

Seasonally Dry Tropical Forest Biodiversity and Conservation Value in Agricultural Landscapes of Mesoamerica

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The Mesoamerican region is blessed with tremendous biological richness, a high level of species endemism, and a diverse cultural heritage. Yet in 2000, only 30 percent of the region's forest cover remained. Overall, 37.4 percent of the land area of Mesoamerica is used for agriculture (CCAD 2002); much of this agriculture is concentrated in the more seasonal areas previously occupied by seasonally dry tropical forest (SDTF). Pasture is the predominant agricultural land use in Central America, constituting 61.1 percent of all agricultural land in 2000 (FAO 2005). Rice, sugarcane, maize, and beans constitute other major agricultural products grown in dry forest zones of Mesoamerica (Donald 2004; Harvey et al. 2005a).

Only 5.7 percent of SDTFs in Central America have protected area status (Miles et al. 2006). As formerly continuous blocks of forest are reduced and fragmented throughout Mesoamerica, remaining forested refuges and protected areas become increasingly embedded within agricultural landscapes (DeClerck et al. 2010). Conservation of biodiversity (including forest specialist species) in these areas therefore requires active management at the landscape level (Janzen 1986a; Daily et al. 2003; McNeely and Schroth 2006; Vandermeer and Perfecto 2007; Harvey et al. 2008a; Chazdon et al. 2009a) and partnerships with farmers who are practicing *circa situm* (on-farm) conservation (Boshier et al. 2004).

Here, we review our present knowledge of plant and animal biodiversity at the landscape level in seasonally dry forest zones of Mesoamerica. We describe how much and what kind of biodiversity is found within agricultural landscapes, and in what kinds of habitats. We highlight the conservation value of agricultural landscapes for protecting forest specialists and endangered species. To examine the potential for secondary forests on abandoned pastures in SDTF regions to support biodiversity, we include a detailed case study of plant, bird, and bat diversity associated with secondary forests of Chamela-Cuixmala in Mexico. Finally, we present recommendations to enhance biodiversity within agricultural landscapes and enumerate research priorities for deepening our knowledge of species, populations, and communities and their interactions in these landscapes.

The Nature of Biodiversity in Agricultural Landscapes

When concern over biodiversity loss in tropical forests became widespread in the 1980s, virtually no detailed information was available on biodiversity status in areas outside the boundaries of intact forest. Janzen (1988b) speculated that “when dry forest habitat is replaced by fencerows, ditchsides, unkempt pastures, and woodlots, the species richness of the breeding fauna and flora is reduced by 90 to 95 percent.” We now know that unkempt pastures, woodlots, and other agricultural habitats can contain significant levels of biodiversity. In the agricultural landscape of Las Cruces, Costa Rica, researchers have detected at least 45 percent of the native bird species and 54 percent of the native mammal species within agricultural and pastoral habitats (Daily et al. 2001, 2003; Ranganathan and Daily 2008). Studies in the fragmented landscape of Los Tuxtlas, in Mexico, have detected 226 bird species, 39 bat species, 39 nonflying mammal species, and 36 dung beetle species, which represent 68 percent of the original bird fauna, 80 percent of the original bat fauna, and 65 percent of the original nonflying mammal species (Estrada 2008).

What is the nature of the biodiversity within tropical agricultural landscapes? Janzen (1986a) classified three groups of species that live and interact in agricultural habitats. The first group is the crop species, which are planted (in the case of crops) or raised (in the case of cattle) and depend upon humans for their well-being and survival. Second are species that can thrive and reproduce in managed systems, disturbance-adapted species, or species associated with human activities. Third are remnant species originating from forested ecosystems that have persisted in the transformed

landscape but are not breeding or regenerating. This group has been termed the “living dead,” as they are not expected to persist beyond the remnant generation (Janzen 1986a).

Many species have been incorrectly labelled as “living dead,” as one-time surveys may not clearly reveal whether breeding and reproduction are occurring within the disturbed landscape. Studies of gene flow (particularly pollen flow) within pastures and between remnant trees and trees in forest fragments show that trees in pastures are not reproductively “dead” but typically form part of the breeding population, despite being physically isolated from other trees (Aldrich and Hamrick 1998; White et al. 1999a; Boshier et al. 2004). Moreover, many tree species are able to reproduce within actively grazed pastures. Esquivel et al. (2008) found that 37 of the 85 tree species present in grazed pastures in Muy Muy, Nicaragua (an area of transition between dry and humid forest), regenerated under the current management conditions, suggesting that these species may be able to maintain their populations over the long term. In other cases, management of heterogeneous landscapes, changes in land use, and restoration practices have the potential to transform the living dead into biological legacies (Bengtsson et al. 2003; Lamb et al. 2005).

Janzen’s initial categorization also omitted species that are considered to be restricted to mature forests but are able to persist and reproduce in types of forest cover within agricultural landscapes. A subset of mature forest species can survive within highly modified landscapes (Chazdon et al. 2009b). In the dry forest pasture landscape of Rivas, Nicaragua, riparian forests, secondary forests, and forest fallows were characterized by tree species typical of SDTF (Harvey et al. 2006). Although most species of birds, butterflies, beetles, and bats were generalist species, 27 bird and 4 bat species classified as forest dependent were observed at low abundance (Harvey et al. 2006). Some bird species typical of forest habitats are capable of persisting and breeding successfully in agricultural areas (Sekercioglu et al. 2007). Clearly, there is still much to learn about the nature of biodiversity and the types of habitats that support forest-dependent species in agricultural landscapes (Chazdon et al. 2009b; Gardner et al. 2009).

The Nature of Agricultural Landscapes in Dry Forest Zones

Biodiversity is most diverse in agricultural landscapes with heterogeneous and abundant vegetation cover (Kindt et al. 2004; Schroth et al. 2004; Bennett et al. 2006). Remnant old-growth forest fragments and riparian

strips provide the highest quality tree cover, with vegetation structure and composition most similar to intact forest areas. Live fences are widely used in Mesoamerica and provide corridors for animal movement and breeding/nesting sites (Budowski 1987; Estrada et al. 2000; Estrada and Coastes-Estrada 2001; Harvey et al. 2005b; Chacón and Harvey 2006). Fallow fields and secondary forest provide sheltered areas and resources for animal species (Dunn 2004) and are often composed of a high diversity of plant species (Finegan and Nasi 2004; Gordon et al. 2004). Remnant trees in pastures provide stepping-stones for animal movement as well as food, shelter, and shade (Harvey and Haber 1998). Finally, there is the agrobiodiversity itself, in the form of annual crops, perennial crops, and tree crops, agroforestry systems, and associated flora and fauna (Power 1996; Perfecto and Vandermeer 2002; Schroth et al. 2004; Jarvis et al. 2007).

Remnant tree cover, tree crops, agroforestry, and tree plantations provide a benign and permeable matrix within agricultural landscapes (Harvey and Haber 1998). The type, size, and spatial configuration of habitat patches influence species composition and movement within the landscape (Medina et al. 2007). Remnant tree cover is not randomly distributed across the landscape; remnant patches are usually associated with steep topography, stream drainages, and river basins or located in areas with limited access (i.e., away from roads). Thus, species utilization of remnant patches of vegetation will be affected by topography, the composition and structure of the surrounding landscape mosaic, and connectivity with other habitats within the landscape.

