



Biodiversity conservation in human-modified landscapes of Mesoamerica: Past, present and future

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ABSTRACT

Mesoamerica provides a unique context for biodiversity conservation in managed landscapes because of its geography, history of human intervention, and present conservation and development initiatives. The long and narrow form of the Mesoamerican landmass, and its division by a central mountain range, has served as both a bridge and a barrier. Conservation efforts in Mesoamerica are unique for the emphasis they place on regional connectivity through the Mesoamerican Biological Corridor and on biodiversity conservation in managed landscapes. The emphasis on conservation in agricultural systems has fostered innovations in payment for ecosystem services, and provides novel insights on the functional role that biodiversity plays in the provisioning of ecosystem services. The increasing rate of economic development in the region and the advent of new payment for ecosystem service schemes have provided new opportunities for forest regeneration and restoration. However, the small scale of private landholdings and the diversity of land uses featured in the region, while contributing to biodiversity conservation due to their structural and floristic complexity, present challenges for biodiversity monitoring and management.

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1. Introduction

Mesoamerica's geographic setting strongly influences the context for biodiversity conservation in the region. Mesoamerica is both a land bridge between two major continents and a barrier between two major oceans. The joining of North America and South America about three million years ago facilitated the Great American Biotic Interchange (Stehli and Webb, 1985), which witnessed species such as opossum and armadillo moving north across the isthmus while ancestors of llamas, felines, and bears crossed into South America. Major exchanges of avian (Weir et al., 2009) and plant (Gentry, 1982) biodiversity also occurred. In part because of this biogeographic history, Mesoamerica is considered one of the original 25 global biodiversity hotspots (Myers et al., 2000), and is home to more than 5000 endemic vascular plant species and 210 endemic mammal species (Greenheck, 2002).

The biogeographical designation of Mesoamerica is distinct from the geopolitical designation of Central America, which ex-

cludes Mexico, Panama, and sometimes Belize. Mesoamerica stretches from the five southernmost states of Mexico (Quintana Roo, Yucatan, Campeche, Chiapas and Tabasco) to the Darien in eastern Panama. The region is narrow (80 km at its narrowest), bordered by the Pacific Ocean to the west and the Caribbean Sea to the east, and divided by a volcanically active central mountain range reaching elevations of 4220 m on Mt. Tajumulco in Guatemala, and 3820 m on Chirripó in Costa Rica. Both the oceans and the mountain range that divides them influence the distribution of four terrestrial biomes and 19 terrestrial ecoregions in Mesoamerica (Estado de la Región, 2008). These biomes vary widely in climate and in natural and anthropogenic disturbance regimes. The tropical dry broadleaf forests of the Pacific slope are strongly influenced by annual dry seasons. These forests are heavily fragmented by agriculture, with 3% officially protected (Estado de la Región, 2008). Tropical coniferous forests and xeric shrublands have 10% and 19.7%, respectively, of their original extent protected (Table 1; Estado de la Región, 2008). The tropical moist broadleaf forests of the Caribbean slopes are less affected by human disturbances but subject to regular hurricanes; 28% of their area is officially protected.

Mesoamerica is home to numerous local and regional conservation programs that initially developed from the US conservation

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Table 1
Species richness for amphibians, birds, mammals and reptiles in each of Mesoamerica's biomes and ecoregions. The proportion of the region in each biome is indicated along with the proportion of that area that is in officially designated protected areas. Data adapted from Corrales (2010) and Estado de la Región (2008).

Biome/ecoregion	Amphibians	Birds	Mammals	Reptiles	Area (km ²)	Regional percent	Percent protected
Tropical moist broadleaf forests					260 575	55.3	28.6
Central American Atlantic moist forests	38	429	172	143	90 513	19.2	21.4
Chocó-Darién moist forests	138	600	215	200	10 294	2.2	50.3
Costa Rican seasonal moist forests	40	373	186	99	7566	1.6	9
Isthmian-Atlantic moist forests	118	518	217	168	45 431	9.6	13.6
Isthmian-Pacific moist forests	99	407	190	143	42 965	9.1	10.8
Petén-Veracruz moist forests	103	468	191	226	2778	0.6	49.3
Central American montane forests	73	303	191	111	17 828	3.8	38
Chiapas montane forests	49	325	163	61	5633	1.2	0
Chimalapas montane forests	19	294	145	31	2096	0.4	ND
Eastern Panamanian montane forests	30	327	198	102	1871	0.4	80.8
Sierra Madre de Chiapas moist forests	44	315	148	118	13 490	2.9	1.2
Talamancan montane forests	124	450	204	132	20 110	4.3	59.2
Tropical dry broadleaf forests					93 113	19.8	3
Central American dry forests	36	330	195	99	74 632	15.9	3.3
Chiapas Depression dry forests	33	188	160	106	13 415	2.8	0
Panamanian dry forests	22	273	165	59	5086	1.1	0.4
Tropical coniferous forests					114 906	24.4	9.9
Central American pine-oak forests	107	349	203	194	97 494	20.7	9.1
Miskito pine forests	0	240	128	0	17 412	3.7	10.7
Xeric shrublands					2200	0.5	0
Motagua Valley thornscrub	23	115	138	88	2200	0.5	19.7

movement but later evolved in response to local conditions by integrating protected areas with conservation in managed landscapes. To this end, Mesoamerica has become an innovator and global leader in developing policy and incentive instruments for promoting conservation outside protected areas, particularly payment for ecosystem service (PES) and eco-certification of agricultural crops (Pagiola et al., 2005, 2007).

Although each country in the region maintains its own ministries of the environment, all participate in the Central American System of Protected Areas (SICAP) formed in 1992. The system currently includes 669 protected areas totaling 124 250 km², with approximately 24 new reserves added per year between 1980 and 2007 (Estado de la Región, 2008). Another regional program, the Mesoamerican Biological Corridor (MBC), integrates regional scale connectivity of protected areas with sustainable development and improvement of human livelihoods. Maintaining connectivity is particularly important and challenging in Mesoamerica because of the region's altitudinal and latitudinal gradients, which pose natural barriers to species movement that can increase the vulnerability of biodiversity to climate change and agricultural expansion.

In this paper, we explore the history of human interaction with biodiversity and the current status of biodiversity conservation in Mesoamerica. We focus on current conservation strategies, including the MBC, conservation in protected and managed forests, and conservation in landscapes dominated by agriculture. Next, we review the potential for forest regeneration and ecosystem restoration and discuss the critical need for effective biodiversity monitoring tools to assess and improve the conservation value of managed landscapes. We conclude with a prognosis for the future of Mesoamerican biodiversity and recommendations for safeguarding this unique biodiversity while promoting sustainable development.

