurement of actual biodiversity. Also, when taking into account biodiversity held outside of parks or reserves, conservation implementation costs are reduced. Another benefit to conservation planning is that a variety of conservation strategies and management plans can be modeled. This is important because, for example, non-traditional conservation areas such as well-managed reforestation or agroforestry areas can provide reasonable habitat for a wide range of species (Wood, Ch.2), and can increasing the permeability of landscapes for wildlife movement (Daily et al. 2003).

Each dissertation chapter addresses research questions pertaining to land use change, landscape and mammalian connectivity, and spatial conservation planning. Chapter two tackled the viability of the NBCP, with its large and complex spatial scale, requires landscape level analyses. While there are initial reports on ecological connectivity and diversity within biological corridors, no study has looked at the effectiveness of targeted PES payments within biological corridors (Céspedes et al. 2008; National System of Conservation Areas SINAC 2009; Vargas 2014). With the spatial complexity, remote sensing provides an effective measurement tool to assess these conservation measures. The purpose of chapter two was to assess landscape changes temporally aligned with initial enactment of the National Biological Corridor Program, specifically on land use change within the CBPN. The objectives of this study were to: (1) identify the major land shifts, pixel by pixel, within the biological corridor; (2) understand how implementation of PES policies overlap with the changes in the corridor from years 2008 to 2012; (3) identify land use changes and proportional changes within the CBPN as compared to similar areas directly outside of the corridor region, to understand the changes and pressures geographically aligned with and without PES targeting; (4) describe changes to forest patch metrics from 2008 to 2012, during the initial years of the NBCP within CBPN.

Chapter three addressed aspects of corridor program effectiveness using the tools of remote sensing, GIS, and wildlife monitoring. Corridor program payments for environmental services are not currently spatially targeted for specific species. Modeling of pathways, mammal routes, and landscape connectivity will provide much needed spatial parameters necessary for successful achievement of the conservation program goals. (1) I used mammalian survey tools to measure medium and large mammalian species occupancy within study region, in PES properties, non-PES properties, and protected areas. (2) Next, I assessed the effectiveness of conservation regions by modeling overall mammal corridor suitability across the Paso de las Nubes Biological Corridor (CBPN) from the inception of the program, and six years into the program using electrical current model theory and specified the role of PES properties in these key areas. Finally, (3) I measured connectivity across the landscape through least cost path, which detailed important mammal corridor routes and pinch points through the CBPN. These approaches allow for an analysis of the efficacy of the national policy, which informs PES actions throughout the biological corridor network. Applications are far-reaching as these policies are used nation-wide in Costa Rica as well as throughout the world (Wünscher et al. 2008) (Morse et al. 2009).

In chapter four, I assessed conservation planning scenarios based on the two official conservation programs, Costa Rica’s Payments for Environmental Services and the National Biological Corridor Programs. Conservation scenario modeling is a necessary step to understand spatial requirements for conservation goals. Due to recent changes to the national biological corridor program in 2006 and the addition of NBCP priority directly into the PES program structure in 2014, planning is an essential final process to understanding how conservation policies shape landscape features and environmental services. Specific objectives of this chapter were to: (1) identify the costs to implement conservation actions on various land use types throughout the region, based on conservation payments and landscape production factors; (2) conduct conservation planning analyses with various scenarios, representing specific goals of active conservation programs within the region; and (3) provide recommendations for spatial priority areas based on conservation goals.

CHAPTER II

LAND USE CHANGE IN PAYMENTS FOR ENVIRONMENTAL SERVICES AND NATIONAL BIOLOGICAL CORRIDOR PROGRAMS

Synopsis

Costa Rica established the National Biological Corridor Program in 2006. Under the National Biological Corridor Program, the long-running Payment for Environmental Services Program was newly prioritized into biological corridors throughout the country. The National Biological Corridor Program caused a nationwide spatial shift in placement of payments for environmental services throughout Costa Rica. We classified ASTER 15-meter resolution imagery in a central Costa Rica corridor connecting the eastern and western protected areas networks to analyze the change in forests during the National Biological Corridor Program with its targeted payments for environmental services effort. We used object-based classification methods, and compared land cover changes over an initial four-year period of corridor policy enactment. We calculated the changes within PES properties and outside of PES regions, and we also calculated forest patch metrics during the same time period. Results indicate a decline in forest cover over the study period, along with an increase in urban and pasture land covers, with higher change and loss of forest centered inside of the biological corridor, near the construction area for the new San Carlos highway, and within eastern pasture areas. We also saw a higher percentage of forest loss inside of the biological corridor area as compared to areas outside of the biological corridor. Forest loss was drastically less within current

and historic PES properties, as compared to the overall study region. Across the entire study region, patch metrics show a decrease in the number of patches and a slight decrease in average patch size. These results suggest that current and past designation of PES prevents forest loss while the current designation of priority conservation status via the National Biological Corridor Program is not increasing connectivity and forest conservation. This is shown by increased land use change and a decrease in forest is associated with designated biological corridors. This is antithetical to the goals of the National Biological Corridor Program.

Introduction

Land conversion and deforestation are closely linked to agriculture throughout much of the world, and within Latin America these drivers have resulted in increased isolation of protected areas (DeFries et al. 2005). Deforestation and land conversion are tied to losses in environmental services, and these services have been shown to benefit human and wildlife populations through mitigation of climate change, stabilization of water resources, and preservation of biodiversity (Foley et al. 2007). Governments and other entities attempt to thwart deforestation and the loss of environmental services through conservation policies, such as neoliberal modeled Payments for Environmental Services (PES) policies (Pagiola 2008; Wunder and Albán 2008). PES is a system where outside benefiters of environmental services pay local communities or landholders to manage their properties to provide those environmental services, either through restoration or protection (Wunder 2005). While many countries in Latin America have experienced forest loss, Costa Rica has seen an increase in forested areas, starting in the 1980s, with 2010 forest coverage totaling ~52% (Aide et al. 2013; FONAFIFO 2012).

Costa Rica is proactive in developing environmental policies to preserve and conserve natural resources. In 1996, Costa Rica established the national PES program, under Costa Rica Forestry Law No. 7575. The goal is to promote watershed stability, biodiversity protection, scenic beauty, and carbon sequestration. This voluntary program solicits applications from landholders with properties that promote conservation, including protection of primary forests, reforestation, or agroforestry; and in return, these registered lands provide environmental services. Well defined land tenure and transparent actors make this system function within the PES framework (Sunderlin et al. 2009). Many entities, including beneficiaries of the environmental services as well as polluters, pay into the program, including national hydroelectric interests and the World Bank (Pagiola 2008). Primary forest payments are eligible for renewal every 5 years, and agroforestry and reforestation are allowed one 5 year contract with no renewal. Most reforestation contract holders have plans to sell the wood for timber after 15 to 20 years, while a few contract holders are using the payments to reforest the land permanently. Contract holders plant both native and non-native tree species. Some tree species include Teak (*Tectona grandis*), American mahogany (*Swietenia humilis)*, Rainbow eucalyptus (*Eucalyptus deglupta*), Melina (*Gmelina arborea*), and Almendro (*Dipteryx panamensis*). Timber products in Costa Rica include wood for pallets or furniture, among others (Floors 1997).

Jointly aligned with the PES program, the National Biological Corridor

Program (NBCP) of Costa Rica was established in 2006 through Executive Order 33106 by the office of the Ministry of Environment, Energy and Telecommunications (MINAE) (National System of Conservation Areas SINAC 2009; Villate et al. 2009). The stated goals of the NBCP are to achieve connectivity among neighboring protected areas and to increase biodiversity through sustainable use (SINAC 2008). The NBCP aims to strengthen existing protected areas, using spatially targeted PES as a tool inside of biological corridors to increase forest cover and connectivity, as well as by supporting cooperatives and local groups to enhance stakeholder alliances and sustainable development in the biological corridor network (National System of Conservation Areas SINAC 2009; Vargas 2014). Along with biological corridors, other priority areas for targeted PES include the Huetar Norte Forest Program region, areas designated for protection of water resources, areas with a Social Development Index of less than 40%, and lastly, areas with expiring PES contracts (Wunscher et al. 2006).

Costa Rica ranks in the top 20 most biodiverse countries in the world, with 0.03% of the earth's land surface holding 4% of the world's species (INBio 2015). Biological corridors and connectivity are integral components to the overall protection of biodiversity, reducing extinction rates from restricted gene flow due to fragmentation and decreasing the impact of stochastic disturbances acting on isolated populations (DeClerck et al. 2010; Hodgson et al. 2011). The Costa Rican biological corridors are embedded within the multinational Mesoamerican biological corridor, which was created in 1998 and runs through eight countries from Mexico to Panama

(Miller et al. 2001). Costa Rica has 47 proposed biological corridors, covering 35% of the country, and in 2010 had 24 active biological corridors, each facing unique conservation challenges (DeClerck et al. 2010). Many of the Costa Rica biological corridors are composed of agricultural matrices, encompassing all forms of land use from private farms to government hydroelectric projects. Extensive human habitation, with its variety of land uses, causes heterogeneous patterns of human pressures within these corridor matrices.

The Paso de las Nubes Biological Corridor (CBPN) is a critical connection point for the eastern and western transects of the greater Mesoamerican corridor within Costa Rica, and is important for national protected area connectivity (Figure 1). Located northwest of the capital of San José, this corridor serves as the northern-most corridor connection for protected areas on either side of the continental divide, and is the main corridor linking the northwestern dry forests to the eastern slopes. The CBPN encompasses a large altitudinal gradient, ranging from 300 to 2100 meters above sea level, making the CBPN well-suited for the protection and persistence of biodiversity in the face of a changing climate (Becker et al. 2007; Loarie et al. 2009). Lastly, this biological corridor and neighboring protected areas serve as the headwaters for more than five major rivers that provide drinking water for cities throughout northern and central Costa Rica. The Juan Castro Blanco National Park on the eastern border is even named “The Park of Water”, because of the wealth of rivers originating within its bounds.

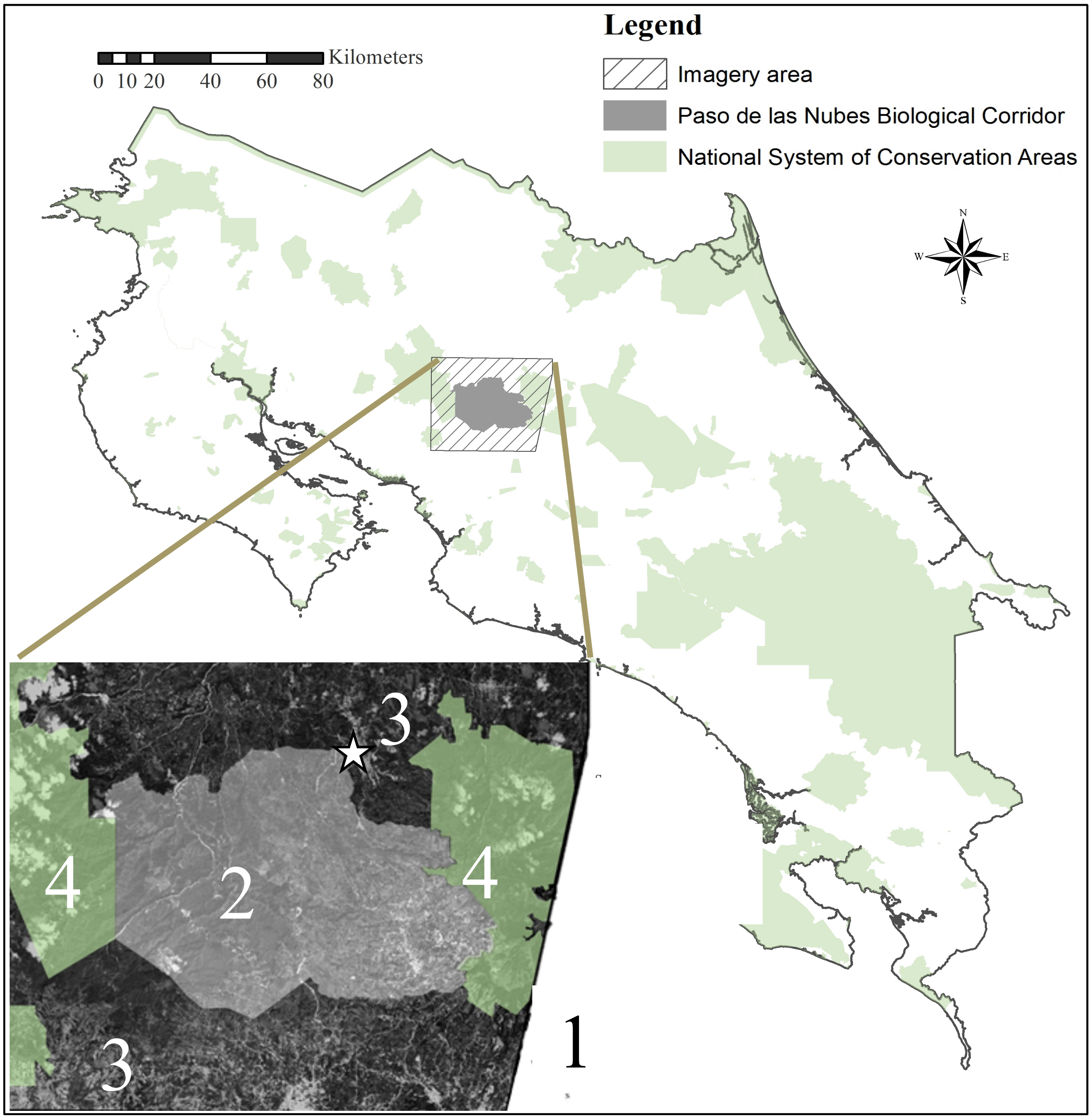

Figure 1. Regional overview, with Paso de las Nubes Biological Corridor and imagery areas outlined. Change analysis areas are found in the lower left corner of the figure. Area 1 encompasses the entire imagery area; area 2: the biological corridor; area 3: the private lands outside of the biological corridor; area 4: the protected areas network, with eastern Juan Castro Blanco and western Manuel Brenes, Monteverde and Arenal protected areas. The star designates Ciudad Quesdad.

The NBCP utilizes the conservation strategy of land sharing to foster connectivity. Land-sharing studies have shown the importance of remnant forests contained in a permeable agricultural matrix (Daily et al. 2003; Horner-Devine et al. 2003; Perfecto and Vandermeer 2010). This matrix is composed of agricultural production areas, human settlements, agroforestry, and remnant forests, and these matrices can function as habitat or as a corridor system linking distant protected areas (Baum et al. 2004; Nagendra et al. 2013; Perfecto and Vandermeer 2002). The existence of Costa Rican protected areas has been shown to decrease deforestation in areas directly outside of protected area boundaries, further aiding in connectivity and enriching the agricultural matrix (Andam et al. 2008). Along with connectivity, the agricultural matrix can provide environmental services to local human populations, and these services are rewarded through the PES program (Jauker et al. 2009). The maintenance of biological corridors within the agricultural matrix is essential for effective management of protected areas, biodiversity, and environmental services.

Within the matrix, some wildlife species are able to persist and travel, but many forest dependent species cannot cross large stretches of open lands between protected areas (Daily et al. 2003; Tabarelli et al. 2010). Within Costa Rica, the majority of large-bodied forest dependent mammal species are nationally endangered due to loss of habitat and hunting (INBio 2015). Within the Mesoamerican multi-national corridor, Costa Rica has one of the highest percentage of land held within protected areas at 26% (World Bank. 2015), but even with large areas under protection, connectivity is key for the utility of protected areas for wildlife species.

The CBPN is essential for the movement of species requiring large home ranges or long dispersal distances. Male jaguars (*Panthera onca*) have a home range between 40-83 km^2, while male puma (*Puma concolor*) require a home range of 200-800 km^2, and male ranges rarely overlap (Rabinowitz and Jr 1986; Reid 1998; Soisalo and Cavalcanti 2006). Even small carnivores such as the jaguarundi (*Puma yaguarondi*) require home ranges of up to 20 km^2 (Michalski et al. 2006). Neighboring protected areas do not have sufficient area to cover the home range of one individual male puma. Thus, the CBPN acts as a buffer zone to the extensive adjacent protected areas of Juan Castro Blanco National Park (145 km^2), Alberto Manuel Brenes Biological Reserve (78 km^2) and Monteverde Cloud Forest Reserve (260 km^2), further extending essential habitat for wildlife species (Figure 1).

The value of natural experiments is indispensible in understanding the utility of conservation programs. Conservation policies must be researched in the same manner as ecological hypotheses, and made to answer the question of additionality; that is, "do interventions work better than no intervention at all?" (Ferraro and Pattanayak 2006). This is exactly what I aim to understand in this study. The study area enables us to examine changes seen under active conservation programs within the CBPN, and I designated a control area outside of biological corridor that currently does not hold priority and since 2006 holds lower probability of receiving PES contracts. While it can be challenging to link changes back to specific policies, identifying changes can provide a quantitative measure to determine if the goals of the conservation policies are being achieved (Ferraro and Pattanayak 2006).

Assessment of the viability of the NBCP, with its large and complex spatial scale, requires landscape level analyses. While there are initial reports on ecological connectivity and diversity within biological corridors, no study has looked at the effectiveness of targeted PES within biological corridors (Céspedes et al. 2008; National System of Conservation Areas SINAC 2009; Vargas 2014). With the spatial complexity, remote sensing provides an effective measurement tool to assess these conservation measures, and can be used in future studies to map other corridors within the biological corridor network through the nation.

We took advantage of this natural landscape experiment to assess landscape changes temporally aligned with initial enactment of the National Biological Corridor Program, specifically on land use change within the CBPN. This information is a necessary assessment of this new targeting program, especially for government agencies and NGOs operating within the country, and in other counties utilizing targeted PES for corridor establishment. The objectives of this study were to: (1) identify the major land shifts, pixel by pixel, within the biological corridor; (2) understand how implementation of PES policies overlap with the changes in the corridor from years 2008 to 2012, with dates also determined through availability of cloud-free imagery; (3) identify land use changes and proportional changes within the CBPN as compared to similar areas directly outside of the corridor region, to understand the changes and pressures geographically aligned with and without PES targeting; (4) describe changes to forest patch metrics from 2008 to 2012, during the initial years of the NBCP within CBPN.

Methods

Study Area

The CBPN is located in the Tilaran and Central mountain ranges of Costa Rica, in Alajuela Province. The corridor is comprised primarily of privately held lands and encompasses an area of ~40,000 ha. Life zones in the region include premontane rain forest, premontane wet forest, lower montane moist forest, lower montane rain forest, and tropical wet forest (Hartshorn 1983). The primary land uses consist of forest, dairy farms, ornamental plant farms, tree plantations, urban areas, and rural towns. The CBPN is bordered to the east by Juan Castro Blanco National Park, and to the west by Alberto Manuel Brenes Biological Reserve and Monteverde Cloud Forest Reserve. North of the corridor, there is extensive agriculture and one of the largest cities in the region, Ciudad Quesada. To the south of the corridor lies many cities emanating from the capitol, including Naranjo de Alajuela and San Ramon, and extensive agriculture, with a wealth of coffee plantations to the southeast.

Before 2006, landholders within the CBPN bounds had an equal opportunity of being selected for PES as compared to areas outside of the not-yet designated CBPN. In 2007, PES priority was moved inside the bounds of the biological corridors, leaving areas outside of the corridor at a lower priority for payments. When looking at general national forest trends, between 2001 and 2005 (before the NBCP) there was a national loss of approximately 63,000 hectares of forest (Global Forest Loss. 2015), and within Alajuela Province, there was a loss of 15,878 hectares (-1.32%) of forest. From 2001 to 2012 there was an overall gain of 7,162 hectares of forest (Global Forest Loss. 2015).

PES properties are diverse within the study region. Registered PES contracts under the 2003 to 2014 period are as follows; 212 forest protection property contracts, 40 agroforestry contracts, and 13 reforestation contracts (Table 1). Forest protection contracts had the highest average property size, and maximum area, while reforestation had the lowest (Table 1). Economic activities conducted by PES property owners were diverse, and included dairy cattle farming, ornamental plant production, subsistence farming, growing trees for timber, ecotourism, teaching, and other employment based in larger regional cities of Ciudad Quesdad and San José. Around a fourth of PES contract holders lived on the property, while the other fourth live off site with managers living on the property. Half of the properties were forest plots with no housing, land managers, residences, or roads.

Table 1. Payments for environmental services contracts information for participants within the study region from 2003 to 2014.

PES Land Use (2003 to 2014)	Total Area (km^2)	Maximum Contract Area (km^2)	Total number of Properties	Average Property Size (km^2)
Reforestation	2.762	0.551	13	0.197
Agroforestry	17.283	3.177	40	0.432
Forest Protection	193.750	7.998	212	0.884

Pre-processing

To quantify land use change, I first acquired Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) imagery from February 2nd, 2008, and February 29th, 2012. I selected dates based on the timing of corridor policy enactment, and for low cloud cover across the CBPN. No other imagery dates with 15-meter resolution (Landsat or ASTER) had less than 30% cloud cover over the CBPN within any season near the implementation of the CBPN or current day. Thus, the two images acquired were the only two available with less than approximately 30% cloud cover over the CBPN and usable for this analysis. Although I did not acquire imagery from the first year after implementation, 2007, I felt the imagery from 2008 was the next best option. Images are from the dry season and within the same month (February) to allow for vegetation comparability; the study area during the dry season receives a monthly rainfall average of approx. 100 mm (http://soltiscentercostarica.tamu.edu/Resources/On-Line-Meteorological-Data). The imagery bands used for the analysis included the first three ASTER bands, visible green/yellow, visible red, and near-infrared, with 15-meter resolution. I used four imagery tiles in this study, two from 2008, and two from 2012, all from ASTER satellites from the approximate location of path 15 and row 53.

During pre-processing, I orthorectified each image, accomplished with the use of software SilcAst with Global ASTER DEM version 2. Then, the imagery was clipped to encompass the corridor, and include private lands within a 6.7 km buffered region around the corridor. This clipping extent was based on the size of the imagery and the accuracy for which the classification could be conducted; areas outside of that buffered region had different vegetation signatures based on mirco-climates causing discrepancies with classification and were not important forTheanalysis, and thus were removed from the analysis. To discriminate between areas of active vegetation growth and senescent or bare land, I calculated the Normalized Difference Vegetation Index (NDVI) by subtracting the red band from the near infrared band, and dividing that value by the near infrared band plus the red band ((nir-r)/(nir+r)) (Carlson and Ripley 1997). I also generated a texture band to create a filter, using the co-occurrence tool in the software ENVI (ENVI version 5.2 2014). The texture band created from the yellow/green band was deemed the most useful in detecting differences in vegetation and non-vegetation. I stacked the texture band with NDVI layer and three ASTER bands to produce a pre-processed imagery product with five layers (Appendix A1).