Vegetation Cover and Diversity in Pastoral Dry-Forest Landscapes

The abundance, diversity, and spatial configuration of tree cover within pasture landscapes strongly determine overall patterns of biodiversity. Tree cover types within these landscapes include riparian forests, old- or second-growth forest fragments, live fences, and remnant trees. The diversity and abundance of remnant tree cover within pastures reflect farmers' management decisions (Barrance et al. 2003; Boshier et al. 2004). When farmers clear an area for pasture or crop production, they sometimes leave forest patches and remnant trees as sources of future timber, fruits, or other materials or as shade for cattle or workers or as protection for steep slopes or riparian areas (Harvey and Haber 1998; Muñoz et al. 2003). Over time,

additional trees regenerate within the area, arising from underground stems, seed banks, and/or incoming seed rain from adjacent land uses. Re-sprouting from root suckers is a particularly important mechanism for tree recruitment in SDTF of central Brazil (Vieira et al. 2006). Even after the area has been cleared and converted to pastures, farmers continue to shape the tree cover within the landscapes by selectively removing some tree species and allowing others (usually species of commercial value as timber species or fruit trees) to grow into adults (Muñoz et al. 2003; Villanueva et al. 2003). These decisions are driven by a variety of socioeconomic factors, particularly the need for timber, fence posts for fencing pastures, and firewood (Villanueva et al. 2003).

Detailed inventories of on-farm tree cover clearly illustrate the extent to which farmers shape patterns of tree cover within agricultural landscapes (table 12-1). A study of isolated trees in pastures in three dry forest regions (Cañas, in Costa Rica, and Rivas and Matiguás in Nicaragua) reported high overall tree species richness within pastures, with 71 to 101 species found in pastures in each landscape (Harvey et al. 2008b). In all three landscapes, a handful of species dominated; these species were either common timber species or important forage species for cattle. In dry forest zones of southern Mexico, Nicaragua, Cuba, Colombia, and Bolivia, silvopastoral systems often involve leguminous species in the genera *Acacia* and *Prosopis*. Pods of these and other legume species, including *A. pennatula*, *Samanea saman*, *Caesalpinia coriaria*, and *Senna atomaria*, are used as supplemental forage for cattle and are locally sold to supplement farmer income (Rice and Greenberg 2004). Management typically reduces the tree diversity considerably, favoring species that provide commercial products or services to farmers (Michon et al. 2007).

Live fences are common and conspicuous elements of agricultural landscapes throughout Mesoamerica (Harvey et al. 2004). In three dry forest pasture landscapes in Costa Rica and Nicaragua, live fences were found on 49 to 89 percent of the farms (Harvey et al. 2005b). These trees contributed to forest connectivity within the landscape; 3.4 to 14.1 percent of the live fences joined directly to forest vegetation. Farmers plant one or two species within the live fences, usually choosing species that resprout easily and can be established from stakes. Consequently, tree diversity within live fences is usually quite low, with most live fences in SDTF regions of Costa Rica and Nicaragua dominated by one of the following species: *Bursera simaruba*, *Pachira quinata*, or *Gliricidia sepium*. Live fences do not contribute greatly to tree biodiversity within individual farms, as they are dominated by a small number of species, but at the

TABLE 12-1. Ten most common trees occurring as dispersed trees and in live fences in three tropical dry forest ecosystems in Costa Rica and Nicaragua

<i>Cañas, Costa Rica</i>		<i>Rivas, Nicaragua</i>		<i>Matiguás, Nicaragua</i>	
<i>Dispersed trees</i>	<i>Live fences</i>	<i>Dispersed trees</i>	<i>Live fences</i>	<i>Dispersed trees</i>	<i>Live fences</i>
<i>Tabebuia rosea</i>	<i>Bursera simaruba</i>	<i>Cordia alliodora</i>	<i>Cordia dentata</i>	<i>Guazuma ulmifolia</i>	<i>Bursera simaruba</i>
<i>Guazuma ulmifolia</i>	<i>Pachira quinata</i>	<i>Guazuma ulmifolia</i>	<i>Guazuma ulmifolia</i>	<i>Cordia alliodora</i>	<i>Guazuma ulmifolia</i>
<i>Cordia alliodora</i>	<i>Spondias purpurea</i>	<i>Tabebuia rosea</i>	<i>Myrospermum frutescens</i>	<i>Tabebuia rosea</i>	<i>Pachira quinata</i>
<i>Acrocomia aculeata</i>	<i>Ficus werckleana</i>	<i>Byrsonima crassifolia</i>	<i>Acacia collinsii</i>	<i>Enterolobium cyclocarpum</i>	<i>Gliricidia sepium</i>
<i>Byrsonima crassifolia</i>	<i>Tabebuia rosea</i>	<i>Gliricidia sepium</i>	<i>Erythrina</i> spp.	<i>Albizia saman</i>	<i>Erythrina</i> sp.
<i>Tabebuia ochracea</i>	<i>Gliricidia sepium</i>	<i>Cordia dentata</i>	<i>Simarouba amara</i>	<i>Platymiscium parviflorum</i>	<i>Cordia alliodora</i>
<i>Pachira quinata</i>	<i>Guazuma ulmifolia</i>	<i>Myrospermum frutescens</i>	<i>Gliricidia sepium</i>	<i>Gliricidia sepium</i>	<i>Tabebuia rosea</i>
<i>Andira inermis</i>	<i>Caesalpinia eriostachys</i>	<i>Acrocomia vinifera</i>	<i>Cordia alliodora</i>	<i>Lonchocarpus minimiflorus</i>	<i>Spondias mombin</i>
<i>Piscidia carthagenensis</i>	<i>Tabebuia ochracea</i>	<i>Enterolobium cyclocarpum</i>	<i>Caesalpinia violacea</i>	<i>Cordia collococca</i>	<i>Enterolobium cyclocarpum</i>
<i>Acosmium panamensis</i>	<i>Byrsonima crassifolia</i>	<i>Swietenia humilis</i>	<i>Tabebuia rosea</i>	<i>Tabebuia ochracea</i>	<i>Spondias</i> spp.

Data are based on complete inventories of all pastures occurring on 15 farms in each landscape. Tree species are ordered in decreasing order of abundance.

Sources are Esquivel et al. 2003 (Cañas), López et al. 2004 (Rivas), and Ruíz-Alemán et al. 2005 (Matiguás).

landscape level, from 72 to 85 species were found within each region because of the presence of remnant trees or pioneer species within the live fences (Harvey et al. 2005b).

To date, only one study has examined nonarboreal vegetation within agricultural landscapes in Mesoamerica. In three wet forest regions of southern Costa Rica, 37 to 42 percent of the species of herbs and shrubs were growing within an agricultural matrix of pastures, coffee plantations,

and small forest fragments (Mayfield and Daily 2005). Similar studies have yet to be conducted in dry forest agricultural landscapes.

