CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Forestry and Wood Sciences

Diploma Thesis Title:

SPATIAL ASSESSMENT OF LAND USE CHANGE PATTERNS AND THEIR IMPACT ON WILDLIFE HABITAT IN TROPICAL FORESTS

This Diploma Thesis has been written and defended at Cranfield University in the United Kingdom under the Double Degree Agreement between the Czech University of Life Sciences Prague, and Cranfield University. In accordance with the Double Degree Agreement, this Diploma Thesis is fully recognized as part of the MSc programme study at the Czech University of Life Sciences Prague.

Diploma Thesis Author: Miriam Zemanová

Diploma Thesis Supervisor: Humberto Perotto-Baldivieso

Diploma Thesis Co-Supervisor: Miroslav Svoboda

GRADE: 74% (ECTS A)

Česká zemědělská univerzita v Praze
Katedra: Pěstování lesů

Fakulta lesnická a dřevařská
Akademický rok: 2010/2011

ZADÁNÍ DIPLOMOVÉ PRÁCE
(PROJEKTU, UMĚLECKÉHO DÍLA, UMĚLECKÉHO VÝKONU)

pro: **Miriam A. Zemanová**
obor: **Forestry, Water and Landscape Management**

Název tématu:

SPATIAL ASSESSMENT OF LAND USE CHANGE PATTERNS AND THEIR IMPACT ON WILDLIFE HABITAT IN TROPICAL FORESTS

Zásady pro vypracování:

This study builds on previous research in the Bolivian lowlands, where significant anthropogenic disturbance has taken place as a result of different social and economic conditions, especially in the last 35 years The overall goal is to gain a better understanding of the impacts of anthropogenic disturbance patterns on landscape structure and connectivity in a tropical forest. The specific objectives of this research are: (1) to understand the impacts of anthropogenic disturbance patterns on landscape structure in the study area; (2) to assess the influence of anthropogenic disturbance on habitat connectivity for wildlife, using an endangered species – jaguar (*Panthera onca*) – as a model organism.

Rozsah grafických prací: **cca 5 stran**

Rozsah průvodní zprávy: **cca 50-60 stran**

Seznam odborné literatury:

Killeen TJ, Calderon V, Soria L et al (2007) Thirty years of land-cover change in Bolivia. Ambio 36 (7):600-606
Millington AC, Velez-Liendo XM, Bradley AV (2003) Scale dependence in multitemporal mapping of forest fragmentation in Bolivia: Implications for explaining temporal trends in landscape ecology and applications to biodiversity conservation. ISPRS J Photogramm 57(4):289-299
Mertens B, Kaimowitz D, Puntodewo A et al (2004) Modeling deforestation at distinct geographic scales and time periods in Santa Cruz, Bolivia. Int Regional Sci Rev 27(3):271-296
Steininger MK, Tucker CJ, Ersts P et al (2001) Clearance and fragmentation of tropical deciduous forest in the Tierras Bajas, Santa Cruz, Bolivia. Conserv Biol 15(4):856-866
Steininger MK, Tucker CJ, Townshend JRG et al (2001) Tropical deforestation in the Bolivian Amazon. Environ Conserv 28(2):127-134

Vedoucí diplomové práce: **doc. Ing. Miroslav Svoboda, Ph.D.**

Konzultant diplomové práce: **Dr Humberto Perotto-Baldivieso (Cranfield University, UK)**

Datum zadání diplomové práce:

Termín odevzdání diplomové práce:

ČESKÁ ZEMĚDĚLSKÁ UNIVERZITA V PRAZE • FAKULTA LESNICKÁ A DŘEVAŘSKÁ •

L.S.

....
Vedoucí katedry

....
Děkan

V Praze dne 5. 10. 2010

Prohlášení

Prohlašuji, že jsem bakalářskou práci na téma „SPATIAL ASSESSMENT OF LAND USE CHANGE PATTERNS AND THEIR IMPACT ON WILDLIFE HABITAT IN TROPICAL FORESTS“ vypracovala samostatně s použitím odborné literatury uvedené v seznamu, který je součástí této práce.

CRANFIELD UNIVERSITY

MIRIAM A ZEMANOVA

SPATIAL ASSESSMENT OF LAND USE CHANGE PATTERNS AND THEIR IMPACT ON WILDLIFE HABITAT IN TROPICAL FORESTS

SCHOOL OF APPLIED SCIENCES

Ecological Conservation (Land Management)

MSc THESIS

Academic year: 2009-2010

Supervisors: ***Humberto Perotto-Baldivieso***

Miroslav Svoboda

September 2010

CRANFIELD UNIVERSITY

SCHOOL OF APPLIED SCIENCES
Ecological Conservation (Land Management)

MSc THESIS

Academic Year 2009-2010

Miriam A ZEMANOVA

SPATIAL ASSESSMENT OF LAND USE CHANGE PATTERNS AND THEIR IMPACT ON WILDLIFE HABITAT IN TROPICAL FORESTS

Supervisors: Humberto Perotto-Baldivieso
Miroslav Svoboda

September 2010

This thesis is submitted in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Habitat loss and fragmentation, caused by deforestation, are considered major threats to biodiversity. In Bolivian tropical forests, different deforestation patterns have evolved due to diverse economic and social drivers. This study aimed to provide a better understanding of the impact of these patterns on habitat fragmentation and connectivity. Classified Landsat imagery was used for the period 1975-2005. Five separate study areas were determined based on their land use history and fragmentation patterns. Vegetation spatial structure was assessed with selected landscape metrics. Since fragmentation impacts differ among species, an emblematic species, jaguar (*Panthera onca*), was selected as a model organism to determine landscape connectivity. The analyses showed a decrease in the amount of natural vegetation and changes in its spatial distribution, with significant alterations for most landscapes in 1991. Connectivity for jaguar declined radically after the year 1991 in all study areas. Although the amount of natural vegetation in 2000 was on average > 35 % in most of the study areas, connectivity values were extremely low (< 0.2). Landscape metrics effectively depicted habitat fragmentation within and among the study areas, but they were not able to fully explain its impact on wildlife habitat. Conservation plans need to incorporate connectivity analyses for multiple species, while combining patch structure and function to study functional connectivity of the landscape.

ACKNOWLEDGEMENTS

I would like to express the deepest appreciation to my supervisors, Humberto Perotto-Baldivieso and Miroslav Svoboda, for whose encouragement, guidance and support I am heartily thankful.

Special thanks are due to Museo Nacional de Historia Natural Noel Kempff Mercado for provision of the satellite imagery.

I would also like to offer my regards and blessings to those who helped me and supported me, my family and friends, and to all the wonderful people – both among fellow students and university staff – I had the pleasure of meeting during my studies at Cranfield.

And I would especially like to thank my father, who never stopped believing in me.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

NOTATION

This thesis has been prepared in the format used for scientific papers appearing in the journal Landscape Ecology. Additional information is available in the Appendices and the paper includes an extended literature review.

SPATIAL ASSESSMENT OF LAND USE CHANGE PATTERNS AND THEIR IMPACT ON WILDLIFE HABITAT IN TROPICAL FORESTS

Miriam A. Zemanova[1,2] & **Humberto Perotto-Baldivieso**[1]

[1] *School of Applied Sciences, Cranfield University, MK43 0AL Bedfordshire, UK*

[2] *Czech University of Life Sciences Prague, Kamycka 129, 165 21 Prague 6, Czech Republic*

ABSTRACT

Habitat loss and fragmentation, caused by deforestation, are considered major threats to biodiversity. In Bolivian tropical forests, different deforestation patterns have evolved due to diverse economic and social drivers. This study aimed to provide a better understanding of the impact of these patterns on habitat fragmentation and connectivity. Classified Landsat imagery was used for the period 1975-2005. Five separate study areas were determined based on their land use history and fragmentation patterns. Vegetation spatial structure was assessed with selected landscape metrics. Since fragmentation impacts differ among species, an emblematic species, jaguar (*Panthera onca*), was selected as a model organism to determine landscape connectivity. The analyses showed a decrease in the amount of natural vegetation and changes in its spatial distribution, with significant alterations for most landscapes in 1991. Connectivity for jaguar declined radically after the year 1991 in all study areas. Although the amount of natural vegetation in 2000 was on average > 35 % in most of the study areas, connectivity values were extremely low (< 0.2). Landscape metrics effectively depicted habitat fragmentation within and among the study areas, but they were not able to fully explain its impact on wildlife habitat. Conservation plans need to incorporate connectivity analyses for multiple species, while combining patch structure and function to study functional connectivity of the landscape.

Keywords: habitat fragmentation, deforestation, Bolivian lowlands, landscape metrics, connectivity

1. INTRODUCTION

Since the adoption of the Convention on Biological Diversity in 1992 (Secretariat of the Convention on Biological Diversity 2005), biodiversity loss has been widely acknowledged as a significant global problem, as the changes in biodiversity might modify ecosystem functions and services (Naeem et al 1994; Chapin III et al 2000; MEA 2005). The main causes of changes in biodiversity are disturbance, fragmentation and destruction of habitat (Spangenberg 2007).

Ecological implications of already severe impacts of habitat loss might be aggravated by the spatial arrangement of remaining habitat. The process of land use change where the whole habitat is broken into smaller pieces is called habitat fragmentation (Ewers and Didham 2006; Hilty et al 2006). There are still many uncertainties surrounding this phenomenon, especially in tropical environments. Our research focused on fragmentation processes in tropical forests.

This study built on previous research in the Bolivian lowlands, where significant anthropogenic disturbance has taken place as a result of different social and economic conditions, especially in the last 35 years (e.g. Steininger et al 2001a,b; Millington et al 2003; Mertens et al 2004; Killeen et al 2007). The overall goal was to gain a better understanding of the impacts of anthropogenic disturbance patterns on landscape structure and connectivity in a tropical forest. The specific objectives of this research were: (1) to understand the impacts of anthropogenic disturbance patterns on landscape structure in the study area; (2) to assess the influence of anthropogenic disturbance on habitat connectivity for wildlife, using an endangered species – jaguar (*Panthera onca*) – as a model organism.

2. LITERATURE REVIEW

Fragmentation is considered the central issue of concern in conservation biology (Wiens 1996; Meffe and Carroll 1997). There are several aspects to fragmentation processes and their effects, and this literature review attempted to summarise some of them. It was divided into three sections: 1) impacts of deforestation in tropical forests as an important example of habitat fragmentation; 2) fragmentation processes and their influence on landscape structure, species abundance, richness and dispersal, and its connection to climate change; and 3) analysis of landscape pattern.

2.1 Deforestation

Deforestation is defined as a change that leads to the long-term or permanent loss of forest cover and it implies transformation into another land use (FAO 2001). Deforestation is a disturbance process that has been present for a long time, but its rate has increased significantly during the last two hundred years, particularly since the 1950's (Williams 2000; Shvidenko 2008). Deforestation is the most pervasive type of habitat destruction, both in temperate and tropical forests. Temperate forests in developed countries were already strongly affected centuries ago (Kaplan et al 2009). The main attention regarding deforestation is nowadays focused on tropical rainforest, a terrestrial biome considered to hold the highest biodiversity (Adam 1998). In most tropical countries more than a half of the habitat has already been lost through deforestation. The highest net loss of forest occurs in Africa and South America (Townsend et al 2003; FAO 2010).

Deforestation might be caused naturally and/or by human activities, which differ in severity, duration, extent and the drivers behind them (Boahene 1998; Peres et al 2010). Natural deforestation may occur through fire, drought, volcanic activity or hurricanes. Periodic droughts leading to higher occurrence of wildfire in Asian and American tropical rainforests are caused by El Niño Southern Oscillation, and its effects might be even more pronounced under climate change (Mason 2001; Malhi and Wright 2005). Anthropogenic activity is however the leading cause of deforestation. Millions of people live in tropical forests or in their vicinity, and depend on them for food, fuel and income (Chomitz et al 2007). Forests are being cut in order to supply the demand for timber and crop production, mineral extraction and/or urban development. The main cause of tropical deforestation is the expansion of agricultural land and pastures (Geist and Lambin 2001; Freitas et al 2010). Agricultural productivity in developing countries is usually low, due to the limited availability of inputs, thus creating even more pressure on land cover conversion (Barbier 2004). In Latin America, deforestation has been correlated with cattle density (Bawa and Dayanandan 1997). Cattle ranching was primarily promoted by government incentives and it is now sustained by economic as well as social pressures (Andersen 2002). While the population growth and economic development leading to a higher demand for land were identified as the main forces behind deforestation, population dynamics cannot explain all the drivers behind this process (Graigner 1993; Sloan 2007). In the today's globalised world landscape change is also driven by economy and international markets, as well as political forces and technology (Bürgi et al 2005).

