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Contribution of live fences to the ecological integrity of agricultural landscapes

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Abstract

Live fences are conspicuous features of agricultural landscapes across Central America but there is remarkably little information about their abundance, distribution, and function. Here we present a detailed analysis of: (1) the abundance, composition, structure and distribution of live fences in four contrasting cattle-producing areas of Costa Rica and Nicaragua; (2) the management of live fences by farmers; and (3) the ecological roles of live fences in providing habitat, resources and connectivity for wildlife. Data on botanical composition and structure are complemented by documentation of local knowledge about live fences and associated management practices, as well as an assessment of fauna that utilize them. Live fences were common, occurring on between 49% and 89% of cattle farms, with an overall mean of 0.14 ± 0.01 km ha^{-1} of farm land and almost 20 fences per farm. They were generally short (164.3 ± 5.4 m), narrow (3.76 ± 0.03 m) and densely planted (323.1 ± 8.6 trees km^{-1}), consisting primarily of planted trees. The mean tree species richness for individual fences in each landscape was low (from 1.4 to 7.5 species per fence), but landscape species richness was higher (from 27 to 85 species, with over 70 species in three out of four sites). A total of 161 tree and palm species were recorded in the live fences across the four sites. The abundance, tree species composition and structure of live fences varied across farms and landscapes, reflecting differences in environmental conditions and management strategies. In all landscapes the main productive roles of live fences were to divide pastures and serve as barriers to animal movement, although they were also sources of fodder, firewood, timber and fruit. The main ecological roles were to provide habitats and resources for animal species and structural connectivity of woody habitat across the agricultural landscape. More than 160 species of birds, bats, dung beetles and butterflies were recorded

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visiting them. Their value for biodiversity conservation depended on their species composition, structural diversity and arrangement within the landscape, all of which were heavily influenced by management currently undertaken by farmers in pursuit of production rather than conservation goals. Live fences are important features of agricultural landscapes that merit much greater attention in sustainable land management strategies and need to be an explicit element in regulations and incentives that aim to enhance the ecological integrity of rural landscapes in Central America.

Keywords: Biodiversity conservation; Costa Rica; Farm management; Faunal diversity; Landscape characterization; Landscape connectivity; Local knowledge; Nicaragua; Central America

1. Introduction

Live fences are common in Central America, delineating crop fields, pastures, and farm boundaries and forming elaborate networks of tree cover across rural landscapes. Not only do live fences occur across areas that are biophysically diverse, with different elevations, ecological life zones, and soil types, but they also occur in areas with distinct cultures, land use histories and agricultural production, notably coffee plantations, pastures and home gardens (Sauer, 1979; Budowski, 1987). In some agricultural regions, where deforestation and conversion to agriculture have been high, live fences constitute the most prevalent form of tree cover remaining in the landscape.

Despite their prevalence throughout Central America, there is remarkably little information about the functional roles of live fences within agricultural landscapes. Aside from a few general descriptions of live fences and their management (Sauer, 1979; Lagemann and Heuveldop, 1983; Budowski, 1987, 1988; Budowski and Russo, 1993; Otarola, 1995), there is little information about their abundance, density or distribution and how these vary across farms and landscapes. Similarly, while several studies have considered specific aspects of live fences such as fodder production (Beer, 1987; Berninger and Salas, 2003; Frank and Salas, 2003), establishment (Somarriba, 1995), growth rates (Picado and Salazar, 1984; Beer, 1987) or rooting abilities (Lozano, 1962), few studies have looked holistically at the range of products, environmental services and ecological functions that live fences provide. The ecological roles of live fences as potential habitats, resources and corridors for wildlife have been particularly neglected, with the exception of a few studies in Mexico (e.g. Estrada et al., 1993, 2000; Estrada and Coates-Estrada, 2001). This paucity of information about live fences is in sharp contrast to the extensive literature on the patterns of hedges and windbreaks in temperate regions (e.g. Baudry et al., 2003; Thenail and Baudry, 2004), where their ecological and productive roles are well understood and highly valued (e.g., Osborne, 1983; Forman and Baudry, 1984; Baudry, 1988; Bennett et al., 1994; Burel, 1996; Baudry et al., 2000; Marshall and Moonen, 2002). It also contrasts with the burgeoning information and growing recognition of the conservation importance of other forms of tree cover in human-dominated landscapes in the tropics, such as forest fragments, riparian strips, and dispersed trees in fields (Schelhas and Greenberg, 1996; Laurance and Bierregaard, 1997; Harvey and Haber, 1999; Daily et al., 2001; Harvey et al., 2004).

The general objective of this paper is to draw attention to the prevalence of live fences within agricultural landscapes in Central America, to highlight both their agronomic and ecological functions, and discuss their potential contribution to sustainable development and conservation initiatives. The specific objectives of this paper are: (1) to characterize the abundance, species composition, structure and distribution of live fences in agricultural landscapes in Central America; (2) to explore how live fences are integrated within farming systems and how farmers manage them; (3) to assess the ecological roles of live fences in providing habitats, resources and landscape connectivity for wildlife; and (4) to explore the potential for incorporating live fences into conservation planning at the landscape scale. Our assessment draws on a set of integrated studies of live fences in four contrasting agricultural landscapes dominated by cattle grazing in Costa Rica and Nicaragua, but the general principles identified here are likely to apply generally across agricultural landscapes in Central America.

For the purpose of this paper, we consider live fences to be ‘‘fences established by planting large cuttings, that easily produce roots and on which several strings of wire are attached with the obvious purpose of keeping livestock in or out’’ (*census* Budowski, 1987). Although their composition and structure vary from one site to the next, most live fences consist of one or two woody perennial species that are evenly planted in a straight line adjacent to agricultural fields or along farm boundaries (Sauer, 1979). Live fences differ from hedges in that they are less dense, contain fewer plant species, usually support one or more strings of wire, and are entirely anthropogenic features, in contrast to hedges which may originate from natural regeneration, relict vegetation or from planting (Baudry et al., 2000). They also differ from windbreaks in that their primary purpose is to provide fencing to contain animal movement, rather than to provide shelter, and they are consequently less densely planted (Finch, 1988; Wight, 1988). However, live fences are similar to hedges and windbreaks in that they are linear woody features that form integral components of farm production systems and are carefully managed by farmers to provide many of the same ecological and production functions.

2. Methods

Live fences were studied in four agricultural landscapes where cattle grazing was the predominant land use; Cañas and Río Frío in Costa Rica, and Matiguás and Rivas in Nicaragua (Table 1). Cañas and Rivas are typical of cattle production systems on the seasonally dry Pacific slope of Central America, with extensively managed cattle systems for beef in Cañas and dual-purpose (beef and dairy) production in Rivas. In contrast, Río Frío is a dairy producing region on the wet Atlantic slope of Costa Rica, with smaller and more intensive farms than those in Cañas. The Matiguás region is one of the key cattle raising zones in central Nicaragua dedicated to dual-purpose cattle production, in a transition area between tropical dry and humid forest. Farms in Matiguás are dedicated almost exclusively to cattle production, while those in Rivas integrate cattle production with agricultural production, rotating areas of pasture with plots of banana, plantain, corn and beans. In each landscape, an area of roughly 10 000–16 000 ha was selected as representative of the landscape in the region. Each of these landscapes was dominated by pasture (48–68% of the land), while the little forest cover remaining (8.2–23.3%) was generally in the form of small forest patches and riparian strips.

