RESEARCH ARTICLE

The effect of land use change and ecotourism on biodiversity: a case study of Manuel Antonio, Costa Rica, from 1985 to 2008

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Abstract Development in biodiversity rich areas is of global concern. While development may lead to socioeconomic benefits, this often comes concomitant with biodiversity loss and deforestation. Biodiversity rich areas present the opportunity for both improvements in socioeconomic conditions and conservation; however numerous challenges exist. Costa Rica's Manuel Antonio National Park presents an ideal case study to investigate the balance between alternative forms of development which have contrasting environmental impacts. The Manuel Antonio region is a highly dynamic landscape experiencing deforestation, from agriculture, cattle ranching and oil palm plantations; and also reforestation from abandonment of land holdings and nature oriented tourism. Landscape dynamics are closely intertwined with the livelihoods and perspectives on biodiversity conservation of local communities, determining ecological sustainability. We use an analysis combining multi-temporal remote sensing of land cover dynamics from 1985 to 2008 with questionnaire data from local families on their socioeconomic status, perspectives on conservation, and perceived changes in local wildlife populations. Our results show that, while regeneration occurred and forest fragmentation in the area decreased from 1985 to 2008, Manuel Antonio National Park is rapidly becoming isolated. Decreasing ecological connectivity is related to the rapid expansion of oil palm plantations adjacent to the park and throughout the lowland areas. Perceived decreases in wildlife abundance and compositional change are evident throughout the area, with local communities attributing this primarily to illegal hunting activities. Nature based tourism in the area presents an effective strategy for conservation, including reductions in hunting, through increased valuation of biodiversity and protected

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areas, and socioeconomic advantages. However, without urgent efforts to limit deforestation and preserve the remaining forested corridor connecting the park to core primary forest, the ability to maintain biodiversity in the park will be reduced.

Keywords Biological corridor · Secondary forests · Land use and land cover change · Sustainable development · Remote sensing

Introduction

Human land use activities have transformed the planet (Foley et al. 2005), resulting in unintended consequences to the natural environment (DeFries et al. 2004). Land-use related change is now considered the primary driving force of biodiversity loss worldwide (Vitousek et al. 1997), especially in tropical ecosystems (Sala et al. 2000). Costa Rica, in particular, presents some of the world's greatest challenges and opportunities for biodiversity conservation. While being one of the world's richest hotspots of biodiversity (MINAE 1992; Soto 1992; Myers et al. 2000), it also has had among the most rapid rates of deforestation (FAO 1990; Jha and Bawa 2006). Costa Rica has sought to address this through the declaration of a globally renowned network of nature reserves—encompassing more than 15% of its land area (Boza 1993).

Natural protected areas have been shown to be an effective strategy for preserving biodiversity and limiting deforestation (Bruner et al. 2001). However, adjacent forested areas are being rapidly cleared or fragmented (DeFries et al. 2005), in part as a result of population growth through migration for tourism related jobs (Wittemyer et al. 2008). Such changes are resulting in the increasing ecological isolation of parks globally (DeFries et al. 2005). Similarly, such dynamics are occurring in Costa Rica's parks, where the loss of tropical forest and ecological connectivity (Goodwin 2003) has been rapid and extensive (Sánchez-Azofeifa et al. 2001, 2003). Causes include rapid touristic development and other concomitant changes in land cover, i.e., oil palm plantations or cattle ranching, which reduce and fragment remaining contiguous forest areas and decrease their ecological connectivity to other natural habitats (Sánchez-Azofeifa et al. 2002; Van Laake 2004). Oil palm plantations

are of particular concern as they are one of the world's most rapidly increasing crops (Fitzherbert et al. 2008). Biodiversity loss also occurs through conversion of native ecosystems to plantations (Curran et al. 2004), which function as barriers to animal movement (Fitzherbert et al. 2008) and support low native biodiversity (Edwards et al. 2010). On the positive side, oil palm plantations provide employment to often-isolated communities with few other local economic opportunities (Koh and Wilcove 2007).

Costa Rica has responded to the rapid loss of connectivity through, among many activities, participation in development of a Mesoamerican Corridor—encompassing 85 Costa Rican protected areas and 14.2% of its national territory—designed to maintain viable wildlife populations (Miller et al. 2001). Although, under optimal conditions, biological corridors may augment wildlife populations of smaller natural areas (Beier and Noss 2010), corridors are easily subjected to negative anthropogenic influences due to their narrow width. In Costa Rica, with numerous smaller parks, hunting is of especial concern and its intensity has been shown to determine wildlife abundance levels within protected areas (Carrillo et al. 2000) and across the surrounding human dominated landscape (Daily et al. 2003). Hunting intensity within communities is, in some cases, controlled by poverty and improvements in income, education and healthcare have been suggested as possible methods to reduce wildlife consumption (Robinson and Bennett 2004).

Simultaneously, the Costa Rican Ministry of Tourism has sought to address the rapid, mostly tourism related, unregulated development occurring adjacent to its protected areas through establishment of the certification for sustainable tourism (CST) in 1997 (Rivera 2002)—a voluntary program that certifies each tourism company according to the ecological and social sustainability of their practices (http://www.turismo-sostenible.co.cr/en/). However, a clear understanding of how certified nature oriented hotels may contribute to biodiversity conservation does not exist (Gössling 1999), especially when considering the multitude of possible land use pressures (Alpízar 2006).