Animal Diversity in Pastoral Dry-Forest Landscapes

The different types of vegetation cover within pasture landscapes support substantial levels of animal diversity, by providing key resources, habitat, and connectivity to sustain animal populations (e.g., Daily et al. 2001, 2003; Harvey et al. 2006; Manning et al. 2006). Numerous studies have documented bird diversity within pastoral dry-forest landscapes. For example, in the inter-Andean Cauca Valley of northwestern Colombia, a preliminary survey of avifauna in a landscape of silvopastures, citrus groves, sugarcane fields under organic management, and remnant forest fragments of El Hatico Ranch and Nature Reserve revealed 135 of the region's 141 bird species, including several species not previously recorded from the valley (Cárdenas et al. 2000). Of these, 66 percent were found within agroecosystems, and 51 species were breeding or feeding fledglings within agricultural or silvopastoral habitats and remnants of natural vegetation. In comparison, for open rangeland in this region, Naranjo (1992) recorded only 42 species in pastureland, and only 14 of them regularly used this habitat. Thus, the presence of forest remnant vegetation, live fences, and silvopastoral management in El Hatico enabled persistence of forest specialist birds.

Studies of bird diversity in agricultural landscapes in the dry region of Nicaragua reported significant numbers of bird species using different types of tree cover (Harvey et al. 2006; Vilchez et al. 2008). In the pastoral landscape of Rivas, 83 bird species were reported within all types of tree cover. Similarly, in Matiguás, 137 bird species were observed in the agricultural landscape, with the greatest species richness occurring in the riparian forests, secondary forests, and forest fallows (table 12-2). In both landscapes, species composition varied greatly across different tree cover types. Forest-dependent birds and birds of conservation concern were generally more abundant in the forestlike types of tree cover than in more open pasture habitats.

Bats, like birds, use a variety of tree cover types within the agricultural matrix, including riparian forests, secondary forests, forest fallows, live fences, and even dispersed trees in pastures (Harvey et al. 2006; Medina et al. 2007). A total of 24 bat species were found in the agricultural landscape of Rivas, Nicaragua (Harvey et al. 2006), whereas 39 species were found

TABLE 12-2. Total species richness of birds, bats, and dung beetles in two agricultural landscapes dominated by pastures in Matiguás and Rivas, Nicaragua

Tree cover type	Birds (point counts)		Bats		Dung beetles	
	Matiguás	Rivas	Matiguás	Rivas	Matiguás	Rivas
Riparian forests	73	42	24	19	20	23
Secondary forests	71	49	21	14	26	29
Forest fallows	63	42	20	14	20	28
Live fences	47	32	20	18	17	24
Pastures with high tree cover	53	41	22	15	23	24
Pastures with low tree cover	51	35	20	15	10	20
Total	137	83	39	24	33	32

Sampling efforts and methods were identical across the two landscapes. Birds were sampled using point counts, bats were sampled using mist nets, and dung beetles were sampled using baited pit-fall traps. Eight plots of each tree cover type were sampled in each landscape. For additional details on methods see the sources.

Harvey et al. 2006 and in press

in the agricultural landscape of Matiguás, Nicaragua (Medina et al. 2007). Within the Matiguás landscape, bats move readily among different types of tree cover within the landscape, easily traveling large distances (more than 10 kilometers) within the landscape (Medina et al. 2007). Riparian forests (and to a lesser degree, live fences) appear to be key travel routes for bats as they cross agricultural landscapes. These linear features help bats orient their flight as they cross the agricultural landscape (as has been reported elsewhere by Verboom and Huitema [1997], Law and Lean [1999], and Galindo-González and Sosa [2003]) and fly over areas of open pasture (Estrada and Coates-Estrada 2001; Medellín et al. 2000; Medina et al. 2007). Moreover, bats feed on fruiting trees in pastures and other habitats within agricultural landscapes and disperse seeds of many tree species important for forest regeneration (Medellín and Gaona 1999; Melo et al. 2009).

Ants are another important indicator group for assessing the biodiversity value of agricultural habitats and landscapes (Power 1996; Perfecto and Vandermeer 2002). Ramírez and Enriquez (2003) sampled ant diversity in two silvopastoral systems (*Prosopis* and *Leucena*) and in remnant dry forest at El Hatico Ranch and Nature Reserve in Colombia. The forest showed the highest species richness, whereas *Prosopis* and *Leucena* silvopastoral sys-

tems supported 62 and 97 percent of the species found in the dry forest fragment, respectively, despite considerably lower vegetation cover (20 to 71 percent). For ants, higher vegetation cover did not correspond with higher species richness across these habitats (Ramírez and Enriquez 2003). In the dry forest region of Veracruz, Mexico, Gove et al. (2005) found that ant species richness was higher in isolated trees in pasture and secondary growth than in pastures lacking trees. Isolated trees also provided unique habitat for some arboreal species such as *Cephalotes*.

Dung beetle diversity within agricultural landscapes can also be high, particularly in landscapes that retain a significant level of tree cover. In many dry forest regions converted to cattle production, the availability of large quantities of cattle dung can provide a plentiful food source for some dung beetle species, and if the landscape still retains sufficient tree cover and shade, the conditions may be quite favorable for certain (but not all) species. In the Rivas landscape of Nicaragua, a total of 32 dung beetles were found, while in the Matiguás landscape, a total of 33 dung beetle species were reported (Harvey et al. in press). In both landscapes, dung beetles were reported across all types of tree cover studied (from forest patches to live fences to pastures with trees), although species richness was generally higher in habitats with greatest tree cover and lowest in pastures with low tree cover.

Conservation of Vulnerable and Endangered Species in Agricultural Landscapes

Agricultural landscapes in dry forest regions support a considerable proportion of the original biodiversity but fewer species than found in intact forest. For most taxa that have been examined, the most abundant and frequent species within agricultural landscapes are generalist species typical of open or disturbed habitats (Boshier et al. 2004; Harvey et al. 2006). Small forest fragments within the agricultural matrix can have high conservation value, however (Sekercioglu et al. 2007). In the Rivas landscape of southwestern Nicaragua, 14 endangered bird species were observed in forest fragments (Harvey et al. 2006).

Conservation value is ranked highest for habitats utilized by species that are highly sensitive to human disturbance. Petit and Petit (2003) studied bird communities in 11 distinct habitat types in Panama, ranging from extensive tracts of lowland humid forest to forest fragments and a variety

of agricultural land uses. Bird species were classified into five broad habitat association guilds and into three classes of “vulnerability,” representing sensitivity of species to human disturbance. Agricultural habitats, such as sugarcane and rice fields, grazed and fallow pasture, and pine plantation, showed no forest-specialist bird species and no species of high vulnerability (Petit and Petit 2003). Yet these habitats did support species with moderate levels of vulnerability. Shade coffee plantations, riparian forest, and lowland forest fragments supported some forest specialists and forest generalists, as well as species of high and moderate vulnerability. These habitats serve as refugia within the broader agricultural landscape in which they are found (Griffith 2000). In regions where most of the forest cover has been lost, shade coffee plantations provide a particularly important habitat for forest-dwelling bird species (Perfecto et al. 1996; Wunderle and Latta 1996; Greenberg et al. 1997; Petit and Petit 2003).