Deforestation has a significant impact at the landscape scale. Species habitat, soil fertility, hydrological regime and water quality are negatively affected by deforestation processes (Dudley et al 2006). The extensive use of slash-and-burn practices leads to the loss of nutrients, organic matter in the fire, and regeneration ability of fallow (Börner et al 2007). Negative impacts on species richness have also been reported (e.g. Miller and Kauffman 1998; Barlow et al 2006).

Climate data from deforested areas in the Amazon region suggest that after forests have been cleared, lower rates in evapotranspiration, increase in maximum daily temperature, and decrease in long-term rainfall amount occur. These changes may be abrupt and not easily predictable (Laurance and Williamson 2001; Laurance et al 2002; Bounoua et al 2004). Deforested areas are also more prone to drought damage (Laurance and Williamson 2001), increased mercury levels in aquatic systems (Roulet et al 2000), and spread of malaria (Guerra et al 2006).

2.2 Habitat fragmentation

2.2.1 Impact on landscape structure

When deforestation occurs, the spatial structure of vegetation cover is transformed into separate patches, causing habitat fragmentation. This process is dynamic and depends on scale (Farina 2000). Important characteristics of a patch are its size, shape and position in the landscape (Franklin and Forman 1987; Saunders et al 1991). Ecological and functional characteristics of patches are determined primarily by their size and shape (Botequilha Leitão et al 2006), but Raheem et al (2009) reported that age of the patch also plays a significant role. When habitat is fragmented into different land uses, the fluxes of radiation, wind, water and nutrients in the landscape change significantly; the impact of external factors becomes greater with the decreasing size of a patch (Saunders et al 1991).

Habitat fragments also have artificial boundaries associated with so called edge effects, which change the ecosystem's structure, composition, dynamics and microclimate (Laurance 2008). Their effect is species-specific and depends on the orientation of edges to biotic and abiotic flows, as well as on adjacent land use (López-Barrera et al 2007). Significant role also play the properties of an edge – its form, width and shape (Opdam and Wiens 2002). In some cases, edge effects will provide new opportunities for certain species, in others they may increase nest predation, and lead to loss of core habitats and connectivity (Arango-Vélez and Kattan 1997; Maczulak 2010).

Impact of fragmentation on ecological processes and functions in tropical rainforests depends on the pattern of deforestation (Zipperer 1993; Rudel and Roper 1997). Several patterns can be distinguished (geometric, corridor, fishbone, diffuse, patchy and island) that are specific for certain deforestation processes (Geist and Lambin 2001). These patterns might be associated with socio-economic features and settlement schemes (Lorena and Lambin 2009), as is the case in this study.

2.2.2 Impact on habitat suitability, species abundance and richness

While landscape heterogeneity is valuable for species that need more than one type of habitat, it also represents reduction of a suitable habitat for a species with specific requirements (Fahrig and Nuttle 2006). Loss of habitat means decline in carrying capacity (i.e. number of species that can be supported in a given environment). The smaller the carrying capacity, the higher the extinction risk for organisms inhabiting it

(Ranta et al 2006). However, reduction in the patch size alone may not affect population density; this depends also on other factors, such as edge effects or dispersal behaviour (Bowman et al 2002). While Fahrig (1997) stated that habitat loss is more detrimental for a species than habitat fragmentation in the sense of extinction risk, habitat fragmentation is also a very significant factor affecting the population survival (Fahrig 2001). Small fragments may not provide sufficient territory for an organism, they lack the inner variety, and they also affect the ecological relationships within and among them (Sandwith and Lockwood 2006). Modification of landscape composition can alter species interactions, such as predation, mutualism, parasitism, or competition (Lindenmayer and Fischer 2006). When a native plant or animal is lost from a certain area, the place is open to invasion of exotic species (Collinge 1996).

The theory of island biogeography (MacArthur and Wilson 1967) has been used as a framework for explaining the effects of habitat fragmentation on species richness. Habitat patches in a landscape are considered as theoretical islands of suitable habitat in the sea of inhospitable surroundings. For instance, a forested landscape after fragmentation consists of habitat "islands" in a matrix of open land types (Johnson and Patil 2006). But this concept might be in some instances too simplistic and inaccurate (Laurance 2008). Some species may even prosper in disturbed habitats (Pimm 1998). Despite several criticisms of the island biogeography theory, it has been an important part in the field of conservation biology, emphasising the effects of size and isolation of habitat patches (Turner et al 2001; Haila 2002).

Habitat fragmentation has been shown to affect the genetic diversity of a population of animals (Gibbs 2001; Telles et al 2007; Craul et al 2009; Dixo et al 2009) as well as plants (Raijmann et al 1994; Lienert 2004). The impacts differ among species.

Impediments caused by fragmentation are more pronounced in the case of species that require a larger amount of specific habitat (Spangenberg 2007), while species that are able to utilise more than one habitat type (i.e. habitat generalists) would be less affected by habitat loss and fragmentation. Species that live in naturally homogeneous ecosystems such as rainforests are less adapted to dealing with landscape discontinuity caused by fragmentation (Opdam and Wiens 2002). Haskell et al (2002) predicted that large species are more sensitive to this process, because they generally have greater requirements for the home range size. Large carnivores are especially vulnerable, since they usually prey on animals with low density and they might not be able to compensate for losses in prey availability. The impact on a population would depend not only on the isolation and size of habitat patches, but to some extent also on the suitability of the adjacent land use (Andrén 1994; Prevedello and Vieira 2010). Collinge (2009) summarised that other factors affecting biodiversity and abundance of a species are habitat quality, age of the fragment, edge effects, and interaction among fragments.

Studies on fragmentation conducted in Amazonian rainforests showed that fragments are inhabited by less species than intact forests (Hilty et al 2006). However, the responses to forest loss are specific for species and guilds (Fredericksen and Fredericksen 2002), and using merely a few selected organisms as indicators might be misleading (Lawton et al 1998). For example Gascon et al (1999) presented the results of a long-term research conducted in central Amazonia, where birds and ants species showed a decrease in the biodiversity, while only a few species of small mammals and frogs seemed to be affected by forest fragmentation. Study by Bell and Donnelly (2006) in Costa Rica reported higher density of lizard species and lower densities of frogs in fragments when compared to intact forests. Gomes et al (2008) showed that also bird species respond to deforestation in a different way, depending on their habitat preferences; species avoiding forest would have the highest incidence in disturbed habitats. Forest fragmentation in Mexico was determined as the main factor leading to local extinction of medium- and large-sized mammals (Chhabra et al 2006). The abundance of dung beetles, which are important for disease control, has also been reported to be negatively correlated with the tropical forest fragmentation (Farina 2000; Nichols et al 2007; Gardner et al 2008). Some groups of bees are sensitive to tropical forest fragmentation as well (Brosi et al 2008).

Specific for a rainforest is that many trees are adapted to growing in large groups, where changes in microclimatic conditions are minimised due to the dense canopy. This protection is lost when forests become fragmented (Laurance et al 1998). Fragmentation is especially detrimental to large trees, since they are more sensitive to the effects of newly created forest edges – increase in wind velocity, parasite occurrence and drought (Laurance et al 2000). Large patches of intact rainforest (over 300 ha) are also vital for sustaining high biodiversity of epiphytes (Alvarenga et al 2010).

2.2.3 Impact on species dispersal

Landscape connectivity (also known as landscape permeability) determines to what extent organisms are able to move through the landscape (Suter et al 2007). It has received a growing interest from landscape managers and conservation planners (Pascual-Hortal and Saura 2006). Fragmentation essentially means the loss of connectivity. There can be distinguished two general types of landscape connectivity – structural and functional; structural connectivity depicts only the physical relationship among fragments and does not consider the response in an organism's behaviour to landscape structure (Taylor et al 2006).

Fragmentation inhibits migration between patches, thus affecting the gene flow within a population and making the species more vulnerable to extinction risks (Vandermeer and Lin 2008). When migration is limited, the population might suffer from genetic drift and inbreeding depression, especially when the number of individuals is small (Hewitt and Nichols 2005; Rockwood 2006). Some species show differences in dispersal between sexes, potentially leading to patches with populations that are not able to reproduce (Lindenmayer and Fischer 2006). That is why connectivity between patches of suitable habitat is so crucial, and it is used as a measure of landscape structure and impacts of land use change (Taylor et al 1993; Goodwin and Fahrig 2002).

In order to predict the organism's susceptibility to extinction due to fragmentation, it is important to know its rates of movement in the landscape (Fahrig 2001). Less mobile species would be affected by the reduction of connectivity more significantly (D'Eon et al 2002). Animals also tend to move faster in areas they are not familiar with in order to minimise mortality risk (Knowlton and Graham 2010). The migration rate of a species largely depends on landscape characteristics, such as spatial arrangement of habitat patches and their suitability, as well as the matrix surrounding them (Collingham and Huntley 2000; Ricketts 2001). Theodorou et al (2009) reported that a larger range of species dispersal rates can be found in landscapes with different sizes of patches; especially valuable for metapopulation dynamics are large patches. As the habitat patches get smaller, the distances between them grow and the probability of migration decreases (Suter et al 2007). In 2007, Walters suggested dividing organisms into two groups: short- and long-ranging dispersers, both of which are affected by the landscape pattern and gradients in a different way, and conservation plans should conform to their needs.

Fragmentation and landscape characteristics do not only affect the dispersal of animals – plants are affected as well (Sork and Smouse 2006). Fragmentation impacts might be particularly severe for tree species that occur more scarcely and are often dependent on animals for dispersal (Young et al 1996; Cramer et al 2007).

2.2.4 Effect of climate change

The term climate change is used by the IPCC for referring to "any change in climate over time, whether due to natural variability or as a result of human activity" (Solomon et al 2007). Malcolm et al (2002) predicted that global warming may require species to migrate faster in the landscape in order to adapt to its impacts. This would be a disadvantage to less mobile species, leading to a certain loss in biodiversity (Honnay et al 2002).

Under the changing climate species will be forced to find new suitable habitats. These shifts in species range have already been observed (Hannah et al 2005). According to Opdam and Wascher (2004), alterations of species range due to climate change might be exacerbated by landscape fragmentation. These constraints could potentially lead to species extinction (McLaughlin et al 2002). Adaptation measures are therefore of high importance, especially for the management of existing protected areas and land use surrounding them (Hannah et al 2002), as well as for designing new reserves (Araújo et al 2004; Higgins 2007).

Since climate change is usually mentioned in the context of carbon dioxide emissions (e.g. Gerlagh and van der Zwaan 2006; Solomon et al 2009), a significant part of mitigation strategies is land reforestation. The second highest carbon stock in vegetation and soil is in tropical forests (after boreal forests) with an average annual uptake of 4 to 8 tonnes of carbon per hectare (IPCC 2000). Intact forests in the Amazon serve as a major carbon sinks, and they lower the rise of atmospheric CO_2 levels (Laurance 1998), although there are some regional and temporal differences (Pimm 1998). Deforestation on the other hand leads to the release of carbon into the atmosphere (Malhi et al 2008). Gullison et al (2007) calculated that deforestation in the tropics during the 1990's was responsible for releasing approximately 1.5 billion metric tons of carbon to the atmosphere every year. The United Nations Framework Convention on Climate Change proposed the introduction of financial incentives to reduce emissions from deforestation and forest degradation (REDD) in developing countries; however, there are some concerns regarding this concept (Miles and Kapos 2008). Venter et al (2009) recommended that these carbon payments should include biodiversity values in order to increase the momentarily low benefits of this scheme for biodiversity.

2.2.5 Summary

Debinski and Holt (2000) summarised that most studies on habitat fragmentation dealt with the impact on species richness, abundance of species, interspecific interactions, movement of individuals, and ecosystem services.

The impacts of fragmentation might be difficult to predict, sometimes the effect could be even positive (Fahrig 2003). The response differs among species, and even the same species may be affected in a different way, namely according to the season (Farina 2000). Species-specific studies are therefore crucial (Fahrig 2003). Also, since ecosystems and habitat fragmentation effects are complex and intricate, models trying to predict the impacts on populations might not reflect reality (Wiegand et al 2005). Species usually do not respond to habitat loss immediately, but with a certain lag (Chomitz et al 2007), and the effect might not be directly evident. Habitat fragmentation caused by human activities is a relatively new phenomenon in the evolution history, and its long-term impacts may have not yet been revealed (Ewers and Didham 2006). There are still many unanswered questions about fragmentation, especially about its effects at the landscape level (McGarigal and Cushman 2002), and further research is needed.