2. Effects of prehistoric human occupation on biodiversity in Mesoamerica

Human have inhabited Mesoamerica, and impacted its biodiversity, for at least 10 000 years. Few lowland areas of Mesoamerica lack archaeological remains (Gomez-Pompa and Kaus, 1990). In the Petén region of Guatemala, late Classic population densities

ranged between 200 and 300 individuals per km² (Rice and Rice, 1990). In the central Maya lowlands, as much as 75% of the landscape was altered by intensive cultivation prior to 1200 BP (Whitmore et al., 1990). This activity left three long-lasting legacies: (1) forest burning, agriculture, and soil erosion; (2) silviculture and forest management; and (3) landscape modifications involving raised fields, canals, and terraces.

The development and spread of agriculture after the Pleistocene (11 500 BP) profoundly impacted the structure and composition of vegetation (Piperno, 2007). Pollen, charcoal, and plant phytoliths in lake and swamp sediments from numerous sites in Mesoamerica show sequences of burning coincident with crop cultivation and declines in arboreal pollen during the early and middle Holocene, 7000–10 000 BP (Neff et al., 2006; Piperno, 2006; Horn, 2007). Throughout Mesoamerica, the abundance of burned phytoliths of Poaceae and *Heliconia* indicate human-set fires in early successional vegetation, evidence of short-fallow shifting cultivation (Piperno, 2007). Impacts of ancient agricultural land use are evident across the full range of tropical forest vegetation, including evergreen, semi-evergreen, and deciduous forest types, from Mexico to the Amazon Basin (Piperno, 2007). Overall, impacts were earlier and more sustained in the lowlands and in highly seasonal forests which have more fertile soils and were more easily cleared of vegetation than aseasonal forests (Denevan, 2007; Piperno, 2007).

Indigenous Mesoamericans cultivated trees, hunted game, and managed forest patches for over 4000 years (Emery, 2007; Ford, 2008). The Maya planted homegardens, practiced shifting cultivation, and managed forests as indicated by high-density aggregations of useful tree species in forests surrounding archeological sites (Gomez-Pompa, 1987; Ford and Fedick, 1992; Fedick, 1995; Campbell et al., 2006; Ross, in press). Abundant tree species favored by the Maya include *Brosimum alicastrum* (Moraceae), *Bursera simarouba* (Burseraceae), *Manilkara zapota* (Sapotaceae), and *Attalea cohune* (Arecaceae). Maya forest gardens were so widespread during the Mayan Pre-Classic period (4000–700 BP) that contemporary forests of the southeastern Petén, eastern Guatemala and western Belize are widely considered to be dominated by species favored by human land-use practices (Gomez-Pompa and Kaus, 1990; Peters, 2000; Campbell et al., 2006; Ford and Nigh, 2009; Ross, in press).

Ancient Mayans used new technologies to intensify and expand agricultural production to meet the needs of growing populations (Whitmore et al., 1990). The Maya of Mesoamerica transformed wetlands by creating raised platforms surrounded by drainage canals (Fedick, 2003). In La Milpa, Belize, and Petexbatun, Guatemala, the Maya constructed terraces and dams to minimize erosion and increase agricultural productivity on slopes during the Late Classic period (1400–1100 BP) (Dunning and Beach, 2000). Terraced agricultural fields were particularly associated with high settlement densities on hilly terrain in the upper Belize River area (Healy et al., 1983; Fedick, 1994).

Despite these interventions, tropical forests rebounded in many areas following the Mayan collapse (1200–1000 BP) and widespread population decline in the Americas after the Spanish Conquest (Wahl et al., 2006; Piperno, 2007). Sufficient areas of remnant and managed forest gave rise to the diverse tropical forests of Mesoamerica that grow today. In the Darien forest of Panama, in northern Petén, and elsewhere in Mesoamerica, today's mature forests have been undergoing secondary succession for approximately 350 years (Bush and Colinvaux, 1994; Clement and Horn, 2001; Wahl et al., 2006). As recently as 300 years ago, corn was cultivated adjacent to a swamp at La Selva Biological Station in Costa Rica (Kennedy and Horn, 1997). Since canopy trees can live in excess of 300 years, these forests—and many other so-called “primary” forests in Mesoamerica—are likely still undergoing gradual changes in composition and structure (Bush and Colinvaux, 1994).

3. Land use in Mesoamerica

In 2003, natural vegetation, including secondary forests and selectively logged forests, was estimated to cover 57% of Mesoamerica. The remaining area was used mostly for crop and cattle production (42%) with 1–2% in urban and other land covers (Fig. 1a). Regionally, pastures cover three times as much land area as all cropping systems combined (FAO, 2008). More than half of Costa Rican, and El Salvadorian territories are in pasture (Harvey et al., 2005a; FAO, 2008). In 2005, annual and perennial crops accounted for less than 10% of land cover in all Mesoamerican countries except for El Salvador, Nicaragua and Guatemala, where they covered 32%, 16% and 13% of land area, respectively.

The main crops cultivated in the region are corn, coffee, beans and sugar cane, covering 38%, 19%, 13% and 12% of agricultural lands, respectively (Estado de la Región, 2008). Export crops such as oil palm, banana, sugar cane and cattle for beef tend to be produced on large farms (>80 ha), whereas local market crops are produced on smaller plots (Harvey et al., 2005a). This distribution of farm sizes has important consequences for biodiversity. Large monoculture farms for pineapple, oil palm, banana, and cattle have created severe habitat loss and fragmentation in both the Pacific and Caribbean lowlands (Harvey et al., 2005a). This contrasts with the finer scale and more heterogeneous mosaic of small and medium farms that predominates in hilly and higher elevation terrain. Coffee is cultivated in the highlands between 600 and 1600 m.a.s.l. on a wide range of plot sizes. Cocoa is typically produced in small rustic plots (<5 ha), primarily in the Caribbean lowlands. These two crops are particularly important for biodiversity conservation because of their perennial nature and adaptability to agroforestry systems retaining high levels of native tree cover (Moguel and Toledo, 1999; Schroth and Harvey, 2007; Philpott et al., 2008).