Data on live fences were collected in a set of integrated studies which included: (1) a socioeconomic survey of a random sample of 53–100 farms in each landscape, in which information about farm characteristics, land use, and tree cover was collected; (2) a complete inventory of the floristic composition, structure and spatial arrangement of live fences present in a sample of 12–16 cattle farms in each landscape; (3) acquisition of local knowledge that farmers held about live fences; (4) the monitoring of farm management, including information on live fence establishment, management and pollarding, in 12–16 farms in each landscape during 1 year; and (5) studies of the fauna (birds, bats, dung beetles, and butterflies) present in live fences. A summary of the research conducted in each landscape is shown in Table 2, and additional details of each study are provided below. Research was conducted from February 2002 to March 2003 in Rivas and Cañas, and from March 2003 to June 2004 in Río Frío and Matiguás.

2.1. Farm survey

In each of the four landscapes, a questionnaire on farm land use and management was completed by interviewing 53–100 farmers, randomly selected from a list of all farmers in each study area. The aim of this survey was to characterize farm types and understand farm management practices. In addition to general statistics of land use, information was collected on the presence of live fences, the number of tree species present in live fences and management practices associated with them. Additional details on the farm survey are available in Villacis (2003) and Gómez et al. (2004).

2.2. Inventory of live fences

Detailed information on live fence abundance, composition and structure was obtained on 12–16

Table 1
Biophysical and productive characteristics of the four study sites in Costa Rica and Nicaragua in which live fences were studied

Variable	Costa Rica		Nicaragua	
	Cañas	Río Frío	Rivas	Matiguás
Biophysical characteristics				
Study area (ha)	13051	15987	11621	10108
Ecological life zone	Tropical dry forest	Tropical wet forest	Tropical dry forest	Transition from tropical dry forest to tropical humid forest
Average annual rainfall (mm)	1544	4120	1400	1800
Average annual temperature (°C)	27.6	25.0	27.0	24.0
% of landscape that is covered by forest (including riparian forest)	23.2	21.8	21.5	8.2
% of landscape that is covered by pasture	48.4	47	56.7	68.2
Production system characteristics				
Main production system	Beef	Dairy (some beef)	Mixed (dual-purpose cattle + agriculture)	Dual purpose cattle
Range of farm size (ha)	5.6–1526	2.5–140	0.7–47.8	5.62–351.3
Mean farm size (ha)	158.2 ± 42.6	22.1 ± 3.1	20.8 ± 1.5	27.9 ± 5.1
Mean herd size (animal units)	84	32	11	20
Mean pasture size (ha)	8.42	4.83	12.3	4.4
Cattle breeds	Crosses of Indobrasil, Brahman, and Gyr	Dairy breeds include crosses of Jersey, Holstein, and Brown Swiss; beef breeds include crosses of Indobrasil and Brahman	Crosses of Brahman, Indobrasil, Holstein, Brown Swiss and Criollo	Crosses of Brahman, Indobrasil, Brown Swiss, Holstein and Criollo
Grass species	*Brachiaria brizantha*, *Brachiaria decumbens*, *Hyparrhenia rufa*	*Ischaemun ciliare*, *Brachiaria arrecta*	*H. rufa*	*Panicum maximum*, *Paspalum virgatum*, *H. rufa*

Table 2
Summary of the data collected on live fences in the four study sites

Live fence data collected	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua	All four sites
No. of farmers interviewed in socioeconomic survey	53	71	57	100	281
Farm types in which live fences were inventoried (number of farms)	Beef farms (5), mixed farms (cattle + crops; 5), dual-purpose farms (5)	Dairy farms (4), mixed (cattle + crops) farms (4), beef farms (4), dual purpose farms (4)	Mixed (cattle + crops) farms held by private farmers (4), mixed farms (cattle + crops) acquired through agricultural reform (4), mixed farms (mainly agriculture, but some cattle; 4)	Mixed campesino farmers (mainly crops, some cattle production; 5), mixed farms (mainly cattle, some crops) <10 ha (5), mixed farms (mainly cattle, some crop production) >10 ha (5)	
Total no. of farms on which live fences were inventoried	15	16	12	15	58
Total farm area surveyed for live fences (ha)	1030.5	157.9	385.4	418.3	1992.1
Total area of pastures surveyed for live fences (ha)	800.7	117.9	248.6	324.6	1491.8
No. of trees (dbh > 10 cm) within live fences measured for diameters, heights and crown radius	3331	1377	530	1737	6975
No. of key informants interviewed about local knowledge of live fences	25	25	20	25	95
No. of people interviewed to validate the knowledge base	50	50	45	69	214
No. of farmers studied for decision-making	15	16	12	15	58
No. of live fences in which birds, bats, dung beetles and butterflies were sampled	8	8 (ongoing)	8	8 (ongoing)	16
Additional studies on birds in live fences	No	Yes	No	No	

farms in each of the four sites, giving a total of 59 farms. The farms were chosen using stratified sampling schemes reflecting the main types of farms present at each site, with 4–5 farms per farm type. The farm typologies surveyed in each site are listed in Table 1, and additional details on these typologies are available in Gómez et al. (2004; Rivas); Villanueva et al. (2003; Cañas), and Villacís et al. (2003; Río Frío). Within each of these farms, a complete census of all live fences was conducted, with data collected on the species composition, number of trees with a stem diameter at breast height (1.3 m) >10 cm, number of wooden fence posts, and fence length. In addition, in each fence, between 5 and 10 randomly chosen trees were measured for diameter at breast height (dbh) and canopy radius (measured as the widest point of the canopy extending perpendicularly from the fence). Each live fence was georeferenced with a GPS XL12 and subsequently mapped onto an aerial photograph of the farm in ArcView 3.3.

2.3. Farmer knowledge and practice

Additional information on live fence establishment, structure and management was generated through studies of farmer knowledge about farm tree cover, including live fences. Detailed, open-ended interviews were conducted with 20–25 key informants at each site, using knowledge based systems methods (Sinclair and Walker, 1998; Walker and Sinclair, 1998). The information collected on live fences included knowledge of the characteristics of live fence species (e.g., rooting ability, phenology, soil requirements, growth rates, wind susceptibility, durability, susceptibility to pests, and wood quality), live fence management (preparation of stakes, seasonality of management, planting distances and pollarding frequency), as well as the roles of live fences within the farming system (value as forage, firewood, timber and medicine, provision of shade to cattle, and their effects on soil). All interviews were tape-recorded, transcribed and entered into a formal knowledge base on computer, using the Agroecological Knowledge Toolkit software (AKT5 version 4.01, Dixon et al., 2001). A more detailed description of the methods for each site can be found in Muñoz et al. (2004; Río Frío and Cañas), Martínez (2003; Matiguás) and Joya et al. (2004, Rivas). Additional information on live fence establishment and management was collected through monthly visits to the 12–16 sample farms in each landscape.