The conservation value of agricultural landscapes is greatly enhanced by linear forms of vegetation that serve as corridors connecting forest fragments. Williams and Vaughan (2001) studied habitat use by white-faced monkeys (*Cebus capucinus*) in an agricultural landscape in Curu Wildlife Refuge of northwestern Costa Rica. Live fences, palm canals, and riparian forest were the most utilized habitats. Management of vegetation corridors in agricultural landscapes is therefore essential to support populations of primates, birds, bats, butterflies, and other animal taxa (Estrada and Coates-Estrada 1996; Sorensen and Fedigan 2000). Forest fragments in Oaxaca, Mexico, are often embedded in an agricultural matrix of land uses, including older secondary forests. These secondary forests and forest fragments have considerably high conservation importance (Gordon et al. 2004).

Restoration and Succession: A Brighter Future for Biodiversity?

In addition to their current value as habitat and resources for certain species, agricultural landscapes also hold the potential to enhance biodiversity through natural and assisted regeneration processes. Increases in vegetation complexity and forest cover will likely benefit biodiversity, potentially ameliorating at least some of the negative effects of forest conversion to agriculture. In the Chorotega dry forest region of northwestern Costa Rica, declining beef prices from 1985 to 1989 caused progressive abandonment of cattle ranches (Arroyo-Mora et al. 2005). In this highly deforested re-

gion, forest cover increased from 1979 to 1986 (at a rate of 1.63 percent per year) and from 1986 to 2000 (4.91 percent per year). Secondary forests now cover large areas of this dry forest region (Kalacska et al. 2004; Arroyo-Mora et al. 2005). Within Guanacaste National Park (700 square kilometers), pasture declined by 28 percent from 1979 to 1985 and is being replaced by successional deciduous or evergreen dry-forest vegetation (Janzen 1988c; Kramer 1997; Kalacska et al. 2004). On a smaller scale, SDTFs are resurging in many areas of the Neotropics (Sánchez-Azofeifa et al. 2005; Wright and Muller-Landau 2006; Hecht and Saatchi 2007; Lebrija-Trejos et al. 2008).

As with their wet-forest counterparts, SDTFs show a high capacity to recover vegetation structure and biodiversity through succession (Vieira and Scariot 2006; Ruiz et al. 2005; Chazdon et al. 2007; Lebrija-Trejos et al. 2008). In Mexico, dry-forest succession differs from humid-forest succession in the low species richness of pioneers and lack of long-lived pioneer species, leading to more rapid recovery of tree species composition (Ewel 1980; Lebrija-Trejos et al. 2008).

Case Study: Biodiversity in Secondary Forests of Chamela-Cuixmala, Mexico

Secondary forests within agricultural landscapes provide critical habitats for biodiversity, but few data are available for SDTF species. To explore the potential value of secondary forests as catalysts for the conservation of plant and animal species, we describe changes in woody vegetation, bat, and bird diversity in successional habitats within one agricultural landscape in a SDTF region surrounding the Chamela reserve in western Mexico. We assess changes in abundance and biodiversity using a chronosequence composed of three pasture sites 0-1 years since abandonment, three sites 3-5 years postabandonment, three sites 8-12 years postabandonment, and three old-growth forest sites representing a late successional stage from the Chamela reserve. In July 2003, one 1-hectare site was delimited for study for each of these sites.

The Chamela-Cuixmala region was opened to human colonization in the late 1960s. Slash-and-burn practices initially established agricultural fields during the first 2 years, and pastures were later established for raising cattle. About 70 percent of the SDTF in the local communal *ejidos* surrounding the biosphere reserve has been converted to pastures (Maass et

al. 2005). Lack of economic or human resources to maintain pastures along with water scarcity (various years of drought) have resulted in the abandonment of pastures in this region (Burgos and Maass 2004; J. Trilleras-Motha and P. Balvanera, unpublished data). Abandoned pastures are rapidly colonized by *Acacia* and *Mimosa* species, which form monospecific-vegetation thick carpets (Ortiz 2001; Burgos and Maass 2004).

Woody Plants

Within each of the 12 study sites, a 30 by 60 meter permanent plot was established using a nested design. All stems of trees, shrubs, and lianas greater than or equal to 1 centimeter in diameter at breast height (or 1.3 meters above ground level) were tagged, measured, and taxonomically identified within 10 by 50 meters, those greater than or equal to 2.5 centimeters in diameter within 20 by 50 meters, and those greater than or equal to 10 centimeters in diameter within 30 by 60 meters. Stem density increases slowly during the first 5 years of succession, followed by rapid increases thereafter; sites with fallow ages of 8-12 years were similar in stem density to old-growth forest sites (fig. 12-1A). This trend was paralleled by changes in alpha diversity (i.e., number of species per plot) observed along the chronosequence. Pasture sites with less than 6 years of abandonment had, on average, a third or less of the number of species recorded at the old-growth forest sites, whereas sites with fallow ages of 8-12 years had a similar alpha diversity (about 80 species in 1800 square meters) compared with the old-growth forest sites (fig. 12-1B).

Facilitation appears to operate at the early successional stages, where few colonizing species can establish and grow under the harsh conditions of the abandoned pastures. Among the colonizing species, *Cnidoculus spinosus* and the legumes *Acacia farnesiana*, *Caesalpinia caladenia*, *Mimosa arenosa*, and *Bahuinia subrotundifolia* were practically restricted to the youngest successional sites (less than 6 years old), accounting for 40 percent of total stem density in such sites. Other relatively abundant colonizing species reached their maximum densities in the 8-12-year-old sites. Among these, *Croton pseudoniveus*, the legumes *Lonchocarpus constrictus* and *Piptadenia constricta*, and *Casearia corymbosa* accounted for 14 percent of total stem density recorded at the youngest successional sites. Yet, other colonizing species were among the 15 most abundant trees found in the old-growth forest sites. Among these, *Caesalpinia eriostachys*, *Lysiloma microphylla*, and *Caesalpinia tremula*, *Cordia alliodora*, and *Heliocarpus pallidus* constituted