3.1. Protected areas and deforestation

Mesoamerica had one of the highest deforestation rates in the world during the last two decades of the 20th century (–0.7%

change in forest area annually) but forest loss has recently slowed from 1.5 million ha lost annually between 1990 and 2000 to 1 million ha lost annually between 2000 and 2005 (Kaimowitz, 2008). Land use change in Mesoamerica between 1990 and 2000 converted 1.9% of the forested area to agricultural uses (Galloway et al., 2005). Deforestation in Mesoamerica, as elsewhere, varies widely in relation to climate, accessibility and agroecological factors (Kaimowitz, 2008 and see Sánchez-Azofeifa et al. (2001) for a case study in Costa Rica). Declining deforestation rates cannot be attributed to effective conservation, however, and deforestation remains a major threat to conservation objectives within both protected areas and biological corridors in some regions (Kaimowitz, 2008; Calvo-Alvarado et al., 2009). Hansen et al. (2008) point to northern Guatemala as a Mesoamerican deforestation hotspot where an estimated overall 1.43% annual deforestation rate for 1992–2001 was made up mainly of loss of lowland humid forest in the Petén Department (Environmental Profile, 2006). Honduras has an even greater average annual deforestation rate estimated at 3% between 1990 and 2005 (FAO, 2008).

Trends are different in other countries (Kaimowitz, 2008). Costa Rica's well-known protected areas system has had little impact on habitat destruction and degradation in unprotected territory (Sánchez-Azofeifa et al., 2001, 2003), but the country has nevertheless facilitated an unprecedented rise in locally-driven conservation initiatives now organized within its National Biological Corridors Program. Morse et al. (2009) document a major decline in deforestation rates in a key Costa Rican biological corridor – from 1.4% to 0.1% annually over the 1987–2001 period and provide evidence that the decline is linked to the measures taken in the country's 1996 Forest Law that restricts forest clearing, promotes sustainable forest management, and includes a payment for ecosystem services program paying land-owners for forest protection and reforestation.

3.2. The Mesoamerican biological corridor

Around 10.7% of Mesoamerica is currently under some category of protection for biodiversity conservation, ranging from <1% in El Salvador to 25% in Costa Rica (Miller et al., 2001; Table 1, Fig. 1b). Protected areas are regionally integrated, at least on paper, into a single functional conservation area (Poiani et al., 2000), the Mesoamerican Biological Corridor (Miller et al., 2001; Fig. 1b). The program seeks to apply the Convention on Biological Diversity's ecosystem approach to support conservation initiatives that are strongly linked to sustainable rural livelihoods. Among the MBC's most significant achievements is the alignment of local priorities, social capital, and political will to carry out grassroots initiatives with both conservation and development objectives (Proyecto Corredor Biológico Mesoamericano, 2007). The MBC concept thus includes a strong focus on local drivers of conservation, recognizing that conservation must be considered a social process (Carroll and Groom, 2006) that addresses contested resources and controversial issues (Rivera et al., 2002; Finley-Brook, 2007; Grandia, 2007). Maps of the MBC (Fig. 1b) emphasize the substantial regional presence of protected areas, although recently compiled GAP analyses suggest that these do not ensure adequate representation of the region's biodiversity (e.g. SINAC, 2007), and the lack of effective management of many or most of these areas is almost axiomatic (Hockings et al., 2000).

Examples from experiences in Costa Rica illustrate these points, but also serve to indicate ways in which effective participatory management of biological corridors can be achieved in Mesoamerica. Since the initiation of the MBC, the government of Costa Rica has officially recognized biological corridors and adopted them as one of its principal conservation strategies, although these areas are not legally defined as conservation areas. Rather, these

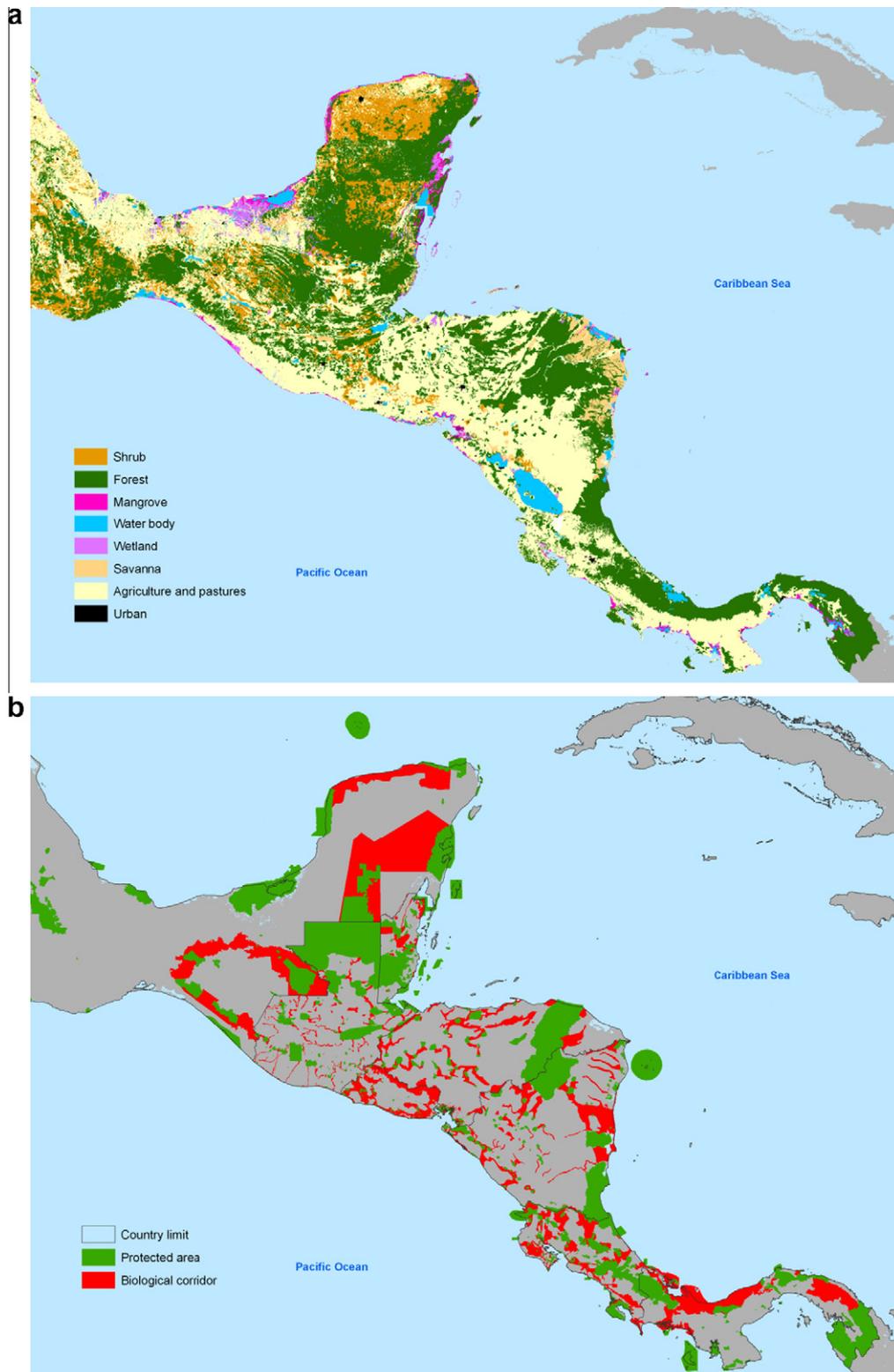


Fig. 1. Maps of Mesoamerica representing (a) dominant natural and agricultural land uses and (b) protected areas (green) and the Mesoamerican Biological Corridor areas (red) attempting to establish structural connectivity between the protected areas. Map data obtained from the Central American Commission on the Environment and Development. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