2.4. Biodiversity

In the Rivas and Cañas sites, data on biodiversity (birds, bats, dung beetles and butterflies) within live fences were collected as part of a study of biodiversity within the overall landscape, in which the abundance, species richness and diversity of these faunal groups was compared among different woody habitat types (forest patches, riparian forests, young areas of secondary growth and pastures with dispersed trees). In each landscape, a total of eight randomly chosen live fences (each a minimum of 250 m long) were surveyed for biodiversity. Birds were registered using point counts (80–90 min of observation per live fence), bats were caught using eight mist nets (total of 96 mist-net hours per live fence), dung beetles were captured using pitfall traps (total of 64 trap-nights per live fence), and butterflies were collected using nets (total of 3 h of netting per live fence). All biodiversity inventories were conducted along a transect that ran along the side of the live fence, with point counts being positioned every 50 m, mist nets (for bats) established at 50 m intervals on alternate sides of the live fence, and pitfall traps positioned at 5 m intervals. All monitoring was conducted in two consecutive days in each live fence.

In the Río Frío site, avian use of live fences was studied in greater detail in 16 live fences, eight of each of two structural types: large ‘complex live fences’, with trees with dbh >10 cm, a canopy with mean spread >4 m, and a mean tree height of >6 m; and smaller ‘simple live fences’, which were below these thresholds. Each fence was observed on 5 days in a 6-week period using a randomized point count method with a total observation time of 250 min per live fence and 67 h overall. Data were collected on bird abundance and activities (foraging, perching, nesting, etc.). Additional observation of bird movement and use of live fences using ringed birds were also collected as part of an ongoing study of bird use of agricultural landscapes by R. Taylor.

3. Results

3.1. Abundance, species composition, structure and spatial distribution of live fences

3.1.1. Abundance

In all four landscapes, live fences were common features and represented an important component of farm tree cover. A total of 1195 live fences were inventoried in the four landscapes, containing a total of 60 536 trees, of which roughly half had dbh >10 cm, and comprising a total length of 196.4 km (Table 3). A total of 51 226 dead wooden posts were recorded within the live fences, showing that live fences generally included some dead fence posts. Farmers typically establish fences using dead posts to facilitate attachment of barbed wire, and then plant live posts in between. Fences consisting of only dead wooden posts were also present in each landscape and accounted for 14.6% of all existing fences across all sites.

The abundance and density of live fences varied across both farms and landscapes. Live fences were present on over 80% of farms in three sites, while at Rivas they occurred on just under half of the farms (Table 4). There were typically more than 22 live fences per farm, although many fewer in Rivas. The total length of live fences per farm was also variable, with an overall mean of just over 3 km farm^{-1}, and the longest in Cañas that also had the largest farms. Expressed on an area basis, the mean length of live fence was 0.14 km ha^{-1} of farmland and 0.22 km ha^{-1} of pasture, and was significantly higher in Río Frío compared to the other sites ($p < 0.001$).

Several factors influenced the abundance of live fences at both farm and landscape scales, including farm size and production system. Not surprisingly, larger farms tended to have a greater total length of live fence, more trees in live fences and greater numbers of live fences than smaller farms but the density of live fences was not related to farm size (Tables 1 and 5). This is illustrated in the Río Frío site, where live fence abundance and density were related to the level of farm intensification (rather than farm size), with the more intensively managed dairy farms having more live fences, a longer length of live fence per farm and a higher density of live fences (km ha^{-1} of farmland) than less intensively managed farms (dual-purpose,

Table 3
Summary of the number of live fences, trees, and wooden posts, and live fence length in the four study sites

Live fence data collected	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua	All four sites
No. of live fences	385	409	71	330	1195
No. of wooden (dead) fences	51	1	69	83	204
% of total fences that are live fences	88.3	99.8	50.8	80	85.4
No. of trees registered with dbh >10 cm	20974	3812	1852	3464	30102
No. of trees registered with dbh <10 cm	11477	12205	1958	4794	30434
No. of wooden fence posts counted (total)	28241	5702	18616	10363	62922
No. of wooden fence posts counted in live fences	25374	5689	12160	8003	51226
Total length of fences surveyed (including both live and wooden fences) (m)	90832	35535	46125	50378	222870
Total length of live fences (m)	83551	35475	35610	41772	196408

Table 4
Live fence abundance and distribution on cattle farms in four landscapes

Variable	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua	All four sites
% of farms with live fences[a]	89	87	49	88	80
Mean no. of live fences per farm	25.7 ± 3.0	25.6 ± 6.3	4.7 ± 0.6	22.2 ± 2.0	19.6 ± 2.1
Min–max no. of live fences per farm	8–46	6–79	2–9	4–32	2–79
Mean total length of live fences per farm (m)	5570 ± 957	2217 ± 249	2374 ± 336	2785 ± 280	3220 ± 314
Mean km of live fence per ha of farm	0.09 ± 0.01	0.23 ± 0.03	0.11 ± 0.02	0.13 ± 0.01	0.14 ± 0.01
Mean km of live fence per ha of pasture	0.14 ± 0.02	0.34 ± 0.05	0.21 ± 0.04	0.16 ± 0.02	0.22 ± 0.02

Means and standard errors represent the means per farm.
[a] Data on the percent of farms with live fences stem from the socioeconomic surveys (n = 53 in Cañas, 73 in Río Frío, 57 in Rivas, and 100 in Matiguás). All other data stem from the field inventories on 12–16 farms per landscape.

beef production systems or mixed cattle and crop farms; Fig. 1); however at the same time, live fences in dairy farms had lower tree densities than live fences in the less intensively managed farms; Table 5).