Effective conservation strategies differ between areas with touristic potential versus less accessible areas. For long-term sustainability of natural parks having high touristic potential, both ecologically and as destinations for nature tourists, biodiversity must be

maintained. Although increased nature oriented tourism can promote greater conservation of natural areas (Aylward et al. 1996) and development of a conservation mentality in local communities (Almeyda Zambrano et al. 2010a), it has in some cases resulted in increased deforestation and forest fragmentation from development and unsustainable levels of visitation (Stem et al. 2003) with limited socioeconomic advantages (Campbell 1999). Changes in land cover dynamics are inter-related with changes in the social and economic dynamics of the families living and working in the region (Almeyda Zambrano et al. 2010b), and especially proximate to national parks (Andam et al. 2010), as well as with their perspectives on conservation and protected areas, which are often contentious topics in many countries (Schwartzman et al. 2000).

The main objective of this study was to evaluate how forest cover and ecological connectivity, resulting from the expansion of oil palm plantations and the development of nature based tourism, affects wildlife populations in the area surrounding Costa Rica's Manuel Antonio National Park (MANP). We investigated the interplay between these contrasting forms of development on both biodiversity conservation and socioeconomic improvement. To achieve this goal, we combined multi-temporal remote sensing analyses of land cover changes from the years 1985 through 2008 with in depth interviews with local families living in different environmental matrices, some of whom work for tourism operations in the area. The driving research question was: what is the effect of contrasting forms of development - nature oriented tourism and oil palm plantations - on wildlife populations and socioeconomic conditions in a biodiversity hotspot experiencing significant land use change? The study aims to provide a better understanding of the effects of tourism, land conversion and forest fragmentation on the viability of small, protected areas in human dominated landscapes.

Methods

Study area

Our study area was located on the Pacific Coast of Costa Rica within a 30 km radius surrounding the Manuel Antonio National Park (MANP) (Fig. 1). The park was established November 15th 1972 and encompasses approximately 620 ha of terrestrial surface, dominated by tropical wet forest, with an additional 55,000 ha of marine area. The Manuel Antonio region is considered a biodiversity hotspot (Myers et al. 2000), with the national park having more than 100 species of mammals and 180 species of birds (personal communication). A pronounced wet season extends from May to November. Costa Rica, in general, represents an ideal location to better understand the interplay between conservation and development as it is considered one world's leaders in biodiversity conservation (Sun 1988). To achieve this, Costa Rica reversed dramatic rates of historical deforestation resulting in more than 50% forest loss between 1940 and 1984 (Sader and Joyce 1988). The forest regrowth in the last two decades has occurred, among other reasons, as a result of government initiatives to promote carbon sequestration (Castro-Salazar and Arias-Murillo 1998) and conservation (Sánchez-Azofeifa et al. 2007), increased governance as shown through development of new forestry laws (Pfaff and Sánchez-Azofeifa 2004), and emigration for jobs in cities (Almeyda Zambrano et al. 2010b). Similar dynamics are occurring throughout the tropics (Chokkalingam and de Jong 2001).

MANP is one of the most visited and greatest income-generating parks within Costa Rica (Sterling 1999), experiencing increasing tourism and related development, including industrial and smaller scale eco-touristic hotels. The flat low-lying areas surrounding the park are ideal for agriculture, cattle ranching and, in particular, oil palm plantation development while proximate mountainous areas exist as potential repositories of biodiversity and reduced anthropogenic impact (Sader and Joyce 1988). The study area includes both deforestation occurring for agriculture, oil palm plantations, and forest regeneration occurring from the large-scale abandonment of previous pasture areas and nature oriented development and conservation (Sánchez-Azofeifa et al. 2001; Almeyda Zambrano et al. 2010a, b). The Manuel Antonio area has great potential to simultaneously conserve biodiversity and provide economic benefits to local communities. Understanding the challenges and successes at MANP is therefore directly relevant to developing effective conservation approaches in similar biodiversity rich areas attractive to ecotourism.
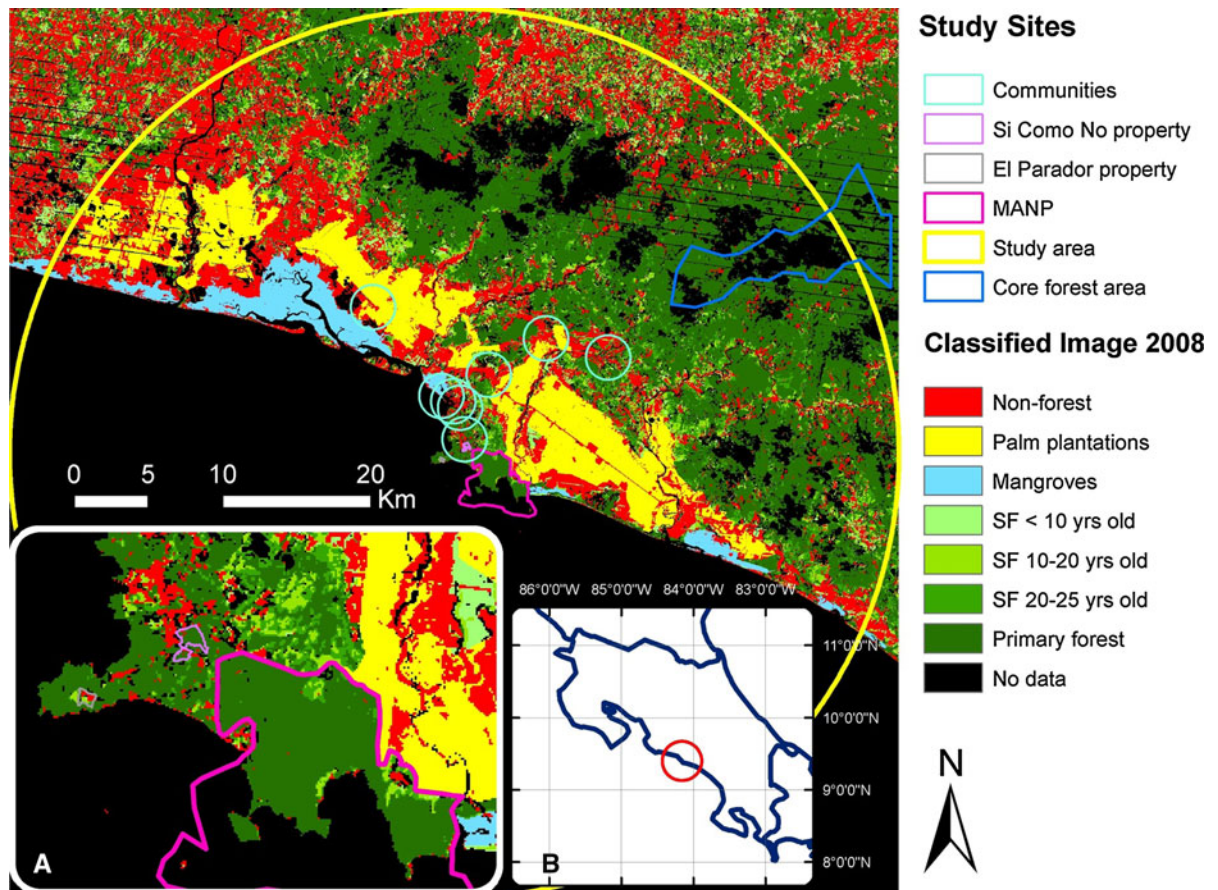
Fig. 1 Detailed forest classification map of the study area in the year 2008. *Insets* show: *A* a close up of the park (MANP) and hotel nature preserves; and *B* the general location of study area in Costa Rica. The *scale bar* applies to the overview map only