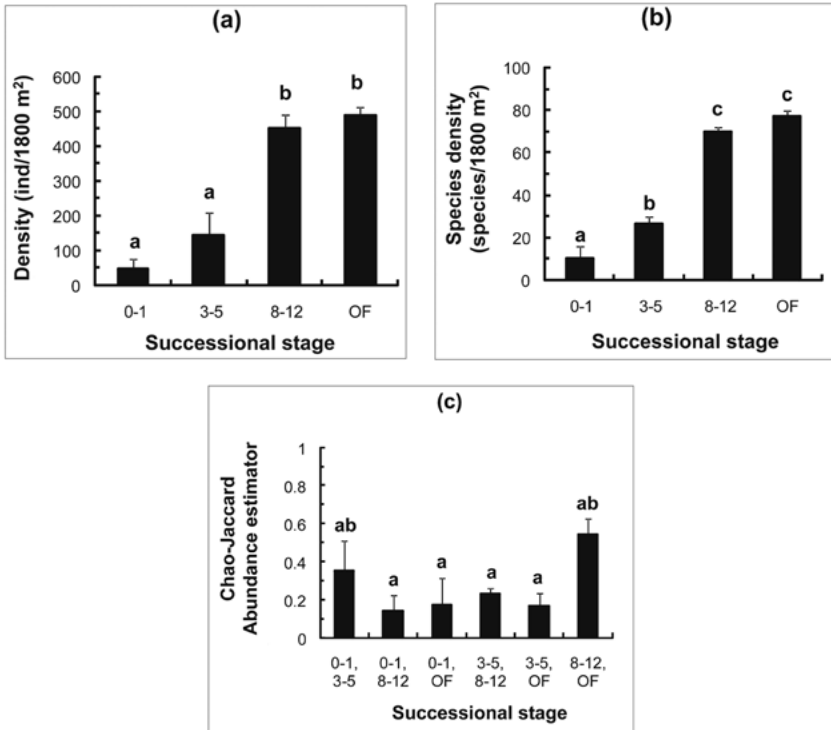


FIGURE 12-1. Structural and species diversity changes of woody plants along a chronosequence of abandoned pasture fields and old-growth forest sites in the Chamela-Cuixmala region, western Mexico. (A) Changes in stem density of trees, shrub, and lianas with diameter at breast height greater than 1 centimeter. (B) Changes in alpha diversity, number of species of trees, shrub, and lianas per sampled area. (C) Changes in beta diversity, proportion of shared species among sites of different successional ages. In all cases, bars represent means plus 1 standard error considering three sites per successional stage. Numbers on the bottom axis indicate intervals of years since field abandonment, and “OF” indicates old-growth forest sites. Different letters on bars indicate significant differences between successional stage classes ($P < 0.05$).

12 percent of total stem density recorded at the youngest successional sites. Thus, early secondary vegetation incorporates tree species that are structurally and functionally important in middle-aged secondary forest as well as in the old-growth forest.

Overall, 229 woody species were recorded in the 12 studied plots (total sampled area = 1.2 hectares). Combining sites from the same successional

age category together, species density in old-growth forest accounted for 65 percent of the gamma diversity value, species density in 8-12-year-old secondary forest accounted for 49 percent, species density in the 3-5-year-old secondary forest accounted for 37 percent, and species density in the 0-1-year-old abandoned pasture fields accounted for only 11 percent. Thus, the secondary forest sites of different ages held a substantial component (about 80 species) of the recorded gamma diversity. Furthermore, on average, species composition of old-growth forest sites showed low similarity with secondary forest sites less than 6 years old and higher similarity with the 8-12-year-old secondary forest sites (fig. 12-1C).

Current agricultural practices appear to promote high species diversity of woody vegetation within the landscape. The small size of clearings, reduced use of heavy machinery, low use of agrochemicals, presence of a large fragment of old-growth forest (the Chamela Biological Station Reserve), low frequency of fire use, low cattle loads for short periods, and generally moderate to low soil degradation in the region facilitate forest regeneration there (J. Trilleras-Motha and P. Balvanera, unpublished data). Contrary to the notion that shrubby legume species of *Acacia* and *Mimosa* arrest succession in abandoned agricultural fields (Ortiz 2001; Burgos and Maass 2004), our results suggest that they constitute a transient successional stage that facilitates the incorporation of a diverse array of woody species after only 6 years since field abandonment. In 30-year-old secondary forests dominated by *Mimosa arenosa* in the region, regenerating primary forest species were found among the youngest saplings. The relative dominance of regenerating primary species was clearly related to the intensity of management (Romero-Duque et al. 2007).

Birds

Effects of the process of ecological succession from pastures to mature forest on resident bird species were studied using both nonradius point counts and mist nets. Point counts were used to estimate bird species richness and abundances, while mist netting was used to complete the inventory of species and determine the reproductive and molting status of birds. Eighty point counts were established in each of the four successional stages, for a total of 320 independent sampling points. Point counts were randomly located inside the different successional stages and at least 250 meters apart to ensure independence of the data collected (Bibby et al. 2000). Sampling was conducted in, and around, two of the three sites used to represent each successional state in

the vegetation study, for a total of eight sampling areas. Mist-netting stations were established inside the eight vegetation plots discussed above. Each sampling area was visited two times during the dry season and two times during the rainy season in 2005, allowing for a better understanding of the effect of agricultural landscapes on the bird species breeding in the area.

Bird species richness and abundances were clearly positively related to increasing complexity of vegetation structure and plant diversity during succession. Bird communities in pastures were very distinct from those of the other successional stages. Pasture communities had low species richness and were dominated by a small number of granivorous species. Bird species richness was similar among secondary and old-growth forests, suggesting that once shrubs establish in abandoned pasture, bird communities can recover their alpha diversity and structure within 8 years (fig. 12-2).

Bird species richness increased rapidly during the first 3 to 5 years of succession and then stabilized, with 8-12-year-old secondary forests being very similar to old-growth forest sites (fig. 12-2A). However, bird abundances increased slowly along the successional gradient, reaching their highest values in the old-growth forest sites (fig. 12-2B).

Patterns of species richness and abundance along the successional gradient seem to be the result of three complementary processes: (1) the loss of forest species when the native vegetation is turned into pastures, (2) the invasion of pastures by granivorous and/or grassland-specialist species, and (3) the recolonization of secondary forest habitats by insectivorous, frugivorous, and nectarivorous species. Pasture sites presented a higher number of granivorous species compared with forest sites, and usually their communities were dominated by one species (*Aimophila ruficauda*). Granivore species richness and abundances decreased during succession, while the number of species and individuals of fruit- and nectar-eating birds increased. Although the number of insectivorous species increased with the time of abandonment (from 16 species in pastures to 30 in old-growth forest), their abundances remained constant (15 plus or minus 2.5 individuals per hectare), increasing the complexity and evenness of insectivorous bird communities. Because insect abundance did not differ significantly among the different sites (C.A. Chávez-Zichinelli, unpublished data), this result suggests that an increase in the complexity of vegetation structure associated with successional age could provide a larger number of feeding niches for insectivorous birds.