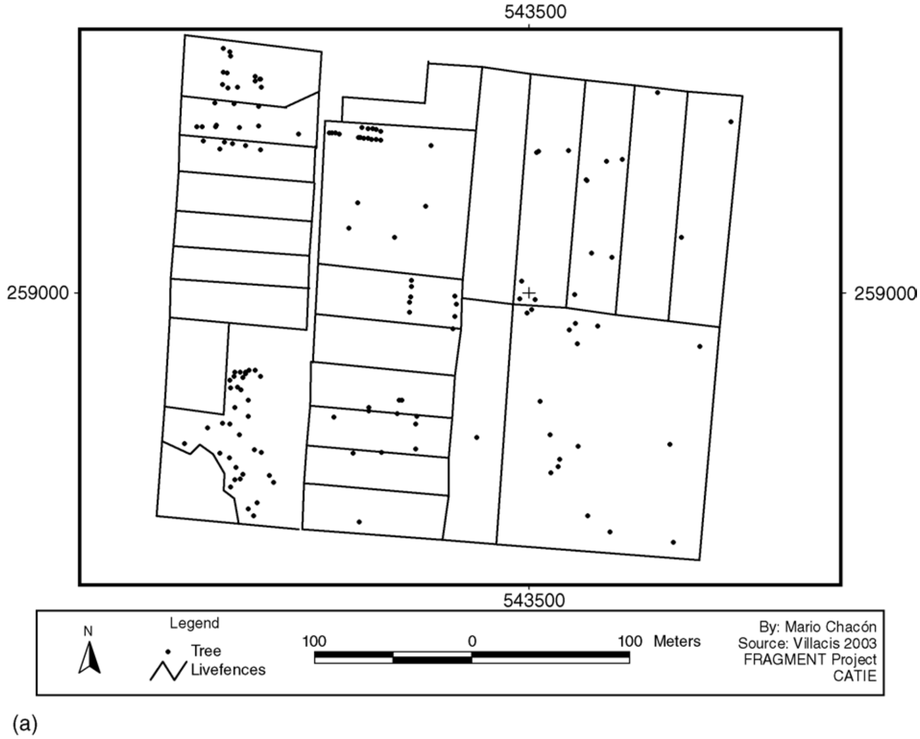
3.1.2. Species composition

A total of 161 plant species were found in live fences across all four sites (Appendix 1), of which 159 were tree species and two were palms. With the exception of Rivas, a handful of species deliberately planted by farmers were dominant (Table 6). In Río Frío, *Erythrina costaricensis* and *Gliricidia sepium* accounted for 75.6% and 11.1% of all trees, respectively, and the mean number of species per fence was 1.5. In Cañas, live fences were more species rich, with a mean of approximately four tree species per fence, but similarly two species, *Bursera simaruba* and *Pachira quinata*, dominated, accounting for 54.2% and 27.6% of all live fence trees, respectively. In the Matiguás site, live fences were also dominated by *B. simaruba* (a planted species accounting for just over half of all trees) and to a lesser extent by *Guazuma ulmifolia* (a species that naturally regenerates within pastures and live fences, and is dispersed by cattle), *P. quinata* (planted), and *G. sepium* (planted). In contrast, live fences in Rivas, where more trees in the fences arose from natural generation, were more diverse. The tree species richness was considerably higher in Rivas than at the other sites (7.5 species per fence, compared to from 1.4 to 4.1 at other

Table 5
Comparison of live fence number, length, density and characteristics in intensified dairy farms versus non-intensified cattle systems in Río Frío, Costa Rica

Variable	Highly intensified dairy farms (n = 4 farms, 236 live fences, 330 trees)	Less intensified cattle farms (n = 12 farms, 264 live fences, 1047 trees)
Type of cattle production system	Specialized dairy production	Dual-purpose, meat and/or mixed production systems (beef/agriculture)
Grass type	Predominantly ‘improved’ grasses (*Brachiaria arrecta*, *Panicum maximum* var. *Tanzania*, *Pennisetum purpureum* var. *King* and *Brachiaria brizanta*)	Naturalized grasses (*Ischaemum ciliare*)
Stocking rate (animal units)	3.8 ± 0.2 a	2.2 ± 0.2 b
Mean number of live fences per farm	59 ± 16.7 a	14.5 ± 1.7 b
Mean total length of live fences per farm	3.2 ± 0.6 a	1.5 ± 0.1 b
Mean number of paddocks per farm	21.2 ± 6.6 a	3.5 ± 0.5 b
Mean km of live fence per ha of farm	0.3 ± 0.06 a	0.16 ± 0.01 b
Mean total number of trees per km of live fence[a]	308.4 ± 51.5 b	707.8 ± 61.0 a
Mean frequency of pollarding (times/year)[b]	1.6	1.3

[a] Data from socioeconomic survey.
[b] Includes trees of all sizes.



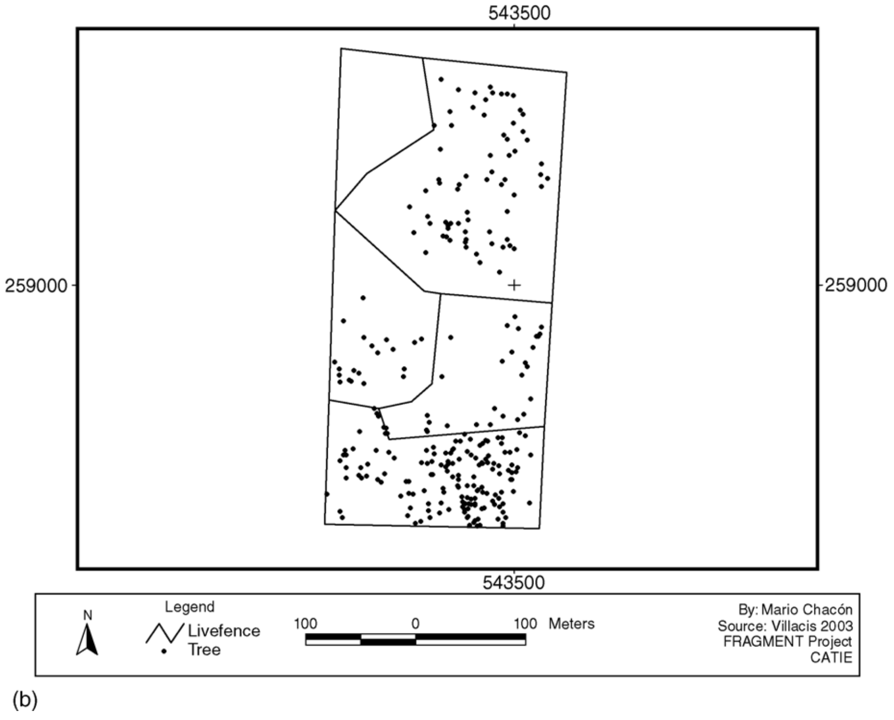


Fig. 1. Examples of the arrangement of live fences (black lines) and dispersed trees (black dots) present in (a) intensified dairy farms and (b) less intensified beef and dual purpose farms. Data are from two farms in Río Frío, Costa Rica where all live fences and dispersed trees were georeferenced.