Study design

Our study design used a "nested-level" approach that combined land cover change analyses using remote sensing paired with participant observation-based ground assessment, interviews and questionnaires (Almeyda Zambrano et al. 2010a). The four levels of data collection and analysis were: landscape, community, hotel-park, and household. Landscape analyses encompassed a 30 km radius surrounding the MANP for a total of 110,000 ha. Community analyses included eight communities that were within the area of influence (in both spatial and cultural contexts) of the MANP. Hotel-park analyses included the MANP, with an area of approximately 620 ha, and two hotels ranked highly by Costa Rica's CST: Hotel *Sí Cómo No* with five CST leaves, and Hotel *El Parador* with four CST leaves. We delineated, using a handheld GPS unit (Garmin

GPSmap 60SCx), the borders of the hotel properties while the borders of the MANP were generated from existing maps. Each hotel had a private nature reserve within its property boundaries encompassing 14 ha for Hotel *Sí Cómo No* and 5 ha for Hotel *El Parador*. The *El Parador* property was located within a peninsula containing mostly intact forest area, with abundant wildlife including monkeys and sloths, but currently not under any protection status. We defined buffer zones for the park and hotels as the 1.5 km zone surrounding their borders. Community areas were defined using a 1.5 km radius around the community center. Household analyses included those directly employed by the park and hotels and those only indirectly affected (e.g., proximate). We used these complementary scales and methods at multiple locations to enable a more thorough understanding of the varied processes affecting biodiversity conservation in the region.

Spatial analyses

We developed multi-temporal maps of the dominant land cover types—forest, mangrove forest, oil palm plantation and non-forest areas —within our study area for the years 1985, 1990, 2000 and 2008 using eighteen Landsat satellite images at a spatial resolution of 30 meters (m) acquired from the USGS (http://glovis.usgs.gov/) (Appendix 1 in Supplementary Material). All remote sensing work was conducted using the ENVI/IDL remote sensing and programming software (ITTVIS, Inc., Boulder, CO, 2000–2010) and spatial analyses were conducted using ArcGIS (V. 9.2., Environmental Systems Research Institute, Inc., Redlands, Calif). Satellite images were georeferenced to two orthorectified Landsat images (RMSE <15 m.) generated through a NASA directive (http://glcf.umiacs.umd.edu/portal/geocover/). Validation GPS (global positioning system) points ($n = 184$) of primary forests (PF), secondary forests, mangroves, oil palm plantations and non-forest areas (i.e., urban, agriculture and pasture) were acquired in July 2009. The spectral angle mapper (SAM) routine in ENVI was used to classify all images as: (a) forest; (b) mangroves; (c) oil palm plantations; (d) non-forest; (e) water; (f) cloud; and (g) cloud shadow. Overall classification accuracy was 90% with a Kappa coefficient of 0.85. To reduce cloud interference and data gaps resulting from the 2003 Landsat ETM + scan line malfunction, multiple classifications covering the same study area during the same year were merged (Appendix 1 in Supplementary Material). One study area mask was generated from the final merged classifications which included any area of cloud, cloud shadow or no data pixel. This was then applied to all classification images, resulting in classification for 88% for the total study area. Using these we calculated a detailed map of primary and secondary forests for the year 2008. PF were defined as those pixels classified as forest in all 4 study years while secondary forest (SF) pixel ages were based on last known non-forest date. The final classes were: PF (>25 years old), SF 20–25 years old, SF 10–20 years old, SF < 10 years old.