2.3 Landscape pattern analysis

Patterns in the landscape can be characterised by landscape metrics (or indices), whose advantage is that they are usually very easy to calculate (Lindenmayer and Fischer 2006; Bolliger et al 2007). Landscape metrics could be used to determine patch properties, such as area, shape, boundary characteristics, and contrast between neighbouring patches (Fortin and Dale 2005). There are three basic levels at which metrics might be calculated: 1) patch level – computed for every patch, 2) class level – for every type or class of patches, and 3) landscape level – for the whole assortment of patches (UMASS 2000).

Commonly used landscape metrics are mean patch size, patch shape index, patch and edge density, and mean Euclidian nearest neighbour distance; equations for their calculation are provided in McGarigal and Marks (1995). Mean patch size is "the arithmetic average size of each patch on the landscape or each patch of a given cover type" (Cardille and Turner 2002). Patch density expresses the number of patches on a per unit area basis and it depicts the subdivision of large patches into smaller ones in the process of fragmentation (Botequilha Leitão et al 2006). Edge density describes edge length of a patch type standardised to a per unit area basis (McGarigal and Marks 1995). Mean Euclidian nearest neighbour distance provides information on the average edge-to-edge distance between nearest patches of the same type; for comparison among landscapes similar extent and known grain are required (Hargis et al 1998). Since fragmentation leads to the reduction in patch size, increased number of patches, and changes in the distances among them, these metrics can be used as measures of habitat fragmentation (McGarigal and Marks 1995).

Although landscape metrics are a very powerful tool for assessing the fragmentation process, there are also several issues one needs to be aware of when analysing the landscape. First, the patch considered in an analysis is defined as "a spatially homogeneous area where at least one variable has similar attributes" (Fortin and Dale 2005). This approach might be easier for the researcher but it is quite simplistic and does not exactly reflect the reality (Mitchell and Powell 2003). Landscape indices usually fail to depict certain factors that are important for biodiversity and abundance, such as the vertical complexity of vegetation cover (Lindenmayer and Fischer 2006).

Second, the probably most important factor in the landscape pattern analysis is that it should be ecologically relevant. The results should be assessed in the context of ecological processes within and among landscape structures (Li and Wu 2004, 2007). However, landscape metrics might not be easy to interpret in relation to ecological processes and they should be denoted as “comparative measures of landscape condition” (Botequilha Leitão et al 2006), rather than absolute measures. The understanding of what an index quantifies in correlation with the considered process is therefore of great importance (Gustafson 1998). Choosing the right evaluation method for a specific study and objective is crucial, and also the interpretation of results might be difficult (Li and Wu 2007).

Finally, most landscape metrics quantify several components of spatial patterns, and the effectiveness of landscape metrics is still not fully understood (Peng et al 2010). For example, there have been proposed many graph-based indices of connectivity, but there is uncertainty about their sensitivity and behaviour, which constrains their interpretation and utility (Pascual-Hortal and Saura 2006). Many metrics are also correlated (Riitters et al 1995), leading to the same or at least similar results, making them redundant in a specific analysis. Furthermore, different measures of landscape connectivity have been shown to provide different values for the same landscape (Goodwin and Fahrig 2002).

Since the ability of a species to move in the landscape is affected by the maximum distance between connected islands of habitat, connectivity and its quantification depend on scale (Johnson and Patil 2006). There is no perfect scale or resolution that can be applied universally, thus it is vital to understand the spatial dependency of biological processes when using landscape metrics (Bissonette 2003). The scale issue might be also problematic in comparing landscape analysis results from different sources with different scale (Turner et al 1989; Saura 2002).

Cushman et al (2008) recommended using a minimum of independent metrics that are able to quantify the specified landscape structure. It is important to select the appropriate subset of landscape measurements for a particular study and questions being asked (De Clercq et al 2006; Johnson and Patil 2006).

3. METHODS

3.1 Study area

Bolivia is located in the central part of South America (Fig. 1). Its topography ranging from the Andes mountains to the lowlands in Amazonia contributes to exceptionally high biodiversity (Ibisch 2005; USAID / Bolivia 2008). The majority of forest can be found in the lowland regions with elevation below 500 m above the sea level, which cover over two thirds of the country's area (Mertens et al 2004; Pacheco 2006). The western part of Santa Cruz and the lowlands of Cochabamba departments are regions particularly strongly affected by anthropogenic activities. Soils in the area are generally of high quality making them suitable for agricultural purposes, but their characteristics also mean vulnerability to degradation (Hecht 2005). Favourable climatic conditions, with rainfall of 900 to 1,400 mm per year, allow two types of crop to be grown annually (Barber et al 1996). Majority of agricultural products in Bolivia come from the lowlands in Santa Cruz department (Hecht 2005).

There are five very distinctive areas of deforestation (study areas – SAs) in the Bolivian tropical lowlands defined by their natural and social dynamics (Fig. 1; Mertens et al 2004):

<u>Chapare (SA 1)</u>

The Chapare area is located in the departments of Cochabamba and Santa Cruz. This region was settled by indigenous Andean colonists driven mainly by coca production, agriculture, timber harvesting and hydrocarbon extraction (Millington et al 2003; Bradley and Millington 2008).

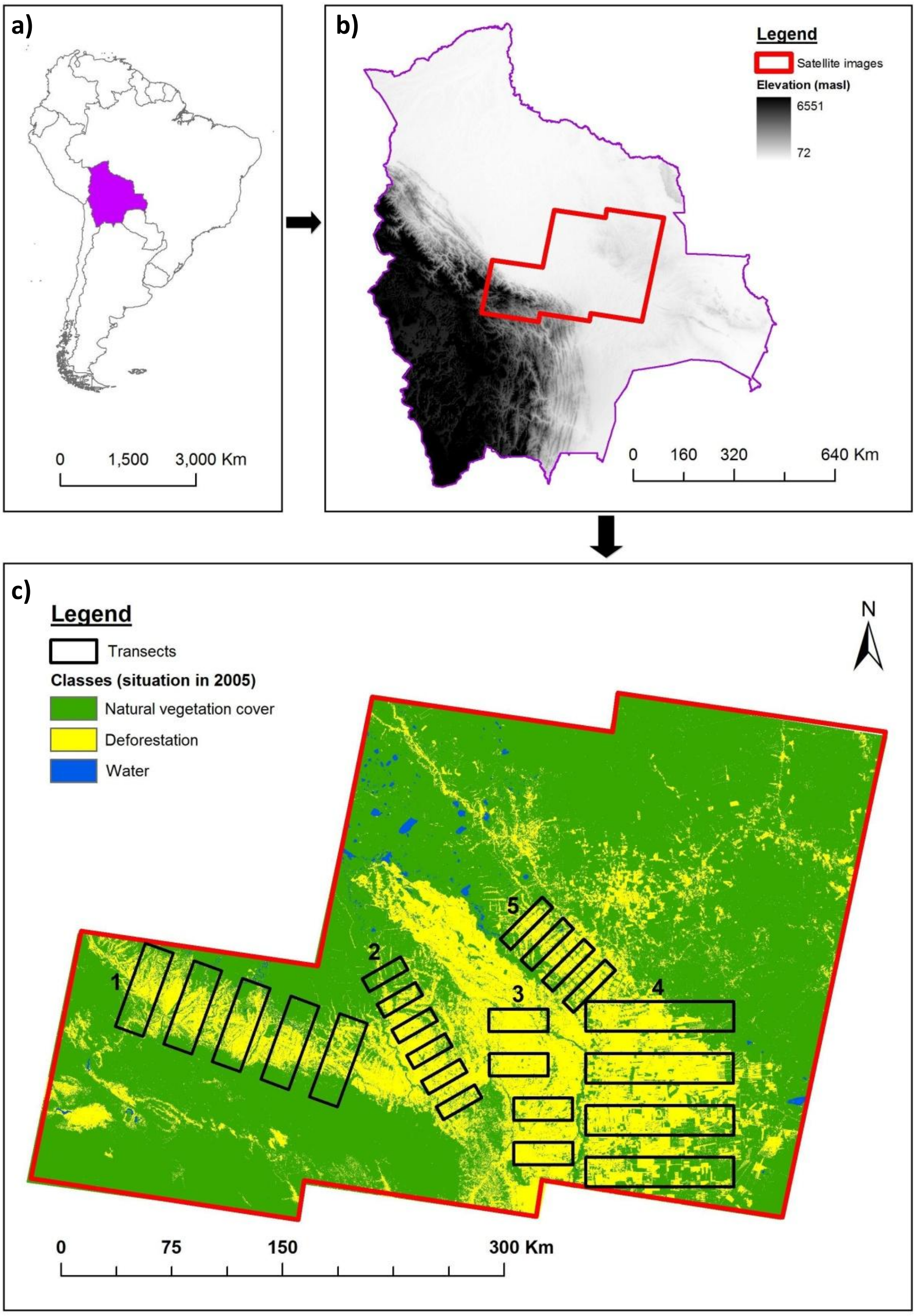


Fig. 1 Study area and location: a) position of Bolivia in South America, b) satellite imagery coverage for the study area, and c) sampling transects for each study area (1 – Chapare, 2 – Northwest colonisation zone, 3 – Integrated zone, 4 – Southern expansion zone and 5 – Northern expansion zone)

Natural vegetation cover consists mainly of evergreen rainforest and evergreen thicket. Crops are mostly perennial and thery are grown in an extensive manner (Superintendencia Agraria 2001). Chapare is specifically important for biodiversity protection since there are two national parks to the south – Carrasco and Amboró – and Isiboro Sécure National Park and indigenous territory to the west. Portions of these protected areas are represented in the transects.

Northwest colonisation zone (SA 2)

This part has been traditionally exploited for large-scale agricultural purposes. Japanese and Mennonite colonists reside in this area (Mertens et al 2004). Crops are grown extensively on a rotational basis. There are also silvopastures in this region, and natural cover is constituted by evergreen rainforest (Superintendencia Agraria 2001).

Integrated zone (SA 3)

This area was delineated above and next to the city Santa Cruz de la Sierra and to the left of the Rio Grande river. It is inhabited by Cruceño farmers (Cruceño refers to the people from the Santa Cruz city). Similarly to SA 2, crops are grown in rotations. Silvopastures and xeromorphic semi-deciduous forests can be also found there (Superintendencia Agraria 2001).

Southern expansion zone (SA 4)

The area east of the river Rio Grande is known as the expansion zone, where mechanised farm sector has been growing steadily (Vanclay et al 1999). It is managed mainly by large agro-industrial corporations. Intensive rotational cropping systems prevail. Natural vegetation cover consists of seasonal and xeromorphic semi-deciduous forests (Superintendencia Agraria 2001). There is the Kaa-Iya del Gran Chaco National Park in the south-eastern direction.

Northern expansion zone (SA 5)

The characteristic radial patterns in this area originated from the San Javier resettlement scheme of indigenous people from the Andes through development projects financed by the United States Agency for International Development. There is a small community in the middle of each circle, from which extend fields, generally with soybean (Steininger et al 2001a; NASA 2008). Crops are grown in rotations and extensively. Forests in the area are seasonal and semi-deciduous (Superintendencia Agraria 2001).

3.2 Data collection and analysis

Classified satellite imagery (Landsat, resolution 30 m) was provided by the Museo Nacional de Historia Natural Noel Kempff Mercado (MNHNNKM) from the Universidad Autónoma Gabriel Rene Moreno (UAGRM), Bolivia. This imagery, covering time period between the years 1975 to 2005, was already processed and used in the study by Killeen et al (2007). Images underwent unsupervised classification using the Leica/Erdas software and were compared to aerial videography for validation (Killeen et al 2007).

Images were classified into several classes: forest, Chaco woodland, Cerrado (savannah), other type of vegetation, plains, Andean plateau, wetlands, water, snow and deforested areas. Since most of the analysed land use changes shifted from forest cover in 1975 (Table 1), these changes were referred to as deforestation.