Table 6
Species composition and structure of live fences in Río Frío, Cañas, and Rivas, based on trees with diameters >10 cm

Variables	Cañas, Costa Rica (n = 20 974 trees in 385 live fences)	Río Frío, Costa Rica (n = 3812 trees in 409 live fences)	Rivas, Nicaragua (n = 1852 trees in 71 live fences)	Matiguás, Nicaragua (n = 3464 in 330 live fences)
Mean no. of tree species per live fence	4.10 ± 0.14	1.38 ± 0.04	7.48 ± 0.64	3.12 ± 0.15
Mean no. of tree species in live fences per farm	24.8 ± 2.4	4.8 ± 0.7	17.3 ± 2.5	20.3 ± 2.0
Total no. of tree species found in live fences	85	27	73	72
Total no. of tree species that are planted deliberately	13	2	28	23
% of trees that are of planted species	92.2	86.6	38.4	31.9
Five most common plant species present in live fences (% of all trees surveyed)	*Bursera simaruba* (54.2%), *Pachira quinata* (27.6%), *Ficus* spp. (3.8%), *Gliricidia sepium* (1.9%), *Tabebuia rosea* (1.9%)	*Erythrina costaricensis* (75.6%), *G. sepium* (11.1%), *Cordia alliodora* (2.8%), *B. simaruba* (2.6%), *Dracaena fragrans* (1.8%)	*Guazuma ulmifolia* (9.06%), *Cordia dentata* (8.44%), *Acacia collinsii* (7.01%), *Myrospermum frutescens* (6.67%), *Simaruba glauca* (6.3%)	*B. simaruba* (50.1%), *G. ulmifolia* (8.7%), *P. quinata* (7.1%), *G. sepium* (5.5%), *Erythrina berteroana* (4.4%)

sites) and no species accounted for more than 9% of all trees. A common feature across sites was that almost all of the species found in live fences were native or naturalized.

Although the tree species richness of individual live fences was generally low, the combined species richness of live fences at farm and landscape scales was higher (Table 6). At the farm level species richness ranged from a mean of 4.8–24.8 species amongst landscapes, whereas at the landscape level, species richness ranged from 27 to 85 species per site.

3.1.3. Structure of live fences

Although in all sites live fences consisted of single rows of trees, the structure of live fences was variable across farms and landscapes due to differences in the tree species, planting distances, and frequency and intensity of pruning (Table 7). Most live fences were short (with an overall mean of 164.3 m), but the length of individual live fences ranged from 4 m to almost 2 km. Live fences were generally longer in the dry forest regions (Rivas and Cañas) than at the other two sites, because these sites had more extensive grazing systems that used larger pastures with fewer divisions (Tables 1 and 7). Total tree density (including all trees planted as live posts, regardless of diameter) ranged from a mean of 148.6 trees km^{-1} in Rivas to 414.6 trees km^{-1} in Río Frío (Table 7). If only trees with diameters >10 cm dbh were considered, the mean tree density across the four sites was 137.5 ± 5.3 km^{-1}, and ranged from 67.5 km^{-1} in Rivas to 241.8 km^{-1} in Cañas. Mean tree heights in live fences at each site were generally between 6 and 10 m with the tallest trees occurring in the Rivas landscape where live fences were infrequently pruned. The overall mean dbh of the measured trees in live fences was 23.6 cm, however, since only trees with dbh >10 cm were measured, this overestimates the mean for all trees. The mean crown radius of live fence trees was fairly uniform across sites, ranging from 3.1 to 4.8 m, with larger crowns occurring in live fences that were either older or had received less frequent pruning.

The distances at which trees were spaced within live fences varied depending on location within the farm. For example, in Río Frío, live fences that were planted along roads were more densely planted (mean of 415 trees km^{-1}) than those not adjacent to roads

Table 7
Structural characteristics of individual live fences in the four study sites

Variable	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua	All four sites
Mean length of individual live fences (m)[a]	217.0 ± 7.7	86.7 ± 3.6	500.3 ± 58.2	126.6 ± 4.4	164.3 ± 5.4
No. of live fences with trees with dbh >10 cm[a]	378	186	68	280	912
No. of live fences that had only trees with dbh <10 cm[a]	7	223	3	50	283
Mean density of trees with dbh >10 cm per km of live fence[a]	241.9 ± 11.8	88.1 ± 7.5	67.5 ± 6.9	92.1 ± 5.8	137.5 ± 5.3
Mean total tree density (trees km^{-1} of live fence)[a]	360.7 ± 16.2	414.6 ± 16.8	148.6 ± 15.2	203.6 ± 8.8	323.1 ± 8.6
Mean density of dead fence posts per km of live fence[a]	335.7 ± 10.5	123.0 ± 9.3	369.9 ± 11.3	216.8 ± 9.8	231.8 ± 6.0
Mean height of trees in live fences (±S.E.) in m	7.57 ± 0.07	6.77 ± 0.11	9.8 ± 0.17	7.02 ± 0.11	7.4 ± 0.05
Mean diameter of trees in live fences (±S.E.) in cm, of trees with dbh >10 cm	28.5 ± 0.3	16.09 ± 0.2	27.6 ± 0.7	19.1 ± 0.3	23.6 ± 0.2
Mean canopy radius of trees in live fences (±S.E.) in m	4.23 ± 0.05	3.07 ± 0.04	4.83 ± 0.12	3.20 ± 0.06	3.79 ± 0.03

[a] Data summarized per live fence (n = 385 in Cañas, 409 in Río Frío, 71 in Rivas, and 330 in Matiguás); all other data summarize data from the individual trees measured within live fences (n = 3331 trees in Cañas, 1377 in Río Frío, 530 in Rivas, and 1737 in Matiguás).

(mean density of 309.2 trees km^{-1}; $p < 0.0001$) to ensure that animals could not stray onto roads and to reinforce farm boundaries. Similarly, those live fences that were along roads had a significantly higher tree species richness (mean of 3.7 spp. versus 3.0 spp. in other fences), because of less frequent pruning and more natural regeneration ($p = 0.006$).

3.1.4. Distribution of live fences within farms and landscapes

In each site, live fences occurred in extensive, rectilinear networks that expanded across the landscape (e.g. Fig. 1), dividing the landscape into smaller areas and enhancing the physical connectivity of the on-farm tree cover. Within farms, most live fences occurred adjacent to (or within) pastures, with a subset outlining farm boundaries or bordering roads (Table 8). Of the 410 live fences mapped in Río Frío, well over half were surrounded on both sides by pastures. Similarly, in Cañas, over 70% of live fences divided pastures, and almost 20% bordered roads; very few (just over 3%) bordered either riparian forest or forest patches. Of the 1195 live fences surveyed, 72% were internal fences, occurring within pastures or fields and not bordering other farms.

Farmers rarely used live fences to cordon off forest patches, but some connected directly to forest patches or riparian strips, increasing the structural connectivity of wooded habitat across the landscape. In each of the sites, between 1% and 14% of the live fences connected directly either to a forest patch or riparian forest and since most of these connected to other live fences in expansive rectilinear networks, the majority of live fences were indirectly connected to forest patches.