The importance of deforestation, forest fragmentation, and topography on landscape dynamics have been previously identified in Costa Rica (Sader and Joyce 1988; Sánchez-Azofeifa et al. 2001, 2003). We investigated changes in these factors across our study area at a spatial scale of 30×30 m. First, we calculated the number of spatially separated forest fragments, and their area (ha), edge length (m) and edge to area ratio (m edge m-2 area) for each study year. Fragmentation analysis was conducted over the entire study area. Second, slope was derived using 10×10 pixel computation cell on a digital elevation model (DEM) of the study area (http://www2.jpl.nasa.gov/srtm/) resampled to 30 m from an original resolution of 90 m. The delineation of lowland areas (0–3° slope) versus mountainous areas (>3° slope) was conducted following visual analysis of the distribution of land cover classes in the Manuel Antonio area. Third, we generated a Euclidean distance (m) map to the park border using the Spatial Analyst extension of ArcGIS. One quarter of the spatial topography and distance data within the study area were randomly selected to avoid spatial auto-correlation issues. Linear regressions were used to identify correlations between land cover dynamics and slope, elevation and distance to park borders. We quantified ecological connectivity between communities and hotel properties and core PF—identified using the detailed 2008 forest age classification. Connectivity was calculated using least cost paths from the park border, the Hotel *El Parador* and Hotel *Sí Cómo No* properties, and the community center points to the core primary forest (Rouget et al. 2006). For this purpose, we assigned relative movement costs to the main land cover classes as follows: 1 for forest, 2 for mangroves, 3 for oil palm plantation, and 4 for non-forest pixels. For this calculation the forest category included both primary and secondary forest as our methods did not permit separation of these classes prior to 2008 and our connectivity analyses extended from 1985 to 2008. Assigned cost values were based on a general review of the related literature and used for spatial and temporal comparisons of land cover change rather than as directly biologically meaningful values.

Socioeconomic analyses

Socioeconomic data were collected to enable comparison of: (a) households working, versus not, in tourism; (b) perceptions of biodiversity conservation; and (c) linkages between these variables. Data were collected through participant observation, interviews and questionnaires during July–August 2009. At the

Table 1 Forest fragmentation and land cover from 1985 to 2008

Study area	Study year			
	1985	1990	2000	2008
Fragments (<1 ha)	6,228	5,066	4,364	2,998
Fragments (>1 ha)	1,140	824	652	509
Median patch size (m²)[a]	24,300	26,100	24,368	26,100
Median edge (m)[a]	1,080	1,080	1,026	1,080
Edge/area ratio	0.0429	0.0415	0.0424	0.0413
Total area in largest fragment (%)	81.7	83.3	86.4	88.7
Lowland forest (%)	13	19	26	23
Lowland palm (%)[b]	19	23	27	31
Lowland non-forest (%)	60	49	37	37
Mountainous forest (%)	57	69	79	77
Mountainous palm (%)[b]	0	0	0	0
Mountainous non-forest (%)	43	31	20	22

[a] Includes only fragments >1 ha in area

[b] Palm refers to oil palm plantations

landscape level we interviewed MANP guides and management, hotels owners, management, staff and neighbors about the development of the study area. At the household scale, we conducted in-depth questionnaires with 121 heads of households. The random sample included employees from each hotel: Hotel *Sí Cómo No* ($n = 37$), Hotel *El Parador* ($n = 41$), as well as non-employee neighbors ($n = 43$). The questionnaire, provided in Spanish, covered the general themes: household demography and economy, education, perceptions of tourism, use of natural resources, including hunting, and perceptions of wildlife abundance and composition. Non-parametric statistics were used for all analyses.

Wildlife analyses

We collected wildlife data at the household scale as part of the in-depth questionnaires with heads of households. Wildlife related questions were administered to households that had lived in the Manuel Antonio area for at least 5 years ($n = 90$). Questions focused on the perception of changes in wildlife abundance and its causes and changes in the abundance of key wildlife groups. Spatial analyses were conducted by extracting the: (a) percent forest and mangrove cover (year 2008); (b) percent regrowth (year 1985–2008); and (c) ecological connectivity. These were then categorized as low, medium or high,

using 33 and 66% as thresholds. We used a logistic regression to gauge the relationship between household residence time and perceived changes in wildlife populations. We acknowledge that perceived wildlife abundance requires additional care in interpretation over that of direct measurements (i.e., camera traps), but no other method allowed for multi-temporal analysis of wildlife composition and abundance in this area. All statistics were conducted using JMP software (V.7. SAS Institute Inc., Cary, NC, 1989–2007) and a significance value of 0.05 were considered for all tests.

Results

Spatial analyses

At the landscape scale, forest cover and oil palm plantations increased from 44 to 58% and from 8 to 14%, respectively, between 1985 and 2008 (Appendix 2 in Supplementary Material). The rate of establishment of new oil palm plantations reduced from 1990 (469 ha year^{-1}) to 2000 (216 ha year^{-1}). Oil palm plantations existed only in the lowlands (from 19% in 1985 to 31% in 2008), with new areas being established on an increasing proportion of previously forested areas (9% in 1990 to 23% in 2008), resulting from decreasing availability of non-forest areas
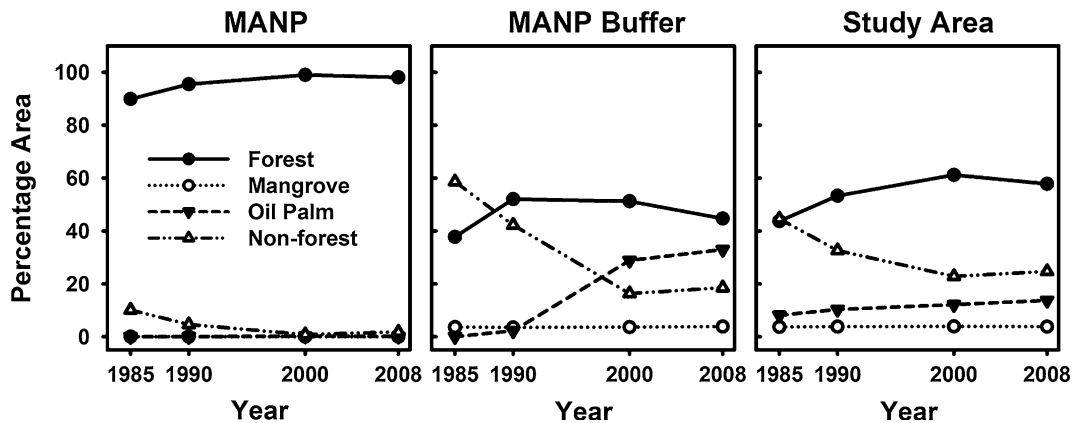
Fig. 2 Land cover change (% area) from 1985 to 2008 within the Manuel Antonio National Park (MANP), its buffer (1.5 km), and across the entire study area