corridors owe their existence to grassroots initiatives that are coordinated by the country's national Biological Corridors Program, a dependency of the National System of Protected Areas SINAC. Corridor management is coordinated by local councils, which bring together a broad range of governmental and non-governmental

organizations. To date, 47 biological corridors have been proposed in Costa Rica, covering some 1 753 822 ha, representing 35% of the country's land area, and potentially uniting the 160 protected areas. Of these 47 proposed corridors, 24 have active and functioning local councils.

To our knowledge, the Costa Rican experience in biological corridor implementation (as opposed to just planning) is unique (Canet-Desanti et al., 2009). The corridors are guided by a set of standardized management principles, criteria and indicators divided among three dimensions of sustainability (environmentally sound, economically viable, and socially responsible) (Canet-Desanti et al., 2009; see Watson et al. (2004) for an example of a multi-dimensional, criteria and indicators-based guidelines for conservation management). In response to criticism of the MBC concept and approach (Finley-Brook, 2007; Grandia, 2007), it is essential to recognize that these corridors represent grassroots initiatives where the greater part of the investment in the initial phases is the creation and consolidation of the human, social, financial and political capital necessary for the long-term management of the corridor (Canet-Desanti et al., 2009).

Future phases of corridor management in turn focus on biological connectivity for forest-dependent species by promoting land management practices favoring biodiversity. Canet-Desanti et al. (2009) found that of the 24 active Costa Rican corridors, 21 are in the initial consolidation phase, two are in secondary phases of impacting land management practices, and one, the San Juan – La Selva corridor (see Chassot et al., 2005; Ramos and Finegan, 2006; Morse et al., 2009) is in the third phase of demonstrating impact on functional connectivity. The San Juan – La Selva initiative has featured strong emphasis on the corridor's flagship species, the green macaw. Measures taken to ensure the conservation of this bird include studies of the abundance of keystone mutualist tree species, restrictions on logging of these species, the installation of artificial nest holes, and environmental education campaigns (Chassot and Monge, 2002).

In spite of the achievements of the MBC initiative, conservation in Mesoamerica is faced with the increasing isolation of protected areas (Defries et al., 2005). To increase the effectiveness of conservation initiatives, local and regional participation is urgently

needed. Most of Mexico's forests are owned by local communities (Bray et al., 2005), whereas much of the forest in the Nicaraguan and Panamanian sectors of the MBC is within indigenous territories (Kaimowitz, 2008). Over 40% of Mesoamerica's protected areas system has is under a sustainable management category but has no restriction for use due to lack of community involvement and enforcement (Estado de la Región, 2008). Finally, the biological corridors that potentially unite protected areas to form the MBC are fragmented landscapes modified by human activity, posing an enormous challenge for the achievement of conservation objectives (Miller et al., 2001, and see below).

Among the needs for spatial information for corridor management are priority-setting exercises for local and landscape-scale actions to maintain or restore connectivity. Several recent exercises illustrate the use of remote sensing imagery and GIS to select structural connectivity routes based on least-cost path modeling, generating Potential Ecological Connectivity Networks (PECN). This approach is based on the assumption that structural connectivity between habitat patches is a key factor for forest-dependent species, and that if these species are provided with landscape scale connectivity then larger numbers of less specialized species will also benefit. Ramos and Finegan (2006) created the first PECN for the San Juan – La Selva Biological Corridor in northern Costa Rica, taking the general ideas of Hoctor et al. (2000) and adapting them to the availability of data sources and computational capacity. The PECN was constructed in four steps (Fig. 2): (a) spatial modeling for prioritizing areas of high ecological integrity, (b) selecting the forest patches with highest ecological integrity to be connected, (c) modeling to find optimum routes for connectivity, and (d) creating PECNs by combining least-cost paths and prioritized forest patches. PECNs have been created for three other biological corridors in Costa Rica and Nicaragua, demonstrating the applicability of the approach (Sánchez, 2006; Murrieta et al., 2007; Cespedes et al., 2008).