3.2. Live fence functions and management within farming systems

3.2.1. Roles of live fences in farming systems

According to the farmers interviewed at each site, although live fences play multiple roles within farming systems, their main intended function is to delineate farm boundaries and divide pastures, thereby restricting animal movement. Farmers mentioned that live fences were an economical way to establish borders along farm boundaries and to divide pastures into paddocks, and were often cheaper than alternative

Table 8
Number of live fences bordering different land uses in different study sites

Land use surrounding live fence	Cañas, Costa Rica ($n = 385$ fences)	Río Frío, Costa Rica ($n = 409$ fences)	Rivas, Nicaragua ($n = 71$ fences)	Matiguás, Nicaragua ($n = 330$ fences)	All four sites
Land use					
% of live fences with pasture on both sides	70.91	71.6	56.3	61.5	67.70
% of live fences with pasture on one side	28.8	21.8	14.1	38.5	28.2
Other land uses	0.26	6.6	29.5	0.0	4.1
Location					
% of live fences that occur along roads	19.2	11.5	11.2	7.0	12.7
% of live fences that join directly to a forest or riparian forest	3.4	0.7	14.1	5.4	3.7

fencing methods such as electric fencing or dead wooden posts while having the added benefit of providing forage and shade for livestock and being self-sustaining.

In addition to serving as fencing, live fences were sources of a wide variety of products, including live stakes for new fences, forage, timber, firewood, and fruits, but the relative importance of these varied amongst sites. In all four landscapes, most farmers harvested the branches of established live fences to use as material for establishing new live fences or increasing the tree density within existing fences. Usually these stakes were used within the same farm or given to neighbours, although occasionally farmers sold them to other farmers in the region. Forage for cattle was an important product, particularly because many of the common live fence species such as *G. sepium* and *Erythrina* spp. are nitrogen-fixing species that provide forage that is of high nutritive quality and available in the dry season when grass is scarce (Beer, 1987; Frank and Salas, 2003). While farmers were aware of the potential value of live fence foliage as cattle fodder, less than 10% of them deliberately pruned their fences to make forage available for cattle because of the large amount of labour required to do this, but it was general practice to leave cut branches and foliage on the ground after fences had been pruned for cattle to feed on.

Other potential products from live fences, principally timber, firewood and fruits were rarely harvested. Of 102 farmers interviewed in Rivas, less than 10% indicated that they harvested firewood from live fences. In the Costa Rican sites, where farmers generally used gas or electricity for cooking, the collection of firewood was even less frequent: no farmers reported collecting firewood from live fences for home use but some use for outdoor fires was noted. The harvesting of timber from live fences was similarly infrequent, with farmers in Rivas and Matiguás harvesting timber from live fences on an occasional and sporadic basis, and farmers in Cañas and Río Frío indicating that they rarely, if ever, harvested timber from live fences, preferring timber from dispersed trees in pastures. Similarly, few farmers reported harvesting fruits from live fences, with the exception of some in Río Frío who had included orange trees within fences, particularly near homes or home gardens, and occasionally sold these to obtain additional income.

Farmers also indicated that live fences fulfilled service functions within the farm, such as the provision of shade and wind protection. In all four sites, farmers were aware that shade from live fences was important for cattle, reducing heat stress, particularly in the dry season, and providing a more comfortable environment for cattle, resulting in higher weight gain, milk production and reproductive rates. At the same time, farmers also saw shade as a potential drawback, since high shade levels can reduce grass productivity, and so overall farm productivity. Farmers were consequently careful not to allow live fences to grow too big, and pollarded them regularly to control tree crown size.

Among the drawbacks of live fences, farmers mentioned shade reducing grass production, the need to frequently pollard or repair fences and their permanence (once planted they are hard to remove or relocate, making it more difficult to change paddock sizes). Farmers who planned to make changes to their pastures, by planting different grasses or adding new divisions, were less likely to use live fences than those who do not require this flexibility. Cattle farmers in Rivas, who had fewer live fences than farmers at the other sites, indicated that live fences were not easy to integrate into farms which rotate livestock and crop production on the same land, as pasture boundaries change from 1 year to the next. Farmers also mentioned drawbacks of individual tree species, such as the tendency for *G. sepium* to fall over because of its superficial root system when propagated from cuttings and its susceptibility to taltuzas (*Orthogeomys* spp.) and the difficulty of managing *P. quinata* and some *Erythrina* species because of their spines.

3.2.2. Management of live fences

Live fence management was an integral component of farm management practised on more than 60% of farms in three of the landscapes but hardly at all in Rivas (Table 9). In Rivas, farmers did not need to manage their live fences because they were few in number and did not shade pastures much. At the other sites, management consisted of two main activities: pollarding of live fence trees to prevent shading of adjacent fields or pastures and planting of trees within

Table 9
Comparison of live fence management across three landscapes (no data are provided for Rivas because live fences are not pollarded at this site)

Variable	Cañas, Costa Rica	Río Frío, Costa Rica	Matiguás, Nicaragua
% of farmers that pollard[a]	62	100	80
Mean no. of times live fences are pollarded each year	1.11 ± 0.91	1.49 ± 0.91	NA
Time of pollarding	Dry season	Year-round	Dry season
Mean height of pollarding (m)	2.18 ± 0.02	2.05 ± 0.02	2.05 ± 0.06
Species frequently pollarded	*P. quinata*[b], *B. simaruba*	*E. costaricensis*, *G. sepium*	*P. quinata*[b], *G. sepium*, *Erythrina* spp.
% of trees in live fences that were pruned or pollarded at the time of inventories conducted during the dry season	31	83	10

[a] Data from socioeconomic survey; all other data are from field inventories of live fences.
[b] Species that is usually pollarded only partially.

fences to fill gaps or increase the tree density within the fence.

In the Cañas, Río Frío and Matiguás sites, live fence trees were pollarded at a height of roughly 2 m, so that resprouting shoots were out of reach of cattle, thereby preventing cattle from eating them and damaging the main tree stem in the process (Table 9). Branches removed from the live fences were either left on the ground for cattle to eat or used to establish new live fences or fill in gaps in existing fences. At all three sites, two types of pollarding were practised: complete pruning, involving the total removal of branches above a certain point, and partial pruning, where a few branches were left unpruned for use in the subsequent year as stakes to repair existing fences or establish new ones. When choosing which branches to leave in partially pollarded trees, farmers typically chose from two to four branches that were straight and closest to the stump. At all three sites farmers managed their live fences in accordance with moon phases, only pollarding and planting trees in a waning moon because they believed that this ensured that they rooted and leafed out quickly.

Although all farms in these three sites pollarded their live fences, the frequency, timing, and intensity of pollarding varied across farms and sites (Table 9), depending on species, location, ecological conditions and labour availability, among other factors. For example, in all sites, farmers almost always pollarded non-timber species (such as *G. sepium*, *B. simaruba* and *Erythrina* spp.), but rarely timber species. In general farmers pollarded live fences within paddocks once or twice a year to prevent the trees from shading the grass, as well as live fences near power lines, but rarely managed live fences along farm boundaries or roads, preferring to let the trees grow tall and so clearly mark the boundary.

Finally, differences in the frequency and timing of pollarding also reflected differences in climatic conditions across sites, which affect the rates at which individual species grow. In the drier climate of Cañas, farmers pollarded their fences less frequently than farmers in Río Frío where trees grow faster and retain their leaves throughout most of the year (once every 2 years compared to at least once a year). Differences in climatic conditions also affected the timing of pollarding: in dry sites, live fences were cut primarily during the dry months (February–April), whereas in wet climates that have no distinct dry season, such as Río Frío, live fences were pollarded year-round.