In total, 110 bird species were recorded in the 320 sampling points and eight mist-netting stations (gamma diversity). Among these, 109 were terrestrial birds, and one was an aquatic species that uses terrestrial habitats to nest (*Dendrocygna autumnalis*). This represents 88 percent of the terrestrial

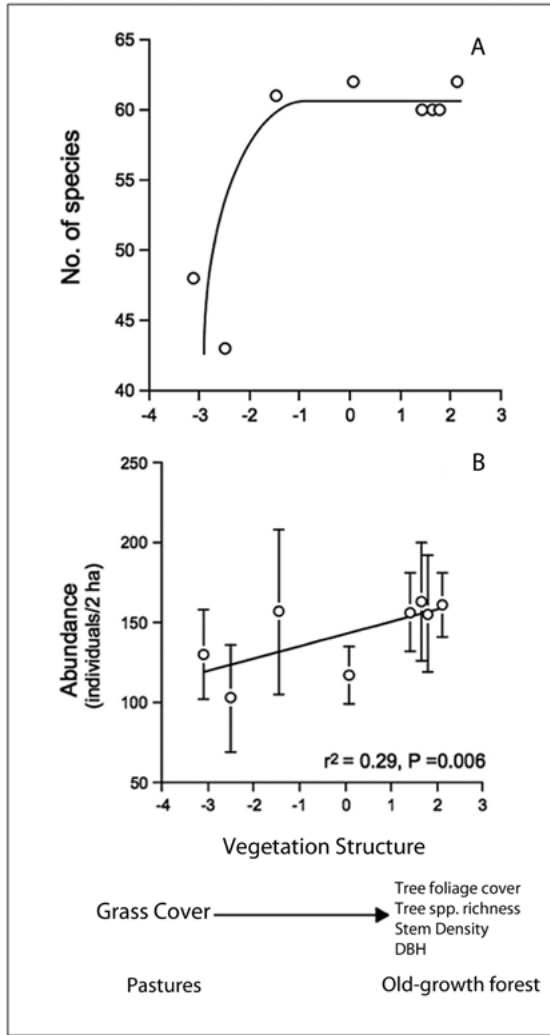


FIGURE 12-2. Effects of vegetation structure on bird species richness and abundance. Vegetation structure was determined by using a principal component analysis that included grass cover, tree foliage cover, density of stems, tree species richness, and diameter at breast height (DBH). The first principal axis (used here as the horizontal axis) comprised 83 percent of the total variation. The analysis ordered the eight sampling sites (each represented by a data point) as a chronosequence, with pasture sites on the left and old-growth forest sites on the right. Number of bird species increase rapidly with succession, reaching a saturation point and staying constant after a few years of pasture abandonment. Bird abundances increase along the successional gradient, reaching their highest values in old-growth forests.

resident species reported for the region (Arizmendi et al. 2002). Lumping data for all sampling points of each successional age category together, species density in old-growth forest accounted for 60.9 percent (67 species) of the gamma diversity, while species density in 8-12-year-old forest, 3-5-year-old forest, and 0-1-year-old abandoned pastures accounted for 61.8 percent (68 species), 67.3 percent (74 species), and 56.3 percent (62 species) of the gamma diversity, respectively. Thus, pastures and secondary forests supported a large fraction of the bird diversity in the landscape (102 species), with only 8 species being restricted to old-growth forest. These old-growth species include one large-sized parrot (*Amazona oratrix*), one large-sized woodpecker (*Campephilus guatemalensis*), a hummingbird (*Chlorostilbon canivetis*), and several species of flycatchers (*Contopus pertinax*, *Myiarchus cinerascens*, *Myiopagis viridicata*, and *Tityra semifasciata*). Old-growth forest sites shared 62 percent of their species with secondary forest sites younger than 6 years old, and 93 percent with the 8-12-year-old secondary forest sites. Surprisingly, 13 percent of all species (12 species) were shared by all successional stages. Among these species are 8 species endemic to Mexico that are considered to be dry forest specialists (*Cacicus melanicterus*, *Deltarhynchus flammulatus*, *Granatellus venustus*, *Melanerpes chrysogenys*, *Passerina lechlanchei*, *Polioptila nigriceps*, *Thryothorus felix*, and *T. sinaloa*).

These results suggest that birds respond quickly to changes in vegetation structure associated with succession. Agricultural landscapes increase bird diversity by allowing grassland species to invade previously forested habitats. Some forest species adapt to pasture conditions, or they start to return to early successional stages as soon as shrubs/young trees get established. Whereas secondary forests showed bird diversity and community structure similar to those found in old-growth forest, the population-level mechanisms that allow these patterns to occur are not yet understood. The patchy configuration of the agricultural landscape in the Chamela-Cuixmala region allows birds to move easily among different successional stages and old-growth forest, promoting the rapid recovery of bird communities despite large-scale land use transformations.

Bats

The structure and composition of bat communities in pasture and different successional stages was investigated by mist net sampling. This method focused on sampling the leaf-nosed family (Phyllostomidae), which includes

the most important Neotropical frugivorous and nectarivorous species. Since most aerial insectivores are adept at detecting and avoiding mist nets, their capture in mist nets is not a reliable method for assessing their abundance or distribution, and data for these species were excluded from this analysis. Every 6 weeks from June 2004 to August 2006, five mist nets (two 6 meters, two 9 meters, and one 12 meters) were placed in each of the 12 sites representing the chronosequence composed of three pasture sites 0-1 years since abandonment, three sites 3-5 years postabandonment, three sites 8-12 years postabandonment, and three old-growth forest sites representing late successional stage. Because of very low capture rate, the three pasture sites were sampled approximately half as much as the other sites. Sampling was conducted from sunset for 5 hours.

During 142 sampling nights, 606 phyllostomid bats were captured, representing 16 species (L.D. Avila Cabadilla and K. Stoner, unpublished data). We captured 87.5 percent of the phyllostomid species reported for this region (Stoner 2002). As with bird communities, bat species richness and abundances were clearly related to successional increases in vegetation structure and plant diversity. However, unlike bird communities, bat communities were less diverse in the youngest successional stages (fig. 12-3).

Sixteen species were captured in mature forest, 9 in late and early successional stages, and only 4 in pastures. Furthermore, a clear change in the

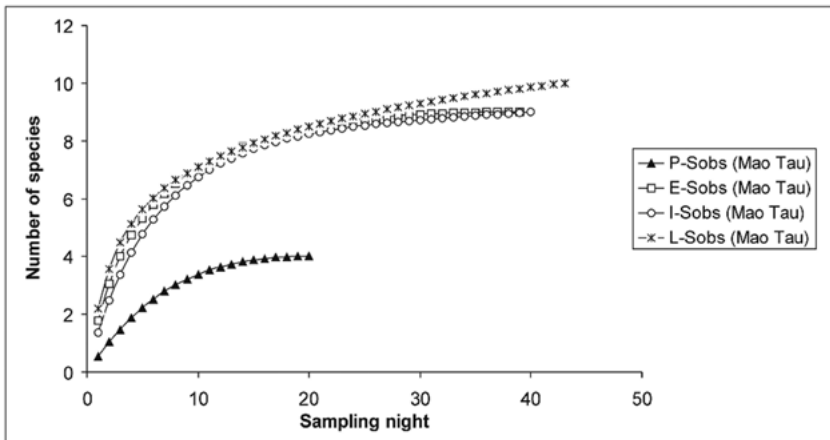


FIGURE 12-3. Species accumulation curve for bats in pastures (triangles), secondary vegetation 3-5 years old (squares), secondary vegetation 8-12 years old (circles), and mature forest representing a late successional stage (asterisks) in the Chamela-Cuixmala region, western Mexico.

number of species within foraging guilds was observed for bats (fig. 12-4). In particular, more species of frugivores and nectarivores were found in mature forest than in either successional stage. The one species of gleaning insectivore (*Micronycteris megalotis*, Phyllostominae) was found only in mature forest.