Processing

We conducted an object-oriented classification of the imagery using Trimble eCognition Developer 9.1 (Trimble 2011). I chose to use object-oriented classification as opposed to pixel-based classification because initial trials using pixel-based methods produced low accuracy and kappa values. Other studies have also shown that object-oriented classification can result in higher accuracy as compared to traditional pixel-based classification (Platt et al. 2008). The parameters developed for the rule set were as follows: scale parameter: 5, shape parameter: 0.1, and compactness: 0.9. Each layer was weighted equally for segmentation, with a value of 1. Segmentation parameters included nearest neighbor feature objects with mean and standard deviation. After the rule-set was developed, I segmented the imagery tiles (Appendix A1).

After segmentation, I identified nine classes based on the vegetation and pixel characteristics of the imagery. The vegetation classification categories included: (1) urban or built up land, (2) pasture, (3) low vegetation, (4) bare ground, (5) forest, (6) dark forest, (7) clouds, (8) cloud shadows, (9) pacific slope low vegetation, (10) water. After classification, I merged classes that represented identical on-the-ground land cover types including pacific slope vegetation and low vegetation classes, cloud and cloud shadow, and forest and dark forest classes. Pacific slope vegetation represented vegetation below 2.5 meters in canopy height located in a region with a distinct dry/wet season rainfall pattern, as opposed to the low vegetation on the Caribbean slope with more constant yearly rainfall. The dark forest class represented forest in shadowed slopes in mountain valleys.

Field Measurements

We collected ground truth and training point data for all class categories except cloud, cloud shadow, and water. Field ground truth points were collected from May to August 2012, 2014, and were collected from all regions of the biological corridor and areas outside of the corridor. Accessibility was the only limiting factor to these points. I collected ground truth points in areas with road networks or trails within properties. PES shapefiles from FONAFIFO (Fondo de Financiamiento Forestal), along with satellite based imagery, were also used to provide additional ground truth points for years 2008 and 2012, especially in regions of the imagery with few roads or difficult accessibility. Due to the steep mountain topography of the high-altitude stream and river channels in the CBPN, I can predict that the streams and rivers have not migrated over the short time scale of this study; because of this, I were able to visually identify water class regions. For both 2008 and 2012, I collected between 40-80 training samples, and approximately 55 ground truth points per class.

Post-processing

First, I conducted a post classification cleaning of all images by manual object identification and classification; this step was especially important for areas of high reflectance along the perimeters of clouds. Next I mosaicked the tiles for each year, conducted an accuracy assessment on the classified imagery, and calculated Kappa statistics (Table 2). The kappa values were 0.97 and 0.95 for 2008 and 0.87 and 0.95 for 2012. The overall accuracy for 2008 was 97.82% and 95.70%, and for 2012, 89.22% and 95.73%. I found these kappa and overall accuracy values satisfactory to proceed with a change detection analysis (Table 2). The final classes for the imagery included forest, pasture, low vegetation, bare ground, urban, water, and cloud, and class descriptions (Appendix A2). Clouded areas from each classification were merged and masked before conducting the change detection. This removed the potential for comparison of cloud to non-cloud areas, eliminating cloud bias in the difference map.

Table 2. Confusion matrix for the two imagery tiles from 2008, 2012 classification of imagery, including user and producer accuracy, kappa coefficients, overall accuracy. Producer accuracy is represented as “P”, and user accuracy is represented as “U”.

	2008-1		2008-2		2012-1		2012-2	
Class	P	U	P	U	P	U	P	U
Forest	98.6	97.3	96.3	96.3	91	93.3	95.2	97.6
Bare land	91.4	100	97.5	90.7	70.7	61.7	92.7	88
Pasture	100	94.7	1000	87.2	90.9	90.9	92.7	100
Low vegetation	98.7	97.4	95	97.4	94.7	93.7	100	92.5
Water	100	100	100	100	88.9	100	93	100
Urban	95	98.7	87.8	100	78.1	84.2	95.7	96.7
Cloud / shadow	100	97.5	97.5	96.3	100	94.7	99.1	95.8
Overall Accuracy (%)	97.8		95.7		89.2		95.7	
Kappa Coefficient	0.974		0.949		0.872		0.949	

Change Detection Analysis

We conducted a post-classification change detection analysis to understand the land use changes and describe the anthropogenic activities occurring in the region during the initial years of the NBCP. A change detection comparison took place within three distinct spatial regions: (1) the entire study area, (2) only within the CBPN, and (3) lands directly outside of the biological corridor within the 6.7 km wide buffered area (Figure 1). Region 3, lands directly outside of the biological corridor, served as control regions to compare with the CBPN; these areas represented areas where the prioritization was not applied after NBCP enactment. This area outside of the biological corridor is primarily private lands within the same region, with similar economic activities, and approximately the same size as the CBPN, making it suitable for comparison. The change detection analysis provided information on the overall differences in land use from 2008 to 2012, and the conversions, pixel by pixel, from one land use category to another.

We then conducted change detection from 2008 to 2012 within regions of current and historic PES properties, analyzing PES contracts from 2003 to 2014. For a PES participant to continue in the program, PES properties are monitored yearly during active contracts, and the owners must follow a number of regulations detailed in their contracts, including prevention of hunting, fires, and deforestation, among others (Pagiola 2008). That said, I do not expect to see forest change during active contracts. However, changes can occur after contracts have expired, as the land uses are unrestricted and decisions are made solely by the landowner and not the PES program.

Forest Patch Metrics

In conjunction with the change detection analysis, I calculated patch metrics for the forest class in 2008 and 2012 across the entire study region, including patch number, and average patch area. These metrics provided information on changes to forest patch dynamics to help understand movement ability of populations across a landscape (Gutiérrez et al. 1999; Hanski and Hanski 1999; Lawes et al. 2000).

Results

Classification Results

We developed a land-use classification map of the study area (Figure 1). The most prevalent class across the entire imagery in 2008 (area 1, Figure 1) was forest, at

399 km2, and the next two largest classes were low vegetation (297 km^2) and bare ground (94 km^2). Urban areas covered 56 km^2 (Table 3). In 2012, forest again was the most prevalent class; with 355.75 km^2 followed by low vegetation and bare ground (Table 3). Within the CBPN in 2008 (area 2, Figure 1) forest totaled 130.48 km^2, declining to 103.68 km^2 in 2012; low vegetation and pasture were also the second and third largest cover types in 2012, with low vegetation at 9% (34 km^2) and pasture at 23% (95 km^2). While the CBPN does have a number of towns and cities located within the boundary, the urban areas were relatively small, 8.43 km^2 in 2008 and 12.53 km^2 or 3% in 2012. The majority of the land throughout the biological corridor was forest and low vegetation, and both land uses were eligible for PES forest or reforestation payments, while only a small percentage of CBPN was comprised of permanently built up lands (Table 3) (Figure 2).

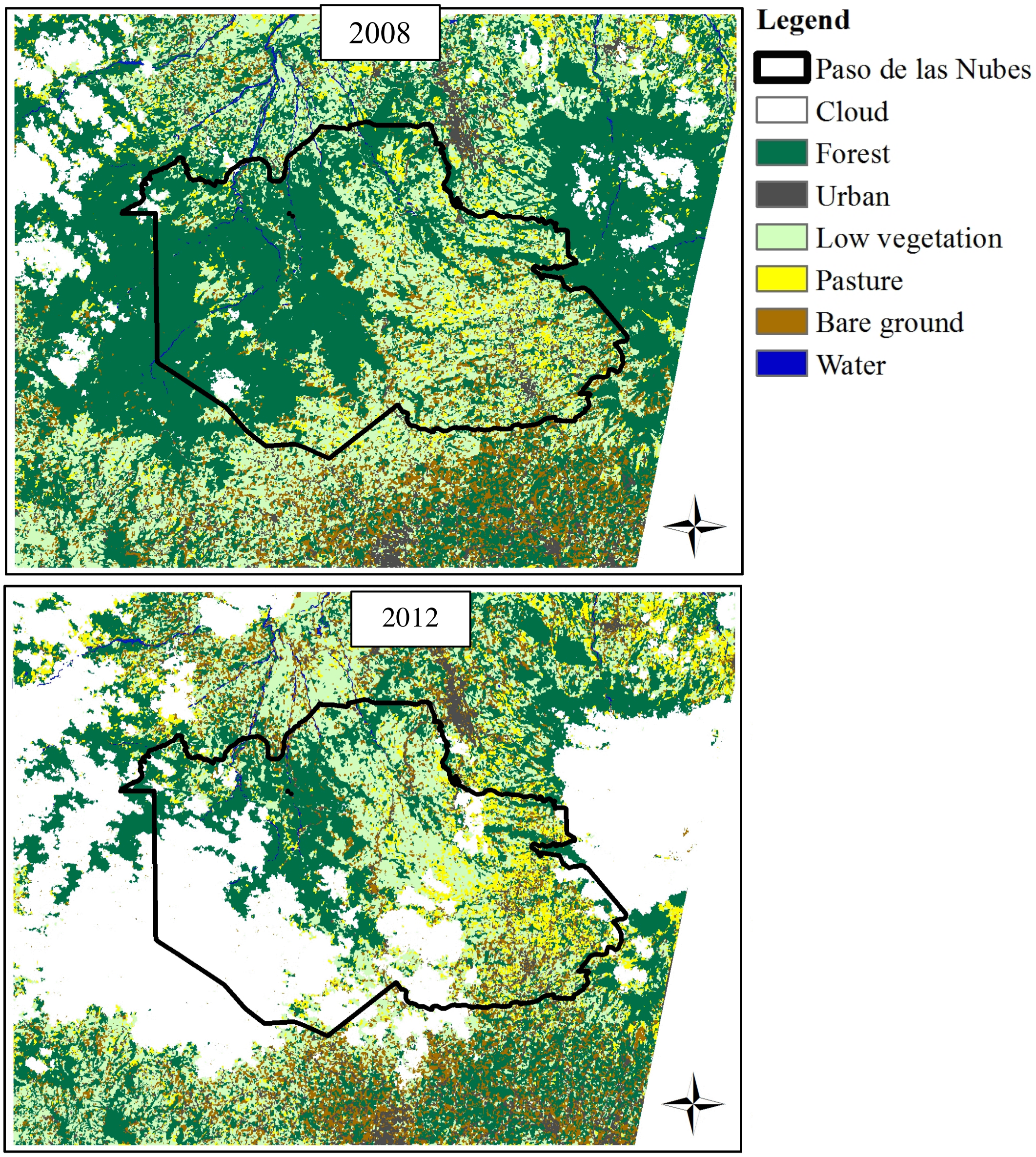

Figure 2. Land use classification for 2008 and 2012, with the Paso de las Nubes Biological Corridor outlined in black. The bare ground and urban linear feature in the center of the 2012 map is the construction of the San Carlos highway and Ciudad Quesada is the grey urban oblong polygon just to the north of the Biological Corridor.

Table 3. Change detection, with values representing change in land use category, within each spatial change analysis area as determined by the remote sensing analysis. Numbers for change analysis area represent: 1. Entire imagery area; 2. Biological corridor; 3: Areas outside biological corridor, excluding protected areas.

Change analysis area		Cloud	Forest	Urban	Low vegetation	Pasture	Bare	Water
1	Total image area 2008 (km^2)	501.53	399.85	55.84	297.39	49.4	94.23	5.58
1	Total image area 2012 (km^2)	501.53	355.75	61.21	283.04	79.45	117.98	4.56
1	Difference in total image area (km^2)	-	-44.1	5.36	-14.35	30.05	23.75	-1.03
1	Difference total image area (%)	-	-11.03	9.61	-4.825	60.84	25.21	-18.36
2	Paso de las Nubes 2008 (km^2)	134.15	130.48	8.43	89.77	20.16	19.01	1.19
2	Paso de las Nubes 2012 (km^2)	134.15	103.68	12.53	95.54	34.44	22.3	1.15
2	Difference Paso de las Nubes (km^2)	-	-26.8	4.1	5.78	14.28	3.3	-0.05
2	Difference Paso de las Nubes (%)	-	-20.54	48.59	6.437	70.83	17.36	-3.85
3	Private Lands Outside Paso de las Nubes Biological Corridor 2008 (km^2)	153.92	193.3	46.25	189.83	26.07	69.89	4.22
3	Private Lands Outside Paso de las Nubes Biological Corridor 2012 (km^2)	153.92	178.85	46.88	171.9	38.29	91.31	3.23
3	Difference Private Outside Paso de las Nubes Biological Corridor (km^2)	-	-14.45	0.63	-17.93	12.22	21.42	-0.99
3	Difference Private Lands Outside Paso de las Nubes Biological Corridor (%)	-	-7.48	1.36	-9.45	46.88	30.64	-23.49

Change Detection Results

When focusing across the entire extent of the imagery (area 1, Figure 1), I observed the largest change in area from 2008 to 2012 in the forest class, with a loss of 44 km^2, or an 11% decrease in forest, corresponding with a 30 km^2 gain in pasture. The largest proportional gain was in pasture, with an increase of 60%. I also observed an increase in bare ground (23 km^2 or 25%) and urban (5.36 km^2).

Within the CBPN (area 2, Figure 1), I observed the largest change in area in the forest class, with a loss of 26 km^2 paralleled by a gain of 14 km^2 in pasture. I also saw minor gains in bare ground, low vegetation and urban areas (3 km^2, 6 km^2, and 4 km^2, respectively). When considering the percentage change, the largest change was observed in pasture with a 70% gain, followed by a 20% loss in forest and a 17% gain in bare ground.

The private lands outside of the CBPN but within the 6.7 km buffered area (area 3, Figure 1) had the largest changes in the bare ground class, with a gain of 21 km^2, followed by a loss of 18 km^2 in low vegetation. I observed a similar gain in pasture and loss in forest, at 12 and 14 km^2, respectively. The largest percent change occurred in the pasture class with an increase of 47%, followed by a 30% gain in bare ground.

When concentrating specifically on the forest class, I observed negative changes in forest cover both inside the CBPN (area 2, Figure 1) and throughout private lands outside of the corridor (area 3, Figure 1). The CBPN exhibited a larger reduction in forest than the surrounding private lands; inside the corridor there was a 27 km^2 loss of forest (-20.5%) while private lands outside of the corridor experienced a loss of 14 km^2

of forest (-7%). Both areas experienced gains in pasture, bare ground, and urban regions, with larger percentage gains in urban areas inside of the corridor (Table 3).

Within the CBPN (area 2, Figure 1), changes were concentrated in gains of pasture and losses of forest, especially along a strip through the center of the 2012 map (Figure 2). This faint bare ground and urban strip bisecting the CBPN is the construction and development pathway of the San Carlos highway, with planned completion in 2016 or 2017. Additionally, there was forest loss on either side of the highway (Figure 2).

While IRB (#IRB2012-0439) regulations do not allow linking landholders to spatial data, I reported the changes seen within the three forms of PES properties compared to non-PES regions (Table 4). All PES regions had slight losses in forests (Table 4), but these losses, by percentage and area, were substantially less than non-PES regions. Percent change in forest protection PES ranged from between -0.17 to -7%, with reforestation PES regions showing the least amount of forest loss at -0.17%, and forest protection regions showing the highest forest loss at 7% (Table 4). I see large percent gains in urban, pasture and bare for all three PES regions, but areas are small when compared to non-PES regional gains, with PES gains in pasture, urban and bare at below 2.6 km^2, with most gains at less than 0.1 km^2 (Table 4).

Lastly, forest patch metrics were reported for 2008 and 2012. There were 4371 forest patches across the entire imagery area (area 1, Figure 1) in 2008, while in 2012 I saw a decrease in forest patches to 3698. The average patch size increased slight from 9.18 km^2 in 2008 to 9.62 km^2 in 2012. Within the CBPN I saw forest patch number decrease from 1325 in 2008 to 1078 in 2012. Average patch size within CBPN decreased from 10.03 km^2 to 9.76 km^2 .

Table 4. Change detection for PES regions, with values representing change in each PES payment type, reforestation, forest protection (forest), and agroforestry. Land use categories are shown within each spatial change analysis area, as determined by the remote sensing analysis. Both percentage change and area gained or lost are shown in the table.

Difference in PES Areas 2008 to 2012	Forest	Urban	Low vegetation	Pasture	Bare	Water
Reforestation (km^2)	-0.0013	0.0410	0.0855	0.0090	-0.0045	-0.0025
Reforestation (%)	-0.17	379.17	18.78	12.09	-5.08	-50.00
Forest (km^2)	-4.1418	0.2533	2.5542	1.8266	2.5747	0.0817
Forest (%)	-7.231	33.021	18.238	84.203	197.497	47.204
Agroforestry (km^2)	-1.1147	0.0504	1.1439	-0.1870	0	-0.0018
Agroforestry (%)	-17.879	22.951	33.114	-32.41	235.906	-9.639

Discussion

Additionality is used to measure effectiveness of conservation programs, and is defined as the conservation effects as compared to baseline outcomes (Wunder 2007). I saw little additionality during the initial years of NBCP enactment, demonstrated by decreased forest cover despite connectivity goals and an increased effort to target conservation using PES inside the CBPN. Forest decreased across the entire landscape, both inside and outside of BPN, indicating a regional transition in forest cover, but with percent loss in forest almost three times higher inside the CBPN (Table 3). I did see additionality within PES property bounds, with substantially less forest change within

PES regions as compared to non-PES regions. And while it can be challenging to link landscape changes back to specific policies, identifying landscape changes can provide a quantitative measure to empirically determine the success or attainment of policy goals and conservation efforts (Ferraro and Pattanayak 2006). I found PES protects forests, but these protections do not extend to other lands outside of the PES property bounds to fulfill the larger NBCP goals.

Past studies have questioned the additionality of Costa Rica PES and deforestation ban programs against baseline scenarios, citing little change in deforestation rates with or without the policy (Miranda et al. 2003; Sanchez-Azofeifa et al. 2007; Sierra and Russman 2006). Specific concerns include payment to lands already destined to be protected while using limited conservation funds (Miranda et al. 2003; Pagiola 2008). A recently study on the forestry ban of 1996 actually showed in an increase in forest. Fagan et al. (2013) described that while perverse incentives could have acted to decrease natural regeneration, instead, as intended, forest area increased. In the study, I also found benefits to PES, in the form of decreased forest lost in current and historic PES regions.

Within the biological corridor, economic pressures and road networks could be a major driving factor in forest loss outside of PES properties, countering conservation efforts (Geist and Lambin 2002). The construction of the San Carlos highway is funded and designed by the government agency CONAVI with supplemental funding from the dairy cooperative Dos Pinos (Figure 2)(Herrera 2011); Dos Pinos owns a dairy factory in Ciudad Quesada, with another plant south, near San José. Dos Pinos is one of the main economic interests in the area, and supplies the country with dairy products. It is also worth noting that many Dos Pinos farmers are participants of the PES program, and hold important forest patches on the eastern side of the corridor. The new highway is a four-lane route able to move agricultural products from the agricultural regions in northeastern Alajuela, Heredia and Limon provinces to the western and central parts of the country, with future increased access to markets. Currently, two 2-lane highways run the length of this 20 km-wide sensitive CBPN area, with the new third highway located in the middle, placing each route approximately 7 km apart, all with similar geographical origins and ends. The necessity for the new highway was questionable if current highway routes had been expanded, however the San Carlos highway is in its final years of construction after approximately 40 years of planning. As such, once the highway is completed, ease of access to forests and the interior of the biological corridor will increase, and without sufficient conservation tools in place, I can predict additional urbanization and deforestation in these newly opened areas. Dos Pinos is unofficially linked to the conservation efforts in the CBPN as many of their dairy farmers receive payments through the PES program, especially along the eastern side of the corridor. Dairy farmer participation could be used as a catalyst to grow an official conservation partnership with the dairy cooperative, the NBCP, and the PES program, working towards conservation goals in the corridor.

The NBCP and PES programs officiated by both SINAC and FONAFIFO, and the highway system run by CONAVI, are all government agencies and programs, with funds that appear to be working without coordination. To eliminate contradictory outcomes in funding, government agencies working within similar geographical areas could create formalized collaborations (the fourth goal the NBCP) to define solutions and mitigate conflicting goals.

Designation of conservation priority lands can in some cases cause the opposite of the desired conservation actions, leading to unintended or perverse consequences such as land grabs, habitat degradation, or in-migration (Liu et al. 2007; Rodriguez-Solorzano 2014). In the neighboring biological corridor of San Juan/La Selva, landowners have expressed anger and protested around corridor designation. In contrast, when interviewing PES landowners in the CBPN, most were not aware that their properties were located within a biological corridor, but showed positive interest in the designation. This unawareness could be partially attributed to the fact that I witnessed no official signage designating the CBPN. And while perverse incentives were observed in other studies (Rodriguez-Solorzano 2014), I feel that the designation of the landscape as a biological corridor did not lead to deforestation and conversion of land through these means. Additional signage and public campaigns delineating the CBPN may even spur collaborations among interested actors within communities.

The loss of forest in the CBPN caused a decrease in the quality of the countryside matrix, resulting in a less permeable landscape for wildlife species and less density or width of movement corridors throughout the region (Daily et al. 2003). There is also a decrease in the size and number of forest patches, increasing the distance required to travel between and among patches. Some species or individuals may not be able to move to or from spatially isolated patches. Further isolation of these patches can negatively impact remnant populations that are dependent on forests for habitat (McGarigal et al. 2009), degrading the quality and conservation potential of this area, antithetical to the goals of the NBCP.

Wunder (2005) describes PES as a valid conservation tool when threats are intermediate, when projected as a future threat, or when land use choices are flexible. Intermediate threats can be defined as mid-level deforestation rates. I have a scenario where land uses are not flexible due to the deforestation ban, with immediate threats such as the opening of the middle of the corridor with the highway, in an area deemed a high priority for conservation. While this study area meets some of the PES recommendations, in this situation, PES has been shown to protect forests across the study region, with areas outside of the PES properties (falling under the NBCP) experiencing the highest losses in forest cover. The current situation in the CBPN is a case for the effective application of a systematic conservation planning process (Margules et al. 2007) to generate optimal solutions using economic costs and benefits under the current constraints.

PES and biological corridor policies could spatially target reforestation and forest protection payments to accomplish the stated goal of the programs. This can occur in several ways. Programs could focus on specific areas with high forest loss and solicit applications from specific farms and regions. There could be an objective to prioritize recently deforested areas near the highway, allowing for renewed connectivity of neighboring mammal populations with short isolation times. This may be beneficial as forest fragments isolated for longer periods may have higher local extirpation of species.

This would also provide PES protection to the newly accessible core areas of the corridor using a forest buffer along the highway route. Lastly, programs can mitigate barrier issues tied to highway development through the use of culverts or overpasses.