In addition to pollarding live fences, farmers in the Cañas, Río Frío and Matiguás sites also planted additional trees within existing live fences to ensure that they remained dense and so were an adequate barrier to cattle. The planting of live stakes to fill in existing live fences usually occurred at around the same time as pollarding, with farmers using the branches from the pruning as new stakes and planting them either immediately, or after a period of a few weeks. In all sites, farmers selected branches that were 6–10 cm wide, at least 2 m long, (usually 2 years old) and as straight as possible, but the handling of stakes before planting varied across sites, with farmers in some sites storing the stakes horizontally, others vertically, and yet others planting them directly without storage. In all sites, live stakes were planted in both the rainy and dry seasons. When adding new live posts to existing fences, farmers first added stakes to the boundary live fences to ensure that their farm boundaries were well protected, and then used any additional stakes to strengthen other live fences with low tree densities.

3.3. Ecological roles of live fences in agricultural landscapes

In the Cañas and Rivas sites where the biodiversity associated with live fences was studied, a total of 167 animal species (including birds, bats, dung beetles and butterflies) were observed using them (Table 10, Appendix 2). This almost certainly under estimates the actual species richness as these initial studies only surveyed eight live fences in each landscape for a short

Table 10
Summary of the number of species of birds, bats, terrestrial small mammals, dung beetles and butterflies found in live fences in Cañas, Costa Rica and Rivas, Nicaragua

Taxon	Cañas, Costa Rica	Rivas, Nicaragua	Total
Bird	45	29	59
Bat	25	18	30
Dung beetle	23	25	44
Butterflies	28	25	34
Total	121	97	167

Data come from eight live fences in each landscape.

Table 11
Examples of bird species found in live fences in Río Frío, Costa Rica that are considered species typical of forest habitats, in alphabetical order

Scientific name	Authority	Common name	Primary habitat (based on Stiles and Skutch, 1989)
Arremon aurantiirostris	Lafresnaye, 1847	Orange-billed Sparrow	Forest, old secondary
Cacicus uropygialis	Lafresnaye, 1843	Scarlet-rumped Cacique	Forest, tree pasture, old secondary growth
Caryothraustes poliogaster	Du Bus, 1847	Black-faced Grosbeak	Forest, shade tree pasture, old secondary growth
Claravis pretiosa	Ferrari-Perez, 1886	Blue Ground Dove	Forest
Cyanocompsa cyanoides		Blue-black Grosbeak	Forest
Dacnis cayana	Lafresnaye, 1847	Blue Dacnis	Forest, tree pasture, old secondary growth
Dendrocincla fuliginosa	Vieillot, 1818	Plain-brown Woodcreeper	Forest, old secondary growth, tree pasture
Dendroica pensylvanica[*]	Linnaeus, 1766	Chestnut-sided Warbler	Forest, edge, secondary, young secondary growth
Empidonax flaviventris[*]	Baird, WM & Baird, SF, 1843	Yellow-bellied Flycatcher	Forest, secondary, young secondary growth
Euphonia gouldi	Sclater, PL, 1857	Olive-backed Euphonia	Forest, old secondary, tree pasture
Glyphorynchus spirurus	Vieillot, 1819	Wedge-billed Woodcreeper	Forest, tree pasture, old secondary growth
Habia fuscicauda	Cabanis, 1861	Red-throated Ant-Tanager	Forest edge, riparian, young secondary growth
Hylophilus decurtatus	Bonaparte, 1838	Lesser Greenlet	Forest edge, secondary, tree pasture
Lepidocolaptes souleyetii	Des Murs, 1849	Streak-headed Woodcreeper	Tree pasture, secondary, young secondary growth
Leptotila cassini	Lawrence, 1867	Gray-chested Dove	Forest, old secondary growth, plantation
Manacus candei	Parzudaki, 1841	White-collared Manakin	Forest, edge, riparian, old secondary growth
Melanerpes pucherani	Malherbe, 1849	Black Cheeked Woodpecker	Young secondary growth
Mniotilta varia[*]	Linnaeus, 1766	Black-and-white Warbler	Forest, old secondary growth
Myiozetetes granadensis	Lawrence, 1862	Gray-capped Flycatcher	Tree pasture, secondary, forest edge
Oryzoborus funereus	Sclater, PL, 1860	Thick-billed Seed-Finch	Young secondary growth pasture, secondary, forest edge
Pachyramphus polychopterus	Vieillot, 1818	White-winged Becard	Tree pasture, plantation, old secondary growth
Pheucticus ludovicianus[*]	Linnaeus, 1766	Rose-breasted Grosbeak	Tree pasture, secondary, forest edge
Piculus simplex	Salvin, 1870	Rufous-winged Woodpecker	Forest, tree pasture
Pteroglossus torquatus	Gmelin, 1788	Collared Aracari	Forest, tree pasture, old secondary growth
Seiurus aurocapillus[*]	Linnaeus, 1766	Ovenbird	Forest understory
Seiurus noveboracensis[*]	Gmelin, 1789	Northern Waterthrush	Riparian forest
Setophaga ruticilla[*]	Linnaeus, 1758	American Redstart	Forest
Synallaxis brachyura	Lafresnaye, 1843	Slaty Spinetail	Young secondary growth, riparian
Tangara larvata	Du Bus, 1846	Golden-hooded Tanager	Forest, tree pasture, old secondary growth
Thamnophilus doliatus	Linnaeus, 1764	Barred Antshrike	Young secondary growth, forest
Thryothorus thoracicus	Salvin, 1865	Stripe-breasted Wren	Forest edge, riparian, plantation
Vermivora chrysoptera[*]	Linnaeus, 1766	Golden-winged Warbler	Forest, tree pasture, old secondary growth
Wilsonia citrina[*]	Boddaert, 1783	Hooded Warbler	Young secondary growth, forest edge, secondary
Xiphorhynchus susurrans costaricensis	Jardine, 1847, Ssp. Ridgway, 1888	Cocoa Woodcreeper	Forest, tree pasture, old secondary growth

Asterisks indicate migratory species.

period of time, and species accumulation curves for individual animal groups suggest that greater sampling effort would result in the detection of more species in both sites (Fig. 2). This was borne out during a more intensive 6-week observation period at Río Frío when 92 bird species were found to be using live fences compared with only 28 species recorded from spot measurements of eight live fences at the same site (Saenz, unpublished data). Most of the bird species observed were generalists that are able to survive in fragmented and modified landscapes, but a smaller set of forest-dependent species also made use of live fences (Table 11). For example, in the Río Frío site, of the 92 bird species recorded, 33 were considered dependent on forest habitats including both forest-dependent resident and migrant species (R. Taylor, personal communication).