Table 1 Vegetation cover in the individual study areas in 1975

Study area	**SA 1**		**SA 2**		**SA 3**		**SA 4**		**SA 5**	
Vegetation cover	**km^2**	**%**	**km^2**	**%**	**km^2**	**%**	**km^2**	**%**	**km^2**	**%**
Forest	5,395.3	89.9	1,298.3	72.1	1,110.1	46.3	5,625.3	70.3	1,508.6	94.3
Chaco woodland	*N/A*	*N/A*	*N/A*	*N/A*	2.3	0.1	2,018.5	25.2	0.1	0.0
Cerrado	2.6	0.0	2.0	0.1	39.4	1.6	318.4	4.0	1.5	0.1
Plains / wetlands	93.4	1.6	17.0	0.9	39.6	1.7	3.4	0.0	72.5	4.5
Other vegetation	131.0	2.2	23.5	1.3	6.9	0.3	15.3	0.2	*N/A*	*N/A*
Total area	**6,000**	**100**	**1,800**	**100**	**2,400**	**100**	**8,000**	**100**	**1,600**	**100**

The classification used by Killeen et al (2007) was reclassified into three classes: 1) natural (forest, Chaco woodland, Cerrado, other type of vegetation, plains, Andean plateau, wetlands and snow), 2) deforestation (land cover change) and 3) water. Reclassification facilitated better understanding of land cover dynamics related to fragmentation and connectivity in tropical forests. Since the type of land use is determined by physical (climate, soil, relief) as well as economic and social factors (Dai et al 2005), the sampling design was prepared in order to reflect different land management policies in the five separate sections, based mainly on the past development and colonisation in the area (Killeen et al 2008). Rectangular transects were used in order to better assess the variability in fragmentation trends (Perotto-Baldivieso et al 2009). Transects were designed perpendicularly to disturbance features (highway patterns, disturbance development) and/or rivers, which constitute natural boundaries in the study areas. Transects differed for each study area and depended on the size of deforestation patterns (Fig. 1; Table 2).

Table 2 Transects and sampling design for each study area

Study area	SA 1	SA 2	SA 3	SA 4	SA 5
Number of transects	5	6	4	4	4
Dimensions (km)	60x20	30x10	40x15	100x20	40x10
Area (km^2)	1200	300	600	2000	400
Spacing (km)	15	10	15	15	10

To assess the visually identified different patterns of fragmentation, FRAGSTATS 3.3 (McGarigal and Marks 1995) was used to calculate a set of metrics that described landscape pattern in each transect. There have been conducted many studies describing deforestation by landscape metrics, applying different indices in their analyses (e.g. Trani and Giles Jr 1999; Imbernon and Branthomme 2001; Southworth et al 2002; Armenteras et al 2006; De Clercq 2006). In this study, the following landscape metrics were used to evaluate the land use change in the area at the class level (Wu et al 2000): percentage of natural vegetation cover, mean patch size (ha), patch density (patches/100 ha), edge density (m/ha) and mean Euclidian nearest neighbour distance (m). These metrics provided information needed to interpret the spatial distribution of natural vegetation cover in the individual transects. They were summarised using mean and standard deviation for each study area (Wu et al 2000; Perotto-Baldivieso et al 2009). Standard deviation helped in the interpretation of variability within study areas and the deforestation processes within them.

Connectivity was assessed using the integral index of connectivity (IIC), which was proposed by Pascual-Hortal and Saura (2006) as a new metric to quantify structural and functional connectivity. IIC is a graph-based connectivity index and it has been used to assess connectivity at multiple scales (Neel 2008; Perotto-Baldivieso et al 2009;

Visconti and Elkin 2009). Connectivity values range from 0 to 1, with best connectivity when the IIC = 1. This index was chosen for its relative robustness (Saura and Pascual-Hortal 2007). For its calculation, the software CONEFOR SENSINODE 2.2 (Saura and Torné 2009) was used. The input variables were the distance among patches and the patch value, in our case the area of a patch. As we were seeking to understand the landscape pattern and its effect on a specific organism, the selection of a model species was vital for the connectivity analysis. For the purposes of this study, an emblematic species in the Amazon was selected – jaguar (*Panthera onca*) (Sanderson et al 2002; Steneck 2005; Zeller 2007). Jaguar is listed on the IUCN Red List (IUCN 2010) under the "near threatened" status. Its protection is therefore of high importance, especially in the areas of persecution from ranchers due to cattle kills (Polisar et al 2003; Michalski et al 2006; Palmeira et al 2008). Jaguar has a large home range size, which makes it vulnerable to habitat fragmentation (Chiarello 1999). It usually inhabits areas with dense vegetation and with access to water bodies, but it can be found also in drier parts of Bolivia. It also requires closed-canopy forest where it stays provided there is enough prey (Michalski and Peres 2005; Ayala and Wallace 2008). There is not much specific information on the dispersal rates and home range size of jaguars available. These differ depending on the season, sex of the individual, and region (Schaller and Crawshaw 1980; Quigley and Crawshaw Jr 1992; Scognamillo et al 2003; Soisalo and Cavalcanti 2006; Cavalcanti and Gese 2009). Females seem to be affected by fragmentation more significantly due to their habitat preferences (Conde et al 2010), and thus the average home range size of females (29 km) reported from Bolivia by Maffei et al (2004) was selected. Average daily movement for female jaguars (1.8 km) reported by Crawshaw Jr and Quigley (1991) was another criterion for the assessment of connectivity.

4. RESULTS

4.1 Fragmentation patterns

Change in the natural vegetation cover between the years 1975 to 2005 was similar for SA 1, SA 2 and SA 3, with the decrease of 41 % (Fig. 2a). Natural cover declined by 64 % and 62 % in SA 4 and SA 5, respectively. SA 2 showed the highest variability. High variability indicated that land conversion processes occurred at different rates even within study areas.

Natural vegetation mean patch size was high in the 1970's, declining sharply with the progress of fragmentation (Table 3). The highest value and variability was observed in SA 4. This is because in 1975 there was almost no anthropogenic disturbance and the natural vegetation was not fragmented. In contrast, SA 3, where human influence was prevalent even before the beginning of the period under investigation, showed the lowest mean patch size values.

Table 3 Mean patch size (Mean) (ha) and standard error (SE) (ha)

	SA 1		SA 2		SA 3		SA 4		SA 5	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
1975	1,450.70	1,290.34	1,738.07	1,090.03	36.44	15.28	74,062.71	43,890.37	7,211.66	2,625.73
1986	196.47	129.23	171.32	117.89	23.06	10.38	10,364.21	6,274.41	265.77	150.58
1991	34.17	11.21	75.63	48.69	10.47	4.16	213.58	77.69	73.60	21.45
2001	14.75	1.35	16.04	8.55	3.92	0.64	30.12	10.01	18.67	5.43
2005	14.84	1.40	16.42	8.92	3.97	0.68	29.71	7.98	18.80	5.38

With increased land cover change, patch density had the highest values in 2001, except for SA 3 and SA 4, where it was in 1991 (Fig. 2b). After reaching the highest value (on average 3.3 patches/100 ha), patch density declined, since the patches began to disappear.

As the landscape was becoming more fragmented, the edge density was increasing (Fig. 2c). The maximum value was observed in 1991 (average 48.2 m/ha; 27.2 m/ha in SA 4), except for SA 5, where the peak was reached in 2001.

Mean Euclidian nearest neighbour distance values between the patches were generally increasing (Fig. 2d). The temporal decrease in some areas in 1991 can be attributed to the creation of new patches with natural vegetation cover. These were transformed into a different land use in the following years. The highest values were observed for the year 2001 (except for SA 3, which also had the highest variability) with an average of 112 m. The greatest change was in SA 4, where the distance increased by 65 m.

4.2 Connectivity

Connectivity for jaguar declined in all study areas, especially after 1991 (Fig. 2e). This decrease showed a similar trend to the loss of natural vegetation cover (Fig. 2a), but was more pronounced. The connectivity values were extremely low after 2000, in spite of the amount of natural vegetation being more than 35% in most of the study areas (with the exception of SA 3).

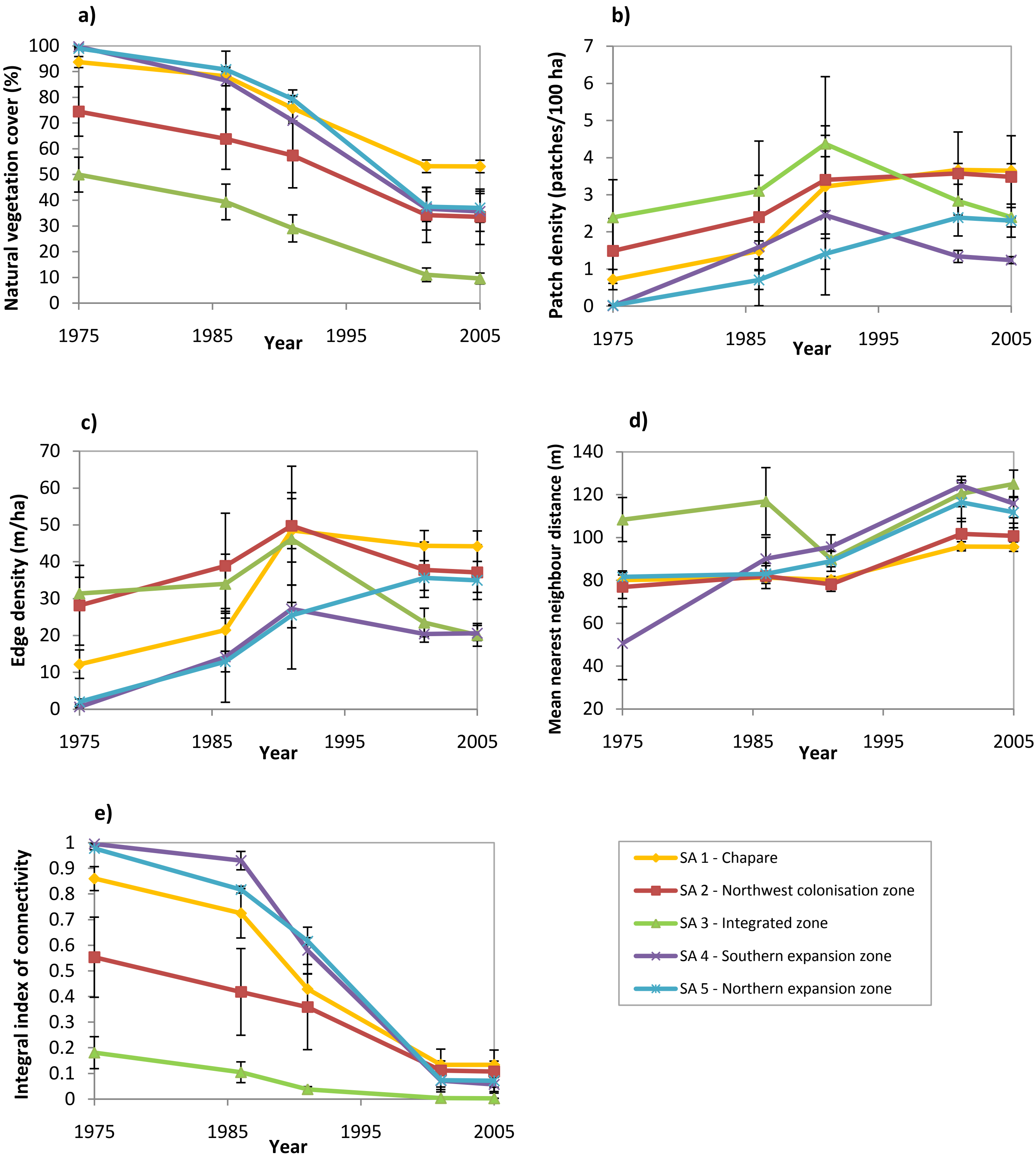


Fig. 2 Mean values of selected landscape metrics for the study areas in the period 1975-2005: a) percentage of natural vegetation cover, b) patch density (patches/100 ha), c) edge density (m/ha), d) mean nearest neighbour distance (m), e) integral index of connectivity. Error bars represent standard errors

5. DISCUSSION

The scale of ecological processes is critical for understanding fragmentation. We used a design that captured anthropogenic patterns and considered species-specific requirements, in order to achieve a more accurate assessment of fragmentation and its possible impacts. This approach of taking into consideration local land use change, rather than for instance changes in the whole area (e.g. country, department), enables obtaining results of higher accuracy, and consequently leads to improvement in land use planning and policy (Van Laake and Sánchez-Azofeifa 2004).

5.1 Land use change development

Natural vegetation cover was very high in 1975 in all study areas (with the exception of SA 3), which corresponded to the general deforestation development in Bolivia. While the anthropogenic disturbance rates in the lowland Bolivian forest were relatively low in comparison to other South American countries during the 1970's, this situation has been changing in the last 30 years as a result of several economic and social trends (Steininger et al 2001b; Kaimowitz et al 2002; Pacheco 2002). Whereas less than 60,000 ha were used for agricultural production in the Department of Santa Cruz in the 1950's, government incentives and policies (e.g. intensive agriculture and road construction between Cochabamba and Santa Cruz) led to gradual changes in land cover and land use. Additional causes such as large scale migration from the highlands, caused by the closure of mines, into the lowlands during the 1980's and 1990's resulted in a significant rise in deforestation rates at the beginning of the 1990's (Steininger et al 2001b; Kaimowitz et al 2002; Pacheco 2002). In the period from 1975 to 1993 the annual deforestation rate in Bolivia was on average 168,012 ha, increasing to 270,333 ha between the years 1993 and 2000 (USAID / Bolivia 2002). Deforestation triggered by agricultural expansion occurred primarily in deciduous lowland forest in the Tierras Bajas, the area east of the city Santa Cruz de la Sierra (Steininger et al 2001b); in fact, 75 % of Bolivian land use change occurred in the Santa Cruz department (Killeen et al 2007).