(Table 1). In 2008, palm plantations occupied most of the coastal areas of the study area, and thus directly bordered the entire North–East section of park (Fig. 1). In addition, we found a 33% increase in plantation area from 1986 to 2008 within the park buffer as compared to 6% over the entire study area (Fig. 2). Regression analyses revealed increasing oil palm area and decreasing forest area closer to the MANP, as well as the importance of increasing elevation and slope on limiting oil palm plantation expansion. MANP showed regrowth from 1985 to 2008, with forest area increasing from 90 to 98%—the highest forest cover for any of our study sites—followed by the hotel properties (92%). The MANP and *Sí Cómo No* properties were dominated by primary forest while the *El Parador* property was half secondary forest (Fig. 3). The park had 50% more forest cover than its buffer, Hotel *Sí Cómo No* had 6% more, whereas the Hotel *El Parador* had 28% less (Appendix 2 in Supplementary Material). In 2008, the hotels' nature reserves were connected to the MANP via intact forest and were likely important to the size of the park's contiguous forest area as well as to help mitigate ecological repercussion of adjacent development. Forest cover within our study communities decreased with increasing distance from the park boundaries (83–6%).

From 1985 to 2008, the number of forest fragments at the landscape level decreased while their median area increased and the percentage of all forest in the largest contiguous forest fragment increased from 82 to 89% (Table 1). Although ecological connectivity increased from 1985 to 2008 for all sites as a result of regrowth, most paths now converge through a small

forested gap remaining between palm plantations to the north east of MANP (Fig. 4). A possible biological corridor (800 m wide) was identified which encompassed 1500 ha and has undergone extensive regrowth (20%). In 2008, the corridor was composed of 59% primary forest, 22% secondary forest, and 18% non-forest (Appendix 2 in Supplementary Material). A portion of the corridor integrated the *Sí Cómo No* nature reserve.

Socioeconomic analyses

Approximately half of the households interviewed—working for tourism or not—were born in the study area. Households involved in tourism were younger, had more years of education, fewer dependent children and lived significantly less time in the MANP area than those having other forms of employment (Appendix 3 in Supplementary Material). Tourism related households had significantly greater income and savings (2–3 times greater) and spent more on the "other" category after covering the basic household's needs, while spending significantly less on food and transportation resulting from hotel related benefits (Appendix 4 in Supplementary Material).