Conclusions

Costa Rica leads among Central American countries in total protected area, and has been proactive in staving off deforestation and degradation of the agricultural matrix since the 1980s. The corridor system exemplifies a policy priority of conservation and connectivity. While the study reveals that PES properties within the corridor provided protection against forest loss, I found that even with official biological corridor designation, non-PES lands within corridors can experience increased land use change and forest loss. The reasons for these changes are varied and complex. Biological corridors are an essential link for the protected areas network in Costa Rica and for greater connectivity throughout the Mesoamerican biological corridor. The Biological Corridor system is a unique and an exceedingly important piece of legislation, for which the goals to enact important conservation measures must be accomplished. Policies and on-the-ground outcomes must be reviewed to understand the drivers of change and the requisite tools needed to accomplish these important goals.

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CHAPTER III

THE ROLE OF PAYMENT FOR ENVIRONMENTAL SERVICES IN MAMMALIAN LANDSCAPE CONNECTIVITY

Synopsis

Connectivity is deemed vital for biodiversity and is explicitly mentioned in Target 11 of the Convention on Biological Diversity Aichi Targets. We used spatially explicit analyses to determine if Costa Rica's Biological Corridor Program enhances connectivity within a specific biological corridor. We assessed the Payment for Environmental Services (PES) program in Costa Rica and its targeted efforts within the biological corridor network, defined in the National Biological Corridor Program (NBCP) of 2006. We examined the changes in overall mammal connectivity, and the role of PES properties within the study corridor. We collected mammal occupancy data through camera traps, and interviews with landowners. We created resistance surfaces parameterized by occupancy data, and base layers from a land-use map. We conduced connectivity modeling, including a least cost path model, and conductance surface models, using Circuitscape. Results indicate that PES properties hold a wide variety of species and guild richness, with higher richness in forest protection than reforestation. We established that active PES properties after NBCP played a larger role in connectivity compared to PES properties before. Overall connectivity within the study region has decreased since program enactment. Our results indicate the importance of PES for mammal communities, and the necessity for increased targeting of payments to

existing forested corridors, in particular pinch points and gaps, to provide connectivity between protected areas. PES properties benefit mammal communities in the corridor. Targeted PES can contribute greatly to the connectivity of the biological corridor network of Costa Rica.

Introduction

Ecological connectivity is deemed vital for both biodiversity and ecosystem services by the Convention on Biological Diversity (CBD), as defined in Aichi Target 11 (Woodley et al. 2012). The CBD describes ecological connectivity as a critical component of protected area management by strengthening the effectiveness of protected area networks. The CBD further specifies that connectivity should be met through employing ecosystem approaches to efficiently enhance critical ecological processes and functions (Convention on Biological Diversity 2011). Landscape and economic diversity are inherent and often conflicting characteristics of biological corridors, but when properly managed can benefit biodiversity, conservation, and local stakeholders by increasing ecosystem resilience (Harvey et al. 2008; Schippers et al. 2015). Management of landscape features and patterns of economic activity within corridors requires collaboration with local landowners to enhance connectivity while also providing appropriate economic incentives.

Corridor designs can take many forms, including linear features along the landscape, lattice shaped networks, or stepping-stones (Saura et al. 2014; Townsend and Masters 2015). Now many corridor spatial designs also take into account the potential future impacts of climate change (Williams et al. 2005), with inclusion of latitudinal gradients and elevation bands to form a lattice network of connectivity along rivers and streams, allowing for elevational movement of species and providing refuge to non-vagile species within specific elevational levels (Townsend and Masters 2015). Connectivity has several definitions, including landscape connectivity, habitat connectivity, ecological connectivity, and evolutionary processes connectivity (Lindenmayer and Fischer 2006) (Worboys et al. 2010). Landscape connectivity is defined as an anthropogenic view of vegetation patterns, while habitat connectivity is connections of habitat patches for species (Lindenmayer and Fischer 2006). Ecological connectivity deals with larger ecosystem and hydrologic processes, and evolutionary connectivity focuses on genetic flow throughout populations (Lindenmayer and Fischer 2006). When exploring corridor connectivity on a mosaic landscape, all four of these definitions come into play during the decision-making process.

Prior to the 2020 Aichi targets, in 2006 Costa Rica created the National Biological Corridors Program (NBCP) to improve ecological connectivity, under Executive Decree #33106, by the office of the Ministry of Environment, Energy and Telecommunications (MINAE) (MINAE 2006). The program promoted the use of payments for environmental services, and technical and financial cooperation with landowners within the bounds of the national corridor network. In the same vein, in 2008 MINAE, under Executive Decree #34433 (MINAE 2008), officially deemed biological corridors as conservation priority areas. Lastly, in 2014, PES applicants within biological corridors received higher scores on their PES applications (MINAE 2014).

The biological corridor network in Costa Rica spans the entire country, and connects most protected areas through the use of corridors. Costa Rican biological corridors are multi-use areas, consisting mainly of private lands[i]. Each biological corridor is unique, and contains a multitude of land uses, including areas of urban use, forest, agriculture, and rural development. The corridor program has four main goals: (1) to strengthen the national biological corridor network; (2) to promote the conservation of biodiversity and restore ecological connectivity; (3) to encourage environmentally friendly development within biological corridors; (4) to increase collaborative endeavors with institutions and actors within the biological corridors (National System of Conservation Areas SINAC 2009) (MINAE 2006). The study evaluates the second stated goal, the maintenance and restoration of ecological connectivity. Sistema Nacional de Areas de Conservación (SINAC) criteria describe that increased ecological connectivity should result in increased natural cover and the presence of indicator species to demonstrate connectivity. The definition specifies that the desired results include landscape, habitat, and ecological connectivity (Lindenmayer and Fischer 2006).

When enacting connectivity plans, there are several considerations, including configuration, and assessment of population sources and sinks. Patches, while beneficial, can act as population sinks for species dispersing out of ideal habitat areas and into areas that do not hold the required resources. Sinks can also place wildlife in direct contact and competition with humans (Kilpatrick et al. 2009; Marshall 2010). The size of the patch can also dictate the utility of the patches for a particular species, with smaller or spatially narrow patches providing less habitat and resources compared to larger patches (Forman 1995) (Levin and Paine 1974).

Costa Rica uses a conservation tool, PES, to increase connectivity in the National Biological Corridor system, as stated above in outcomes and goals of the SINAC strategic plan (National System of Conservation Areas SINAC 2009). All PES participants within biological corridors are given an increased probability of application selection (MINAE 2014). Precise property locations within the biological corridors, however, are not a separate factor for selection within this program; the level of spatial specificity is at the level of the biological corridor. Nevertheless, the configuration of patches and the matrix in which they are embedded is essential to determine the degree of connectivity and the potential utility for wildlife (Baum et al. 2004).

We addressed aspects of corridor program effectiveness using remote sensing, GIS, and wildlife monitoring. First, I used mammalian survey tools to measure medium and large mammalian species occupancy within the study region, in PES properties, non-PES properties, and protected areas. Next, I assessed the effectiveness of conservation regions by modeling overall mammal corridor suitability across the Paso de las Nubes Biological Corridor (CBPN) from the inception of the program, and 6 years into the program, using electrical current model theory, specifying the role of PES properties. Finally, I measured connectivity across the landscape through least cost path analysis, which detailed important mammal corridor routes and pinch points through the CBPN. These approaches allow for an analysis of the efficacy of the national policy, which can inform PES actions throughout the biological corridor network. Applications are far-reaching as these policies are used nation-wide in Costa Rica as well as throughout the world (Wünscher et al. 2008) (Morse et al. 2009).

Methods

Study Area

We applied a natural experiment approach to test the effectiveness of the NBCP within a specific biological corridor, the Paso de las Nubes Biological Corridor (Figure 1). The corridor is located at approximately 10.343392 latitude and -84.540478 longitude. This corridor covers an area of 40,000 ha, and is located northwest of the capitol of San José, in the Tilaran and Central mountain ranges of Alajuela Province. CBPN is an essential connection point for the eastern and western protected areas, providing the only linkage for the Pacific and Caribbean slopes on the northern half of the country. Life zones in the corridor include premontane rain forest, premontane wet forest, lower montane moist forest, lower montane rain forest, and tropical wet forest (Hartshorn 1983). The primary land uses consist of private forests, dairy farms, ornamental plant agriculture, tree plantations, urban areas, rural towns, and agroforestry. CBPN is bordered to the east by Juan Castro Blanco National Park, named the Park of the Waters, as it is the headwaters for five large rivers making it essential for water source in this watershed. The CBPN is bordered to the west by Alberto Manuel Brenes Biological Reserve and Monteverde Cloud Forest Reserve, and these forests hold important tracts of cloud forest and areas of high biodiversity as the parks straddle the continental divide, encompassing both the Pacific and Caribbean slopes (Figure 3). This corridor was chosen as a study site because of its important central location and because it acts as the main connection point to the northwestern protected areas, including the threatened dry forests and the famed Monteverde cloud forest reserve.

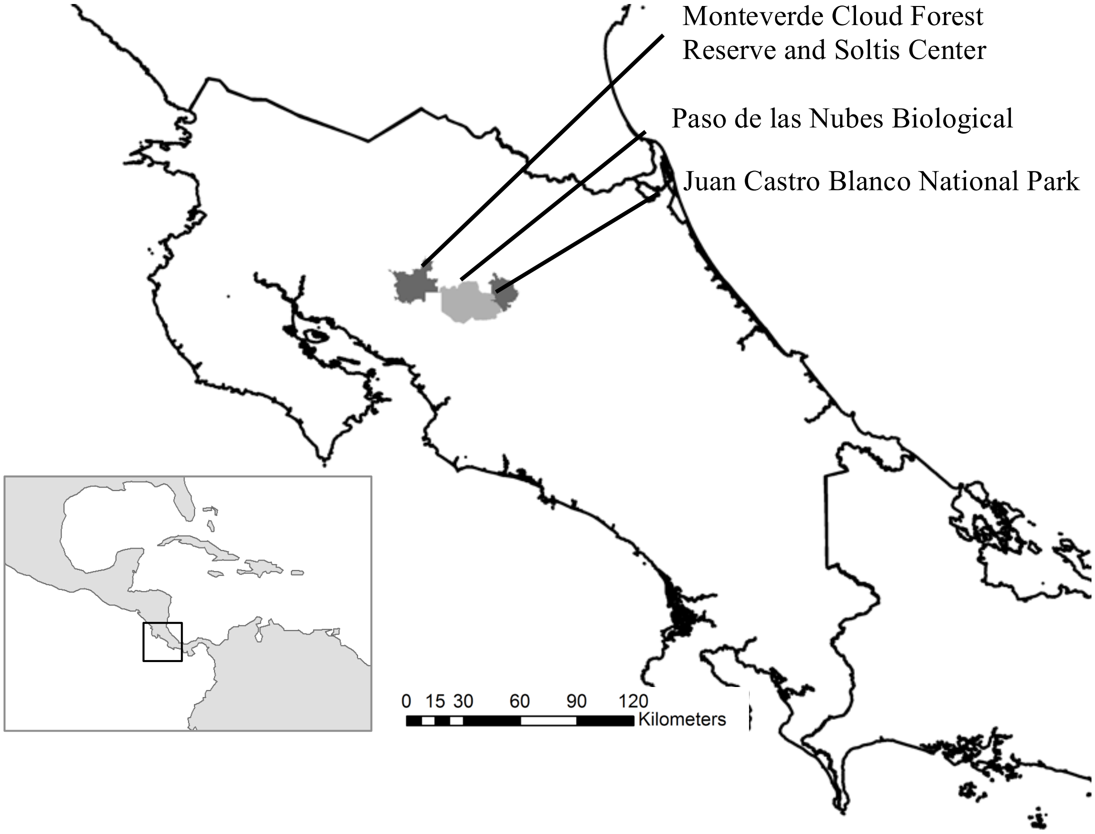

Figure 3. Location of study sites in Costa Rica, including Paso de las Nubes Biological Corridor, Monteverde Cloud Forest Reserve, and Juan Castro Blanco National Park.

Species Occupancy

Identifying species occupancy allowed us to parameterize corridor connectivity models. To accomplish this, I placed 47 camera traps within PES and non-PES properties throughout the CBPN and adjoining protected areas, from May to August

2014 and 2015 (Figure 3). I used a combination of Bushnell 6MP®, Browning 3XR®, and Moultrie M-550® cameras. PES land uses include primary forest, agroforestry, and tree plantations, although no agroforestry properties were present within the CBPN. The national parks surveyed included western Juan Castro Blanco National Park and eastern side of the Monteverde Cloud Forest Reserve. Placement of camera traps was non-random, situated in areas detailed by landowners and managers to have high rates of mammal passage, usually along game trails, human trails, near streams, or in areas with food resources. This was done to maximize capture rate, providing the most complete presence data. Cameras were placed at least 100 meters apart, and approximately 1 meter off the ground, depending upon the slope of the landscape. Traps were set at least 100 meters from forest edges and property lines. The camera traps were activated for 21-45 days, and set with a five second delay to avoid unnecessary multiple captures of the same individual. Each camera was checked and batteries changed once during the activation period, between days 10-18, to ensure sufficient battery and memory card life. Directly in front of each camera trap was a hair trap used as a scent bait station. Each hair trap contained Calvin Klein men's Obsession cologne and catnip spray or loose catnip. All willing PES properties within the CBPN were surveyed, and each PES property held five active cameras at a time, and the larger protected areas contained between 10-30 active cameras at a time. The number of properties surveyed was 14, along with 4 sites in Juan Castro Blanco National Park, and 4 sites in or near protected forests adjacent to the Monteverde Cloud Forest Reserve; the total number of sites in the entire region was 22. This study had 2,179 trapping nights in 2014 and 781 trapping nights in 2015, for a total of 2,960 trapping nights over the duration of the study.

We conducted semi-structured interviews with landowners and managers of PES properties in 2014 and 2015. These interviews corroborated camera trap data with first-hand local ecological knowledge. Interviews are used as a method to estimate mammal richness, and interviews can be as accurate as camera trap data, specifically when interviews are conducted with people who work and live closely to the land (Canale et al. 2012). Prior to conducting field interviews, institutional permission was gained through the Institutional Review Board at Texas A&M University (IRB study #IRB2012-0439). I recruited PES participants using public records of PES contracts, acquired from NGO contacts. I obtained verbal permission for all interviews, and persons interviewed were kept anonymous and their information was not linked to spatial data. Participants of interviews included PES participants who actively worked on their land and were familiar with local mammals, determined by initial questions about time residing on the land, time working on the property, and familiarity with mammals, among other attributes. During the interviews, I used a pictorial guide of local mammals to decrease confusion with local mammal nomenclature. Within the picture guide, I included taxonomically similar non-regional Central American mammals to test for type II errors (Canale, Peres et al. 2012). The interviewees reported mammal presence and absence, frequency of sighting (rare to frequent), type of sighting (actual mammal, prints, scat), and location of sighting.

Cost and Resistance Surfaces

Cost surfaces were used to model movement resistance across the landscape. I used raster algebra to create the cost surfaces for the connectivity analyses. I combined three environmental variable layers to construct the cost surface: land use, slope, and road network. The land use surface was created through object-oriented classification of ASTER imagery in 2008 and 2012 (Wood Ch.2). I created cost surfaces for 2008 and 2012, representing the second year of on the ground implementation of the NBCP (2008), and six years after implementation (2012). The clouded areas in the 2012 classification were mosaicked with the 2008 classification, with clouded regions mainly occurring over protected forested areas due to the climate and topography; effectively, I replaced clouded areas in 2012 with protected area forest from 2008. The land use surface contained seven classes, including forest, low vegetation, pasture, urban, water, cloud, and bare ground. Forest is described as areas with primary or mature secondary forest. Low vegetation is undergrowth below five meters in height. Pasture is actively grazed grassland, mainly used for dairy production. Urban describes built up areas such as cities, roads and towns. Water is largely comprised of high gradient streams and rivers. Bare ground indicates areas cleared of vegetation, including burned areas, coffee shade structures, and construction that exposes bare soil.

The slope surface was derived from the Digital Elevation Model (DEM), with 30-m resolution, using the slope tool in ArcGIS 10.2 (ESRI 2011). The slopes in the study area range from 0 to 88 degrees (with a maximum possible slope of 90 degrees). Lastly, the road network layer was acquired from the Costa Rican government agency

FONAFIFO (Fondo de Financiamiento Forestal de Costa Rica), and provided details on road size, with four categories: primary, secondary, tertiary, and quaternary. Primary roads are larger, heavily traveled highways, while quaternary roads are unpaved local roads, with the approximate width of one car.

Parameterization of Cost Surfaces

The land use change map was parameterized with occurrence data collected from occupancy of medium and large mammal species in camera traps and interviews. Initially, wildlife populations were grouped by guild, and these categories included herbivores, omnivores and carnivores. Frugivores and insectivores were not included in the mapping effort because of low camera trap and interview records of these guilds. When conducting preliminary connectivity maps by guild, I found only minor differences, and determined that a general mammal connectivity map would be appropriate for this study. Most studies use species-specific movement paths but because the National Biological Corridor Program has the goal of restoring ecological connectivity, this study aims to understand and evaluate general corridor goals of connectivity, and thus a broader corridor model was used.

All cost surfaces used for the analyses have a 130 by 130 meter resolution. To create cost surfaces, I weighted each pixel surface using a scale of 1-10 (Appendix, Table A2), and then added the raster surfaces using raster calculator. Within the resulting surface, lower pixel values represented more favorable areas for movement, while higher pixel values represented less favorable areas for movement. For the land use surface (Y), I determined the weights with species occupancy gained from interviews (η) and camera traps (χ) for each land use; this was accomplished by creating a fractional value of the total number of species found in each land use type ($\chi+\eta$) over the total potential medium and large mammal species (τ). This fractional value (Y) was estimated for urban and bare areas, as these are known to be poor habitat areas.

$$Y = \sum(\chi+\eta) \; / \; \tau$$

Y = land use surface value for mammal richness

χ = species recorded on camera traps within each land use

η = species recorded during interviews within each land use

τ = total mammal species with distributions within study region

Then, the fractional values were inverted and scaled to a value 1 through 10. For the slope surface, I weighted steeper slopes with a higher cost for movement, since dispersal across steep surfaces is not preferred, but also is not impossible (Alexander and Waters 2000). Larger, more heavily traveled roads (Benítez-López et al. 2010) had a higher cost value than narrow dirt roads because animals are less likely to traverse large paved roads (Forman and Alexander 1998) (Forman and Deblinger 2000) (Benítez-López et al. 2010).

Lastly, each of the three cost surfaces was weighted. For the first series of weights, land use was weighted at 50%, slope was regarded least important at 20%, and the road network was ranked intermediate and slightly higher than slope, at 30%. Slope is relatively consistent across the mountainous corridor, and the difference when slope was weighted at 50% between 2008 and 2012 was insignificant and was added to the appendix (Figure A1, E). I observed a similar lack of an effect when roads were weighted to 50% (Figure A1, F), and weights and class values for the analyses are reported (Table A2, appendix). The final cost layers were then used for analyses on mammal connectivity across the corridor. Cost surfaces could hold potential biases based on collection of mammal data, weighting of surfaces and interview responses. I used both camera and interview methods to decrease potential error in presence and absence data. And ran many iterations of surface weights to determine the appropriate weights for the model (Figure A1).

Connectivity

The corridor movement model was created using Circuitscape, an open-source ArcGIS extension tool (McRae et al. 2013). This tool was developed using circuit theory; the landscape cost surface represents a conductance surface, with high and low resistance depending on the cost surface value. The tool utilizes a network of nodes that hold varying resistance values (McRae et al. 2013). Circuitscape map scenarios were projected using quantile classification in ArcGIS (Watts et al. 2008). I created four scenarios to understand connectivity at various scales. The four scenarios were: (A) General mammal connectivity 2008; (B) General mammal connectivity 2012; (C) PES before NBCP; and (D) PES after NBCP. With each scenario, I removed areas that contained below 50% current density level, as these areas were deemed unsuitable for connectivity; connectivity displayed includes areas of connectivity density higher than 50%. For each scenario, I reported the cumulative current, defined as the sum of current values contained within all nodes across all iterations within the scenario (McRae et al. 2013). I weighted the cumulative currents on a percentage scale to compare across scenarios, with the highest cumulative current scenario as the maximum available cumulative current in the study.

Scenario A: General Mammal Connectivity 2008

Under this scenario, I model general connectivity of the medium and large mammal community during 2008, the initial years of NBCP. Functional landscape connectivity was based on occupancy data derived from camera traps and interviews, and these data were used to parameterize land use maps. Within the model, protected areas were deemed the source of mammal populations and the model runs across the CBPN landscape (Figure 3). Species have distinctive movement patterns and habitat choices, with some species more able to cross open areas such as pastures, and other species more reliant on forest cover (Daily et al. 2003). The land use covers were parameterized based on overall mammal presence. The resulting map will show general connectivity based on species richness, however species connectivity will vary depending on dispersal abilities of each species.

Scenario B: General Mammal Connectivity 2012

Under this scenario, I modeled connectivity six years after establishment of NBCP. The same occupancy data were used, but the land use map from 2012 was used as the land use cost layer for the cost surface. This layer differs from scenario A in that it shows there to be less forested areas, less patches, and more urban and pasture areas. Again, this scenario details connectivity for the general mammal community.

Scenarios C & D: PES Removal Before, After the National Biological Corridor Program

Under scenario C and D, I determine spatial connectivity importance of PES property locations before and after targeted NBCP PES payments (new properties were chosen each year throughout the time period). I accomplished this by masking PES property locations from years of 2003 to 2006, before NBCP, and then I ran connectivity modeling across this new landscape. Essentially, this scenario represents connectivity under the assumption that PES properties were not conserved, and no longer acted as conservation regions, removing these areas as beneficial for dispersal. Under scenario D, I conducted the same analysis as scenario C, but with PES property locations from 2007 to 2014, the years with active spatial targeting of PES within the CBPN. Properties were masked to uncover connectivity loss had these properties not been conserved.

Scenarios E & F (Appendix): Road, Slope Priority

For scenario E, I weighted roads within the study region higher at 50%, with slope at 20% and land use at 30%. Many studies have shown the significance of roads as barriers to movement of species (Forman and Alexander 1998) (Benítez-López et al.

2010). Road networks are extensive throughout this region, and could act as a major barrier to movement, hence the need for a road focused scenario E. Under scenario F, the slope scenario, I use the general occupancy connectivity model and prioritized slopes, as opposed to land use and roads. Slope can also be a rather ominous barrier; especially across a volcanic landscape with steep valleys and peaks spotting the landscape, and sheer cliffs are barriers in the landscape, hence the slope scenario.