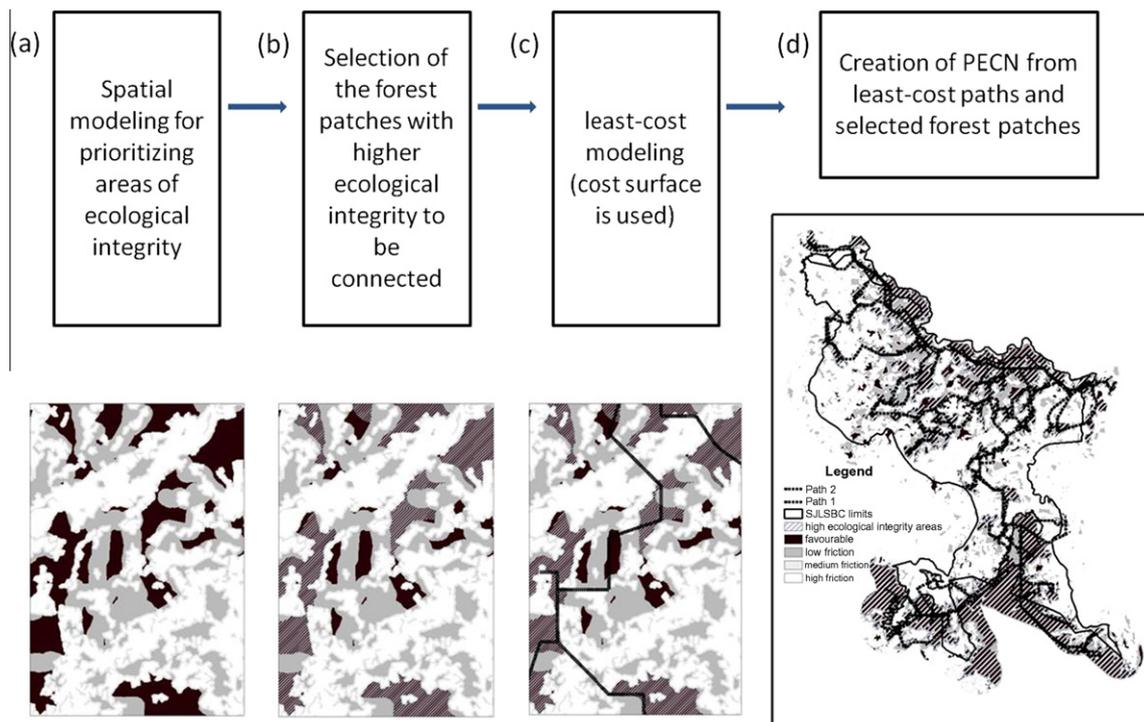


Fig. 2. Steps in the construction of a potential ecological connectivity network and an example of the final product, for Costa Rica's San Juan – La Selva Biological Corridor (see Ramos and Finegan, 2006).

4. Conservation in the agricultural matrix

Conservation of biodiversity within Mesoamerica's managed landscapes calls for a multipronged strategy that includes increasing the conservation value of the agricultural matrix both in terms of providing viable habitat for forest-dependent species, as well as increasing connectivity between protected areas and forest fragments. Although many regions of Mesoamerica are dominated by agriculture, a global analysis by Zomer et al. (2009) of tree cover found that 98% of Central America's agricultural area has >10% tree cover, 81% with >20% tree cover and 52% with >30%. These values are significantly greater than any other region analyzed.

Numerous studies in the region focus on the conservation role of embedded trees in the agricultural matrix, including isolated trees in pasture, plantations, agroforestry systems and forest fragments (Daily et al., 2001; Harvey et al., 2008; Philpott et al., 2008; Chazdon et al., 2009a, 2010; Gardner et al., 2009). These studies highlight four main observations complementing research conducted in other regions. First, they conclude that significant biodiversity persists in agricultural landscapes (Daily et al., 2001, 2003; Ricketts et al., 2001; Koh and Ghazoul, *in press*). Second, they conclude that simple land-use classifications (coffee, cacao, pasture) are not suitable to the highly heterogeneous agricultural matrices of Mesoamerica where farms are often small, comprised of multiple land uses, and where a single land use can show tremendous structural and floristic diversity (Harvey et al., 2006a). Third, there is increasing evidence that landscape context plays an important role in determining the agricultural value of managed landscapes (Ranganathan et al., 2007). Finally, studies increasingly recognize that the integration of non-domesticated or wild biodiversity in the agricultural context can make important contributions to the provisioning of ecosystem services (Ricketts, 2004; Ricketts et al., 2004; Perfecto and Vandermeer, 2006; Philpott et al., 2009).

Harvey et al. (2006a) demonstrate that not all pastures are equal, but that a pasture with high tree cover (upwards of 30%) or a pasture that is surrounded by a multistrata live fence can harbor 2–3 times as many species as a pasture devoid of tree cover for multiple taxonomic groups. In most regional analyses, however, all pastures, or all coffee fields are treated equal. Likewise in coffee systems, several authors demonstrate that most crop classifications fail to recognize the tremendous diversity within differentiated coffee management systems (Moguel and Toledo, 1999; Philpott et al., 2008). Harvey and Villalobos (2007) found similar results in cacao and plantain agroforestry systems where bird and bat richness and abundance was equal to or greater than in adjacent monocultures and forests.

At the plot level, most studies concur that the conservation value of agricultural systems increases with floristic complexity, particularly by increasing tree species richness, density, canopy cover, canopy height, canopy depth, and number of vertical strata (Perfecto et al., 1996; Greenberg et al., 1997a,b; Cruz-Angón and Greenberg, 2005; Komar, 2006; Philpott et al., 2008). Epiphytes can also contribute to this structural complexity. Cruz-Angón and Greenberg (2005) found increased avian abundance and presence of forest dwelling species with greater epiphyte abundance. One of the little studied contributions of this increased plant diversity to avian conservation may be in ensuring the seasonal availability of foraging resources through complementary fruiting and flowering phenology (Dietsch et al., 2007). Not all taxonomic groups respond in the same way to increasing tree cover in different land uses however. Harvey et al. (2006a) found greatest abundances of birds in forests, bats in riparian forest and live fences, beetles in secondary forests and forest fallows, and butterflies in pastures with low tree diversity.

There is little doubt that in the absence of tree cover within the agricultural matrix, regional biodiversity would continue to be lost. However, these same studies demonstrate two important points.

First, species turnover between simplified agricultural systems, agroforestry systems and forests is quite high; in other words each land use host some unique species. Second, agricultural systems, including agroforestry systems, record low species richness and abundances of forest-dependent species (Canterbury et al., 2000; Daily et al., 2001; Cárdenas et al., 2003; Lang et al., 2003; Petit and Petit, 2003; Robinson et al., 2004; Taylor, 2006; Harvey et al., 2006a,b; Harvey and Villalobos, 2007; Vilchez-Mendoza et al., 2008). How to increase the conservation value of these agroforestry systems to species of conservation concern remains a primary challenge.

Landscape scale effects can have a significant impact on conservation, and this may explain some of the differences between landscapes. Species with different levels of sensitivity towards deforested habitats depend a great deal on the trees outside of forest patches in fragmented landscapes (Graham, 2001; Hughes et al., 2002; Cohen and Lindell, 2005; Sekercioglu et al., 2007), and the distance to the nearest forest fragment impacts avian community composition. Luck and Daily (2003) found that a greater diversity of frugivorous bird species (21 species) used isolated fruit trees <2 km from forest patches and immersed in a matrix of low intensity land uses when compared to isolated trees located up to 7 km away from the same fragments (14 species), and/or immersed in a more intensively managed matrix. Moths, in contrast, showed no response in species richness to changing land-use, but responded to the distance from the forest fragment with greater species richness <1 km from forest fragments than >3.5 km from them (Ricketts et al., 2001). Other studies however found no landscape scale effects (Daily et al. (2003) for mammals and Milder, 2010). We conclude that there is anecdotal evidence of landscape effects such as the importance of maintaining closely spaced (<2 km) forest fragments but the paucity of study sites for this work, combined with the lack of consistent methodology across sites and studies, means that we cannot yet make well-supported general statements about these effects.