Deforestation patterns in our study areas were connected with the proximity to Santa Cruz de la Sierra and other large settlements (Pacheco and Mertens 2004). Deforestation proceeded from an already inhabited or agriculturally exploited area or a road (in SA 1, described in Millington et al (2003), and SA 2). SA 3 was already very fragmented in 1976 due to the developed infrastructure facilitating land use conversion and transport of agricultural products to markets (Mertens et al 2004). This area had the highest levels of fragmentation in the whole region. That contrasts with SA 4 on the opposite side of the river Rio Grande. The land there was converted at the beginning from forest, then (in 2001) also from chaco woodland. Chaco consists mainly of low, dense, spiny trees and cacti (Parker III et al 1993), which could have contributed to the reluctance of converting this type of vegetation cover into agricultural fields. The lack of water has been another constraint for agricultural practices (Steininger et al 2001a). But the limited land use change in this area before 1986 was mainly caused by the poor transportation routes to markets (Mertens et al 2004). These different land use changes and deforestation rates within our study areas were also reflected in the results of landscape pattern analysis.

5.2 Landscape pattern and connectivity

The landscape pattern analysis showed a decrease in natural vegetation cover and changes in its spatial distribution with significant changes for most study areas in 1991. The variability in the results means that it is not easy to predict habitat loss and fragmentation. The factors affecting the metrics behaviour are likely to be multifaceted, and there is a need for assessment and research specific for the area under investigation. The differences in the results can be explained by different shapes of agricultural areas and the land use change development. The variations were most likely the consequence of agricultural and economic policies which benefited certain groups and supported the expansion of large-scale agriculture (Mertens et al 2004; Pacheco and Mertens 2004).

Millington et al (2003) used certain metrics to assess the fragmentation for Chapare region (represented in our SA 1) during the years 1986, 1993 and 2000. From the metrics they used, we were able to compare only the mean Euclidian nearest neighbour distance and patch density. Results of the former were relatively similar to ours, but the latter differed in the order of magnitude. This divergence could be attributed to the different design of the study area. The fact that in our study were used transects specifically capturing deforestation enabled observation of more pronounced alterations of natural vegetation cover over the time period.

The important question for habitat connectivity is not how much habitat is lost, but where it is lost. We observed extremely low values of connectivity for jaguar (less than 0.2), even though the vegetation cover was more than 35 % (except for SA 3). Our results contradicted the theory assuming that 30 % of native vegetation cover is a threshold below which the impacts of habitat fragmentation become severe (Andrén 1994). This threshold would however depend on the species and the type of habitat

(Huggett 2005; Lindenmayer et al 2005; Radford et al 2005; De Oliveira Filho and Metzger 2006; Fischer and Lindenmayer 2007; Rhodes et al 2008), and cannot be universally applied. As Swift and Hannon (2010) pointed out, there is still lack of knowledge about the topic of critical thresholds and habitat loss or fragmentation. As has also been shown in our study, the practical use of these thresholds is questionable.

5.3 Implications for conservation efforts

Well connected patch networks combined with large patches are able to efficiently support ecological functions, such as water management, cycling of nutrients, and soil protection by vegetation cover, and provide more valuable habitat. Different mean patch size in 2005 suggested variable severity of the impact on ecological processes. Also the increasing edge density can have negative implications for the physical and biotic conditions within the forest patches (Laurance 2005). Of the vegetation types found in the region, dry forest is especially vulnerable to being cut, as this endangered ecosystem can be cleared and managed with fire very easily (Janzen 1988).

The amount and spatial distribution of fragmentation is critical to wildlife habitat. However, landscape metrics values alone do not fully represent the impact of fragmentation on a specific species. Despite the great variability of remaining land cover in our study areas, connectivity values for jaguar were very small (IIC < 0.2). The issue of hindered connectivity for jaguar movement within our study area to move between breeding populations was already studied by Rabinowitz and Zeller (2010) and deserves more attention. Action should be taken to improve landscape connectivity by using general principles, even though specific data for particular species may not yet be known (Watts and Handley 2010).

The implications of deforestation depend on the new land use – deforested areas may not be uniformly unsuitable for species and their migration (Kupfer et al 2006). We expect agriculture to be less detrimental than urban areas (in the vicinity of SA 3). Regarding agriculture, a small scale and extensive production might be less detrimental than a large scale and intensive one (in SA 4). Spatial pattern also affects the way of prospective habitat restoration (Malanson et al 2007). Although secondary forest could add some ecological values, such as habitat and food provision, this habitat may not be as valuable as the original one (Barlow et al 2007; Gardner et al 2007).

Landscape analysis should provide a tool for decisions about where to target limited funding to improve the connectivity of the landscape and prioritise nature conservation efforts. Protected areas cover 16 % of the Bolivian territory (Ibisch 2005). National parks are generally associated with low cutting and logging rates, but even they might be under threat, especially if they are in the vicinity of roads or already deforested regions (Sánchez-Azofeifa et al 1999; Forrest et al 2008; Asner et al 2009). Although these areas may not be significantly affected by land cover change, connectivity with other adjacent ecosystems could be at risk due to land cover change outside the protected areas, which is the case in SA 1 and SA 4.

One of the constraints to nature conservation in this region might be the fact that Bolivia is the country with the lowest national income in Latin America (UNFPA 2008). The lack of will and capacity to implement environmental policies is a well-known problem in most developing countries (Kaimowitz et al 1999). Even though some measures are already being made to control deforestation and promote sustainable forest management in Bolivia, it remains to be seen how effective these policies will be (Pacheco et al 2010). It might be important to incorporate economic incentives into nature protection recommendations and practices. This should reconcile environmental and economic needs, and gain more support from the government as well as local people (Pfund 2010). Nature conservation can also be supported by the profits from tourism. However, strict measures need to be implemented so that this concept is viable and beneficial to the biodiversity (Gössling 1999; Tollefson 2009). The scientific knowledge should also be transferred to local people in order to encourage nature conservation as a means for obtaining ecosystem services (Becker and Ghimire 2003). Non-governmental organisations should play an important role in educating local people in nature conservation efforts (Tole 2006). Recommended is the promotion of certain agricultural practices that are ecologically sound and sustainable, and establishment of remnant forest strips and set-aside forested regions to provide habitat for species, carbon offsetting and ecotourism (Fredericksen 2003; Hawes et al 2008).

5.4 Recommendations for further research

Landscape metrics can be utilised for developing conservation plans, but only to a limited degree. New approaches are needed to integrate the arrangement of habitat spatial patterns into functional habitat networks for multiple species within and among different trophic levels. This study used data for female jaguars, which – as a predator – plays an important regulatory role in an ecosystem. There is a need to develop further multiple-species analyses and assess the value for different habitat patches for wildlife species – the functional connectivity. This would provide a more comprehensive understanding of the landscape structure importance for ecosystem processes and functions, which is vital for designing conservation strategies (e.g. corridors and protected areas), in regions highly affected by anthropogenic activity.

6. CONCLUSIONS

The aim of this study was to provide a better understanding of the impacts of anthropogenic disturbance patterns on landscape structure and connectivity in a tropical forest. The goals were fulfilled by providing new knowledge about the development of changes in landscape pattern in Bolivian lowlands. We showed that different settlement schemes and agricultural practices lead to distinct habitat fragmentation effects. This study is the first step for the following research efforts and design of conservation measures specific for the area under investigation.

A method was presented to identify and assess land use change and the impact on connectivity for a specific species. We recommend that conservation plans incorporate connectivity analyses to assess, design, and implement habitats and corridors for wildlife.

Studies on deforestation and other land use change in tropical areas usually focus on how much of the habitat is lost. We emphasise the need to assess the arrangement, i.e. where it is lost, as well. Landscape management should focus on both – connectivity restoration and protection of the remaining habitat fragments in order to minimise extinction risk of the targeted organisms.

7. ACKNOWLEDGEMENTS

Authors thank Museo Nacional de Historia Natural Noel Kempff Mercado for provision of the satellite imagery, and Cranfield University for technical support. Thanks are also due to the European Commission for the grant to Miriam Zemanova, supporting her studies in the UK.

8. REFERENCES

Adam P (1998) History and ecology of rainforest diversity. Trends Plant Sci 3(8): 287-288

Alvarenga LDP, Pôrto KC, Oliveira JRdPM (2010) Habitat loss effects on spatial distribution of non-vascular epiphytes in a Brazilian Atlantic forest. Biodivers Conserv 19(3):619-635

Andersen LE, Granger CWJ, Reis EJ et al (2002) The Dynamics of Deforestation and Economic Growth in the Brazilian Amazon. Cambridge University Press, New York

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. Oikos 71(3):355–366

Arango-Vélez N, Kattan GH (1997) Effects of forest fragmentation on experimental nest predation in Andean cloud forest. Biol Cons 81(1-2):137-143

Araújo MB, Cabeza M, Thuiller W et al (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biol 10(9):1618-1626

Armenteras D, Rudas G, Rodriguez N et al (2006) Patterns and causes of deforestation in the Colombian Amazon. Ecol Indic 6(2):353-368

Asner GP, Rudel TK, Aide TM et al (2009) A contemporary assessment of change in humid tropical forests. Conserv Biol 23(6):1386-1395

Ayala G, Wallace R (2008) El jaguar en el Parque Nacional Madidi. Wildlife Conservation Society, La Paz

Barber RG, Orellana M, Navarro F et al (1996) Effects of conservation and conventional tillage systems after land clearing on soil properties and crop yield in Santa Cruz, Bolivia. Soil Tillage Res 38(1-2):133-152

Barbier EB (2004) Agricultural expansion, resource booms and growth in Latin America: Implications for long-run economic development. World Dev 32 (1):137-157

Barlow J, Overal WL, Araujo IS et al (2007) The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. J Appl Ecol 44(5):1001-1012

Barlow J, Peres CA, Henriques LMP et al (2006) The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis. Biol Cons 128(2):182-192

Bawa KS, Dayanandan S (1997) Socioeconomic factors and tropical deforestation. Nature 386(6625):562-563

Becker CD, Ghimire K (2003) Synergy between traditional ecological knowledge and conservation science supports forest preservation in Ecuador. Ecol Soc 8(1):1. Available from http://www.consecol.org/vol8/iss1/art1 (accessed June 2010)

Bell KE, Donnelly MA (2006) Influence of forest fragmentation on community structure of frogs and lizards in northeastern Costa Rica. Conserv Biol 20(6):1750-1760

Bissonette JA (2003) Linking landscape patterns to biological reality. In: Bissonette JA, Storch I (eds) Landscape Ecology and Resource Management: Linking Theory with Practice. Island Press, Washington, pp 15-34

Boahene K (1998) The challenge of deforestation in tropical Africa: reflections on its principal causes, consequences and solutions. Land Degrad Dev 9(3):247-258

Bolliger J, Wagner HH, Turner MG (2007) Identifying and quantifying landscape patterns in space and time. In: Kienast F, Wildi O, Ghosh S (eds) A changing world: challenges for landscape research. Springer, Dordrecht, pp 177-194

Börner J, Denich M, Mendoza-Escalante A et al (2007) Alternatives to slash-and-burn in forest-based fallow systems of the eastern Brazilian Amazon region: Technology and policy options to halt ecological degradation and improve rural welfare. In: Tscharntke T, Leuschner C, Zeller M et al (eds) Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation. Springer-Verlag, Heidelberg, pp 333-362

Botequilha Leitão A, Miller J, Ahern J, McGarigal K (2006) Measuring landscapes: a planner’s handbook. Island Press, Washington

Bounoua L, DeFries RS, Imhoff ML, Steininger MK (2004) Land use and local climate: A case study near Santa Cruz, Bolivia. Meteorol Atmos Phys 86(1-2):73-85

Bowman J, Cappuccino N, Fahrig L (2002) Patch size and population density: The effect of immigration behavior. Conserv Ecol 6(1):9. Available from http://www.consecol.org/vol6/iss1/art9 (accessed June 2010)