Tourism was, on average, perceived to have positive effects on biodiversity through increased values of flora and fauna and decreased hunting and deforestation. Although the two hotels were perceived to have greater positive impacts for all categories Hotel *Sí Cómo No* had significantly greater positive effects on deforestation and value of flora and fauna. Tourism was perceived to have both positive and
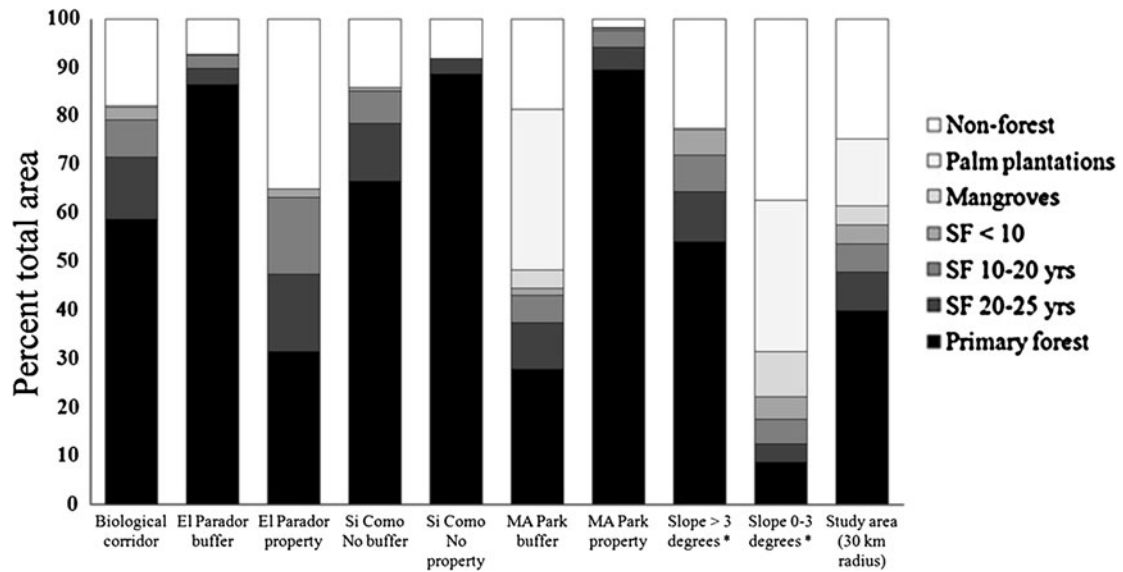
Fig. 3 Land cover classes (% area) in the year 2008 within selected study sites, including the Manuel Antonio National Park (MA), and their adjacent buffer areas (1.5 km)
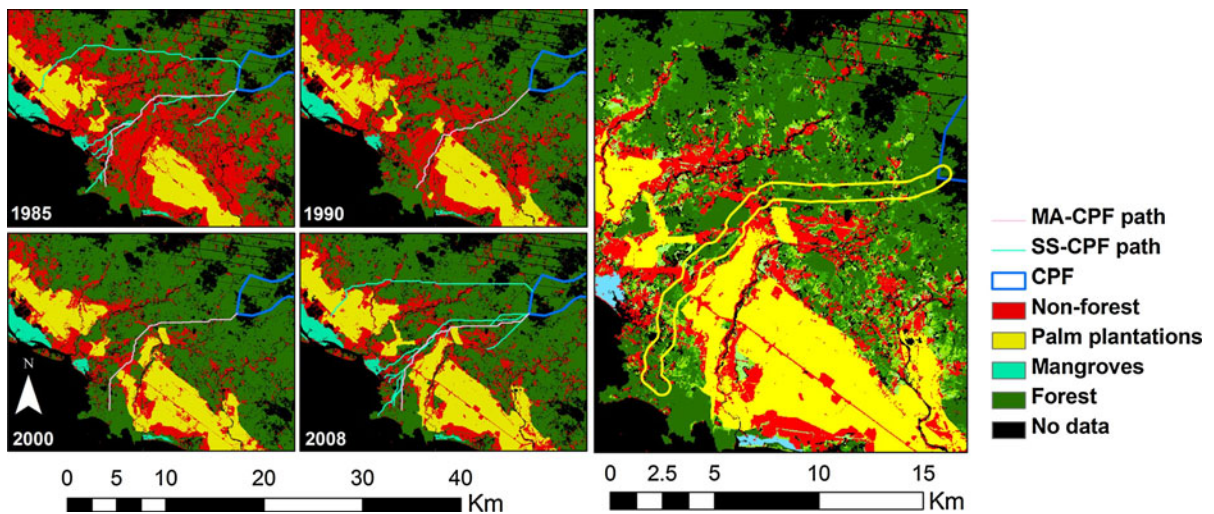

Fig. 4 Least cost paths between all study sites (SS), including the Manuel Antonio National Park (MA) and core primary forest (CPF). The proposed biological corridor (800 m width) location is provided in the right inset

negative effects on socioeconomic conditions. Positive effects were increased health, education and job training opportunities. Negative effects were increased land and product prices, as well as alcoholism, drug addiction, and prostitution (Table 2) by both tourists and locals. The two hotels were perceived as having a more positive effect than tourism in general for all variables with the exception of education.

Sixty-seven percent responded that the local forest was disappearing and 100% of respondents' felt it was important to conserve the remaining forest. When asked why it was important to conserve the forest (Table 3), the respondent's top three answers were: (1) save the animals ($n = 36$); (2) provide clean air ($n = 33$); and (3) attract tourism ($n = 19$). Ninety-two percent of respondents felt it was important to have natural protected areas, with the top three reasons being: (1) attract tourists ($n = 48$); (2) protect the animals ($n = 46$); and (3) protect the environment in general ($n = 20$) (Table 3). Many residents

Table 2 Perceived impacts of the *Sí Cómo No* (SCN) and *El Parador* (EP) hotels versus tourism in general (T)

Category	Mean ± Std. Dev. (N)			P value	
	SCN	EP	T	SCN	EP
Health	1.6 ± 0.9 (33)	2.0 ± 0.9 (32)	2.5 ± 0.8 (104)	<0.0001	0.0766
Education	1.8 ± 0.8 (32)	2.0 ± 1.0 (33)	1.9 ± 0.9 (104)	1	0.1865
Job training	1.7 ± 0.9 (31)	1.5 ± 0.8 (29)	1.9 ± 1.0 (96)	0.0699	0.2064
Hunting	1.8 ± 0.7 (32)	1.9 ± 1.0 (32)	2.1 ± 0.9 (95)	0.4743	0.8312
Deforestation	1.7 ± 0.7 (31)	2.3 ± 1.1 (33)	2.7 ± 1.4 (100)	<0.0001	0.2089
Value of flora and fauna	1.2 ± 0.6 (33)	1.5 ± 0.7 (35)	1.6 ± 0.9 (107)	0.0006	0.5206
Land price	3.2 ± 1.1 (33)	3.0 ± 0.9 (32)	3.3 ± 0.8 (104)	0.3441	0.5608
Products price	3.2 ± 0.9 (33)	3.1 ± 0.9 (35)	3.6 ± 1.1 (103)	0.0368	0.1022
Alcoholism	2.7 ± 0.5 (32)	2.8 ± 0.7 (33)	3.4 ± 0.8 (101)	<0.0001	0.0002
Drug addiction	2.8 ± 0.6 (31)	2.8 ± 0.8 (34)	3.7 ± 0.9 (104)	<0.0001	<0.0001
Prostitution	2.7 ± 0.8 (30)	2.5 ± 0.9 (32)	4.0 ± 1.0 (94)	<0.0001	<0.0001

Ranks range from 1–5; values >3 indicate a negative impact and <3 a positive impact. The matched pairs statistical analysis was used for mean comparisons

reported having changed their behaviors, stopped hunting, and started working to increase regrowth as a result of feeling it could increase their economic wellbeing. Even in remote communities with little tourism, many expressed a desire to reforest areas and conserve the wildlife populations in the hope of attracting tourists to their area. A similar sentiment was expressed for mangrove conservation. There was no statistical difference in "feeling if protected areas were important" between % forest classes.