Least-Cost Path

To corroborate the above electrical connectivity models, I conducted a least-cost path (LCP) analysis. This method provides a path of least resistance across a minimum number of barriers between two points. A cost weighted surface is used to determine the best movement paths dependent on surface weights. I created the cost surface using raster algebra, and the direction raster was created using the ArcToolbox cost raster, with the protected areas to the east and west used as source and destination localities. The LCP analysis was parameterized with the same variables as the cost surface in the Circuitscape model, using slope, roads, and land use from 2012. Cost paths were created from west to east and east to west. This identified the most direct path between the two protected areas, to further specify the best areas for conservation priority, and to provide additional criteria for specific regions of conservation concern. Paths that were bi-directional were displayed as the main route, and only one path fell under this criterion. A 1 km buffer was clipped from around the main LCP, and the land use layer was described, with percentage area of urban, forest, pasture, low vegetation, etc. held within the LCP, as compared to the general landscape and to the biological corridor.

Results

Species Occupancy in PES and Protected Areas

Interview participants reported, on average, 16 species of medium and large mammals on forest protection PES properties (N = 11), and 12 species within reforestation PES properties (N = 4). In forest protection properties, interviewees reported on average 6 herbivore species, 2 insectivore species, 1 frugivore species, 8 omnivore species, and 3 carnivore species. For reforestation PES properties, interviewees reported an average of 3 herbivore species, 2 insectivore species, 1 frugivore species, 4 omnivore species, and 2 carnivore species. Total species reported from interviews for PES primary forest properties was 34 species (Table A4, appendix). Total species reported in interviews on reforestation properties was 17 (Table A4, appendix). Selection of non-native mammals was negligible, with error rate of 0.0076.

Camera trap occupancy shows an average of 7 species (N = 11) on primary forest PES properties with a total of 19 species across all PES forest properties, and an average of 2 species of herbivores, insectivores and omnivores, 1 carnivore, and no frugivores. An average of 5 species were found on reforestation PES properties (N = 4), with a total of 16 species across all reforestation properties, and an average of 1 species from each guild. The average number of species found in protected area sites (N = 6) was 10, with the total number of species at 15. Camera trap species lists for forest protection PES, reforestation PES, and protected areas are provided in appendix (Table A3); this list also takes into account arboreal medium and large species sighted while setting traps. A list of medium and large mammal species presented on the pictorial interview guide can be found in the appendix (Table A1).

Corridor Connectivity, Circuitscape

Across all scenarios, I found no solid connections from North to South, as there are no large tracts of forests either north or south of the biological corridor to act as sources and sinks for the circuit model. All connections are reported from east to west, as the circuit model is rooted in forest patches within protected areas.

Scenario A: Areas with higher density currents, and hence higher probability for mammal presence and movement, were represented in red and orange, while yellow and green represent intermediate areas, and white represented areas with current densities below 50%. When examining the 2008 scenario, the western portion of the corridor supports higher mammal movement capacity, represented by large areas of red and orange paths, compared to the eastern side of the corridor, that contains only a few high current paths (Figure 4, Map A). There were more forested areas on the western side, along with a less extensive road network. Many pinch points were found along this route, with some movement current paths only 1 pixel wide (130 meters). One main connection remains across the entirety of the corridor, located in the northern half of the CBPN. Other areas of connectivity include northern and southern routes, outside of the CBPN. Ciudad Quesada, the largest city in the region with a population of approximately 44,000, is located along the northeastern border of the CBPN, and with potential expansion there is a potential loss of the northern paths (Booth et al. 2014).

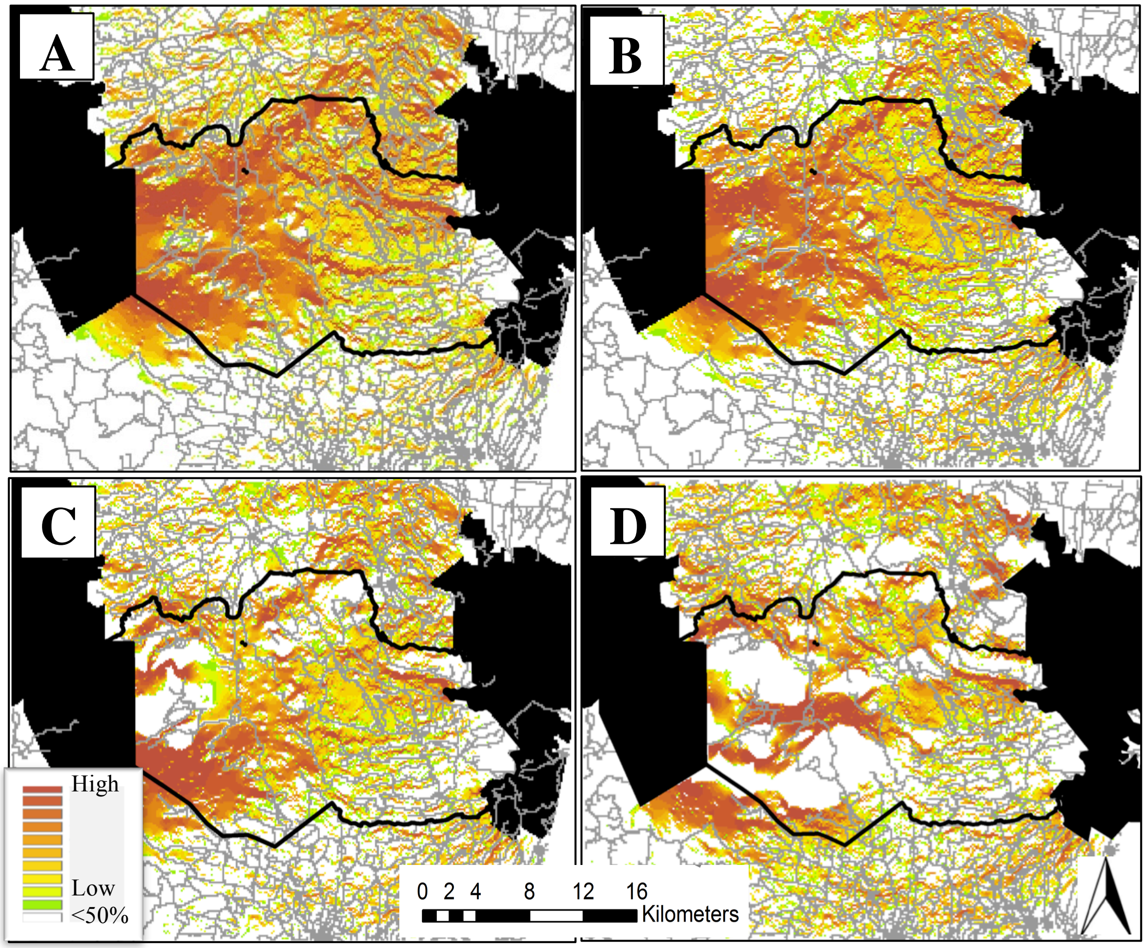

Figure 4. Electrical connectivity using Circuitscape models across the Paso de las Nubes Biological Corridor. Scale to the left: white represents areas below 50% connectivity, red representing the highest level of connection density, and green at 50% connectivity density. Map A: 2008 connectivity; Map B: 2012 connectivity; Map C: PES before national biological corridor policy, removed from available conservation; Map D: PES after national biological corridor policy, removed from available conservation.

Scenario B: In 2012, six years after NBCP inception, the sole central connection line in 2008 (delineated in red, high density of current) decreased to intermediate connectivity in orange/yellow along the central portion after the initial construction path of the new San Carlos highway moved through the corridor between 2008 and 2012 (Figure 4, Map B). Additionally, two 500 m breaks occur with currents lower than 50% were present in the corridor I still see higher connectivity levels on the western as opposed to eastern side, and again I see the potential for other connectivity paths north outside of the CBPN.

Cumulative currents for Scenarios A & B: To understand changes in electrical current across the landscape from scenario A to B, the cumulative percent current was reported (the sum of current values contained within all nodes across the iterations of the scenario) (McRae et al. 2013). 2008 held the maximum cumulative of all scenarios, with cumulative current at 100%, whereas the maximum cumulative current for 2012 decreases to 94%. In 2008, 98.2% of pixels held currents below 50% current (white pixels), while 2.8% held current above 50% (red, orange and yellow pixels). In 2012, 99.5% of pixels held current below 50%, and only 0.5% above 50%, showing a decrease in available pixels for ideal movement areas.

Scenario C: Removal of PES property locations before 2006 from the conservation landscape produced a connectivity gap in northwestern connectivity within the corridor, represented in large white spaces (Figure 4, Map C). Because of this, I also lose the sole connectivity path seen in red in 2008. When examining the other areas of the CBPN, there were no large changes in connectivity, which can be seen when comparing this scenario with scenario B (Figure 4, Map B, C). Overall cumulative current change between scenario C and D was negligible, with only a 1% difference, but overall path connections differed drastically (Figure 4, Map C, D).

Scenario D: Removal of 2007-2014 PES properties from the conservation landscape produced large gaps in connectivity represented in white, and cut connectivity spanning east to west on the map, particularly within the CBPN (Figure 4, Map D). Under this scenario, there were no connected paths that hold high or intermediate connectivity across the CBPN. I do find one large south central area ideal for connectivity, in red, but this patch was not connected to eastern protected areas through red high corridor paths, leaving it as island inside the corridor (Figure 4, Map D).

Corridor Connectivity, Least-Cost Path

The least-cost path displays many linkages across the western portion of the corridor while the eastern region holds only one main linear connection. Bi-directional paths were defined as paths that overlap and were present from east to west and west to east; there was only one path that fits this criterion (Figure 5). All least-cost paths were represented, either from east to west or west to east (Figure 5). The least-cost path analysis was consistent with the electrical circuit mapping scenarios above, and shows similar regions for connection of the protected areas across the CBPN (Figure 5). The 1 km buffered main LCP showed the following land use information: forest encompassed the majority of the area, at 56%, followed by low vegetation at 26%, pasture at 8%, bare ground at 6%, and urban at 3% (Table 5, Figure 6). When those values were compared to the overall regional land covers or the land covers within the CBPN, both CBPN and within the overall region, forest was also the dominant cover followed by low vegetation (Table 5). Surprisingly, within the LCP, forest was less dominant than in the broader landscape, and low vegetation was marginally higher when compared to the broader landscape (Table 5). Lastly, similar percentage values were found in urban, bare ground and water land cover classes.

Table 5. Percentage land cover within a 1km buffer of the Least-Cost Path compared with regional value and CBPN values.

Land cover	Entire region 2012 (%)	CBPN 2012 (%)	Inside 1km LCP buffer (%)
Forest	61	59	56
Urban	4	3	3
Low vegetation	20	24	26
Pasture	6	9	8
Bare ground	8	6	6
Water	0	0	0

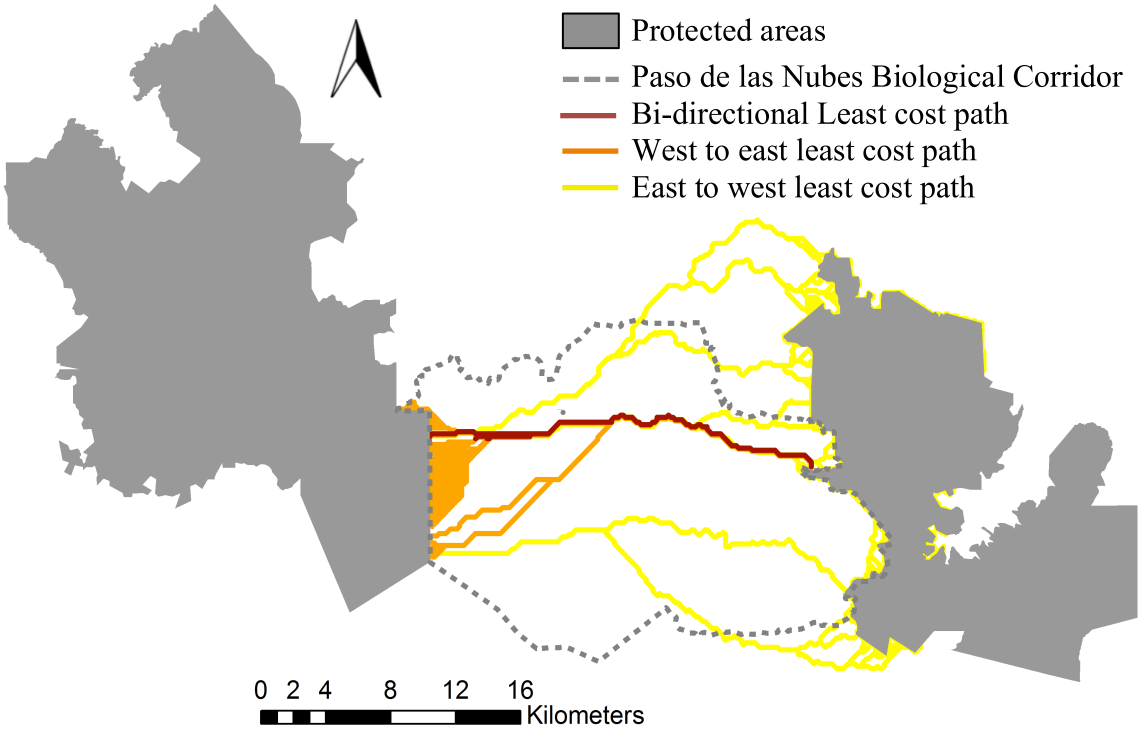

Figure 5. All least-cost paths from both directions (east to west in yellow and west to east in orange) between eastern Juan Castro Blanco Protected Area, and western Monteverde and Alberto Brenes Protected Areas, in grey. With the bi-directional least-cost path represented in red. The dotted line represents the outline of the Paso de las Nubes Biological Corridor border.

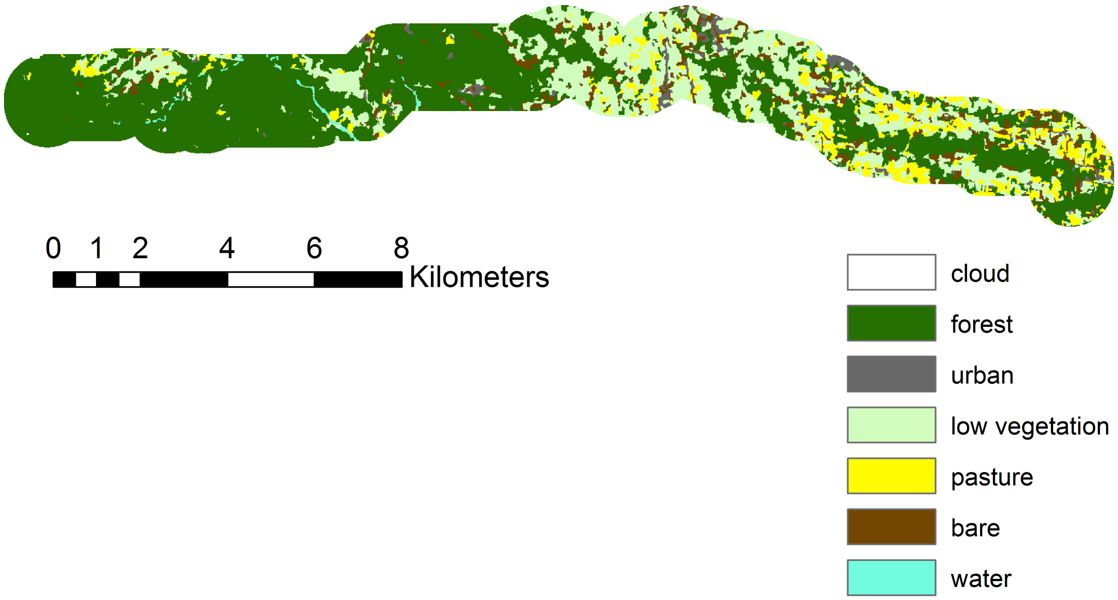

Figure 6. Bi-directional least-cost path, with 1km buffer. Land uses from 2012 are displayed within that buffer.

Discussion

A main goal of the Costa Rica Biological Corridor Program is to enhance conservation through improved connectivity. Corridors are regarded as important for dispersal of mammals, and a key component of the conservation toolbox (Gilbert-Norton et al. 2010). Since 2006, Costa Rica has made an increased commitment to the biological corridors (MINAE 2008, 2014). the study suggests that, while the PES conservation focus within biological corridors is beneficial for connectivity, the spatial scale at which the program targets investments could be further focused to ensure protection of vulnerable core connections and pinch points. the research shows that PES properties are beneficial for a wide range of mammal species, with forest properties holding more richness than reforestation properties. To create a cohesive corridor conservation plan, I recommend removing barriers, and using PES properties in strategic corridor locations to bolster corridor effectiveness.

The CBPN could be experiencing a social-scale mismatch within the land-use policies and ecological properties of the system (Cumming et al. 2006); the conservation program functions at a larger scale than the ecological necessities of the system, with changes occurring at the individual property level within a regional scale policy. At the individual property level, landholders and managers are responsible for making bottom up changes to the system, while the regional policies are directed from the top-down by government and NGO organizers (Muñoz-Rojas et al. 2015). Until the scale of policy enactment aligns with the spatial scale of the properties, and is placed into the context of internal priority conservation corridors, the selection of properties will not likely contribute to large enhancements in connectivity.

Scale mismatches among policy objectives and landscape outcomes can lead to unattainable ecological goals (Cumming et al. 2006). the results indicate that while I do not see large losses of overall connectivity across the landscape, I also do not see creation of additional, newer, or wider corridors using PES within the NBCP. The LCP shows that portions of routes are only 130 meters wide, and in 2012, I see two 500 m breaks in the corridor, including a barrier feature, the new four-lane San Carlos highway. These issues could cause the CBPN to become a non-functioning corridor. While the minimum width of the corridor falls within one standard measure, it is difficult to determine an exact width needed for corridors within the CBPN as each system and species group requires different needs (Spackman and Hughes 1995). I can also assume that large gaps of inhospitable land (roads, highways) do not increase corridor efficacy. Furthermore, other studies show similar challenges with corridor implementation and policy mismatch. In Nepal, necessary measures to enact conservation of target species resulted in recommendations of additional protection, monitoring, and restoration of corridors to increase habitat connectivity (Aryal et al. 2012). A Scottish study examined forest policy and corridor planning to find lags in existing planning and policy, and argued that a more spatially explicit policy and planning instrument was needed to coordinate across institutions and actors (Muñoz-Rojas et al. 2015). The "Nature Ways" corridor network in Singapore provided no financial initiatives to prevent anthropogenic changes in a corridor, and the future of the functional corridor was at risk, with some corridors already too narrow to function (Jain et al. 2014). I see a reoccurring theme of the necessity for more corridor based actions, especially as the benefits of corridors have already been explicitly acknowledged (Woodley et al. 2012).

The benefits, along with the challenges, of PES have been shown on multiple levels (Pagiola 2008). I have revealed that both reforestation and forest protection PES properties acted as effective mammalian habitat, and these benefits are consistent with the program goal of biodiversity conservation. I have displayed that PES properties can serve multiple conservation goals, including protecting forests and providing habitat for biodiversity. This is consistent with De Barros et al. (2014), who showed additional benefits to biodiversity from REDD+ conservation projects. Based on the mammal richness study, I recommend that PES properties continue to be used for the purpose of increasing connectivity. It must be noted that the type of PES property is important, as forest protection provides suitable habitat for a larger number of species, while fewer species were present in reforestation properties. I also found more rare species in forest protection properties, as defined by a species being listed as endangered within Costa Rica. While forest protection properties held more rare species, species from all guilds were found in both types of PES properties, with forests containing higher numbers of species in each guild. Whereas forest protection holds more species richness, reforestation properties can create new habitats and close gaps, which is an essential component to mitigating fragmentation and barrier features. Hence, both PES property types serve important functions within the biological corridor.

A review of connectivity studies has called for assessing multiple landscape variables to understand connectivity. Humphrey et al. (2015) recommended increasing the size of existing patches and decreasing isolation of patches to develop successful ecological networks and corridors. To obtain suitable movement paths throughout biological corridors, other studies suggest that conservation focus on riverine and riparian areas, which provides a slight increased benefit to biodiversity as compared to conservation without a riverine focus (Rouget et al. 2006). A riverine focused policy is already in place within Costa Rica; Forestry Law Number 75757 prohibits cutting of trees along riparian corridors. By pairing PES programs with riparian corridor conservation, these forested areas could be expanded to provide a more viable elevational connectivity, especially if reforestation payments could be used to further protect riverine corridors along elevational gradients. Townsend and Masters (2015), built on the riverine method to protect elevational bands or strips of land, to produce a lattice network to allow for a climate change induced elevational movement of species while providing refuge to non-vagile species within specific elevational levels. The protection of riparian corridors meets the additional objectives of protecting and maintaining river flows. On the western side of the CBPN, there appears to be elevational gradient connectivity already in place, within the large tracts of forest. Horizontal bands are not found on either side of the corridor; these bands are defined as horizontal connections within one elevational level, for example, a band between forested habitats at an elevation of 100 meters. Elevation bands on the eastern side would be harder to implement because of the presence of extensive dairy production. One method to incorporate these bands into the landscape would be to develop wider windbreaks within the eastern regional farms; then, these corridors could be used for movement, and could also benefit local landholders by providing wind shelter for cattle, additional timber trees, increased milk production, decreased soil erosion, and increased forage (Ferber 1958; Harvey 2000; Murgueitio et al. 2011). Another method to enhance connectivity is through habitat creation with reforestation payments or by creating a new payment system for natural regeneration to increase the quality and size of already existing forest patches, to subsequently act as stepping-stones (Saura et al. 2014).

While achieving connectivity through addition or maintenance of corridors is a key focus of the NBCP, one of the most cost effective techniques is to remove barriers (McRae et al. 2012). In the region, bypassing barriers, such as the new highway, is a necessary step to create connectivity among the neighboring national parks. Without mitigation of barriers through underpasses or overpasses (Kleist et al. 2007) (Gloyne and Clevenger 2001), conservation efforts, such as PES, will spend funds that pool conservation efforts on either side of the barrier. While this method meets other conservation goals such as carbon sequestration, it lags in connectivity goals.

The National Biological Corridor Program was formed in 2006 to provide connectivity to the protected areas network, and to improve connections along the larger Mesoamerican biological corridor. In doing so, the country's policy is aligned with the newer Convention on Biological Diversity's Aichi targets. the analysis presents evidence that PES properties serve as habitat for medium and large mammal species, however overall connectivity has slightly decreased over the initial years of the program. With the increased pressure to complete the highway, and the recent government commitment to fast-track the construction, mitigation of connectivity issues is timely (Arias 2015). Currently, mammal connectivity routes are limited to a few pathways that span highways and large gaps. Given that PES properties are used as habitat for many mammal species, I recommend they be used as a tool for enacting connectivity across the landscape. Because of the high reliance of the Costa Rican economy on ecotourism, and in particular, on charismatic mammalian species, the protection of this habitat benefits ecotourism initiatives. National policy goals are already aligned with connectivity, however changes need to be made to ensure that actions are prioritized and implemented at appropriate regional and local levels to realize ecological connectivity.