Bradley AV, Millington AC (2008) Coca and colonists: Quantifying and explaining forest clearance under coca and anti-narcotics policy regimes, Ecol Soc 13(1):31. Available from http://www.ecologyandsociety.org/vol13/iss1/art31/ (accessed June 2010)

Brosi BJ, Daily GC, Shih TM et al (2008) The effects of forest fragmentation on bee communities in tropical countryside. J Appl Ecol 45(3):773-783

Bürgi M, Hersperger AM, Schneeberger N (2005) Driving forces of landscape change – Current and new directions. Landscape Ecol 19(8):857-868

Cardille JA, Turner MG (2002) Understanding landscape metrics I. In: Gergel SE, Turner MG (eds) Learning landscape ecology: a practical guide to concepts and techniques. Springer-Verlag, New York, pp 85-100

Cavalcanti SMC, Gese EM (2009) Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern pantanal, Brazil. J Mammal 90(4):935-945

Chapin III FS, Zavaleta ES, Eviner VT et al (2000) Consequences of changing biodiversity. Nature 405(6783):234-242

Chhabra A, Geist H, Houghton RA et al (2006) Multiple Impacts of Land-Use/Cover Change. In: Labmin EF, Geist H (eds) Land-Use and Land-Cover Change: Local Processes and Global Impacts. Springer-Verlag, Heidelberg, pp 71-116

Chiarello AG (1999) Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. Biol Cons 89(1):71-82

Chomitz KM, Buys P, De Luca G et al (2007) At Loggerheads? Agricultural Expansion, Poverty Reduction, and Environment in the Tropical Forests. The World Bank, Washington DC

Collinge SK (1996) Ecological consequences of habitat fragmentation: Implications for landscape architecture and planning. Landscape and Urban Plan 36(1):59-77

Collinge SK (2009) Ecology of fragmented landscapes. The Johns Hopkins University Press, Baltimore

Collingham YC, Huntley B (2000) Impacts of habitat fragmentation and patch size upon migration rates. Ecol Appl 10(1):131-144

Conde DA, Colchero F, Zarza H et al (2010) Sex matters: Modeling male and female habitat differences for jaguar conservation. Biol Cons (in press)

Cramer JM, Mesquita RCG, Williamson GB (2007) Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. Biol Cons 137(3):415-423

Craul M, Chikhi L, Sousa V et al (2009) Influence of forest fragmentation on an endangered large-bodied lemur in northwestern Madagascar. Biol Cons 142(12):2862-2871

Crawshaw Jr PG, Quigley HB (1991) Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. J Zool 223(3):357-370

Cushman SA, McGarigal K, Neel MC (2008) Parsimony in landscape metrics: Strength, universality, and consistency. Ecol Indic 8(5):691-703

D'Eon RG, Glenn SM, Parfitt I, Fortin M-J (2002) Landscape connectivity as a function of scale and organism vagility in a real forested landscape. Conserv Ecol 6(2), available from http://www.consecol.org/vol6/iss2/art10 (accessed July 2010)

Dai E, Wu S, Shi W et al (2005) Modeling Change-Pattern-Value dynamics on land use: An integrated GIS and Artificial Neural Networks approach. Environ Manage 36(4):576-591

De Clercq EM, Vandemoortele F, De Wulf RR (2006) A method for the selection of relevant pattern indices for monitoring of spatial forest cover pattern at a regional scale. Int J Appl Earth Obs 8(2):113-125

De Oliveira Filho FJB, Metzger JP (2006) Thresholds in landscape structure for three common deforestation patterns in the Brazilian Amazon. Landscape Ecol 21(7):1061-1073

Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. Conserv Biol 14(2):342-355

Dixo M, Metzger JP, Morgante JS, Zamudio KR (2009) Habitat fragmentation reduces genetic diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest. Biol Cons 142(8):1560-1569

Dudley N, Schlaepfer R, Jackson W et al (2006) Forest Quality: Assessing Forests at a Landscape Scale. Earthscan, London

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev Camb Philos Soc 81(1):117-142

Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. J Wildlife Manage 61(3):603-610

Fahrig L (2001) How much habitat is enough? Biol Cons 100(1):65-74

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Ann Rev Ecol Evol Syst 34:487-515

Fahrig L, Nuttle WK (2006) Population Ecology in Spatially Heterogeneous Environments. In: Lovett GM, Jones CG, Turner MG, Weathers KC (eds) Ecosystem Function in Heterogeneous Landscapes. Springer, New York, pp 95-118

FAO (2001) Global Forest Resources Assessment 2000, Forestry Paper 140. Available from ftp://ftp.fao.org/docrep/fao/003/Y1997E/FRA%202000%20Main%20report.pdf (accessed May 2010)

FAO (2010) Global Forest Resources Assessment 2010: Key Findings. Available from http://foris.fao.org/static/data/fra2010/KeyFindings-en.pdf (accessed May 2010)

Farina A (2000) Principles and methods in landscape ecology. Kluwer Academic Publishers, Dodrecht

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. Global Ecol Biogeogr 16(3):265-280

Forrest JL, Sanderson EW, Wallace R et al (2008) Patterns of Land Cover Change in and Around Madidi National Park, Bolivia. Biotropica 40(3):285-294

Fortin M-J, Dale MRT (2005) Spatial analysis: A guide for ecologists. Cambridge Universtiy Press, New York

Franklin JF, Forman RTT (1987) Creating landscape patterns by forest cutting: Ecological consequences and principles. Landscape Ecol 1(1):5-18

Fredericksen TS (2003) Forest Management and Biodiversity Conservation in Bolivian Tropical Forests. Lyonia 5(1):9-14

Fredericksen NJ, Fredericksen TS (2002) Terrestrial wildlife responses to logging and fire in a Bolivian tropical humid forest. Biodivers Conserv 11(1):27-38

Freitas SR, Hawbaker TJ, Metzger JP (2010) Effects of roads, topography, and land use on forest cover dynamics in the Brazilian Atlantic Forest. Forest Ecol Manag 259(3):410-417

Gardner TA, Hernández MIM, Barlow J, Peres CA (2008) Understanding the biodiversity consequences of habitat change: The value of secondary and plantation forests for neotropical dung beetles. J Appl Ecol 45(3):883-893

Gardner TA, Ribeiro-Júnior MA, Barlow J et al (2007) The value of primary, secondary, and plantation forests for a neotropical herpetofauna. Conserv Biol 21(3):775-787

Gascon C, Lovejoy TE, Bierregaard Jr RO et al (1999) Matrix habitat and species richness in tropical forest remnants. Biol Cons 91(2-3):223-229

Geist HJ, Lambin EF (2001) What drives tropical deforestation? A meta-analysis of proximate underlying causes of deforestation based on subnational case study evidence, LUCC Report Series No. 4. LUCC International Project Office, Louvain-la-Neuve

Gerlagh R, van der Zwaan B (2006) Options and instruments for a deep cut in CO_2 emissions: Carbon dioxide capture or renewables, taxes or subsidies. Energy J 27(3):25-48

Gibbs JP (2001) Demography versus habitat fragmentation as determinants of genetic variation in wild populations. Biol Cons 100(1):15-20

Gomes LGL, Oostra V, Nijman V et al (2008) Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. Biol Cons 141(3):860-871

Goodwin BJ, Fahrig L (2002) How does landscape structure influence landscape connectivity? Oikos 99(3):552-570

Gössling S (1999) Ecotourism: A means to safeguard biodiversity and ecosystem functions? Ecol Econ 29(2):303-320

Graigner A (1993) Controlling tropical deforestation. Earthscan Publications, London

Guerra CA, Snow RW, Hay SI (2006) A global assessment of closed forests, deforestation and malaria risk. Ann Trop Med Parasit 100(3):189-204

Gullison RE, Frumhoff PC, Canadell JG et al (2007) Tropical forests and climate policy. Science 316(5827):985-986

Gustafson EJ (1998) Quantifying landscape spatial pattern: What is the state of the art? Ecosystems 1(2):143-156

Haila Y (2002) A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. Ecol Appl 12(2):321-334

Hannah L, Lovejoy TE, Schneider SH (2005) Biodiversity and climate change in context. In: Lovejoy TE, Hannah L (eds) Climate change and biodiversity. Yale University Press, New Haven & London, pp 3-14

Hannah L, Midgley GF, Millar D (2002) Climate change-integrated conservation strategies. Global Ecol Biogeogr 11(6):485-495

Hargis CD, Bissonette JA, David JL (1998) The behavior of landscape metrics commonly used in the study of habitat fragmentation. Landscape Ecol 13(3):167-186

Haskell JP, Ritchie ME, Olff H (2002) Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature 418(6897):527-530

Hawes J, Barlow J, Gardner TA, Peres CA (2008) The value of forest strips for understorey birds in an Amazonian plantation landscape. Biol Cons 141(9):2262-2278

Hecht SB (2005) Soybeans, development and conservation on the Amazon frontier. Dev Change 36(2):375-404

Hewitt GM, Nichols RA (2005) Genetic and evolutionary impacts of climate change. In: Lovejoy TE, Hannah L (eds) Climate change and biodiversity. Yale University Press, New Haven & London, pp 176-192

Higgins PAT (2007) Biodiversity loss under existing land use and climate change: An illustration using northern South America. Global Ecol Biogeogr 16(2):197-204

Hilty JA, Lidicker Jr WZ, Merenlender AM (2006) Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation. Island Press, Washington

Honnay O, Verheyen K, Butaye J et al (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecology Lett 5(4):525-530

Huggett AJ (2005) The concept and utility of 'ecological thresholds' in biodiversity conservation. Biol Cons 124(3):301-310

Ibisch PL (2005) Biodiversity Conservation in Bolivia: History, Trends and Challenges. In: Romero A and West SE (eds) Environmental Issues in Latin America and the Caribbean. Springer, Netherlands, pp 55-71

Imbernon J, Branthomme A (2001) Characterization of lanscape patterns of deforestation in tropical rain forests. Int J Remote Sens 22(9):1753-1765

IPCC (2000) Land Use, Land-Use Change, and Forestry. Cambridge University Press, Cambridge

IUCN (2010) IUCN Red List of Threatened Species, Version 2010.2. Available from http://www.iucnredlist.org (accessed July 2010)

Janzen D (1988) Tropical dry forests, The most endangered major tropical ecosystem. In: Wilson EO (ed) Biodiversity. National Academy of Sciences/Smithsonian Institution, Washington DC, pp 130-137

Johnson GD, Patil GP (2006) Landscape pattern analysis for assessing ecosystem condition. Springer, New York

Kaimowitz D, Mendez P, Puntodewo A, Vanclay J (2002) Spatial regression analysis of deforestation in Santa Cruz, Bolivia. In: Wood CH, Porro R (eds) Deforestation and land use in the Amazon. University Press of Florida, Gainesville, pp 41-65

Kaimowitz D, Thiele G, Pacheco P (1999) The effects of structural adjustment on deforestation and forest degradation in lowland Bolivia. World Dev 27(3):505-520

Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe. Quaternary Science Reviews 28(27-28):3016-3034

Killeen TJ, Calderon V, Soria L et al (2007) Thirty years of land-cover change in Bolivia. Ambio 36 (7):600-606

Killeen TJ, Guerra A, Calzada M et al (2008) Total historical land-use change in eastern Bolivia: Who, where, when, and how much? Ecol Soc 13(1):36. Available from http://www.ecologyandsociety.org/vol13/iss1/art36/ (accessed May 2010)

Knowlton JL, Graham CH (2010) Using behavioral landscape ecology to predict species' responses to land-use and climate change. Biol Cons 143(6):1342-1354

Kupfer JA, Malanson GP, Franklin SB (2006) Not seeing the ocean for the islands: The mediating influence of matrix-based processes on forest fragmentation effects. Global Ecol Biogeogr 15(1):8-20

Laurance WF (1998) A crisis in the making: responses of Amazonian forests to land use and climate change. Trends Ecol Evolut 13(10):411-415

Laurance WF (2005) Forest-climate interactions in fragmented tropical landscapes. In: Malhi Y, Phillips OL (eds) Tropical Forests & Global Atmospheric Change. Oxford University Press, New York, pp 31-38

Laurance WF (2008) Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. Biol Cons 141(7):1731-1744

Laurance WF, Delamônica P, Laurance SG et al (2000) Conservation: Rainforest fragmentation kills big trees. Nature 404(6780):836

Laurance WF, Laurance SG, Delamonica P (1998) Tropical forest fragmentation and greenhouse gas emissions. Forest Ecol Manag 110(1-3):173-180

Laurance WF, Powell G, Hansen L (2002) A precarious future for Amazonia. Trends Ecol Evolut 17(6):251-252

Laurance WF, Williamson BG (2001) Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. Conserv Biol 15(6):1529-1535