The role of tree cover within agricultural land uses is more important for maintaining connectivity between forest fragments rather than as a habitat for forest-dependent species (Harvey et al., 2005b; Martinez-Salinas, 2008; Sekercioglu et al., 2007). Live fences, the use of living trees as fence posts in pastures, maintain such connectivity (Harvey et al., 2005b) when they are comprised of high species and structural tree diversity (Lang et al., 2003) doubling the species richness and abundance of birds observed. At landscape scales, live fences make significant contributions to structural connectivity for tree dependent and forest-dependent species that would become locally extinct in the absence of these features (Fig. 3). DeClerck (2009) found that at least 67% of the forest fragments in the heavily fragmented pasture-dominated landscape of Matiguas in Nicaragua are connected by at least one live fence, which facilitates the movements of bird species among the fragments (Martinez-Salinas, 2008). Less understood is the importance of placement of these live fences within the landscape, and the maximum distance that a forest-dependent species will travel between forest patches using these elements.

4.1. Biodiversity contributions to ecosystem services

While increasing tree cover in the agriculture matrix appears to play a support role for conservation, there is increasing interest in the functional contribution that biodiversity makes to production systems through the provisioning of ecosystem services (the aspects of ecosystems utilized to produce human well-being, Fisher et al., 2009). Few ecological studies in Mesoamerica have successfully demonstrated strong mechanistic links between biodiversity and ecosystem services, while payment of ecosystem service



Fig. 3. Two toed sloth (*Choloepus didactylus*) using a live fence to move across the landscape. Linear elements such as live fences and riparian forests can be managed to increase their value for connectivity (photo by Leonardo Ramirez).

schemes continue to be rapidly developed, often with little grounding in the ecological mechanisms that drive these services.

There are a few notable exceptions however. Ricketts (2004) and Ricketts et al. (2004) published a study on the pollination of coffee in Costa Rica that considered the economic value of forest fragments adjacent to coffee plantations. Their study showed greater pollinator activity and resilience to change adjacent to forest fragments (<50 m) when compared to distances >100 m from the forest edge. Moreover, Perfecto and Vandermeer (2008) and Perfecto et al. (2004) have found that coffee agroforests maintain ecological complexity which contribute to controlling coffee pests. Mutualistic relationships between *Azteca* ants and coccids in coffee agroforests have positive indirect effects on coffee by reducing coffee borer beetles abundance (Perfecto and Vandermeer, 2008). Resident neotropical birds also control pest outbreaks when coffee farms retain greater tree cover and diversity. Perfecto et al. (2004) lepidopteran larvae removal rates were twice as high in a coffee farm with 60% tree cover and seven tree species per 20 × 20 m plot when compared to an adjacent farm with 30% tree cover and three tree species. Phillipott et al. (2009) conducted a meta-analysis that demonstrates a strong link between measures of bird species diversity and arthropod removal. Although we are still far from understanding the mechanisms behind biodiversity and ecosystem function in agricultural landscapes, these studies and others support the notion that biodiversity conserved in managed landscapes contributes to production goals.

5. Species conservation through forest regeneration and restoration

Although tropical forests continue to be cleared in many regions in Mesoamerica, some agricultural lands are being abandoned due to declines in commodity prices, changes in agricultural policy and subsidies, industrialization, or land being set aside for conservation

of biodiversity and/or ecosystem services (Grau et al., 2003; Arroyo-Mora et al., 2005; Hecht et al., 2005). Much former agricultural land is undergoing natural regeneration or is being actively restored through a range of human interventions (Holl, 2002; Chazdon, 2008a). The most common restoration strategy is planting trees, with an increasing focus on native species. Many tropical forest restoration projects plant large areas with a small number of species that enhance seed dispersal by fauna, shade out competitive grasses and other pioneer vegetation, ameliorate microclimate conditions, and improve nutrient availability, facilitating the establishment of a range of flora and fauna (reviewed by Holl (2002)). Increasingly, restoration ecologists are diversifying plantings (e.g. up to 60–80 species, Rodrigues et al., 2009) and exploring new planting designs such as creating small tree patches to serve as nuclei for recovery (Zahawi and Augspurger, 2006; Cole et al., in press). Other restoration methods with mixed success include installing perching structures to attract seed-dispersing fauna (Holl, 1998; Shiels and Walker, 2003), reducing fire frequency (Janzen, 2002), and reducing cover of aggressive exotic grasses and ferns (Sampaio et al., 2007; Shono et al., 2007; Hooper, 2008; Douterlungne et al., in press).

Short-term studies of forest regeneration and restoration in Mesoamerica (e.g., Uhl, 1987; Aide and Cavellier, 1994; Holl et al., 2000; Ferguson et al., 2003) provide limited insights into prospects for long-term recovery of biodiversity (Gardner et al., 2009). Evidence from chronosequence studies suggests that the number of species and proportion of later-succession plant and animal species increases over time, enhancing the conservation value of secondary forests with age (Chazdon et al., 2009b; Dent and Wright, 2009). But chronosequence patterns may not accurately predict changes in species abundance and composition within individual secondary forests (Chazdon et al., 2007). To date, only one study has evaluated changes in the abundance and species richness of old-growth tree seedlings and saplings over time in secondary forests of NE Costa Rica (Norden et al., 2009). Nonetheless, we

highlight three main conclusions about the effect of forest recovery on biodiversity in Mesoamerica.

First, the rate of forest recovery in post-agricultural lands in Mesoamerica, both with and without human intervention, is extremely variable. Many sites are quite resilient with woody biomass and a large percentage of species recovering within 15–60 years (e.g., Reiners et al., 1994; Aide et al., 2000; Silver et al., 2000; Janzen, 2002; Letcher and Chazdon, 2009). In other sites, particularly with aggressive ruderal vegetation and degraded soils, recovery may be arrested, at least temporarily (Aide et al., 1995; Zahawi and Augspurger, 1999; Holl et al., 2000). Species composition in post-agricultural sites often varies widely even among nearby sites sharing similar soils and topography (Ewel, 1980; Guariguata and Ostertag, 2001). Previous land use significantly affects the abundance and composition of initial colonization, creating long-term legacies in successional pathways (Holl, 2007; Chazdon, 2008a).