CHAPTER IV

CONSERVATION SPATIAL PLANNING REVEALS SPATIALLY DISTINCT REGIONS BASED ON POLICY GOALS

Synopsis

Conservation planning is an essential tool to prioritize spatial arrangements of conservation actions, considering a variety of factors, such as biodiversity protection, implementation costs, and management options. Conservation planning has advanced to consider protected areas as well as public lands, various land management regimes, and overlapping land use and conservation priorities. Spatial planning has become a necessary and exceedingly valuable tool in conservation when facing conservation decisions. The Paso de las Nubes Biological Corridor in northwestern Costa Rica has two overlapping conservation programs, the Payments for Ecosystem Services Program (1997) and the National Biological Corridor Program (2006), each with differing goals. The Payments for Environmental Services goals focus on preservation of biodiversity, scenic beauty, watershed protection, and carbon sequestration, whereas the National Biological Corridor Program focuses on sustainable development to increase connectivity within biological corridors. New legislative actions in 2014 have placed spatial bounds on Payments for Environmental Services funding based on the National Biological Corridor Program official corridors. Due to these conservation policy changes and differing goals, it is important to critically analyze the spatial needs of each policy goal across a heterogeneous biodiversity landscape and a variety of ownerships regimes,

including private property, government lands, and national parks. In this study we used Marxan, a decision algorithm conservation-planning tool, to model potential reserve networks that aim to meet the specified policy goals of these two conservation programs while minimizing implementation costs. Stated goals from these two national conservation programs were used to create scenarios that prioritized increased biodiversity, watershed and flood protection, increased carbon, and protected area connectivity to the larger landscape. Costs were based upon payment plans for conservation programs, and labor and cost inputs gained from interviews with farmers and landholders. Biodiversity values were based upon mammal richness data, and were collected from occupancy data within the region. The scenario results provided regional conservation management recommendations for future Payments for Environmental Services and National Biological Corridor Program planning efforts. Results indicate that goals within these two programs have differing spatial requirements, with minimal planning unit overlap, especially regarding watershed protection. In our study case, connectivity, biodiversity, and carbon sequestration appeared to provide the highest regional overlap among the scenarios. Watershed protection fell outside of the above region and outside of the core conservation area, indicating efforts need to be prioritized in the broader context to achieve this goal. While there was regional overlap, we found minimal planning unit overlap among scenarios, and because of this, multi-goal programs must determine which goals are most important and can strategically select goals with the highest overlap to accomplish the highest returns.

Introduction

Conservation planning has become an indispensable step in the examination and enactment of conservation policies. Planning provides spatial targets based on social and biological variables. There is growing literature on conservation landscape scenario modeling, with integration of biodiversity measures and social management land cover costs (Reyers et al. 2012) (Cowling et al. 2008) (De Groot et al. 2010) (Nelson et al. 2009) (Tallis and Polasky 2009). Conservation planning was developed for use in the marine field to determine overlapping sustainable fishing regions and priority no-take zones (Klein et al. 2009) (Mazor et al. 2014); and this method has also been used extensively on terrestrial ecosystems (Levin et al. 2013) (Chan et al. 2006). Conservation planning allows for a cost-benefit analysis of a series of scenarios, and projects the resulting options onto the landscape, in a spatially explicit form with detailed costs for each reserve scenario.

Conservation planning can now take into account both private and public lands to provide an optimal solution across various ownership and land use management (Ball et al. 2009). Conservation planning studies have illuminated the level of overlap between ecosystem service oriented goals and biodiversity oriented goals, allowing for the understanding of both needs within a study system (Chan et al. 2006). The focus of conservation programs has changed from solely protected areas to creating more permeable landscapes and healthy ecosystems (Perfecto and Vandermeer 2010). Because of these larger and more complex goals, conservation planning has become a necessary tool to understand trade-offs and relationships among costs within ecosystems. Taking into account biodiversity held within private lands increases the biodiversity value of the landscape and provides a more representative measurement of actual biodiversity. Also, when taking into account biodiversity held outside of parks or reserves, conservation implementation costs are reduced. Another benefit to conservation planning is that a variety of conservation strategies and management plans can be modeled. This is important because, for example, non-traditional conservation areas such as well-managed reforestation or agroforestry areas can provide reasonable habitat for a wide range of species (Wood, Ch.3), and can increase the permeability of landscapes for wildlife movement (Daily et al. 2003).

The Paso de las Nubes Biological Corridor in northwestern Costa Rica has two overlapping conservation programs, the Payments for Ecosystem Services Program (1997) and the National Biological Corridor Program (2006), each with various and separate goals (Figure 7) (MINAE 2006, 2014). The Payments for Environmental Services goals focus on preservation of biodiversity, scenic beauty, watershed protection, and carbon sequestration, whereas the National Biological Corridor Program focuses on sustainable use to increase connectivity within biological corridors (MINAE 2008). New legislative actions in 2014 have placed spatial bounds on Payments for Environmental Services funding based on the National Biological Corridor Program's official corridors (MINAE 2014). Due to these conservation policy changes and differing goals, it is important to critically analyze the spatial needs of each policy goal across the heterogeneous biodiversity landscape within a variety of ownerships regimes, including private property, government lands, and national parks.

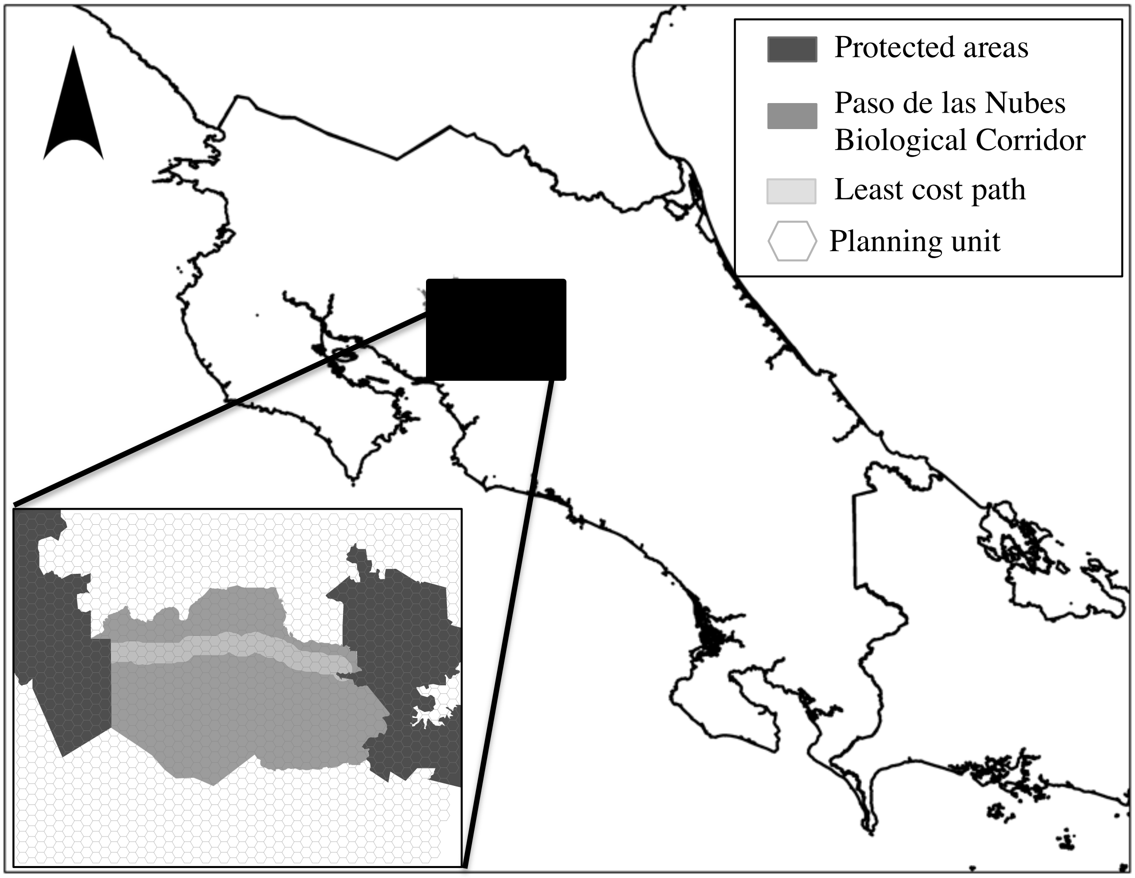

Figure 7. Overview of the study region, including the hexagonal planning units, protected areas, biological corridor, and 1 km buffered least cost path.

The Paso de las Nubes Biological Corridor and surrounding areas (Figure 7) are located in northwestern Costa Rica. (Wood, Ch.2, Ch.3) has shown the need for conservation planning because of a decrease in forest cover and a slight decline in connectivity throughout the corridor during the initial years of the National Biological Corridor Program. In addition, this region is the exclusive connection point in the northern half of the country between the western and eastern slopes of the continental divide, and the sole connection point for all threatened dry forest western protected areas. The neighboring protected areas and Huetar Norte region are facing drastic conservation issues, chiefly agricultural intensification through pineapple and banana production, and timber extraction. Endangered species, such as the great green macaw (*Ara ambiguus)*, rely on these landscapes for nesting sites and habitat (Monge-Arias and Chassot). To the west, on the pacific slope of Monteverde, efforts are in place to create a hiking corridor, termed the Sendero Pacifico, that links Monteverde in the east to the western coastal mangroves along the bellbird biological corridor; this plan takes a multifaceted conservation approach that ties farmers to conservation to public recreation use (Ryan 2012; Sendero Pacifico 2016). Recent studies in the northeastern region of Costa Rica have shown that forest clearing bans are successful in decreasing forest loss of mature growth, but do not increase regrowth of forests, which is precisely the need to increase forested connectivity between parks (Fagan et al. 2013).

In this study, I assessed conservation planning scenarios based on two official conservation programs, Costa Rica's Payments for Environmental Services and the National Biological Corridor Programs. Specific objectives of this study were to: (1) identify the costs to implement conservation actions on land use types throughout the region, based on conservation payments and landscape production factors; (2) conduct conservation planning analyses with various scenarios, representing specific goals of active conservation programs within the region; and (3) provide recommendations for spatial priority areas based on conservation goals.

Methods

Study Area

We conducted the study in the Paso de las Nubes Biological Corridor (CBPN) in the northwestern portion of Costa Rica, approximately 60 km northwest of the capital, San Jose. This corridor is part of the larger national biological corridor network. The Paso de las Nubes Biological Corridor covers an area of approximately 400 km2, and contains many different land uses, such as private forests, small towns, ornamental plant production, dairy cattle, and small scale farming (Figure 7 and Figure 8). Ecoregions within the corridor include premontane rain forest, premontane wet forest, lower montane moist forest, lower montane rain forest, and tropical wet forest (Hartshorn 1983). This corridor was selected because of its important central location between two expansive protected areas, with Monteverde and Arenal protected areas on the western side, and Juan Castro Blanco on the eastern side (Figure 7). This area has overlapping conservation programs, the Payments for Environmental Services and National Biological Corridor Programs. I also chose this location because previous work has provided a high resolution (15 meters) base layer map of land use cover, necessary to conduct quality conservation landscape modeling within an area of this size (Wood Ch.2).

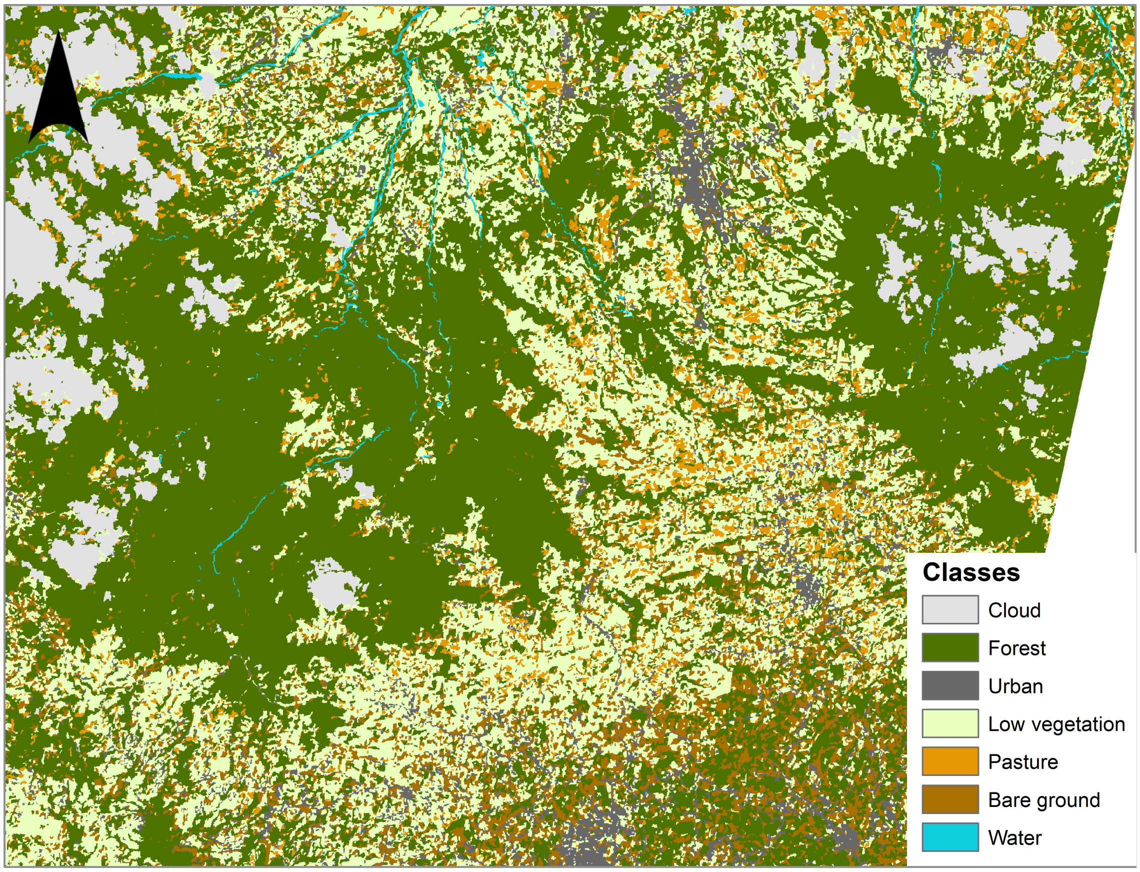

Figure 8. Study region land use classification map, at 15 meter resolution.

Marxan Model

For this study, I selected the spatial conservation-planning tool Marxan (Watts et al. 2008). Marxan uses spatial algorithms to identify the most cost-effective conservation landscape zones. Cost is calculated and defined as the cost to implement conservation management across specific areas. The different scenarios within the model address future potential conservation outcomes in the corridor, which are ultimately influenced by the active conservation goals. Marxan provides reserve design recommendations that maximize biodiversity targets while minimizing boundary length and cost, to create the potential reserve network. This is accomplished with the use of spatial data paired with cost and biodiversity target data, and uses the optimization technique of simultaneous annealing to provide multiple solutions with information on the cost and connectivity for each solution (Watts et al. 2008)

The study region must be broken into "planning units" based on regularly spaced shapes such as hexagons or squares, or by biological boundaries, such as watersheds. I determined that 10 km^2 hexagonal planning units would best fit the study area, as the maximum PES property within the Paso de las Nubes Biological Corridor was 8.1 km^2, making 10 km^2 an ideal planning unit size to fully encompass large PES properties. The total number of hexagonal planning units in the study region was 1,547. The hexagonal planning units were preferred over square planning units as they are more efficient and produce less fragmented results (Nhancale and Smith 2011).

Conservation Programs

We modeled two conservation programs in the conservation-planning model scenarios, using program goals to define scenarios and targets. The first program was the Payments for Environmental Services Program. This program pays landholders for a variety of land uses, and current payments go to forest protection, reforestation, and agroforestry. The four goals of this program include protection of biodiversity, scenic beauty, and watersheds, and also sequestration of carbon (MINAE) (National System of Conservation Areas SINAC 2009; Villate et al. 2009). The second program was the Biological Corridors Program (MINAE 2006). The corridor program has four main goals: (1) to strengthen the national biological corridor network; (2) to promote the conservation of biodiversity and restore ecological connectivity; (3) to encourage environmentally friendly development within biological corridors; (4) to increase collaborative endeavors with institutions and actors within the biological corridors (National System of Conservation Areas SINAC 2009) (MINAE 2006). (SINAC 2008).

Biodiversity and Cost Data

Biodiversity can be measured in a variety of ways, including species richness, taxonomic diversity, and endangered species presence, along with many other surrogates (Rodrigues and Brooks 2007). In the study system, I chose to use mammal species richness as the measure of biodiversity. Mammals were chosen because they are known beneficiaries of improved connectivity, and are primary species of interest when interviewing managers and government officials with reference to biodiversity goals (Minor and Lookingbill 2010). Mammals were also chosen because Costa Rica's economy is heavily reliant on ecotourism, and mammal species are among the top ecotourism attractions of the country (Eagles 1992).

We gathered biodiversity data from May to August 2014 and 2015. I collected richness data through interview surveys, camera traps, and hair traps. To identify species occupancy in PES properties, I placed 47 camera traps within PES and non-PES properties throughout the Paso de las Nubes Biological Corridor and adjoining protected areas, from May to August 2014 and 2015 (Figure 7). PES land uses can include primary forest, agroforestry, and tree plantations, although no agroforestry properties were present within the Paso de las Nubes Biological Corridor. The national parks surveyed included western Juan Castro Blanco National Park and eastern Monteverde Cloud Forest Reserve. I used a combination of Bushnell 6MP®, Browning 3XR®, and Moultrie M-550® cameras. Placement of camera traps was non-random, situated in areas detailed by landowners and managers to have high rates of mammal passage, usually along game trails, human trails, near streams, or in areas with food resources. The goal was to maximize the capture rate, providing the most complete presence data. Cameras were placed at least 100 meters apart, and approximately 1 meter off the ground, dependent on the slope of the landscape. The camera traps were activated for 21-45 days, and set with a five second delay to avoid unnecessary multiple captures of the same individual. All willing Payments for Environmental Services properties within the Paso de las Nubes Biological Corridor were surveyed, and each Payments for Environmental Services property held five active cameras at a time. Protected areas, with their larger areas, contained between 10-30 active cameras at a time. The number of landowner properties surveyed was 14, with 4 additional sites in Juan Castro Blanco National Park, and 4 others in or in protected forests adjacent to the Monteverde Cloud Forest Reserve; the total number of sites in the entire region was 22. This study had 2,179 trapping nights in 2014 and 781 trapping nights in 2015, for a total of 2,960 trapping nights over the duration of the study.

We conducted semi-structured interviews with landowners and managers of PES properties in 2014 (Wood, Ch.3). These interviews corroborated camera trap data with first-hand local ecological knowledge. Costs gained from interview data was also used to understand the costs associated with executing conservation actions, and costs associated with diary and ornamental plant production. Interviews were used as a method to estimate mammal diversity, and have been shown to be as accurate as camera trap data, specifically when interviews are conducted with people who work and live closely on the land (Canale et al. 2012). Prior to conducting field interviews, institutional permission was gained through the Institutional Review Board at Texas A&M University (IRB study #IRB2012-0439). I recruited PES participants using public records of PES contracts, acquired from NGO contacts. I obtained verbal permission for all interviews, and persons interviewed were kept anonymous, ensuring that identifying information was anonymous and was not linked to spatial data. Participants of interviews included PES participants who actively worked on the land and were familiar with local mammals, determined by initial questions about time residing on the land, time working on the property, and familiarity with mammals, among other attributes. During the interviews, I used a picture guide of local mammals to decrease confusion from local mammal nomenclature. Within the picture guide, I included taxonomically similar non-Costa Rican mammals to test for type II errors (Canale, Peres et al. 2012).

To weight the landscape based on biodiversity values I used mammal richness, calculated as the sum of species present in interviews and camera trap data (Wood, Ch.3). Each land use was given a specific richness value, along with the national parks. Through scenario modeling I aimed to increase land uses that had high biodiversity value (forests), while decreasing land uses that had low biodiversity value (urban, bare, pasture). Through conservation payment programs, forests can receive forest protection payments, while low vegetation, bare and pasture can be converted to forest through reforestation payments. I deemed urban too permanent to be eligible to be converted to conservation lands. Mammal connectivity analyses were performed through least cost path and electrical conductivity modeling (Wood, Ch.3), and these analyses illustrated core mammal dispersal routes within the CBPN, and were used to model sites of interest for connectivity goals.

Cost values were assigned to each specific land use type, and were based on the cost values within the PES system (reforestation and forest protection), and the production value of the lands based on interview data (MINAE 2014) (Table 6). I did not use agroforestry payments as a PES payment option within the modeling because there were no agroforestry property payments within the study region. I obtained cost values from interviews with PES landholder participants (IRB study #IRB2012-0439). Interviewees reported yearly labor costs associated with upkeep of PES properties, conversion of property to PES reforestation, or food/livelihood production and income per hectare. Costs for forest protection or reforestation were gained from official FONAFIFO payment plans (MINAE 2014). I used those values to calculate the yearly average payment per km^2 (Table 6). Costs to convert pasture to conservation (through reforestation) were derived from interviews with dairy farmers and substantiated by tropical dairy production data (Falvey and Čhanthalakkhanā 1999). Urban property values within the region vary greatly, with Ciudad Quesada prices highest throughout the region when looking at local property pricing. Because of this variability and the lack of lot-specific price data, I removed planning units from the potential solution that contained greater than 30% urban area, as those areas are not suitable or likely to be converted to conservation areas due to costs and the permanence of human settlements. This only removed a small number of planning units, mainly within Ciudad Quesada, which was exactly what was desired. Urban regions that remained within the analysis carried an average price of $65,000 USD per km^2. For all cost values, I assumed cost was homogeneous throughout the study region, and costs are in 2016 USD values, as this was the unit used in official PES payment plans (MINAE 2014).

Table 6. Costs to convert or add land use feature into conservation network. Costs are in current day USD and are assumed to be homogeneous across the landscape.