Lawton JH, Bignell DE, Bolton B et al (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391(6662):72-76

Li H, Wu J (2004) Use and misuse of landscape indices. Landscape Ecol 19(4):389-399

Li H, Wu J (2007) Landscape pattern analysis: key issues and challenges. In: Wu J, Hobbs RJ (eds) Key topics in landscape ecology. Cambridge University Press, New York, pp 39-61

Lienert J (2004) Habitat fragmentation effects of fitness of plant populations – A review. J Nat Conserv 12(1):53-72

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

Lindenmayer DB, Fischer J, Cunningham RB (2005) Native vegetation cover thresholds associated with species responses. Biol Cons 124(3):311-316

López-Barrera F, Armesto JJ, Williams-Linera G et al (2007) Fragmentation and edge effects on plant-animal interactions, ecological processes and biodiversity. In: Newton AC (ed) Biodiversity loss and Conservation in Fragmented forest Landscapes: The Forests of Montane Mexico and Temperate South America. CABI, Wallingford, pp 69-101

Lorena RB, Lambin EF (2009) The spatial dynamics of deforestation and agent use in the Amazon. Appl Geogr 29(2):171-181

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton

Maczulak A (2010) Biodiversity: conserving endangered species. Facts On File Inc., New York

Maffei L, Cuéllar E, Noss A (2004) One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. J Zool 262(3):295-304

Malanson GP, Wang Q, Kupfer JA (2007) Ecological processes and spatial patterns before, during and after simulated deforestation. Ecol Model 202(3-4):397-409

Malcolm JR, Markham A, Neilson RP, Garaci M (2002) Impacts of habitat fragmentation and patch size upon migration rates. J Biogeogr 29(7):835-849

Malhi Y, Roberts JT, Betts RA et al (2008) Climate change, deforestation and the fate of the Amazon. Science 319(5860):169-172

Malhi Y, Wright J (2005) Late twentieth-century patterns and trends in the climate of tropical forest regions. In: Malhi Y, Phillips OL (eds) Tropical Forests & Global Atmospheric Change. Oxford University Press, New York, pp 3-16

Mason SJ (2001) El Niño, climate change, and southern African climate. Environmetrics 12(4):327-345

McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12(2):335-345

McGarigal K, Marks BJ (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report – US Department of Agriculture, Forest Service (PNW-GTR-351)

McLaughlin JF, Hellmann JJ, Boggs CL, Ehrlich PR (2002) Climate change hastens population extinctions. P Natl Acad Sci USA 99(9):6070-6074

MEA (2005) Ecosystems and human well-being: general synthesis. Island Press and World Resources Institute, Washington

Meffe GK, Carroll CR (1997) Principles of Conservation Biology, 2nd edition. Sinauer Associates, New York

Mertens B, Kaimowitz D, Puntodewo A et al (2004) Modeling deforestation at distinct geographic scales and time periods in Santa Cruz, Bolivia. Int Regional Sci Rev 27(3):271-296

Michalski F, Boulhosa RLP, Faria A, Peres CA (2006) Human-wildlife conflicts in a fragmented Amazonian forest landscape: Determinants of large felid depredation on livestock. Anim Conserv 9(2):179-188

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

Miles L, Kapos V (2008) Reducing Greenhouse Gas Emissions from Deforestation and Forest Degradation: Global Land-Use Implications. Science 320(5882):1454-1455

Miller PM, Kauffman JB (1998) Effects of slash and burn agriculture on species abundance and composition of a tropical deciduous forest. Forest Ecol Manag 103(2-3):191-201

Millington AC, Velez-Liendo XM, Bradley AV (2003) Scale dependence in multitemporal mapping of forest fragmentation in Bolivia: Implications for explaining temporal trends in landscape ecology and applications to biodiversity conservation. ISPRS J Photogramm 57(4):289-299

Mitchell MS, Powell RA (2003) Linking Fitness Landscapes with the Behaviour and Distribution of Animals. In: Bissonette JA, Storch I (eds) Landscape Ecology and Resource Management: Linking Theory with Practice. Island Press, Washington, pp 93-124

Naeem S, Thompson LJ, Lawler SP et al (1994) Declining biodiversity can alter the performance of ecosystems. Nature 368(6473):734-737

NASA (2008) Deforestation in Santa Cruz, Bolivia: Image of the Day. Available from http://earthobservatory.nasa.gov/IOTD/view.php?id=3721 (accessed June 2010)

Neel MC (2008) Patch connectivity and genetic diversity conservation in the federally endangered and narrowly endemic plant species *Astragalus albens* (*Fabaceae*). Biol Conserv 141(4):938-955

Nichols E, Larsen T, Spector S et al (2007) Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. Biol Cons 137(1):1-19

Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol Cons 117(3):285-297

Opdam P, Wiens JA (2002) Fragmentation, habitat loss and landscape management. In: Norris K, Pain DJ (eds) Conserving bird biodiversity: general principles and their application. Cambridge University Press, New York, pp 202-223

Pacheco P (2002) Deforestation and forest degradation in lowland Bolivia. In: Wood CH, Porro R (eds) Deforestation and land use in the Amazon. University Press of Florida, Gainesville, pp 41-65

Pacheco P (2006) Agricultural expansion and deforestation in lowland Bolivia: the import substitution versus the structural adjustment model. Land Use Policy 23(3):205-225

Pacheco P, de Jong W, Johnson J (2010) The evolution of the timber sector in lowland Bolivia: Examining the influence of three disparate policy approaches. Forest Policy Econ 12(4):271-276

Pacheco P, Mertens B (2004) Land use change and agricultural development in Santa Cruz, Bolivia. Bois et Forêt des Tropiques 280(2):29-40

Palmeira FBL, Crawshaw Jr PG, Haddad CM et al (2008) Cattle depredation by puma (*Puma concolor*) and jaguar (*Panthera onca*) in central-western Brazil. Biol Cons 141(1):118-125

Parker III TA, Gentry AH, Foster RB et al (1993) The Lowland Dry Forests of Santa Cruz, Bolivia: A Global Conservation Priority, Rapid Assessment Program. Conservation International, Fundación Amigos de la Naturaleza. Available from http://www.conservation.org/Documents/RAP_Reports/RAP04_Santa_Cruz_Bolivia_Jul-1993.pdf (accessed July 2010)

Pascual-Hortal L, Saura S (2006) Comparison and development of new graph-based landscape connectivity indices: Towards the priorization of habitat patches and corridors for conservation. Landscape Ecol 21(7):959-967

Peng J, Wang Y, Zhang Y et al (2010) Evaluating the effectiveness of landscape metrics in quantifying spatial patterns. Ecol Indic 10(2):217-223

Peres CA, Gardner TA, Barlow J et al (2010) Biodiversity conservation in human-modified Amazonian forest landscapes. Biol Cons (in press)

Perotto-Baldivieso HL, Meléndez-Ackerman E, García MA et al (2009) Spatial distribution, connectivity, and the influence of scale: Habitat availability for the endangered Mona Island rock iguana. Biodivers Conserv 18(4):905-917

Pfund J-L (2010) Landscape-scale research for conservation and development in the tropics: Fighting persisting challenges. Curr Opin Env Sust 2(1-2):117-126.

Pimm SL (1998) Ecology: The forest fragment classic. Nature 393(6680):23-24

Polisar J, Maxit I, Scognamillo D et al (2003) Jaguars, pumas, their prey base, and cattle ranching: Ecological interpretations of a management problem. Biol Cons 109(2):297-310

Prevedello JA, Vieira MV (2010) Does the type of matrix matter? A quantitative review of the evidence. Biodivers Conserv 19(5):1205-1223

Quigley HB, Crawshaw Jr PG (1992) A conservation plan for the jaguar *Panthera onca* in the Pantanal region of Brazil. Biol Cons 61(3):149-157

Rabinowitz A, Zeller KA (2010) A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. Biol Cons 143(4):939-945

Radford JQ, Bennett AF, Cheers GJ (2005) Landscape-level thresholds of habitat cover for woodland-dependent birds. Biol Cons 124(3):317-337

Raheem DC, Naggs F, Chimonides J et al (2009) Fragmentation and pre-existing species turnover determine land-snail assemblages of tropical rain forest. J Biogeogr 36(10):1923-1938

Raijmann LEL, Van Leeuwen NC, Kersten R et al (1994) Genetic variation and outcrossing rate in relation to population size in *Gentiana pneumonanthe* L. Conserv Biol 8(4):1014-1026

Ranta E, Lundberg P, Kaitala V (2006) Ecology of populations. Cambridge University Press, New York

Rhodes JR, Callaghan JG, McAlpine CA et al (2008) Regional variation in habitat-occupancy thresholds: A warning for conservation planning. J Appl Ecol 45(2):549-557

Ricketts TH (2001) The matrix matters: Effective isolation in fragmented landscapes. Am Nat 158(1):87-99

Riitters KH, O'Neill RV, Hunsaker CT et al (1995) A factor analysis of landscape pattern and structure metrics. Landscape Ecol 10(1):23-39

Rockwood LL (2006) Introduction to population ecology. Blackwell Publishing, Oxford

Roulet M, Lucotte M, Canuel R et al (2000) Increase in mercury contamination recorded in lacustrine sediments following deforestation in the central Amazon. Chem Geol 165(3-4):243-266

Rudel T, Roper J (1997) Forest fragmentation in the humid tropics: A cross-national analysis. Singapore J Trop Geo 18(1):99-109

Sánchez-Azofeifa GA, Quesada-Mateo C, Gonzalez-Quesada P et al (1999) Protected areas and conservation of biodiversity in the tropics. Conserv Biol 13(2):407-411

Sanderson EW, Redford KH, Chetkiewicz C-LB et al (2002) Planning to save a species: The jaguar as a model. Conserv Biol 16(1):58-72

Sandwith T, Lockwood M (2006) Linking the Landscape. In: Lockwood M, Worboys GL, Kothari A (eds) Managing Protected Areas: A Global Guide. Earthscan, London, pp 574-602

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5(1):18-32

Saura S (2002) Effects of minimum mapping unit on land cover data spatial configuration and composition. Int J Remote Sens 23(22):4853-4880

Saura S, Pascual-Hortal L (2007) A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. Landscape Urban Plan 83(2-3):91-103

Saura S, Torné J (2009) Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environ Modell Softw 24(1): 135-139

Schaller GB, Crawshaw PG (1980) Movement Patterns of Jaguar. Biotropica 12(3):161-168

Scognamillo D, Maxit IE, Sunquist M, Polisar J (2003) Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. J Zool 259(3):269-279

Secretariat of the Convention on Biological Diversity (2005) Handbook of the Convention on Biological Diversity Including its Cartagena Protocol on Biosafety, 3rd ed. Montreal. Available from http://www.cbd.int/doc/handbook/cbd-hb-all-en.pdf (accessed May 2010)

Shvidenko A (2008) Deforestation. In: Jorgensen SE, Fath B (eds) Encyclopedia of Ecology. Elsevier, Oxford, pp 853-859

Sloan S (2007) Fewer people may not mean more forest for Latin American forest frontiers. Biotropica 39(4):443-446

Soisalo MK, Cavalcanti SMC (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. Biol Cons 129(4):487-496

Solomon S, Plattner G-K, Knutti R, Friedlingstein P (2009) Irreversible climate change due to carbon dioxide emissions. P Natl Acad Sci Usa 106(6):1704-1709

Solomon S, Qin D, Manning M et al (2007) Climate Change 2007: The Physical Science Basis, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Sork VL, Smouse PE (2006) Genetic analysis of landscape connectivity in tree populations. Landscape Ecol 21(6):821-836

Southworth J, Nagendra H, Tucker C (2002) Fragmentation of a landscape: Incorporating landscape metrics into satellite analyses of land-cover change. Landscape Res 27(3):253-269

Spangenberg JH (2007) Biodiversity pressure and the driving forces behind. Ecol Econ 61(1):146-158

Steininger MK, Tucker CJ, Ersts P et al (2001a) Clearance and fragmentation of tropical deciduous forest in the Tierras Bajas, Santa Cruz, Bolivia. Conserv Biol 15(4):856-866

Steininger MK, Tucker CJ, Townshend JRG et al (2001b) Tropical deforestation in the Bolivian Amazon. Environ Conserv 28(2):127-134

Steneck RS (2005) An ecological context for the role of large carnivores in conserving biodiversity. In: Ray JC, Redford KH, Steneck RS, Berger J (eds) Large carnivores and the conservation of biodiversity. Island Press, Washington DC, pp 9-33

Superintendencia Agraria (2001) Cobertura de Uso Actual de la Tierra 2001. Available from http://essm.tamu.edu/bolivia/info_geoespacial_vector_es.htm (accessed July 2010)