Several factors affect the pace and composition of recovery of the full complement of biodiversity in secondary tropical forests. Compared to moist forests, dry forests commonly have a larger percentage of trees that resprout or have wind-dispersed seeds (Vieira and Scariot, 2006), so they often recover more quickly (Lebrija-Trejos et al., 2008). Likewise, soil type and elevation influence the rate of recovery (reviewed in Holl, 2007). The surrounding landscape, proximity to remnant forests, and agricultural management techniques (see above) affect the number and composition of plant and animal species that establish, which in turn drive their interactions (e.g. seed dispersal, herbivory, seed predation). Finally, the type and intensity of agriculture prior to abandonment are primary factors affecting both the rate and trajectory of old field succession within a given soil type (reviewed in Guariguata and Ostertag, 2001; Myster, 2004; Holl, 2007; Chazdon, 2008a). Past land use influences forest recovery through a number of mechanisms, including differences in fire frequency, soil physical and chemical properties, and remnant vegetation (Fernandes and Sanford, 1995; Ferguson et al., 2003), which in turn affect species composition and successional trajectories (Aide et al., 1995; Pascarella et al., 2000; Mesquita et al., 2001).

Second, whereas natural regrowth and restored tropical forest provide habitats for an increasing number of species over time, they tend to favor generalist species and lack the full complement of species even in sites that have been abandoned for several decades (e.g., Aide et al., 2000; Zimmerman et al., 2000; Chinea, 2002; Bowen et al., 2007; Grimbacher and Catterall, 2007). Chazdon et al. (2009b) found that the range in the proportion of old-growth species found in secondary forests varies greatly both for animals (33–86%) and trees ≥ 10 cm dbh (diameter breast height) (4–44%). Large-seeded species that are animal dispersed may be particularly at risk of disappearing from fragmented areas due to loss of dispersers (Cole et al., *in press*).

More species will continue to colonize secondary forests over time if propagule pools are available and habitat conditions improve. Nonetheless, restoration efforts, particularly on lands with rapid colonization of early-successional species, should focus on introducing later-successional species in order to restore the full complement of species (Martínez-Garza and Howe, 2003; Lamb et al., 2005; Bonilla-Moheno and Holl, *in press*). Although a large proportion of species have been found in many older restoration sites, it usually is not clear whether these sites are hosting stable reproducing populations, or whether the second growth forests may provide habitat that only meets part of the species' needs and potentially provide 'sink' habitat.

Third, taxa vary widely in their abilities to colonize and persist in secondary forests and restoration sites (Barlow et al., 2007; Stork et al., 2009). Secondary forests in Quintana Roo Mexico, support fewer species and individuals of lizards and snakes than do mature forests (Luja et al., 2008). In contrast, the richness, diver-

sity, and abundance of bats were statistically indistinguishable across four stages of tropical evergreen forest regrowth in Tabasco, Mexico (Castro-Luna et al., 2007). In a tropical deciduous forest landscape of Veracruz, Mexico, species richness of vegetation was higher in secondary forests than in areas of mature forest, and the presence of a range of ages maximizes floristic diversity within the landscape (Castillo-Campos et al., 2008).

In summary, forest restoration in Mesoamerica with and without human intervention will help to conserve a large number of tropical forest species, although active management promoting late-successional species and complex forest structure will be required to protect the most vulnerable species. Heterogeneity of species composition among restored forests and mature forests, can serve to maintain high levels of biodiversity at the landscape scale in many areas. However, due to the unpredictability of the rate and direction of recovery and the potential loss of mature forest specialists, relying on restoration to prevent mass extinctions is a risky prospect for biodiversity conservation (Stork et al., 2009) and restoring forests should not be considered as a substitute for protecting primary forests that have not been extensively logged or cleared for agriculture (Chazdon, 2008b; Chazdon et al., 2009b).

6. Biodiversity monitoring in human-modified landscapes

Biodiversity conservation in human-modified landscapes of Mesoamerica cannot be effectively advanced if it cannot be defined and measured. Rigorous yet cost-effective monitoring and evaluation tools are therefore essential for designing conservation strategies and evaluating the success of these strategies (Chazdon et al., 2009a). Because monitoring biodiversity in the field across entire landscapes is almost always impractical and cost-prohibitive, researchers have sought to identify surrogate measures. Approaches to evaluating conservation in human-modified landscapes can be characterized according to the biodiversity response variable(s) of interest, the predictor or surrogate variable(s) considered, and the spatial and temporal scales of analysis. These factors are explored below.

Biodiversity response variables quantify characteristics of individuals, populations, or species assemblages. A handful of studies in Mesoamerica have evaluated the behavior, habitat use, or reproductive success of single species in human-modified settings (e.g., Sekercioglu et al., 2007; Martínez-Salinas, 2008). By linking habitat characteristics to metapopulation dynamics, such studies are essential for shedding light on the ecological mechanisms underlying the persistence of wild biodiversity in human-modified settings (Donovan and Strong, 2003).

More commonly, however, research in Mesoamerica has used presence/absence or abundance data from field surveys to quantify biodiversity response variables. The choice of metrics for characterizing species assemblages raises questions about which elements of biodiversity matter to researchers or to society at large (Duelli and Obrist, 2003). Standard measures such as species richness, abundance, or Shannon index have been widely used in Mesoamerican research. However, these metrics tend to mask important compositional shifts associated with agricultural intensification, as forest-dependent species are replaced by generalists or disturbance-adapted species (Petit and Petit, 2003; Bennett et al., 2006; Milder, 2010). Such metrics may also overstate the conservation value of production systems relative to forests.

Response variables that consider species composition and attributes of conservation value are more informative than simple species richness or abundance measures. Existing inventories of species of high conservation value (e.g., the IUCN Red List and national threatened species lists) can be a helpful starting point; however such species are often absent or extremely uncommon

in human-modified landscapes. Much of the conservation interest in mosaic landscapes lies with species that are not officially listed, but that are regionally uncommon, in decline, or play critical roles in local ecosystems (Gardner et al., 2009). Such values can be quantified by assessing the prevalence of species possessing characteristics of conservation interest such as forest dependence (Stiles, 1983), vulnerability to human disturbance (Petit and Petit, 2003), declining population trend, and high degree of threat (Carter et al., 2000).

Both taxonomic and environmental surrogates have been used to monitor conservation outcomes across large scales. Taxonomic surrogates are groups of species that serve as proxies for much broader sets of taxa. Across the tropics, with a few exceptions, plant and animal taxa generally do not appear to respond similarly enough to habitat parameters to allow for broadly-applicable indicator taxa (Lawton et al., 1998; Barlow et al., 2007). In Mesoamerica, evaluation of multiple taxa in a pasture-dominated landscape in Nicaragua (Harvey et al., 2006a) and a coffee production area in southern Mexico (Perfecto et al., 2003) revealed limited consistency in the responses of vertebrate and invertebrate taxa to environmental heterogeneity.