Land use	Rule	USD/km^2
Urban	Urban values based on property values within the corridor. Planning units with over 30% urban area removed from solution.	$65,300
Forest	Forest protection (64$ per ha per year). No other legal option for forest other than to leave as forest.	$6,400
Low vegetation	Reforestation option (196$ per ha per year on average). Low vegetation indicates area is not currently being used for production or pasture, making it “easier” to add to the solution.	$19,600
Pasture	Reforestation option. Because this area is currently being used for dairy production, less likely to be added to the solution. Interview data reports that PES value less than 80-90%% of income from dairy production.	$52,000
Bare ground	Reforestation option ($196 per ha per year on average). Bare ground more often associated with urban or crop production, less favorable for placement into "reserve" than low vegetation, but more favorable that pasture.	$32,600

Land Use Maps

The previously published regional map was used as the base layer for the conservation scenario modeling (Wood, Ch.2). The 15-meter resolution land cover map was created by first acquiring Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) imagery from February 2nd, 2008, and February 29th, 2012. The dates were selected based on the timing of corridor policy enactment, and for low cloud cover across the Paso de las Nubes Biological Corridor. During pre-processing, I orthorectified each image, accomplished with the use of software SilcAst with Global ASTER DEM version 2. Then, the imagery was clipped to encompass the corridor, with a 6.7 km buffer, that provided the largest area possible based on the imagery tiles. I conducted an object-oriented classification of the imagery using Trimble eCognition Developer 9.1 (Trimble 2011). I used object-oriented classification because initial trials using pixel-based methods produced low accuracy and kappa values. After segmentation, I identified seven final classes based on the vegetation and pixel characteristics of the imagery. The vegetation classification categories included (1) urban, (2) pasture, (3) low vegetation, (4) bare ground, (5) forest, (6) clouds, and (7) water. The slope surface was derived from the Digital Elevation Model (DEM), with 30-m resolution, using the slope tool in ArcGIS 10.2 (ESRI 2011).

Scenarios

We tested seven scenarios based on the two conservation program goals, with outcomes for each scenario favoring increased conservation targets at minimal cost. All scenarios, because of the increase in forest component, fulfilled PES carbon sequestration goals by increasing protected forested areas in the region. The seven scenarios represent the following goals: biodiversity, forest protection, connectivity, and watershed protection. Table 7 holds a full list of scenario variables, rules, and data.

Table 7. Scenario conservation goals, data used, and targets set. Units: PA – Protected Areas; CBPN - Paso de las Nubes Biological Corridor; LCP – Least Cost Path.

	Feature	Goal	Data	Unit / status	Targets
1	10% forest increase	Biodiversity, carbon	Forest cover, species richness	PA, CBPN	10% forest increase
2	20% forest increase	Biodiversity, carbon	Forest cover, species richness	PA, CBPN	20% forest increase
3	30% forest increase	Biodiversity, carbon	Forest cover, species richness	PA, CBPN	30% forest increase
4	Boundary	Connectivity	Species richness, forest cover and boundary	PA, CBPN	20% forest increase
5	Eastern CBPN	Sustainable development	Species richness, forest cover	PA, eastern CBPN	20% forest increase in developed areas Biological Corridor
6	Least Cost Path	Mammal corridor	Species richness, forest cover, mammal dispersal corridor	PA, LCP	20% forest increase in LCP
7	Watershed protection	Watershed and flood control protection	% Slope + % pasture/bare ground/urban, species richness	PA, CBPN	20% forest increase in landslide, flooding areas

Specifically, scenarios 1, 2, and 3 are based on the PES goal of increased biodiversity (and forest protection), targeted within the biological corridor system in Costa Rica (National System of Conservation Areas SINAC 2009). These scenarios were termed 10%, 20% and 30% increase in forest within the Paso de las Nubes Biological Corridor. I calculated overlap in planning unit selection because these scenarios have comparable conservation targets, only varying in the forest percent within the target. Scenario 4 is the connectivity scenario and based on the National Biological Corridor connectivity goals (National System of Conservation Areas SINAC 2009). The conservation solution for this scenario prioritized a clumped solution, which allows for spatial targeting within a specified region, contiguous within already established protected area. Under this scenario, I used the boundary length modifier in Marxan, set at 0.5, and designated conservation targets at 20% forest increase. The boundary length modifier preferentially selects planning units bordering other planning units within the system. Scenario 5 is termed eastern Paso de las Nubes Biological Corridor prioritization, and under this scenario I prioritized 20% forest increase along the more heavily used eastern portion of the Paso de las Nubes Biological Corridor, where much of the dairy pastures are located. This scenario focused on the sustainable use goals set within the National Biological Corridor Program (National System of Conservation Areas SINAC 2009). Scenario 6 is the least cost path scenario (LCP), and prioritizes a 20% increase in forest to the LCP region of the Paso de las Nubes Biological Corridor; this is similar to scenario 4, but with a different focus on connectivity within the Paso de las Nubes Biological Corridor. This scenario differs from scenario 4 in that solutions are fixed within an already determined mammal connectivity path, rather than targeting general connectivity throughout the Paso de las Nubes Biological Corridor. The final scenario 7 is termed watershed protection and based on the Payments for Environmental Services watershed protection goal. With this scenario, I keep the same conservation target as seen in the last four scenarios, 20% increase in forest, and targeted areas that protect the watershed, contributing to a decrease in flood and landslide risk (Chan et al. 2006). This was obtained through targeting areas heavily deforested and areas with a high slope; both of those variables are indicative of landslides and flooding events (Chan et al. 2006).

We kept the following Marxan model parameters constant across all scenarios to allow for comparability: I ran each with 10,000 iterations, with a random seed number of -1. The annealing parameters were set to the default, at simulated annealing, followed by the normal iterative improvement algorithm. The threshold cost function was not enabled. And the starting proportion of planning units was set to zero (Ball et al. 2009).

Results

Overall, I found that in all scenarios, except the watershed protection scenario, planning units with more forest were favored (Figure 9). Most scenarios except for the watershed protection scenario placed units either within or near the already designated conservation areas (Paso de las Nubes Biological Corridor or national parks). The watershed protection scenario (7) was the only scenario to place the majority of units outside of Paso de las Nubes Biological Corridor (Figure 9). No scenario greatly outperformed the others in costs, as most scenarios were approximately the same cost to implement. The LCP scenario was the most expensive at 3.7 million, with all others falling between 2.5 and 3 million per year (Figure 10).

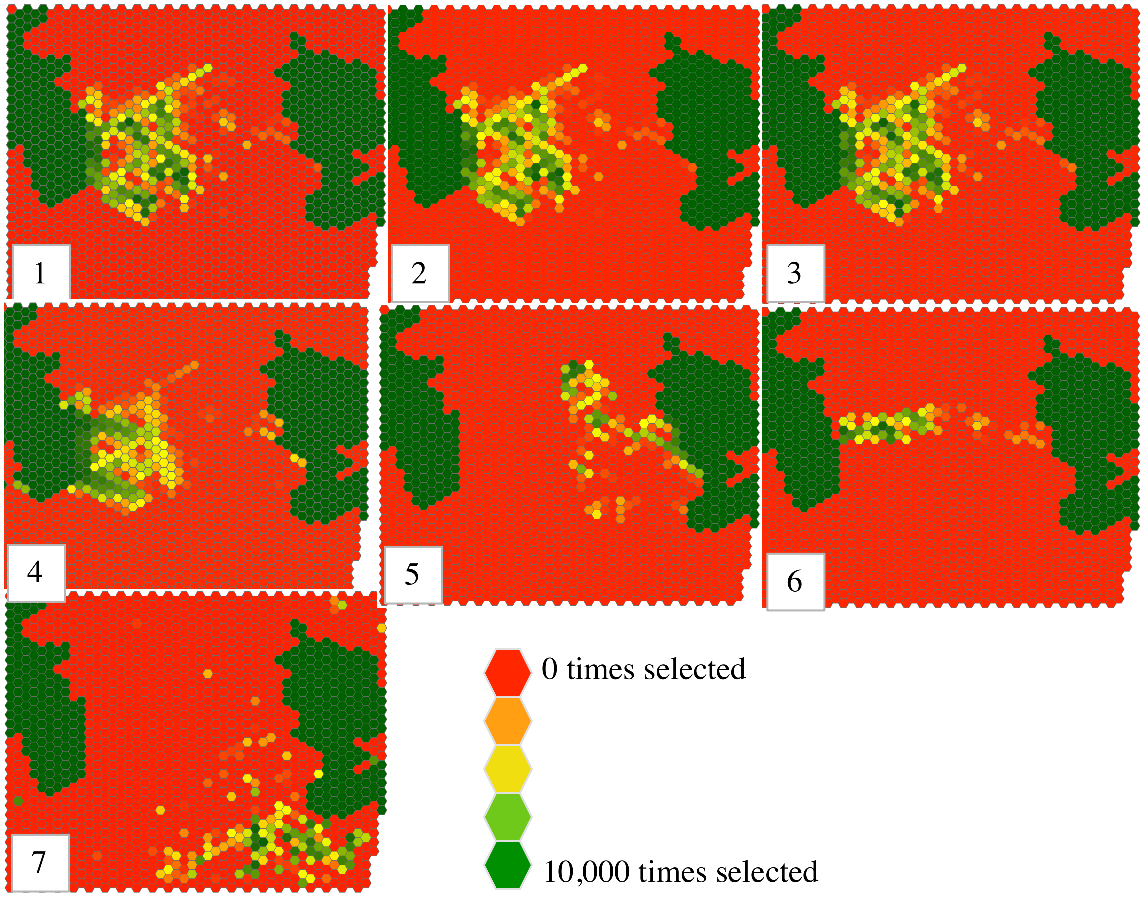

Figure 9. Solutions for each Marxan scenario for 10,000 iterations. The color of the planning unit hexagon represents the number of times that unit was selected over the model runs. Green planning units were selected more often and red planning units were not selected. Light green, yellow and orange planning units are intermediate values. Scenarios 1-3 are 10, 20 and 30% forest increase, respectively. Scenario 4 is the boundary scenario, scenario 5 is sustainable development, scenario 6 is least-cost path, and scenario 7 is watershed protection.

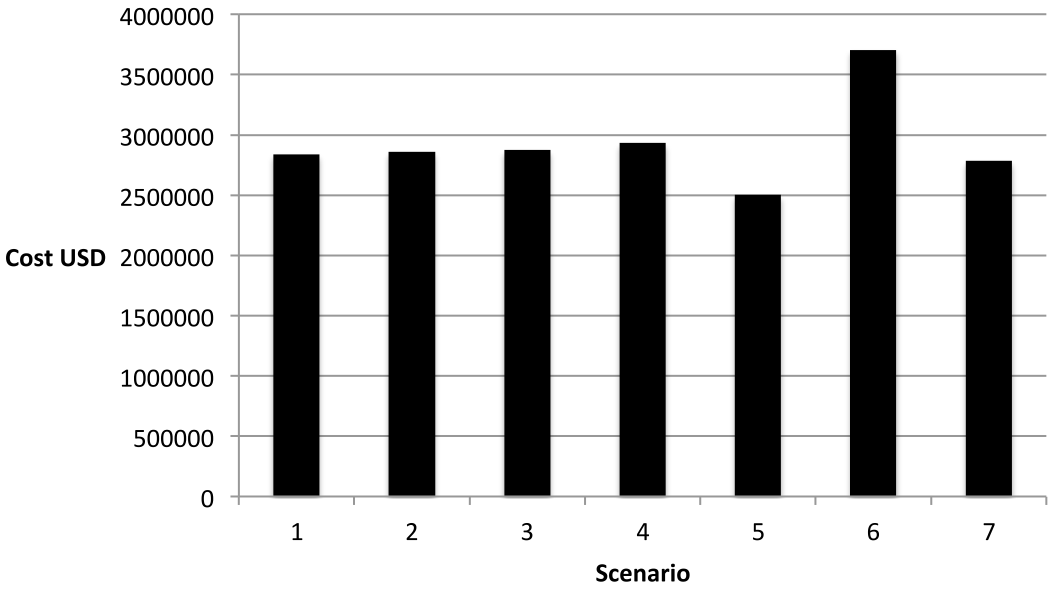

Figure 10. Cost of the best Marxan solution for each associated scenario. Scenarios 1-3 are 10, 20 and 30% forest increase, respectively. Scenario 4 is the boundary scenario, scenario 5 is sustainable development, scenario 6 is least-cost path, and scenario 7 is watershed protection.

Scenario overlap is minimal, except for the preferential selection of western, more forested, units across scenarios 1-4, 6 (Figure 9). Scenario 5, because of scenario boundaries and goals, was not allowed to select western units hence the lack of overlap with the previous mentioned scenarios, by design. The only scenario that did not choose western units, but could have, was scenario 7, watershed protection scenario (Figure 9).

Each scenario within figure 9 represents the number of times a planning unit was selected over the 10,000 runs of the model. When looking at scenarios 1, 2 and 3, I see that the selection of planning units was within a similar area, even with the increase in forest cover from 10% to 30%. This indicates that while conservation targets change, the same spatial areas remain important. In scenario 4, I see that preferred units are on the western side of the corridor where the area is already heavily forested. I also see that units were preferentially added to the borders of protected areas, decreasing the number of isolated or unconnected units. Under scenario 5, the model selected for units close to the eastern national park and units to the north of the corridor, near the large regional city Ciudad Quesada. Under scenario 6, I see planning units selected on the western side of the LCP within the Paso de las Nubes Biological Corridor, mirroring scenarios 1-3. Scenario 7 units are distinct from the previous scenarios, as they do not select units within the Paso de las Nubes Biological Corridor, but rather, units to the southeast of the study region.

The best solution for each scenario (Figure 11) was defined by Marxan as the solution with the lowest score, where score is derived from the cost, boundary length, and penalty for unmet targets. The best solution indicates the optimal selection of planning units based on the number of model iterations, and in the case across the 10,000 iterations. Starting with the forest scenarios of 1, 2, and 3, I see the best solution planning units are on the western side of the Paso de las Nubes Biological Corridor, but each presents solutions that have isolated unconnected units. Planning unit overlap across the CBPN for scenarios 1-3 are as follows: overlap between scenario 1 scenario 2 was 51%, overlap between scenario 2 and 3 was 62%, and overlap between scenario 1 and 3 was 46% (Figure 11). With scenario 4 I see units selected solely along the border of the national parks, aside from one planning unit to the west. Scenario 5 has units against the protected area bounds and a few units selected away from the border of the national parks, located in the center-north of the Paso de las Nubes Biological Corridor.

Scenario 6 shows only a few units selected on the western side of the corridor area. In the final scenario, best unit selection is in the southeast portion of the region, between the national park and the greater San Jose capitol region to the south of the study region.

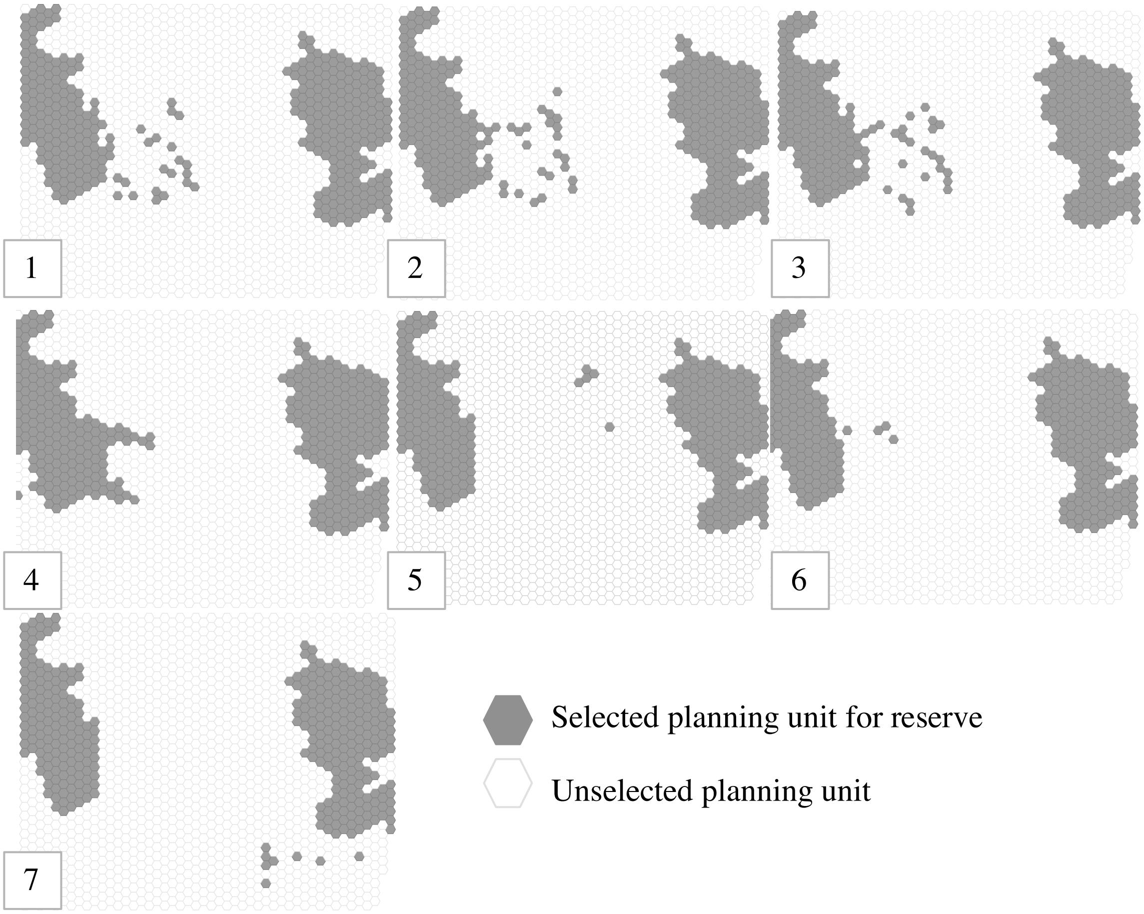

Figure 11. The best reserve configuration solutions for each scenario during the 10,000 model iterations. Best reserve is determined by the best score (cost, conservation targets, boundary length, etc.) determined by Marxan. Scenarios 1-3 are 10, 20 and 30% forest increase, respectively. Scenario 4 is the boundary scenario, scenario 5 is sustainable development, scenario 6 is least-cost path, and scenario 7 is watershed protection.

Discussion

Systematic conservation planning is an important tool to spatially prioritize conservation efforts while minimizing costs. The findings help to support conservation organizations and government agencies by providing spatial prioritization across the conservation landscape of the Paso de las Nubes Biological Corridor, focused on biodiversity, watershed protection, carbon sequestration, sustainable development, and connectivity. I demonstrate few areas of spatial planning unit overlap under each conservation goal. I do find regional preferences, namely the western portion of the CBPN. Factors such as carbon sequestration and biodiversity protection were easily attainable across all scenarios, while watershed protection areas lie well outside of the conservation priority area of the Paso de las Nubes Biological Corridor, and are spatially isolated from other scenario regions. Payments are not currently being placed in the watershed protection region, and benefits from this goal are exceedingly important to local water users and agriculturalists in the area. The relative lack of overlap of planning units based on conservation goals are consistent with Chan et al. (2006), who found that ecosystem goals and biodiversity goals aligned only 40% of the time, and spatial priority areas must be designated for each to create the desired conservation outcomes.

Our scenario outcomes could be used as a tool for conservation managers. Scenario maps (Figure 9) can be used to place initial funds within the dark green planning units, and subsequent additional funds expanded into the light green, orange and yellow planning units. the work provides optimal areas for placement while minimizing costs, and color represents level of selection of that planning unit, which can be used as the starting blocks for conservation actions.

When looking at the best solutions (Figure 11), and specifically scenarios 1-4 as compared to scenarios 5-7, I find less spatial area is conserved in the latter scenarios with similar costs. This is due to the fact that each scenario represents a compilation of two different conservation methods, reforestation and forest protection. Forest protection costs substantially less (three times less) to perform than reforestation. Scenarios 1-4 appear to prioritize forest protection (protection of existing forests), while the subsequent figures have fewer planning units, but those units have less forested areas within each unit, meaning that unit needs to receive the more expensive reforestation payments. That is why costs for scenarios 5-7 are higher for less area protected.

Another factor to consider when creating conservation areas is connectivity. The Marxan connectivity designation, depicted in scenario 4, shows connectivity based around existing parks and protected areas, while scenario 6 (LCP) provides a different view of connectivity, representing physical linkages between the two protected areas based on medium and large mammal data. Each has its advantages and disadvantages; scenario 4 provides a clumped configuration that expands the existing park to extend the area of protection by connecting nearby forested areas, while scenario 6 attempts to connect forests in private lands between national parks. And while the best solution scenarios 1-3 (Figure 11) appear to have little connectivity across planning units, forests around those units must be taken into account (Figure 8). For example, planning units may be embedded within the forest matrix. For example, if the planning units within scenario 1 (Figure 11) are protecting existing forest patches, there is no increased connectivity through new forests, but rather, an increase in the amount of forest under official protection. Scenario 6 (Figure 11) appears to have isolated units, but this scenario could be prioritizing reforestation between large, already existing forests on the western side, thus increasing connectivity more so than protecting existing forests. Each scenario is an instrument to start addressing specific conservation concerns, be it through reforesting or protecting existing forests, in various spatial configurations. It is especially apparent that conservation planning units on the eastern side, because of the lack of forest and hence lack of the potential for forest conservation payments, results in the necessity of reforestation payments and subsequently less land for the cost.

The cost values and scenarios are based upon the best data available. Data on regional property costs and quantitative measurements on what is deemed important with regards to the PES goal of scenic beauty could provide more exact cost values and projections for additional scenarios. However, it has been shown that even conservation planning analyses using uncertain costs, with appropriate prioritization of conservation targets, can still provide suitable results (Carwardine et al. 2010). Additionally, all conservation targets were met within the scenarios. This indicates that targets were attainable with the given landscape configuration, and also signifies that spatial location, rather than availability of quality lands, was more important. Because the CBPN is a working landscape comprised of public and private lands, stakeholders such as the landholders should be taken into consideration when determining where to place sustainable use and protection conservation program. It is worth noting the popularity of the PES program; it always has more applicants than available payments.

Other studies (Evans et al. 2015) have found that without actually conducting conservation planning, the management costs and conservation measures of the system will fail to efficiently and effectively design conservation plans, further indicating the importance of planning. And because Marxan takes into account both protected and unprotected lands, this form of conservation planning modeling can provide better estimates of conservation costs, when compared with past methods that only account for protected area contribution to the conservation landscape (excluding private forests), which then overestimates cost, and area required to meet conservation targets (Wilson et al. 2010). Research has confirmed the benefit of conservation modeling when coordinating across multiple nations or across multiple conservation programs, as it saves money, while still resulting in similar conservation outcomes (Kark et al. 2009). Current and past PES payment placement has focused on the western portion of the Paso de las Nubes Biological Corridor, which validates the conservation planning scenarios, as that was the preferred region for many scenarios because of the availability of forest protection payments (the least expensive conservation option) as opposed to reforestation payments.

While the study focuses on the Paso de las Nubes Biological Corridor region, the importance of neighboring corridors cannot be understated, as broad-based landscape conservation approaches are key to protecting wide ranging species. Watershed protection must also take into account the water needs of downstream and upstream users. Adequate consideration of these factors will require collaboration across conservation efforts throughout the northern region of Costa Rica, including across the both the San Juan-La Selva and Bell Bird biological corridors, and their neighboring protected areas. the results highlight that while the various conservation goals are assumed to be aligned, in fact, actual landscape actions and spatial needs vary among goals and require special spatial consideration during the planning process.