Suter W, Bollmann K, Holderegger R (2007) Landscape permeability: from individual dispersal to population persistence. In: Kienast F, Wildi O, Ghosh S (eds) A changing world: challenges for landscape research. Springer, Dordrecht, pp 157-174

Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: A review of the concepts, evidence, and applications. Biol Rev 85(1):35-53

Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. Oikos 68(3):571-573

Taylor PD, Fahrig L, With KA (2006) Landscape connectivity: a return to the basics. In: Crooks KR, Sanjayan M (eds) Connectivity conservation. Cambridge University Press, New York, pp 29-43

Telles MPdC, Diniz-Filho JAF, Bastos RP et al (2007) Landscape genetics of *Physalaemus cuvieri* in Brazilian Cerrado: Correspondence between population structure and patterns of human occupation and habitat loss. Biol Cons 139(1-2):37-46

Theodorou K, Souan H, Couvet D (2009) Metapopulation persistence in fragmented landscapes: Significant interactions between genetic and demographic processes. J Evolution Biol 22(1):152-162

Tole L (2006) Measurement and management of human-induced patterns of forest fragmentation: A case study. Environ Manage 37(6):788-801

Tollefson J (2009) Paying to save the rainforests. Nature 460(7258):936-937

Townsend CR, Begon M, Harper JL (2003) Essentials of ecology, 2nd ed. Blackwell Science Ltd, Oxford

Trani MK, Giles Jr RH (1999) An analysis of deforestation: Metrics used to describe pattern change. Forest Ecol Manag 114(2-3):459-470

Turner MG, Gardner RH, O'Neill RV (2001) Landscape ecology in theory and practice: Pattern and process. Springer-Verlag, New York

Turner MG, O'Neill RV, Gardner RH, Milne BT (1989) Effects of changing spatial scale on the analysis of landscape pattern. Landscape Ecol 3(3-4):153-162

UMASS (2000) Fragstats metrics. Available from http://www.umass.edu/landeco/research/fragstats/documents/Metrics/Metrics%20TOC.htm (accessed July 2010)

UNFPA (2008) State of World Population – Demographic, Social and Economic Indicators. Available from http://www.unfpa.org/swp/2008/presskit/docs/en_indicators-sowp08.pdf (accessed July 2010)

USAID / Bolivia (2002) USAID / Bolivia's Country Strategy 2004-2009, Bolivia Country Analysis of Tropical Forests and Biological Diversity. ARD Inc. Available from http://bolivia.usaid.gov/StudiesAndReports/US/BoliviaReport-English.pdf (accessed May 2010)

USAID / Bolivia (2008) Bolivia tropical forestry and biodiversity assessment – final report. ARD Inc. Available from http://pdf.usaid.gov/pdf_docs/PNADO440.pdf (accessed May 2010)

Van Laake PE, Sánchez-Azofeifa GA (2004) Focus on deforestation: Zooming in on hot spots in highly fragmented ecosystems in Costa Rica. Agric Ecosyst Environ 102(1):3-15

Vanclay J, Kaimowitz D, Puntodewo A, Mendez P (1999) Spatially explicit model of deforestation in Bolivia. In: Laumonier Y, King B, Legg C, Rennolls K (eds) Data Management and Modelling using Remote Sensing and GIS for Tropical Forest Land Inventory. Rodeo, Jakarta, pp 371-382

Vandermeer J, Lin BB (2008) The importance of matrix quality in fragmented landscapes: Understanding ecosystem collapse through a combination of deterministic and stochastic forces. Ecol Complex 5(3):222-227

Venter O, Laurance WF, Iwamura T et al (2009) Harnessing carbon payments to protect biodiversity. Science 326(5958):1368

Visconti P, Elkin C (2009) Using connectivity metrics in conservation planning – when does habitat quality matter? Divers Distrib 15(4):602-612

Walters S (2007) Modeling scale-dependent landscape pattern, dispersal, and connectivity from the perspective of the organism. Landscape Ecol 22(6):867-881

Watts K, Handley P (2010) Developing a functional connectivity indicator to detect change in fragmented landscapes. Ecol Indic 10(2):552-557

Wiegand T, Revilla E, Moloney KA (2005) Effects of habitat loss and fragmentation on population dynamics. Conserv Biol 19(1):108-121

Wiens JA (1996) Wildlife in patchy environments: metapopulations, mosaics, and management. In: McCullough DR (ed) Metapopulations and wildlife conservation. Island Press, Washington DC, pp 53-84

Williams M (2000) Dark ages and dark areas: global deforestation in the deep past. J Hist Geogr 26(1):28-46

Wu XB, Thurow TL, Whisenant SG (2000) Fragmentation and changes in hydrologic function of tiger bush landscapes, south-west Niger. J Ecol 88(5):790-800

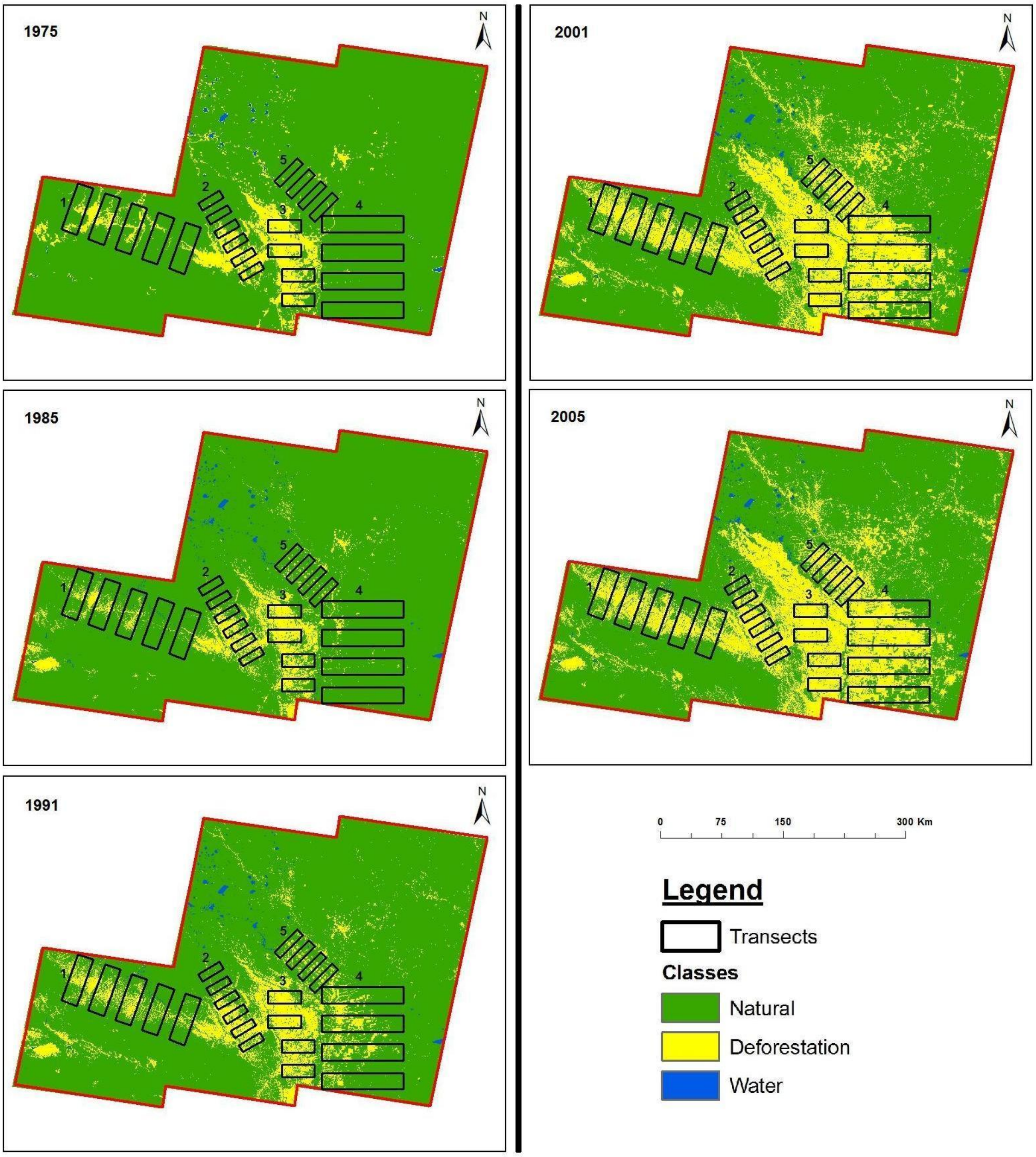
Young A, Boyle T, Brown T (1996) The population genetic consequences of habitat fragmentation for plants. Trends Ecol Evolut 11(10):413-418

Zeller KA (2007) Jaguars in the New Millennium Data Set Update: The State of the Jaguar in 2006. Wildlife Conservation Society, New York

Zipperer WC (1993) Deforestation patterns and their effects on forest patches. Landscape Ecol 8(3):177-184

9. APPENDICES

Appendix A: Development of deforestation within the study area (1975-2005) (1 – Chapare, 2 – Northwest colonisation zone, 3 – Integrated zone, 4 – Southern expansion zone and 5 – Northern expansion zone)



Appendix B: Landscape metrics results in a tabular form

Percentage of natural vegetation cover										
	SA 1		***SA 2***		***SA 3***		***SA 4***		***SA 5***	
Year	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**
1975	93.71	2.14	74.49	9.60	49.95	6.77	99.70	0.16	98.96	0.33
1986	88.16	3.68	63.81	11.79	39.34	6.92	86.55	11.40	90.77	0.74
1991	75.74	4.94	57.38	12.58	29.04	5.27	70.95	11.94	79.29	1.03
2001	53.18	2.45	34.24	10.66	11.01	2.65	36.73	8.32	37.49	5.76
2005	53.13	2.43	33.56	10.76	9.56	2.12	35.69	7.81	37.00	5.60
Mean Euclidian nearest neighbour distance (m)										
	SA 1		***SA 2***		***SA 3***		***SA 4***		***SA 5***	
Year	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**
1975	80.14	3.43	76.96	5.49	108.32	10.28	50.60	16.98	81.60	2.74
1986	81.36	2.89	82.04	5.94	116.87	15.68	90.12	9.88	83.08	3.68
1991	80.24	1.51	78.15	3.34	89.85	3.56	95.73	5.47	88.96	4.80
2001	95.85	2.12	101.72	7.15	120.54	6.20	124.18	4.29	116.40	9.04
2005	95.68	2.21	100.74	5.86	124.98	6.40	115.90	6.73	111.75	7.26
Patch density (patches/100 ha)										
	SA 1		***SA 2***		***SA 3***		***SA 4***		***SA 5***	
Year	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**
1975	0.72	0.27	1.49	0.87	2.39	1.02	0.01	0.00	0.02	0.01
1986	1.49	0.51	2.40	1.13	3.10	1.34	1.59	1.58	0.70	0.25
1991	3.22	0.80	3.40	1.46	4.37	1.81	2.45	2.15	1.41	0.42
2001	3.67	0.18	3.57	1.12	2.84	0.45	1.34	0.16	2.39	0.49
2005	3.65	0.19	3.48	1.11	2.40	0.26	1.24	0.09	2.30	0.45
Edge density (m/ha)										
	SA 1		***SA 2***		***SA 3***		***SA 4***		***SA 5***	
Year	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**
1975	12.16	3.86	28.15	10.83	31.42	4.31	0.61	0.27	2.01	0.72
1986	21.46	5.82	38.90	14.23	33.99	8.02	14.17	12.35	12.89	2.81
1991	48.48	8.61	49.76	16.12	46.17	12.54	27.20	16.33	25.48	3.44
2001	44.33	4.10	37.79	7.50	23.48	3.86	20.37	2.23	35.64	3.45
2005	44.18	4.14	37.14	7.42	20.13	3.09	20.62	2.05	34.94	3.30
Integral index of connectivity										
	SA 1		***SA 2***		***SA 3***		***SA 4***		***SA 5***	
Year	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**	**MEAN**	**SE**
1975	0.86	0.05	0.55	0.16	0.18	0.06	0.99	0.00	0.98	0.01
1986	0.72	0.10	0.42	0.17	0.10	0.04	0.93	0.04	0.82	0.01
1991	0.43	0.06	0.36	0.17	0.04	0.01	0.58	0.09	0.62	0.01
2001	0.13	0.01	0.11	0.08	0.00	0.00	0.07	0.03	0.07	0.03
2005	0.13	0.01	0.11	0.08	0.00	0.00	0.06	0.03	0.07	0.03