Wildlife analyses

Eighty-seven species, dominated by mammals, birds and reptiles, were identified as among the top five most common at arrival or at present. Eighty percent of respondents stated that the abundance of wildlife in general, and specifically large cats and wild pigs, had declined since their arrival to the area, versus 14 and 6% for had increased and no change, respectively. The tepezcuintle (*Cuniculus paca*), macaw (*Ara spp.*) and white-tailed deer (*Odocoileus virginianus*) were identified as previously common species no longer seen. No significant relationship was detected between time of residence and perceived changes in wildlife populations across all communities or for changes in wildlife populations for communities having more forest, greater regrowth or increased ecological connectivity. Monkeys (Ceboidea, several species), iguanas (Iguanidae, several species) and raccoons (Procyonidae, several species) were reported as among the five most abundant animals at present. The leading reported causes for the perceived decline in wildlife were: (1) hunting (36%); (2) construction (24%); and (3) deforestation (22%). We expected that wildlife populations in more forested communities would have declined for reasons different from the declines in wildlife in general. However, when asked the primary reasons for wildlife population changes, hunting was ranked number one regardless of the surrounding land cover. Our semi-structured interviews with park officials and guides highlighted that within the MANP and immediate surrounding areas, forest fragmentation and uncontrolled development of hotels were perceived as the most important factors negatively impacting wildlife populations. Hunting, including the collection of turtle eggs, was stated to occur primarily outside the MANP boundaries. The increasing isolation of the park, however, was evidenced by the lack of large mammals which indicated that the current extent and connectivity of existing natural habitats are insufficient (Chiarello 1999; Newmark 1996).

Discussion

Conservation strategies based on parks and nature-based tourism requires consideration of accessibility, biodiversity, and political stability. They must include a legally delineated system of natural areas with

Table 3 Ranked household perceptions of most important reasons to protect forest and for having natural protected areas

Category	Most important reasons N (rank)*	
	To protect forests	To have natural protected areas
So the animals can live	36 (1)	0
Pure air	33 (2)	9
Attractive to tourists	19 (3)	48 (1)
Clean water	16	11
So our children can see it/plants and animals	13	5
Conservation/Protection of the environment	11	20 (3)
Conservation of plants and animals	10	20 (3)
The source of life	9	0
Prevent global warming	8	0
Nature is beautiful	6	0
Protect the plants	0	10
Recreation	0	10
To protect the animals, there is no hunting	0	46 (2)
To stop humans from destroying it	0	14

adequate governance, effective employment of local populations, and be an economically competitive alternative to other land use practices (Defries et al. 2007; Fitzherbert et al. 2008; Yaap et al. 2010). Biodiversity conservation becomes more complex when multiple viable land uses exist and trade-offs become necessary. In biodiversity rich and tourist friendly areas, such as the Manuel Antonio area, conservation can best occur using an approach combining public and private protected areas, including national parks, ecotourism ventures, and private properties. Regrowth in abandoned agricultural fields or pastures due to increased land values or migration to cities may reduce forest fragmentation (Moran et al. 1996)—sometimes at the expense of the wellbeing of local communities. Further study of the interactions, feedbacks and trade-offs between household social and economic factors and conservation is crucial to simultaneously address livelihood and conservation needs.

Although parks can present an effective conservation strategy (Bruner et al. 2001), many parks globally

have shown encroachment and the park system in Costa Rica has been described as "inadequately funded, minimally policed, and threatened by encroachment" (Brockett and Gottfried 2002). As a result, the integrity of the MANP forest cover throughout our study period was contrary to our expectations and likely a result of both the small size, and therefore easier policing, of the park, as well as apparently effective park policies towards protection against encroachment, as has been found in other parks globally (Hayes 2006). Additional threats to parks however exist and include fragmentation and ecological isolation from other intact forest areas.

One important source of fragmentation and ecological isolation at present is oil palm plantations. Oil palm plantations are one of the most rapidly expanding forms of agriculture in tropical regions today (Tilman et al. 2001; Fitzherbert et al. 2008). Although oil palm plantations do present employment opportunities, often in self-contained communities with schools, health care and infrastructure (Koh and Wilcove 2007), their rapid growth throughout the tropics is problematic. Recent studies have shown that palm plantations are very low in diversity, with abandoned pastures supporting higher species richness (Fitzherbert et al. 2008), and act as barriers to animal movement (Edwards et al. 2010). Like findings in Southeast Asia by Koh et al. (2011), we found palm plantation establishment occurred increasingly on previously forested lands as the availability of easily converted non-forested lowland areas declined. This is contrary to many oil palm producers' arguments that palm plantations do not represent a threat to biodiversity as they are established on disturbed forests or old croplands (Koh and Wilcove 2007). Similar dynamics were identified by Koh (2008) who found that ameliorating the negative impacts of oil palm plantations directly was not viable and suggested that the focus should instead by on maintaining remaining natural forests and creating buffer zones around oil palm estates.