CHAPTER V

CONCLUSIONS

The Paso de las Nubes Biological Corridor is a dynamic landscape, and this research has shown the importance of this region for biodiversity and conservation. I have concluded the following; first, I found a decrease in forest during the years of 2008 to 2012, with large changes seen through the center of the corridor with the construction of the San Carlos highway. Pasture and bare ground increase across the region, and specifically within the biological corridor. Within PES properties there is little forest loss, with forest lost focused outside of PES. Second, through connectivity analyses, I found slightly lower connectivity across the corridor between 2008 and 2012, with one main corridor route present in the northern part of the Paso de las Nubes Biological Corridor. PES properties were essential components to the conservation lands, and more pinch points and narrow passageways could be protected under this program. PES forest properties held similar medium and large mammal species richness as compared to protected areas, and reforestation properties held less species richness, although still had species representing each guild. Lastly, I found the conservation program goals and spatial requirement occurrences in spatially distinct locations in the region, and that corridor conservation must tae into account spatial configurations of natural systems that are deemed important for protection. Overlap of environmental services and corridor areas are minimal, with some environmental services falling outside of the government designated priority regions.

Within the land use change study, chapter two, additionality is used to measure effectiveness of conservation programs, and is defined as the conservation effects as compared to baseline outcomes (Wunder 2007). I saw little additionality during the initial years of NBCP enactment, demonstrated by decreased forest cover despite connectivity goals and an increased effort to target conservation using PES inside the CBPN. Forest decreased across the entire landscape, both inside and outside of CBPN, indicating a regional transition in forest cover, but with percent loss in forest almost three times higher inside the CBPN (Table 3). I did see additionality within PES property bounds, with substantially less forest change within PES regions as compared to non-PES regions. And while it can be challenging to link landscape changes back to specific policies, identifying landscape changes can provide a quantitative measure to empirically determine the success or attainment of policy goals and conservation efforts (Ferraro and Pattanayak 2006). I found PES protects forests, but these protections do not extend to other lands outside of the PES property bounds to fulfill the larger NBCP goals.

Past studies have questioned the additionality of Costa Rica PES and deforestation ban programs against baseline scenarios, citing little change in deforestation rates with or without the policy (Miranda et al. 2003; Sanchez-Azofeifa et al. 2007; Sierra and Russman 2006). Specific concerns include payment to lands already destined to be protected while using limited conservation funds (Miranda et al. 2003; Pagiola 2008). A recently study on the forestry ban of 1996 actually showed in an increase in forest. Fagan et al. (2013) described that while perverse incentives could have acted to decrease natural regeneration, instead, as intended, forest area increased. In the study, I also found benefits to PES, in the form of decreased forest lost in current and historic PES regions.

Within the biological corridor, economic pressures and road networks could be a major driving factor in forest loss outside of PES properties, countering conservation efforts (Geist and Lambin 2002). The construction of the San Carlos highway is funded and designed by the government agency CONAVI with supplemental funding from the dairy cooperative Dos Pinos (Figure 2) (Herrera 2011); Dos Pinos owns a dairy factory in Ciudad Quesada, with another plant south, near San José. Dos Pinos is one of the main economic interests in the area, and supplies the country with dairy products. It is also worth noting that many Dos Pinos farmers are participants of the PES program, and hold important forest patches on the eastern side of the corridor. The new highway is a four-lane route able to move agricultural products from the agricultural regions in northeastern Alajuela, Heredia and Limon provinces to the western and central parts of the country, with future increased access to markets. Currently, two 2-lane highways run the length of this 20 km-wide sensitive CBPN area, with the new third highway located in the middle, placing each route approximately 7 km apart, all with similar geographical origins and ends. The necessity for the new highway was questionable if current highway routes had been expanded, however the San Carlos highway is in its final years of construction after approximately 40 years of planning. As such, once the highway is completed, ease of access to forests and the interior of the biological corridor will increase, and without sufficient conservation tools in place, I can predict additional urbanization and deforestation in these newly opened areas. Dos Pinos is unofficially linked to the conservation efforts in the CBPN as many of their dairy farmers receive payments through the PES program, especially along the eastern side of the corridor. Dairy farmer participation could be used as a catalyst to grow an official conservation partnership with the dairy cooperative, the NBCP, and the PES program, working towards conservation goals in the corridor.

The NBCP and PES programs officiated by both SINAC and FONAFIFO, and the highway system run by CONAVI, are all government agencies and programs, with funds that appear to be working without coordination. To eliminate contradictory outcomes in funding, government agencies working within similar geographical areas could create formalized collaborations (the fourth goal the NBCP) to define solutions and mitigate conflicting goals.

Designation of conservation priority lands can in some cases cause the opposite of the desired conservation actions, leading to unintended or perverse consequences such as land grabs, habitat degradation, or in-migration (Liu et al. 2007; Rodriguez-Solorzano 2014). In the neighboring biological corridor of San Juan/La Selva, landowners have expressed anger and protested around corridor designation. In contrast, when interviewing PES landowners in the CBPN, most were not aware that their properties were located within a biological corridor, but showed positive interest in the designation. This unawareness could be partially attributed to the fact that I witnessed no official signage designating the CBPN. And while perverse incentives were observed in other studies {Rodriguez-Solorzano, 2014 #493), I feel that the designation of the landscape as a biological corridor did not lead to deforestation and conversion of land through these means. Additional signage and public campaigns delineating the CBPN may even spur collaborations among interested actors within communities.

The loss of forest in the CBPN caused a decrease in the quality of the countryside matrix, resulting in a less permeable landscape for wildlife species and less density or width of movement corridors throughout the region (Daily et al. 2003). There is also a decrease in the size and number of forest patches, increasing the distance required to travel between and among patches. Some species or individuals may not be able to move to or from spatially isolated patches. Further isolation of these patches can negatively impact remnant populations that are dependent on forests for habitat (McGarigal et al. 2009), degrading the quality and conservation potential of this area, antithetical to the goals of the NBCP.

Wunder (2005) describes PES as a valid conservation tool when threats are intermediate, when projected as a future threat, or when land use choices are flexible. Intermediate threats can be defined as mid-level deforestation rates. I have a scenario where land uses are not flexible due to the deforestation ban, with immediate threats such as the opening of the middle of the corridor with the highway, in an area deemed a high priority for conservation. While this study area meets some of the PES recommendations, in this situation, PES has been shown to protect forests across the study region, with areas outside of the PES properties (falling under the NBCP) experiencing the highest losses in forest cover. The current situation in the CBPN is a case for the effective application of a systematic conservation planning process

(Margules et al. 2007) to generate optimal solutions using economic costs and benefits under the current constraints.

PES and biological corridor policies could spatially target reforestation and forest protection payments to accomplish the stated goal of the programs. This can occur in several ways. Programs could focus on specific areas with high forest loss and solicit applications from specific farms and regions. There could be an objective to prioritize recently deforested areas near the highway, allowing for renewed connectivity of neighboring mammal populations with short isolation times. This may be beneficial as forest fragments isolated for longer periods may have higher local extirpation of species. This would also provide PES protection to the newly accessible core areas of the corridor using a forest buffer along the highway route. Lastly, programs can mitigate barrier issues tied to highway development through the use of culverts or overpasses.

Costa Rica leads among Central American countries in total protected area, and has been proactive in staving off deforestation and degradation of the agricultural matrix since the 1980s. The corridor system exemplifies a policy priority of conservation and connectivity. While the study reveals that PES properties within the corridor provided protection against forest loss, I found that even with official biological corridor designation, non-PES lands within corridors can experience increased land use change and forest loss. The reasons for these changes are varied and complex. Biological corridors are an essential link for the protected areas network in Costa Rica and for greater connectivity throughout the Mesoamerican biological corridor. The Biological Corridor system is a unique and an exceedingly important piece of legislation, for which the goals to enact important conservation measures must be accomplished. Policies and on-the-ground outcomes must be reviewed to understand the drivers of change and the requisite tools needed to accomplish these important goals.

Within chapter three, I determined that a more productive use of PES and biological corridor funding could be obtained through spatially targeting reforestation and forest protection payments to accomplish the stated goal of maximum connectivity. This could be conducted in several ways. Programs could focus on specific corridor connections and solicit applications from specific farms and regions. There should be a goal to prioritize areas that have been recently deforested near the highway, allowing for renewed connectivity of neighboring mammal populations with short isolation times. This second option may be beneficial as forest fragments isolated for longer periods of time may have higher local expatriation of species. Lastly, mitigate highway barrier issues through the development of culverts or overpasses.

Costa Rica leads among Central American countries in total protected area, and has been proactive in staving off deforestation and degradation of the agricultural matrix since the 1980s. The corridor system exemplifies a policy priority of conservation and connectivity. Yet, the study reveals that even as an official conservation priority, degradation, forest loss, and decreased connectivity can take place. The reasons for these changes are varied and complex. These corridors are an essential link for the protected areas network in Costa Rica and for greater connectivity throughout the Mesoamerican biological corridor. Policies and on-the-ground outcomes must be reviewed to understand the drivers of change and the requisite tools needed to accomplish important connectivity goals.

Connectivity analyses illuminated corridor routes and passageways for mammal species. And a main goal of the Costa Rica Biological Corridor Program is to enhance conservation through improved connectivity. Corridors are regarded as important for dispersal areas of mammals, and a key component of the conservation toolbox (Gilbert-Norton et al. 2010). Since 2006, there has been an increased commitment to biological corridors (MINAE 2008, 2014). the study suggests that, while the PES conservation focus within biological corridors has been beneficial for connectivity, the spatial scale at which the program targets investment could be further focused to ensure protection of vulnerable core connections and pinch points. I could be seeing a social-scale mismatch within the policies and ecological properties of the system (Cumming et al. 2006); the conservation program functions at a scale and grain larger than the ecological necessities and forested corridors, and changes occur at the individual property level while the policy works on a regional spatial scale. The levels of policy enactment and changes are occurring at differing levels of society. Currently, landholders are the actors who are responsible for making changes to the system, from the bottom up, while the policies themselves are coming from the top-down from government and NGO organizers (Muñoz-Rojas et al. 2015).

Scale mismatch among policy objectives and landscape outcomes can lead to unattainable ecological goals (Cumming et al. 2006). the results indicate that while I do not see large losses of overall connectivity across the landscape, I also do not see creation of additional, newer, or wider corridors using PES within the NBCP. The LCP shows that portions of routes are only 130 meters wide, and in 2012, there are two 500 m breaks in the corridor, including a barrier feature, the new four-lane San Carlos highway. These issues could cause this to become a non-functioning corridor. While the minimum width of the corridor falls within the minimal width deemed by other corridor studies, it is difficult to determine a set minimum width as each system and species group requires different needs (Spackman and Hughes 1995). And I can assume that large gaps of inhospitable land (roads, highways) do not increase corridor efficacy. Other studies show similar challenges with corridor implementation and policy mismatch. In Nepal, necessary measures to enact conservation of target species resulted in recommendations of additional protection, monitoring, and restoration of corridors to increase habitat connectivity (Aryal et al. 2012). A Scottish study examined forest policy and corridor planning to find lags in existing planning and policy, and argued that a more spatially explicit policy and planning instrument was needed to coordinate across institutions and actors (Muñoz-Rojas et al. 2015). In the "Nature Ways" corridor network in Singapore, there were no financial initiatives to prevent anthropogenic changes in a corridor, and the future of the functional corridor was at risk, with some corridors currently too narrow to function (Jain et al. 2014).

The benefits and challenges of PES properties have been shown on multiple levels (Pagiola 2008), and I have shown that PES properties, both reforestation and forest protection properties, were active mammalian habitat locations when compared with protected area mammal populations. The benefits from these PES properties are consistent with to the goal of biodiversity within the program. I have shown that PES properties can serve multiple conservation goals, including protecting forests and providing habitat for biodiversity. This is consistent with De Barros et al. (2014), who show additional benefits to biodiversity from REDD+ conservation projects. Based on the mammal richness study, I recommend that PES properties continue to be used for the purpose of increasing connectivity. It must be noted that type of PES property is important, with forest protection provides suitable habitat for a larger number of species, while fewer species were found using reforestation properties. I also found more rare species in forest protection properties, as defined by a species being listed as endangered within Costa Rica. But while forest protected properties had more rare species, species from all guilds were found in both types of PES properties present in the study area, with forests containing higher numbers of species in each guild. Because of the utilization of PES properties by mammals, I recommend that these properties be placed in strategic localities, so as to increase connectivity and provide habitat, while also accomplishing the other goals of the program. Current placement of PES properties since enactment of NBCP aids in connectivity in specific locations, but does not prevent loss of connectivity throughout the corridor. And while the majority of properties are located in areas of high mammal movement, the LCP within the corridor would benefit from additional PES protection. Because PES is a voluntary program, I suggest micro-targeting to incentivize PES properties within mammal movement corridors and pinch points to gain additional conservation benefit and protection through the program.

A review of connectivity studies has called for assessing multiple landscape variables to understand connectivity. Humphrey et al. (2015) recommended increasing the size of existing patches and decreasing isolation of patches to develop successful ecological networks and corridors. To obtain suitable movement paths throughout biological corridors, other studies suggest that conservation focus on riverine and riparian areas, which provides a slight benefit to biodiversity as compared to conservation without a riverine focus (Rouget et al. 2006). A riverine focused policy is already in place within Costa Rica; Forestry Law Number 75757 prohibits cutting of trees along riparian corridors. By pairing PES programs with riparian corridor conservation, these forested areas could be expanded to provide a more viable elevational connectivity, especially if reforestation payments can be used to protect riverine corridors along elevational gradients. Townsend and Masters (2015), built on the riverine method to protect elevational bands or strips of land, to produce a lattice network to allow for elevational movement of species in the face of climate change while also providing refuge to non-vagile species within specific elevational levels. The protection of riparian corridors also meets the multiple objectives of protecting and maintaining river flows. On the western side of the CBPN, there appear to be elevational gradient connectivity already in place, within the large tracts of forest from high elevations to lower elevations. Horizontal bands are not found on either side of the corridor; these bands are defined as horizontal connections within one elevational level, like a band between forested habitat at an elevation of 100 meters. Elevation bands on the eastern side would be harder to implement because of the presence of extensive dairy production. One method to incorporate these bands into the landscape would be to develop wider windbreaks within the eastern regional farms; then, these corridors could be used for movement, and could also benefit local landholders by providing wind shelter for cattle, additional timber trees, increased milk production, decreased soil erosion, and increased forage (Ferber 1958) (Murgueitio et al. 2011). Another method to enhance connectivity is to use reforestation payments or create payments for natural regeneration to increase the quality and size of already existing forest patches to allow them to act as stepping-stones (Saura et al. 2014). And with larger patches, there could be higher wildlife population persistence and decreased edge effects, as compared to small patches (Michalski and Peres 2005).

While achieving connectivity through addition or maintenance of corridors is a key focus of the NBCP, one of the most cost effective techniques is to remove barriers (McRae et al. 2012). In the study, bypassing barriers such as the new highway is a necessary step to create connectivity among the neighboring national parks. Without mitigation of this barrier with either underpasses or overpasses (Kleist et al. 2007) (Gloyne and Clevenger 2001), PES and other conservation efforts will spend funds that pool conservation efforts on either side of this barrier, meeting other conservation goals such as carbon sequestration, but lagging on connectivity goals.

The National Biological Corridor Program was formed in 2006 to provide connectivity to the protected areas network, and to improve connections along the larger Mesoamerican biological corridor. In doing so, the country’s policy is aligned with the newer Convention on Biological Diversity’s Aichi targets. the analysis presents evidence that overall connectivity has slightly decreased over the initial years of the program, and PES properties serve as habitat for medium and large mammal species. With the increased pressure to complete the highway, and the recent government commitment to fast-track the construction, mitigation of connectivity issues is timely (Arias 2015). Currently, mammal connectivity routes are limited to a few pathways that span highways and large gaps. Given that PES properties are used as habitat for many mammal species, re recommend they be used as a beneficial tool for enacting connectivity across the landscape. And conversely, because of the high reliance on ecotourism, and reliance on charismatic mammalian species, habitat is an important area to conserve for tourism. Policy goals are already aligned with connectivity, however changes need to be made to ensure that actions are prioritized and implemented at appropriate regional and local levels to realize these connectivity priorities.

Finally, in chapter four, systematic conservation planning showed that spatial priority areas for conservation program goals are distinct, and biological corridor spatial bounds do not cover all conservation goals. Conservation planning is an important tool to spatially prioritize conservation efforts while minimizing costs. My findings support conservation organizations and government agencies by providing spatial prioritization across the conservation landscape of the Paso de las Nubes Biological Corridor, focused on biodiversity, watershed protection, carbon sequestration, sustainable development, and connectivity. I demonstrate few areas of spatial planning unit overlap under each conservation goal. I do find regional preferences, namely the western portion of the CBPN. Factors such as carbon sequestration and biodiversity protection were easily attainable across all scenarios, while watershed protection areas lie well outside of the conservation priority area of the Paso de las Nubes Biological Corridor, and are spatially isolated from other scenario regions. Payments are not currently being placed in the watershed protection region, and benefits from this goal are exceedingly important to local water users and agriculturalists in the area the relative lack of overlap of planning units based on conservation goals are consistent with Chan et al. (2006), who found that ecosystem goals and biodiversity goals aligned approximately 40%, and spatial priority areas must be designated for each to create the desired conservation outcomes.

The scenario outcomes could be used as a tool for conservation managers. They can use the scenario maps (Figure 9, Figure 11) to set placement of initial funds within the dark green higher selected planning units, and with subsequent additional funds, expand out into the light green, orange and yellow planning unit regions. The work delivers optimal areas for placement while minimizing costs, and color represents level of selection of that planning unit, which can be used as the starting blocks for actions.

Additionally, all conservation targets were met within the scenarios. This indicates that targets were attainable with the given landscape configuration, and also signifies that spatial location, rather than availability of quality lands, was more important. Because this is a working landscape comprised of public and private lands, stakeholders such as the landholders, should be taken into consideration when determining where to place sustainable use and protection conservation program.

Other studies, including (Evans et al. 2015), have found that without actually conducting conservation planning, the management costs and conservation measures of the system will fail to efficiently and effectively design conservation plans, further indicating the importance of planning. And because Marxan takes into account both protected and unprotected lands, this form of conservation planning modeling can provide better estimates of conservation costs(Wilson et al. 2010). Confirmation of the benefit of conservation modeling when coordinating across multiple nations or across multiple conservation programs has been shown to save money, while still resulting in similar conservation outcomes (Kark et al. 2009). Also, current and past PES payment placement has focused on the western portion of the Paso de las Nubes Biological Corridor, which validates the conservation planning scenarios.

While the study focuses on the Paso de las Nubes Biological Corridor and surrounding region, the importance of neighboring corridors cannot be understated, as landscape approaches to conservation are key to protecting long ranging species. Watershed protection must also take into account water needs of downstream users and upstream users. Adequate consideration of these factors will require collaboration across conservation efforts throughout the northern region of Costa Rica, including across the San Juan La Selva and the Bell Bird biological corridors, and their neighboring protected areas. The results highlight that while conservation goals are assumed to be aligned, in fact, actual landscape actions and spatial requirements are not aligned and consideration during planning processes. In conclusion, conservation policies act within a dynamic and complex system of human and natural landscape. Each component has distinct spatial requirements and aligning policy goals is a challenging, but critical component of conservation research to enact the desired ecological outcomes and changes.