Environmental surrogates have the conceptual appeal of being readily measurable and related to human management practices. In Mesoamerica, several plot level surrogates related to vegetation characteristics and agroecosystem management were found to have significant relationships to conservation outcomes. These include tree species richness (Reitsma et al., 2001; Harvey et al., 2006a), percent canopy cover (Montero, 2003), height of ground vegetation (Saab and Petit, 1992), vegetation structural complexity (Estrada et al., 1994, 1998), live fence structure and management (Harvey et al., 2005b), and agricultural management intensity (Luck and Daily, 2003; Mas and Dietsch, 2003).

Another common approach has been to classify landscapes into discrete land cover classes and compare biodiversity across these classes. Such classifications are based on the patch paradigm of landscape analysis, which is most appropriate when there are clear demarcations between adjacent land classes and little internal heterogeneity within each class (Leitao et al., 2006). However, much of Mesoamerica is dominated by diversified small farms and agroforestry systems that defy traditional land use classification and exhibit significant temporal heterogeneity (e.g., shifting cultivation). Nevertheless, numerous studies in Mesoamerica have found land classes to be significant predictors of faunal assemblage characteristics (Estrada et al., 1993, 1994, 1997, 1998; Moreno and Halffter, 2001; Ricketts et al., 2001; Hughes et al., 2002; Daily et al., 2003; Petit and Petit, 2003; Perfecto et al., 2003; Harvey et al., 2006a,b). Land classes have the added advantage of being intuitive to farmers and laypersons, thus increasing their appeal as surrogates for conservation-friendly management in applications such as government incentive programs and PES (Scherr et al., 2007).

Several theoretical shortcomings of the patch paradigm in heterogeneous landscapes are addressed by the gradient paradigm, which considers environmental factors as continuous variables rather than discrete classes. This approach offers several inherent advantages, including scale independence (subject to the grain and extent of the underlying data), ability to detect the full range of variation in land patterns, decreased subjectivity, and opportunities for increased statistical power (Faith and Walker, 1996; Ferrier, 2002). Several studies in Mesoamerica have evaluated continuous predictor variables that are based on underlying land classifications (*sensu* McGarigal and Cushman, 2005), such as percent forest in the surrounding area or distance to the nearest forest patch. However, few studies have attempted to characterize landscape composition and structure without reference to an initial land use map, by using pixel-based methods or spatial interpolation of point data (but see Ranganathan et al., 2007). The effective-

ness of such techniques for characterizing Mesoamerican biodiversity is thus largely unknown.

The vast majority of biodiversity research in Mesoamerican human-modified landscapes has consisted of “snapshot” studies that inventory biodiversity over a few months or, at most, a few years. Such studies characterize only a fleeting moment in a dynamic landscape trajectory. Particularly in smallholder-dominated landscapes, rapid cycles of shifting cultivation and fallow management suggest that plot-scale biodiversity is unlikely to reach any sort of equilibrium. At the landscape scale, more gradual trajectories of agricultural expansion, intensification, or abandonment are likely to create disequilibria such as “extinction debts” (Tilman et al., 1994), which may come due slowly over a period of decades (Brooks et al., 1999).

For researchers, the challenge of understanding biodiversity in dynamic landscapes can be addressed in at least three ways. First, as the quantity of snapshot studies increases, meta-analyses may be able to filter out some of the noise of biodiversity disequilibria to reveal the direction and magnitude of longer-term patterns and trajectories. Second, chronosequence or “space-for-time” studies that evaluate landscapes in different stages of transformation can help determine the factors influencing persistence of different biodiversity elements in human-modified settings. Finally, as mentioned above, detailed studies of species behavior and population processes (e.g., habitat use, survival, and reproductive success) can help reveal dynamic processes as they occur, allowing for inferences on the trajectory of biodiversity at a given location (Chazdon et al., 2009a). While no single approach is a substitute for detailed, long-term study of landscapes, taken together the three approaches may inform inferences on the long-term conservation potential of different types of human-modified systems.

7. Conclusions

Mesoamerican biodiversity cannot be protected in reserves alone as they are too isolated, too expensive to manage, and too controversial in a region where poverty alleviation remains a more immediate priority than conservation. Although conservation of countryside biodiversity shows promise, conservation in the agricultural matrix will be insufficient to protect the entirety of Mesoamerica's biodiversity. Of particular concern is the conservation of forest-dependent species unable to persist in the agricultural matrix even in areas with significant on-farm tree cover. The conservation of these species depends on the effective establishment of protected areas and connectivity between them.

Expanding conservation benefits in agricultural landscapes will require significant investment by local farming communities and the private sector. It will also require increased collaboration with local governments to encourage appropriate land use regulation, and with national governments to define supportive agricultural policies and incentives (Harvey et al., 2008). One angle that has been approached, but which still requires much work is the relationship between conservation and the provisioning of ecosystem services. While the ecological community has made tremendous scientific progress in arguing for the value of functional diversity, and politicians and the public are increasingly aware of the notion of ecosystem services, the direct causal link between conservation of ecosystem systems, the valuing of the services they provide, and the marketing of these services remains tenuous at best. Critical gaps include better indicators of how conservation investments directly impact ecosystem services being sold – or guaranteeing the buyer that the ecosystem service they paid for is being provided. A second critical gap is in targeting these payments to portions of the landscape where the service is most needed, including conservation services. Improved farm and landscape tools for monitoring

biodiversity and ecosystem services are critically needed. Finally, payments ecosystem service programs must find means to equitably compensate land-owners for conservation practices. One means may be through the bundling of ecosystem services that recognize the contribution of conservation interventions to the provisioning of multiple services at multiple scales.

Although deforestation remains a threat to the region, other areas that were formerly converted to agriculture are now being abandoned or managed for ecosystem services (see the Hojanca example in Tekelenburg et al. (2009)). The restoration of these lands critically depends on a sound understanding of restoration practices that include a substantial complement of the native biodiversity, including forest dependent, late-successional species.

The fate of Mesoamerican biodiversity is fundamentally dependent on these processes: (1) successful establishment and management of protected areas with minimal human intervention; (2) an agricultural matrix that includes a full complement of tree cover including forest fragments, riparian forests, multistrata agroforestry systems, and corridors such as live fences; (3) effective and rapid assessment tools aimed at informing conservationists and policy makers with critical hotspots for biodiversity conservation and ecosystem services; and (4) a suite of restoration tools adaptable to both land abandonment and on-farm conservation scenarios.

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