Given the negative ecological repercussions of forest conversion a 'win–win' scenario would have local communities employed in ecological sustainable enterprises, especially in areas of high biodiversity. Nature tourism represents one possible solution. To be effective it should: (a) have minimal environmental impact, (b) promote conservation, and (c) improve local livelihoods (Ceballos-Lascurrain 1987;

Scheyvens 1999; Christ et al. 2003). Similar to previous studies (Almeyda Zambrano et al. 2010a, b) we found this 'win–win' scenario could exist as households employed by nature oriented tourism often have socio-economic advantages over those with non-tourism related employment, including at oil palm plantations. In addition, nature oriented hotels—as found in our study—sometimes have private nature reserves resulting in the maintenance, or regeneration, of forest cover. However, while nature oriented tourism was perceived to have mostly positive socio-economic effects, versus tourism in general, negative effects, such as the increase of land and product prices, remained. Complicating matters, improvements in household economy do not necessarily correlate to increased conservation or valuation of biodiversity—conversely, they sometimes lead to increased environmental degradation (Rock 1996).

The perceptions of biodiversity held by local communities play a key role in determining whether conservation efforts succeed or fail (Abbot et al. 2001). To maximize conservation we recommend a two pronged approach to environmental education, that: (a) emphasizes the unique cultural and environmental value of biodiversity to the local communities; and (b) highlights the economic importance that biodiversity plays in the local areas. Tourism can play a critical role in local residents' perception of the value of fauna, flora and conservation. However, in our study area, the perceived biodiversity benefits of nature oriented tourism and the high importance of forests and natural protected areas being developed within local communities had yet to translate to an increase in wildlife abundance or change in hunting behavior. This ongoing hunting pressure has been demonstrated for other national parks in Costa Rica where reductions in hunting vigilance resulted in immediate increases in hunting activities and concomitant declines in wildlife populations (Carrillo et al. 2000). This disjunction may be a result of ongoing poverty requiring subsistence activities. Alternatively, hunting may be seen as part of the local culture and not contradict their valuation of biodiversity and protected areas—although the majority of interviewed households perceived hunting as a negative impact.

In this context, the viability of an ecological corridor approach faces two main challenges: (a) is it feasible to establish an ecological corridor of sufficient size across this landscape where other land uses are potentially more economically rewarding? And (b) if feasible can an isolated reserve of insufficient size to support large animal species benefit from increased connectivity? In our study area an ecological corridor is likely more feasible than in more remote-less touristic locations due to the high income (the greatest of any Costa Rican protected area; Sterling 1999) of the MANP relative to its size. In addition, income from ecotourism and the interest of even remote communities to participate in ecotourism activities provide added leverage to offset other land use possibilities. Given the extensive areas already occupied by oil palm plantations and their desire to appear green (Koh and Wilcove 2007), opportunity may exist to include such companies in the effort to increase ecological connectivity of the MANP. If such a corridor becomes feasible, will it be useful? Studies addressing this topic have showed that corridor utility differs by species group, with few benefits identified for boreal bird species (Hannon and Schmiegelow 2002), but found to be the most efficient approach for mammal conservation in Eastern North America (Gurd et al. 2001). Simberloff et al. (1992) highlight this issue and present the argument that corridors and other landscape conservation approaches are not mutually exclusive. The value of an approach simultaneously integrating protected areas, conservation corridors and landscape permeability is highlighted by Kostyack et al. (2011). Such an effort would necessarily include the MANP, ecotourism and private nature reserves, community based initiatives for reforestation and biodiversity conservation and cooperation—or involvement—of oil palm producers.

The methods used in this study have several caveats: (a) our remote sensing approach did not allow identification of secondary forest age prior to 2008. While for immediate conservation purposes this is sufficient, improvements to this method would be required to better understand the temporal dynamics of wildlife populations in our area; (b) while secondary forests are clearly superior to pasture or oil palm plantations for supporting fauna, their value has not been well defined (Bowen et al. 2007). A more detailed literature review coupled with field studies is required to enable better allocation of pixel costs for quantification of ecological connectivity; and (c) our study did not directly address linkages between the spatial configuration of remaining habitat and fauna dynamics (McAlpine et al. 2006).

Conclusions

Although we found net regrowth in the study area over the interval 1985–2000, we also found that MANP is becoming increasingly isolated from core primary forest areas in the nearby mountainous regions. Areas immediately to the North–West of the park have undergone more consistent regrowth, due in part to nature-based ecotourism with private protected areas. Ecotourism activities resulted in additional economic and educational gains by households directly employed as well as by those in surrounding areas. In spite of regrowth, wildlife populations are widely perceived to be in decline throughout both the area surrounding the park and in outlying communities. This decline is attributed primarily to ongoing hunting activities among local communities, habitat fragmentation and continued deforestation. Efforts to maintain viable wildlife populations within the park and to maintain connectivity between the park and core primary forest areas in the mountains will be impeded until better regulation of hunting takes place. In addition, regardless of hunting activities, oil palm plantations pose an increasing threat to the park, given their encirclement directly adjacent to the MANP border. Further oil palm expansion could soon isolate the park geographically, as the last remaining forested corridor connecting the park to core primary forest areas is cut off. Similar dynamics of fragmentation and isolation, in particular from the expansion of palm plantations, are likely occurring throughout the many low lying park areas in Central America and will be the focus of future research.

Based on the results of this study we recommend the following be conducted for conservation areas undergoing similar land use pressures: (a) calculation of standardized movement costs for connectivity analyses; (b) development of regulations to limit hunting and uncontrolled expansion of oil palm plantations; (c) remote sensing analyses of changes in land cover and ecological connectivity; (d) estimation of the viability of alternate land uses, including nature oriented tourism; (e) development, implementation and monitoring of conservation and management approaches incorporating both socio-economic considerations and biodiversity; and (f) conservation of forested properties adjacent to parks and within potential biological corridors. Further research on the complex and contrasting effects of land cover change and sustainable development in areas of high biodiversity is warranted.

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