REFERENCES

Aide TM, Clark ML, Grau HR et al (2013) Deforestation and reforestation of Latin America and the Caribbean (2001–2010). Biotropica 45(2):262-271

Alexander SM, Waters NM (2000) The effects of highway transportation corridors on wildlife: a case study of Banff National Park. Transportation Research Part C: Emerging Technologies 8(1):307-320

Andam KS, Ferraro PJ, Pfaff A, Sanchez-Azofeifa GA, Robalino JA (2008) Measuring the effectiveness of protected area networks in reducing deforestation. Proceedings of the National Academy of Sciences 105(42):16089-16094

Arias L (2015) Government pledges to speed up construction of San Carlos highway. Tico Times. Costa Rica

Aryal A, Brunton D, Shrestha T et al (2012) Biological diversity and management regimes of the northern Barandabhar Forest Corridor: an essential habitat for ecological connectivity in Nepal. Tropical Conservation Sciences 5(1):38-49

Ball IR, Possingham HP, Watts M (2009) Marxan and relatives: software for spatial conservation prioritisation. Spatial conservation prioritisation: quantitative methods and computational tools. Oxford University Press, Oxford:185-195

Baum KA, Haynes KJ, Dillemuth FP, Cronin JT (2004) The matrix enhances the effectiveness of corridors and stepping stones. Ecology 85(10):2671-2676

Becker A, Körner C, Brun J-J, Guisan A, Tappeiner U (2007) Ecological and land use studies along elevational gradients. Mountain Research and Development 27(1):58-65

Benítez-López A, Alkemade R, Verweij PA (2010) The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biological Conservation 143(6):1307-1316

Booth JA, Wade CJ, Walker T (2014) Understanding Central America: global forces, rebellion, and change. Westview Press, Boulder CO

Canale GR, Peres CA, Guidorizzi CE, Gatto CAF, Kierulff MCM (2012) Pervasive defaunation of forest remnants in a tropical biodiversity hotspot. PloS One 7(8)

Carlson TN, Ripley DA (1997) On the relation between NDVI, fractional vegetation cover, and leaf area index. Remote Sensing of Environment 62(3):241-252

Carwardine J, Wilson KA, Hajkowicz SA et al (2010) Conservation planning when costs are uncertain. Conservation Biology 24(6):1529-1537

Céspedes M, Finegan B, Herrera B, Delgado L, Velásquez S, Campos JJ (2008) Diseño de una red ecológica de conservación entre la Reserva de Biosfera La Amistad y las áreas protegidas del Área de Conservación Osa, Costa Rica. Recursos Naturales y del Ambiente 54:44-50

Chan KM, Shaw MR, Cameron DR, Underwood EC, Daily GC (2006) Conservation planning for ecosystem services. PLoS Biology 4(11):e379

Convention on Biological Diversity (2011) Target 11. In: Diversity C. o. B. (ed) https://www.cbd.int/sp/targets/rationale/target-11/

Cowling RM, Egoh B, Knight AT et al (2008) An operational model for mainstreaming ecosystem services for implementation. Proceedings of the National Academy of Sciences 105(28):9483-9488

Cumming GS, Cumming DH, Redman CL (2006) Scale mismatches in social-ecological systems: causes, consequences, and solutions. Ecology and Society 11(1):14

Daily GC, Ceballos G, Pacheco J, Suzán G, Sanchez-Azofeifa A (2003) Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conservation Biology 17(6):1814-1826

De Barros AE, Macdonald EA, Matsumoto MH et al (2014) Identification of areas in Brazil that optimize conservation of forest carbon, jaguars, and biodiversity. Conservation Biology 28(2):580-593

De Groot RS, Alkemade R, Braat L, Hein L, Willemen L (2010) Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. Ecological Complexity 7(3):260-272

DeClerck FAJ, Chazdon R, Holl KD et al (2010) Biodiversity conservation in human-modified landscapes of Mesoamerica: Past, present and future. Biological Conservation 143(10):2301-2313

DeFries R, Hansen A, Newton AC, Hansen MC (2005) Increasing isolation of protected areas in tropical forests over the past twenty years. Ecological Applications 15(1):19-26

Eagles PF (1992) The travel motivations of Canadian ecotourists. Journal of Travel Research 31(2):3-7

ENVI version 5.2 (2014), 5.2 edn. Excelis Visual Information Solutions, Boulder, CO

ESRI (2011) ArcGIS Desktop: Release 10. Environmental Systems Research Institute Redlands, CA

Evans MC, Tulloch AI, Law EA, Raiter KG, Possingham HP, Wilson KA (2015) Clear consideration of costs, condition and conservation benefits yields better planning outcomes. Biological Conservation 191:716-727

Fagan M, DeFries R, Sesnie S et al (2013) Land cover dynamics following a deforestation ban in northern Costa Rica. Environmental Research Letters 8(3):034017

Falvey L, Čhanthalakkhanā Č (1999) Smallholder dairying in the tropics. ILRI (aka ILCA and ILRAD) New York

Ferber AE (1958) Windbreaks in conservation farming. US Department of Agriculture, Soil Conservation Service, USA

Ferraro PJ, Pattanayak SK (2006) Money for nothing? A call for empirical evaluation of biodiversity conservation investments. PLoS Biology 4(4):e105

Floors A (1997) Plantation forestry in Guanacaste, Costa Rica. Bib. Orton IICA/CATIE Costa Rica

Foley JA, Asner GP, Costa MH et al (2007) Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. Frontiers in Ecology and the Environment 5(1):25-32

FONAFIFO (2012) Cobertura forestal del pais alcanza el 52.38%. In: FONAFIFO (ed). MINAE, San Jose, Costa Rica, pp. 1-2

Forman RT (1995) Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge

Forman RT, Alexander LE (1998) Roads and their major ecological effects. Annual Review of Ecology and Systematics:207-C2

Forman RT, Deblinger RD (2000) The ecological road-effect zone of a Massachusetts (USA) suburban highway. Conservation Biology 14(1):36-46

Geist HJ, Lambin EF (2002) Proximate causes and underlying driving forces of tropical deforestation. BioScience 52(2):143-150

Gilbert-Norton L, Wilson R, Stevens JR, Beard KH (2010) A meta-analytic review of corridor effectiveness. Conservation Biology 24(3):660-668

Global Forest Loss. (2015) Tree cover loss. Global Forest Watch, Washington DC

Gloyne CC, Clevenger AP (2001) Cougar Puma concolor use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. Wildlife Biology 7(2):117-124

Gutiérrez D, Thomas CD, León-Cortés JL (1999) Dispersal, distribution, patch network and metapopulation dynamics of the dingy skipper butterfly (Erynnis tages). Oecologia 121(4):506-517

Hanski I, Hanski IA (1999) Metapopulation ecology. Oxford University Press, Oxford

Hartshorn G (1983) Plants, Costa Rican natural history DH Janzen, 118–157. University of Chicago Press, Chicago

Harvey CA (2000) Windbreaks enhance seed dispersal into agricultural landscapes in Monteverde, Costa Rica. Ecological Applications 10(1):155-173

Harvey CA, Komar O, Chazdon R et al (2008) Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. Conservation Biology 22(1):8-15

Herrera W (2011) La urgencia de la carretera a San Carlos. La Nacion. San Jose, Costa Rica

Hodgson JA, Moilanen A, Wintle BA, Thomas CD (2011) Habitat area, quality and connectivity: striking the balance for efficient conservation. Journal of Applied Ecology 48(1):148-152

Horner-Devine MC, Daily GC, Ehrlich PR, Boggs CL (2003) Countryside biogeography of tropical butterflies. Conservation Biology 17(1):168-177

Humphrey JW, Watts K, Fuentes-Montemayor E, Macgregor NA, Peace AJ, Park KJ (2015) What can studies of woodland fragmentation and creation tell us about ecological networks? A literature review and synthesis. Landscape Ecology 30(1):21-50

INBio (2015) Biodiversity in Cost Rica. Biodiversity of Costa Rica, Mammals, June 10, 2015. INBio, http://www2.inbio.ac.cr/en/biod/bio_biodiver.htm

Jain A, Chong KY, Chua MAH, Clements GR (2014) Moving away from paper corridors in Southeast Asia. Conservation Biology 28(4):889-891

Jauker F, Diekoetter T, Schwarzbach F, Wolters V (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecology 24(4):547-555

Kark S, Levin N, Grantham HS, Possingham HP (2009) Between-country collaboration and consideration of costs increase conservation planning efficiency in the Mediterranean Basin. Proceedings of the National Academy of Sciences 106(36):15368-15373

Kilpatrick AM, Gillin CM, Daszak P (2009) Wildlife–livestock conflict: the risk of pathogen transmission from bison to cattle outside Yellowstone National Park. Journal of Applied Ecology 46(2):476-485

Klein CJ, Steinback C, Watts M, Scholz AJ, Possingham HP (2009) Spatial marine zoning for fisheries and conservation. Frontiers in Ecology and the Environment 8(7):349-353

Kleist AM, Lancia RA, Doerr PD (2007) Using video surveillance to estimate wildlife use of a highway underpass. The Journal of Wildlife Management 71(8):2792-2800

Lawes MJ, Mealin PE, Piper SE (2000) Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented afromontane forest in South Africa. Conservation Biology 14(4):1088-1098

Levin N, Watson JE, Joseph LN et al (2013) A framework for systematic conservation planning and management of Mediterranean landscapes. Biological Conservation 158:371-383

Levin SA, Paine RT (1974) Disturbance, patch formation, and community structure. Proceedings of the National Academy of Sciences 71(7):2744-2747

Lindenmayer DB, Fischer J (2006) Habitat fragmentation and landscape change: an ecological and conservation synthesis. Island Press, Washington DC

Liu J, Dietz T, Carpenter SR et al (2007) Complexity of coupled human and natural systems. Science 317(5844):1513-1516

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. Nature 462(7276):1052-1055

Margules C, Sarkar S, Margules C (2007) Systematic conservation planning. Cambridge University Press, Cambridge

Marshall AJ (2010) Effect of habitat quality on primate populations in Kalimantan: Gibbons and leaf monkeys as case studies. Indonesian primates. Springer, New York, pp. 157-177

Mazor T, Possingham HP, Edelist D, Brokovich E, Kark S (2014) The crowded sea: incorporating multiple marine activities in conservation plans can significantly alter spatial priorities. PloS One 9.8:e104489

McGarigal K, Tagil S, Cushman SA (2009) Surface metrics: an alternative to patch metrics for the quantification of landscape structure. Landscape Ecology 24(3):433-450

McRae BH, Hall SA, Beier P, Theobald DM (2012) Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. PLoS One 7(12):e52604

McRae BH, Shah VB, Mohapatra TK (2013) Circuitscape 4 User Guide. The Nature Conservancy

Michalski F, Crawshaw PG, Oliveira TGd, Fabián ME (2006) Notes on home range and habitat use of three small carnivore species in a disturbed vegetation mosaic of southeastern Brazil/Notes sur le territoire et l'utilisation de l'habitat de trois espèces de petits carnivores dans une végétation mosaïque perturbée au Sud Est du Brésil. Mammalia 70(1-2):52-57

Michalski F, Peres CA (2005) Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. Biological Conservation 124(3):383-396

Miller K, Chang E, Johnson N (2001) Defining common ground for the Mesoamerican Biological Corridor. World Resources Institute Washington DC

MINAE (2006) Descreto 33106-MINAE. In: El Presidente de la Republica y el Ministro del Ambiente y Energia (ed). La Gaceta, Costa Rica

MINAE (2008) Reglamento a la ley de biodiversidad. In: Ministro del Ambiente y Energia (ed). Sistema Costarricense de Información Jurídica, Costa Rica

MINAE (2014) N° 38323-MINAE. In: Ministro del Ambiente y Energia (ed). La Gaceta, Costa Rica

Minor ES, Lookingbill TR (2010) A multiscale network analysis of protected-area connectivity for mammals in the United States. Conservation Biology 24(6):1549-1558

Miranda M, Porras IT, Moreno ML (2003) The social impacts of payments for environmental services in Costa Rica: a quantitative field survey and analysis of the Virilla watershed. IIED, Costa Rica

Monge-Arias G, Chassot O (2000) La lapa verde (Ara ambigua) a un paso de la extinción. Organization for Tropical Studies

Morse WC, Schedlbauer JL, Sesnie SE et al (2009) Consequences of environmental service payments for forest retention and recruitment in a Costa Rican biological corridor. Ecology and Society 14(1):23

Muñoz-Rojas J, Nijnik M, González-Puente M, Cortines-García F (2015) Synergies and conflicts in the use of policy and planning instruments for implementing forest and woodland corridors and networks; a case study in NE Scotland. Forest Policy and Economics 57:47-64

Murgueitio E, Calle Z, Uribe F, Calle A, Solorio B (2011) Native trees and shrubs for the productive rehabilitation of tropical cattle ranching lands. Forest Ecology and Management 261(10):1654-1663

Nagendra H, Lucas R, Honrado JP et al (2013) Remote sensing for conservation monitoring: Assessing protected areas, habitat extent, habitat condition, species diversity, and threats. Ecological Indicators 33:45-59

National System of Conservation Areas SINAC (2009) Five year strategic plan of the National Program of Biological Corridors Costa Rica 2009-2014. In: SINAC (ed). San José, Costa Rica, pp. 1-40

Nelson E, Mendoza G, Regetz J et al (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in Ecology and the Environment 7(1):4-11

Nhancale BA, Smith RJ (2011) The influence of planning unit characteristics on the efficiency and spatial pattern of systematic conservation planning assessments. Biodiversity and Conservation 20(8):1821-1835

Pagiola S (2008) Payments for environmental services in Costa Rica. Ecological Economics 65(4):712-724

Perfecto I, Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. Conservation Biology 16(1):174-182

Perfecto I, Vandermeer J (2010) The agroecological matrix as alternative to the land-sparing/agriculture intensification model. Proceedings of the National Academy of Sciences 107(13):5786-5791

Platt R, Platt L, Rapoza (2008) An evaluation of an object-oriented paradigm for land use/land cover classification. The Professional Geographer 60(1):87-100

Rabinowitz AR, Jr B (1986) Ecology and behaviour of the jaguar (Panthers onca) in Belize, Central America. Journal of Zoology 210(1):149-159

Reid FA (1998) A field guide to the mammals of Central America and southeast Mexico. Oxford University Press, USA

Reyers B, O'Farrell PJ, Nel JL, Wilson K (2012) Expanding the conservation toolbox: conservation planning of multifunctional landscapes. Landscape Ecology 27.8:1-14

Rodrigues AS, Brooks TM (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. Annual Review of Ecology, Evolution, and Systematics:713-737

Rodriguez-Solorzano C (2014) Unintended outcomes of farmers' adaptation to climate variability: deforestation and conservation in Calakmul and Maya biosphere reserves. Ecology and Society 19(2):53

Rouget M, Cowling RM, Lombard AT, Knight AT, Kerley GI (2006) Designing large-scale conservation corridors for pattern and process. Conservation Biology 20(2):549-561

Ryan KA (2012) Bellbird biological corridor water monitoring program: Objectives, current state, and future directions. University of Georgia, Costa Rica,

Sanchez-Azofeifa GA, Pfaff A, Robalino JA, Boomhower JP (2007) Costa Rica's payment for environmental services program: intention, implementation, and impact. Conservation Biology 21(5):1165-1173

Saura S, Bodin Ö, Fortin MJ (2014) Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. Journal of Applied Ecology 51(1):171-182

Schippers P, van der Heide CM, Koelewijn HP et al (2015) Landscape diversity enhances the resilience of populations, ecosystems and local economy in rural areas. Landscape Ecology 30(2):193-202

Sendero Pacifico (2016) Mountain stewards. http://mountainsteward.net/sendero/

Sierra R, Russman E (2006) On the efficiency of environmental service payments: a forest conservation assessment in the Osa Peninsula, Costa Rica. Ecological Economics 59(1):131-141

SINAC (2008) Corredores biologicos. June http://www.sinac.go.cr/corredoresbiologicos/boletines/2008/boletin200801.html

Soisalo MK, Cavalcanti SM (2006) Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. Biological Conservation 129(4):487-496

Spackman SC, Hughes JW (1995) Assessment of minimum stream corridor width for biological conservation: species richness and distribution along mid-order streams in Vermont, USA. Biological Conservation 71(3):325-332

Sunderlin WD, Larson AM, Cronkleton P (2009) Forest tenure rights and REDD. Realising REDD, Denmark

Tabarelli M, Aguiar AV, Ribeiro MC, Metzger JP, Peres CA (2010) Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human-modified landscapes. Biological Conservation 143(10):2328-2340

Tallis H, Polasky S (2009) Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. Annals of the New York Academy of Sciences 1162(1):265-283

Townsend PA, Masters KL (2015) Lattice-work corridors for climate change: a conceptual framework for biodiversity conservation and social-ecological resilience in a tropical elevational gradient. Ecology and Society 20(2):1

Trimble (2011) eCognition® Developer 9.1. Trimble Germany GmbH Munich, Germany

Vargas YE (2014) Ficha technica para la propuesta del corredor biologico Paso de las Nubes (CBPN) In: Sistema Nacional de Areas de Conservacion SINAC (ed). Online Report, pp. 1-45

Villate R, Canet-Desanti L, Chassot O, Monge-Arias G (2009) The San Juan-La Selva Biological Corridor: a successful conservation strategy. SINAC, Costa Rica, pp. 1-96

Watts M, Klein C, Stewart R, Ball I, Possingham H (2008) Marxan with zones (V1. 0.1): Conservation zoning using spatially explicit annealing, a manual. University of Queensland, Brisbane

Williams P, Hannah L, Andelman S et al (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape proteaceae. Conservation Biology 19(4):1063-1074

Wilson KA, Meijaard E, Drummond S et al (2010) Conserving biodiversity in production landscapes. Ecological Applications 20(6):1721-1732

Woodley S, Bertzky B, Crawhall N et al (2012) Meeting Aichi Target 11: what does success look like for protected area systems. Parks 18(1):23-36

Worboys G, Francis WL, Lockwood M (2010) Connectivity conservation management: a global guide (with particular reference to mountain connectivity conservation). Earthscan, New York

World Bank. (2015) Terrestrial protected areas. http://data.worldbank.org/indicator/ER.LND.PTLD.ZS

Wunder S (2005) Payments for environmental services: some nuts and bolts. CIFOR Jakarta, Indonesia

Wunder S (2007) The efficiency of payments for environmental services in tropical conservation. Conservation Biology 21(1):48-58

Wunder S, Albán M (2008) Decentralized payments for environmental services: the cases of Pimampiro and PROFAFOR in Ecuador. Ecological Economics 65(4):685-698

Wunscher T, Engel S, Wunder S (2006) Payments for environmental services in Costa Rica: increasing efficiency through spatial differentiation. Quarterly Journal of International Agriculture 45(4):319-338

Wünscher T, Engel S, Wunder S (2008) Spatial targeting of payments for environmental services: a tool for boosting conservation benefits. Ecological Economics 65(4):822-833

APPENDIX

MATERIALS

Table A1: Large and medium species of the region, names, IUCN status and guild (herbivore (H), omnivore (O), carnivore (C), insectivore (I), frugivore (f)

	Species name	Scientific name	IUCN (Global) (2014)	IUCN (National, InBio, 2014)	Guild
1	Mantled howler monkey	*Alouatta palliata*	LC	EN	H
2	Red brocket deer	*Mazama americana*	DD	-	H
3	White-tailed deer	*Odocoileus virginianus*	LC	-	H
4	Jaguarundi	*Puma yagouaroundi*	LC	EN	C
5	Puma	*Puma concolor*	LC	EN	C
6	Jaguar	*Panthera onca*	NT	EN	C
7	Cacomistle	*Bassariscus sumichrasti*	LC	EN	O
8	Olingo	*Bassaricyon gabbii*	LC	EN	F
9	Kinkajou	*Potos flavus*	LC	-	O
10	Oncilla	*Leopardus tigrinus*	VU	EN	C
11	Margay	*Leopardus wiedii*	NT	EN	C
12	Ocelot	*Leopardus pardalis*	LC	EN	C
13	Collared peccary	*Pecari tajacu*	LC	-	O
14	White-lipped peccary	*Tayassu pecari*	VU	EN	O
15	Baird's tapir	*Tapirus bairdii*	EN	EN	H
16	Central American agouti	*Dasyprocta punctata*	LC	-	H
17	Paca	*Cuniculus paca*	LC	-	H
18	Mexican porcupine	*Coendou mexicanus*	LC	-	H
19	Water opossum	*Chironectes minimus*	LC	-	C
20	Virginia opossum	*Didelphis virginiana*	LC	-	O
21	Common opossum	*Didelphis marsupialis*	LC	-	O
22	Long-tailed weasel	*Mustela frenata*	LC	-	C
23	Greater grison	*Galictis vittata*	LC	EN	C
24	Tayra	*Eira barbara*	LC	-	O
25	Three-toed sloth	*Bradypus variegatus*	LC	-	H
26	Two-toed sloth	*Choloepus hoffmanni*	LC	EN	H
27	Northern naked-tailed armadillo	*Cabassous centralis*	DD	T	I

28	Nine-banded armadillo	*Dasypus novemcinctus*	LC	-	I
29	White-faced capuchin	*Cebus capucinus*	LC	EN	O
30	Central American spider monkey	*Ateles geoffroyi*	EN	EN	F
31	Silky anteater	*Cyclopes didactylus*	LC	-	I
32	Northern tamandua	*Tamandua mexicana*	LC	-	I
33	Giant anteater	*Myrmecophaga tridactyla*	VU	EN- EX	I
34	Gray fox	*Urocyon cinereoargenteus*	LC	-	O
35	Coyote	*Canis latrans*	LC	-	O
36	Northern raccoon	*Procyon lotor*	LC	-	O
37	Crab-eating raccoon	*Procyon cancrivorus*	LC	-	O
38	White-nosed coati	Nasua narica	LC	-	O

Table A2. Parameterization of cost surfaces. Each weight, transformed to the scale of 1-10, with 1 being most favorable for conductance, and 10 being least favorable for electrical conductance.

Slope Category (degrees)	Weight	Road Category (road size)	Weight	Land use Category (class)	Weight
0-40	1	Primary	8	Forest	1
40-60	5	Secondary	6	Cloud	1
60-80	8	Tertiary	4	Water	2
80-90	9	Quaternary	3	Low vegetation	5
				Pasture	7
				Bare	9
				Urban	10

Table A3: Species lists for camera traps placed in PES forest protection, reforestation, and protected areas. Species with a star were sighted during camera and hair trap set up.

	Forest Protection (PES)	Reforestation (PES)	Protected Areas
1	*Allouata palliata**	*Allouata palliata**	*Allouata palliata**
2	*Canis latrans*	*Bradypus variegatus**	*Bradypus variegatus**
3	*Cebus capucinus*	*Canis latrans*	*Cebus capucinus*
4	*Conepatus semistriatus*	*Cebus capucinus*	*Cuniculus paca*
5	*Cuniculus paca*	*Conepatus semistriatus*	*Dasyprocta punctata*
6	*Dasyprocta punctata*	*Cuniculus paca*	*Dasypus novemcinctus*
7	*Dasypus novemcinctus*	*Dasyprocta punctata*	*Eira barbara*
8	*Eira barbara*	*Dasypus novemcinctus*	*Leopardus pardalis*
9	*Leopardus pardalis*	*Eira barbara*	*Leopardus Wiedii*
10	*Leopardus Wiedii*	*Leopardus Pardalis*	*Nasua narica*
11	*Nasua narica*	*Nasua narica*	*Pecari tajacu*
12	*Pecari tajacu*	*Pecari tajacu*	*Puma concolor*
13	*Philander opossum*	*Philander opossum*	*Sciurus variegatoides*
14	*Procyon lotor*	*Procyon lotor*	*Sylvilagus brasiliensis*
15	*Puma concolor*	*Sciurus granatensis*	*Tamandua mexicana*
16	*Sciurus granatensis*	*Sylvilagus brasiliensis/dicei*	
17	*Sylvilagus brasiliensis/dicei*		
18	*Syntheosciurus mimulus*		
19	*Tamandua mexicana*		

Table A4: Species list of selected medium and large mammals indicated as present on their property by the interviewee.

	Forest Protection (PES)	**Reforestation (PES)**
1	*Tapirus bairdii*	*Dasyprocta punctata*
2	*Bassariscus sumichristi*	*Pecari tajacu*
3	*Dasyprocta punctata*	*Didelphis virginiana*
4	*Ateles geoffroyi*	*Canis latrans*
5	*Pecari tajacu*	*Galictis vittata*
6	*Didelphis marsupialis*	*Poto flavus*
7	*Canis latrans*	*Allouatta palliate*
8	*Procyon cancrivorus*	*Leopardus wiedii*
9	*Myrmecophaga tridactyla*	*Coendou mexicanus*
10	*Urocyon cinereoargenteus*	*Dasypus novemcinctus*
11	*Galictis vittata*	*Cabassous centralis*
12	*Panthera onca*	*Procyon lotor*
13	*Puma yagouaroundi*	*Tamandua mexicana*
14	*Potos flavus*	*Cuniculus paca*
15	*Leopardus wiedii*	*Bradypus variegatus*
16	*Dasypus novemcinctus*	*Choloepus hoffmannii*
17	*Coendou mexicanus*	*Nasua narica*
18	*Cabassous centralis*	
19	*Procyon lotor*	
20	*Allouatta palliata*	
21	*Tamandua mexicana*	
22	*Leopardus pardalis*	
23	*Bassaricyon gabbii*	
24	*Leopardus tigrinus*	
25	*Cuniculus paca*	
26	*Puma concolor*	
27	*Mazama americana*	
28	*Eira barbara*	
29	*Bradypus variegatus*	
30	*Choloepus hoffmannii*	
31	*Didelphis vriginiana*	
32	*Cebus capucinus*	
33	*Nasua narica*	
34	*Odocoileus virginianus*	

Figure A1: Electrical connectivity using Circuitscape models across the Paso de las Nubes biological corridor. The scale to the left: white represents areas with below 50% connectivity, red representing the highest level of connection density, and green at 50% connectivity density. Map E: slope higher importance connectivity map; Map F: roads higher importance connectivity map.