Although these trends suggest that bird communities recover more quickly than bat communities during succession, more studies in SDTF are needed. Given the importance of bats in both seed dispersal (Geiselman et al. 2002; Muscarella and Fleming 2007) and pollination (Winter and von Helversen 2001; Stoner et al. 2003) in Neotropical ecosystems, the lag time in the recovery of this important group of animals may have negative consequences for the regeneration of SDTF ecosystems.

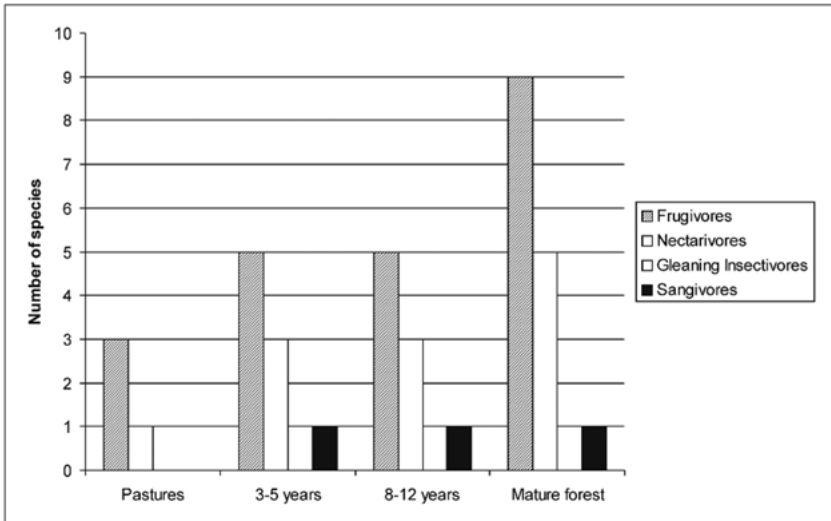


FIGURE 12-4. The number of phyllostomid species observed in pasture, successional forest, and mature forest in the Chamela-Cuixmala region, western Mexico, classified by foraging guilds.

Steps to Enhance Biodiversity and Conservation Value of Agricultural Landscapes

Under favorable conditions, abandonment of pastures in SDTF regions can lead to substantial recovery of biodiversity through forest succession. The negative effects of agricultural land use for biodiversity can be further

reduced through a range of specific farm management strategies and agricultural policies (Harvey et al. 2008a; Chazdon et al. 2009a; table 12-3).

The most fundamental approach to enhancing biodiversity in agricul-

TABLE 12-3. Examples of farm management activities that influence the biodiversity value of agricultural landscapes

<i>Activities that increase the conservation value of agricultural landscapes</i>	<i>Activities that decrease the conservation value of agricultural landscapes</i>
Controlled burning (avoiding escape of fire into intact forests by establishing firebreaks)	Indiscriminant use of fire (and escape of fires into adjacent forests)
Rotational and controlled grazing systems	Overgrazing and unsustainable stocking rates
Maintenance of natural regeneration within pastures	Elimination of natural regeneration in pastures and crop fields
Establishment of diversified forest plantations and agroforestry systems	Establishment of monocultures and exotic species
Planting of multistory, diverse live fences (preferably connected to forest patches)	Removal of existing live fences or simplification of live fence structure and diversity
Sustainable management of forests	Unsustainable harvesting of timber, firewood, and/or nontimber forest products from forest patches, riparian areas, fallow areas, and pastures
Establishment of fallows within agricultural areas	Uncontrolled grazing and trampling of riparian areas by cattle
Restoration of degraded areas to native forest cover	Conversion of forests or fallow areas to pasture or crop land
Use of sustainable land use practices (e.g., organic agriculture, agroforestry)	Unsustainable hunting or collection (for pet trade) of wildlife within forests and fallow areas
Use of integrated pest management strategies	Pollution or contamination of soils and water from agrochemicals (fertilizers, pesticides, etc.)

Sources are Harvey et al. 2005 and in press.

tural landscapes is to increase the amount, diversity, and connectivity of tree cover. Protecting existing forest fragments, riparian forests, and remnants of native habitat within agricultural landscapes should be a high priority (Bengtsson et al. 2003; Daily et al. 2001, 2003; Harvey et al. 2005b, 2006). Different taxa and guilds vary in their response to the types of on-farm tree cover present in agricultural landscapes. Highly degraded, unproductive areas within these landscapes should be restored through reforestation, natural regeneration, and/or enrichment planting. The establishment and management of diverse forms of tree cover will ensure heterogeneous habitats for wildlife and resources for migratory species of birds and butterflies. Linear forms of tree cover, such as riparian strips and live fences, can increase habitat connectivity and enhance biodiversity within agricultural landscapes (Chacón and Harvey 2006). Diversification of agroforestry systems offers another mechanism for enhancing tree cover, particularly in buffer zones surrounding existing protected areas and in biological corridors linking protected areas within the Mesoamerican Biological Corridor (Kaiser 2001; Miller et al. 2001).

Tree cover within agricultural landscapes is highly dynamic, largely due to changes in the way farmers design and manage their farms (Boshier et al. 2004; Harvey et al. 2004, 2005a, 2008b). Conservation biologists need to actively engage farmers in seeking long-term, landscape-level management plans that address both conservation and production concerns. Tree diversity within pastures can be enhanced by encouraging farmers to retain a greater diversity of adult trees within pastures and to select (and retain) a greater number of regenerating trees within pastures. Diversity within live fences can be enhanced by providing farmers with a greater selection of tree species to plant (Zahawi 2005). Tree species that show limited regeneration in pastures could also potentially be promoted through specific management strategies such as retention of adult trees as seed sources, protection of saplings and seedlings from weeding and grazing, and enrichment planting. Farm management practices are thought to be responsible for saving *Leucena salvadorensis* from extinction in Mesoamerica, through maintenance of genetic diversity on farms (Hughes 1998; Chamberlain et al. 1996).

Remnant trees in pastures can serve as seed sources to promote regeneration of many species within the surrounding landscape. Unfortunately, many forestry laws do not restrict harvesting of trees from pastures or regulate their densities or use, due to the misconception that these trees have little or no conservation value. On-farm tree cover also provides critical resources for migratory species. Many dry forest butterfly

species migrate seasonally to wetter lowland forests or to higher-elevation cloud forests (Haber and Stevenson 2004) and require tree cover along their migratory routes.

Challenges to Biodiversity Conservation within Agricultural Landscapes

Any efforts to conserve biodiversity within agroecosystems in the SDTF of Mesoamerica will require strong alliances with the farmers who own and manage agricultural land (Vandermeer and Perfecto 2005, 2007; Harvey et al. 2008a). Decisions about tree cover within these landscapes may have negative or positive impacts on the value of this land for biodiversity conservation by changing the amount or type of tree cover, its structural and floristic complexity, or its arrangement in the landscape (Harvey et al. 2005a).

Common management practices such as the indiscriminant use of fire, cattle grazing in riparian areas and forest patches, hunting, conversion of fallow areas to pastures, or conversion of forests to pastures reduce the quality of the agricultural landscape for biodiversity conservation. Fire is used widely throughout the region to clear new areas for shifting cultivation, prepare land for the planting of crops, eliminate weeds and stimulate regrowth in existing pastures, or eliminate weeds and pests (snakes, rats) from pastures and crop fields prior to planting grass or crops, and also prior to harvesting sugarcane (another key land use in the dry forest region). Although the information on the number and extent of fires is scarce, each year larger areas of land are burned—particularly in the dry season when farmers use fire to prepare lands for cultivation (Middleton et al. 1997; Billings and Schmidtke 2002). For example, it is estimated that 1.1 million hectares of land were burned in Central America during 1998 (of which 653.3 hectares were in agricultural landscapes and the remainder in forest areas), while an estimated 1.5 million hectares were burned in Central America and Mexico during 1999 (SCBD 2001). A significant proportion of these fires occur in dry forest ecosystems. A study in 1998 estimated that 42,486 wildfires occurred in Central America, burning 1.1 million hectares of land.

Harvesting of firewood presents a second important threat to on-farm tree cover. Particularly in rural areas where firewood is the key fuel, indiscriminant harvesting of firewood from forests and fallow areas can severely reduce tree diversity and negatively impact wildlife. In Masaya, Nicaragua, at least 64 tree species were being commercialized in the fuelwood market

by vendors (McCrary et al. 2005). The majority of the fuelwood comes from on-farm tree cover, such as live fences, windbreaks, and fallow areas, yet as much as one-third to one-half of the fuelwood was harvested from natural forests (including protected areas). Harvesting of fuelwood from natural forests is particularly prevalent during the dry season, when these forests are most easily accessed.

Decisions by farmers to increase tree cover within their farms by retaining forest patches, fencing off forests and riparian areas to prevent cattle entry, planting new live fences, establishing forest plantations, or converting agricultural systems to agroforestry systems will rarely be made without financial incentives. Therefore, payments to subsidize reforestation efforts or to cover fencing costs are required to encourage practices that enhance on-farm tree cover and increase the diversity and quality of forested habitats. For example, in projects where payments for environmental services are available to farmers to help offset the costs of establishing on-farm tree cover, farmers have readily increased the number of live fences in pastures and allowed greater natural regeneration of trees (e.g., Pagiola et al. 2005).

A further challenge in biodiversity conservation within agricultural landscapes is that land use and landscape composition are subject to rapid change with minimal regulation. Changes in agrarian and economic policies, such as the adoption of the Central American Free Trade Agreement or sudden increases in prices for cattle or other commodities, can rapidly change the composition of the landscape, with certain impacts on biodiversity (Harvey et al. 2005a). The 1996 Forestry Law of Costa Rica prohibits clearing of existing forest for agricultural land use—but farmers are now hesitant to abandon agricultural lands, as they will lose their rights to use these lands for agriculture in the future. Similarly, if sugarcane becomes more profitable because of changes in the Central American Free Trade Agreement, many pasture areas may be converted to sugarcane, further decreasing the potential for forest regeneration.

Research Priorities for Assessing Biodiversity in Agricultural Landscapes

Our synthesis clearly reveals the need for further research to assess the biodiversity of species utilizing agricultural areas and to promote application of adaptive management to changing agricultural systems and landscapes, changing socioeconomic contexts, and emerging threats to biodiversity.

Landscape-level studies should be conducted in a broad range of different types of agricultural landscapes in dry forest zones encompassing different countries and different historic and current patterns of land use and agricultural management (Chazdon et al. 2009a). These studies will provide critical information needed to maximize biodiversity conservation potential in agricultural landscapes of dry tropical forest regions:

- investigations of demography, breeding behavior, and population genetics of wild flora and fauna in agricultural landscapes
- studies of habitat use, resource use, species interactions, range sizes, and movement patterns of animals within the agricultural landscape
- assessments of the effectiveness of buffer zones and corridors for the conservation of target species of conservation concern
- assessments of the effects of agrochemicals (and pesticide drift), human disturbance, fire, and harvesting of natural products on plant and animal communities
- characterization of relationships between biodiversity, farm productivity, and ecosystem services to provide a more rigorous scientific basis for environmental payment schemes and other incentives for conservation
- assessment of the economic value (and costs) of biodiversity to agriculture (e.g., Ricketts et al. 2004) to evaluate the gains, losses, and trade-offs of encouraging wildlife presence on farms
- investigations of long-term dynamics of natural forest regeneration and succession in agricultural landscapes, including studies of vegetation, vertebrate and invertebrate taxa, and comparisons with wet-forest successional dynamics

Conclusions

Because of their great extent and proximity to protected areas, agricultural landscapes of the tropics are critically important for biodiversity conservation. Within Mesoamerica today, agricultural landscapes still contain significant levels of biodiversity (DeClerck et al. 2010). Urgent action is needed to promote sustainable farming practices that enhance conservation of wild species within these landscapes (Harvey et al. 2008a). At the same time, basic ecological knowledge regarding the habitat utilization, movements, breeding biology, and diversity of species within these landscapes is urgently needed to provide a sound basis for conservation policies and action.

As illustrated in chapter 11, SDTF fragmentation represents a significant threat to the maintenance of species interactions, particularly those relevant to plant reproductive success and genetic diversity. Given that agricultural landscapes bring about forest fragmentation, work is urgently needed to define to what extent agrosapes can support significant proportions not only of the local biodiversity but also of the ecological processes that generate and maintain such biodiversity. Conservation biologists need to extend the scope of their research activities to include studies within agricultural areas (Chazdon et al. 2009a). Ultimately, the fate of tropical biodiversity will be determined by management decisions and government policies that affect entire landscapes and regions. Despite many challenges, agricultural landscapes in dry forest regions offer the potential to cultivate a more secure future for biodiversity.

Acknowledgments

Our synthesis was stimulated by a working group on Biodiversity and Conservation Value in Agricultural Landscapes of Mesoamerica, supported by the National Center for Ecological Analysis and Synthesis (NCEAS) Center funded by the NSF (Grant #DEB-0072909), the University of California, and the Santa Barbara campus. Robin L. Chazdon's research was supported by NSF DEB-0424767 and NSF DEB 0639393. Research by Celia Harvey was supported by the FRAGMENT and CORRIDOR projects, funded by the European Union (INCO-DEV ICA4-CT-2001-10099 and INCO-CT-2005-517644). Research by Kathryn E. Stoner and Luis Daniel Avila Cabadilla was partially supported by the Inter-American Institute for Global Change Research (IAI CRN2-21). Funding for the Chamela successional research was provided by a grant from SEMARNAT-CONACYT (CB-2005-01, No. 24843) and SEP-CONACYT (CB-2005-01-51043). We thank Lorena Morales-Pérez for use of unpublished data.