Animal species used live fences for a variety of different purposes, including feeding on fruits, flowers and nectar. Preliminary observations of birds in live fences in Río Frío indicated that 23% of the birds were actively seeking food within live fences, 37% were perching, 10% were using the live fences as display posts, and 30% were observed traveling along the live

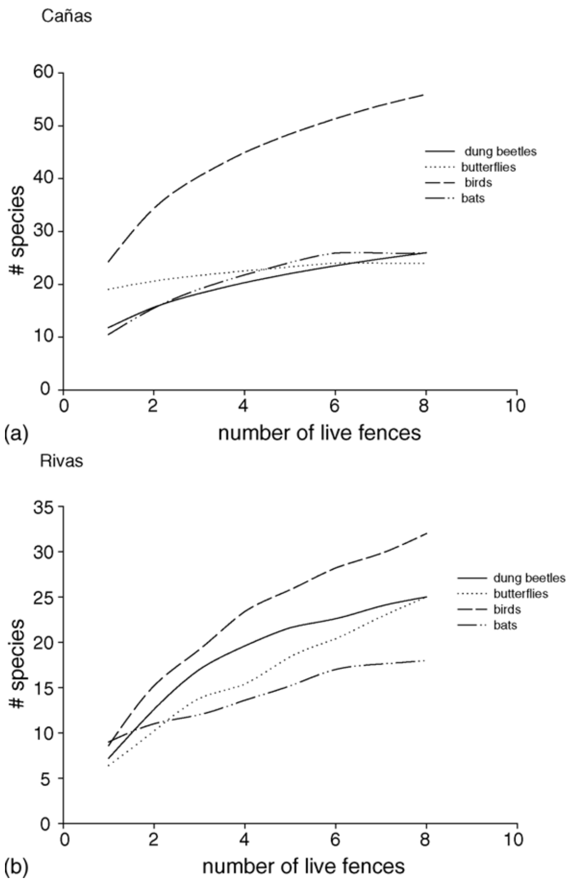


Fig. 2. Species accumulation curves of birds, bats, dung beetles and butterfly species in live fences in (a) Cañas, Costa Rica, and (b) Rivas, Nicaragua. Details on sampling effort can be found in Section 2.

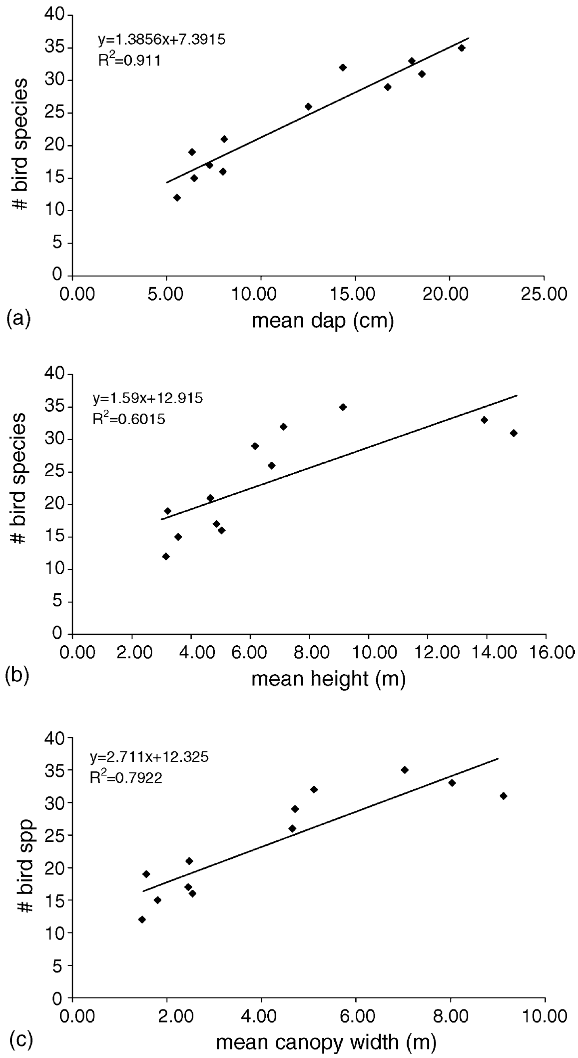


Fig. 3. Relationship between live fence structure (a) mean diameter, (b) height and (c) crown radius and bird species richness in Río Frío, Costa Rica. Data are from Lang et al. (2003), with each point representing a single live fence.

Table 12
Summary of the value of the most common tree species in live fence as sources of food and year-round habitat, based on field observations in the four sites

Scientific name	Family	% of all trees in live fences	Important food source for different organisms?			Deciduous?
			Bats?	Birds?	Butterflies?	
Bursera simaruba	Burseraceae	43.84	X			Yes
Pachira quinata	Bombacaceae	20.05	X	X	X	Yes
Erythrina costaricensis	Fabaceae-Mimosaceae	9.55	X	X		Yes
Gliricidia sepium	Fabaceae-Papilionoideae	3.72	X	X		Yes
Spondias purpurea	Anacardiaceae	3.06	X	X	X	Yes
Ficus werckleana	Moraceae	2.65	X	X		No
Guazuma ulmifolia	Sterculiaceae	2.24		X		Yes
Tabebuia rosea	Bignoniaceae	1.85		X	X	Yes
Cordia alliodora	Boraginaceae	1.23		X	X	Yes

fence (R. Taylor, unpublished data). The trees within live fences provided resources for many bird species. For example, in Río Frío many nectarivorous bird species (hummingbirds, Bananaquit *Coereba flaveola*) and nectarivore-frugivores (such as Baltimore Oriole *Icterus galbula*, Black-cowled Oriole *Icterus dominicensis*, Golden-hooded Tanager *Tangara larvata*) were observed feeding on the flowers of *E. costaricensis*, whereas other bird species (such as Paltry Tyrannulet *Zimmerius vilissimus*, Barred Antshrike *Thamnophilus doliatus*, Red Throated Ant Tanager *Habia fuscicauda*, Slaty Spinetail *Synallaxis brachyura* and Black Striped Sparrow *Arremonops conirostris*) were observed feeding on shrubs, vines and mistletoes present in dense, infrequently pollarded fences. In addition, observations suggest that the nine most common trees in live fences, which represent 89% of the trees present overall, provide food for either birds, bats or butterflies (Table 12).

Ongoing studies of birds in the Río Frío area indicate that live fences may act as movement corridors across the agricultural landscape for some bird species. Of 96 behavioral observations of birds in live fences, 66% were moving longitudinally through the fences, from tree to tree or flying along the fence line (R. Taylor, unpublished data). In addition, individual birds (such as a Ringed Streaked Headed Woodcreeper, *Lepidocolaptes souleyetii*) have been observed using the same live fences repeatedly as they move from one forest patch to the next, suggesting their use as movement corridors to other habitats. Capture rates of bats within live fence networks in both the Rivas (0.57 bats per mist net hour) and Cañas sites (0.67 bats per mist net hour) were greater than that of capture rates within forested habitats (0.37 bats per mist net hour in Rivas and 0.60 in Cañas) suggesting that some bat species may also be using live fences as travel corridors to cross open habitats.

The abundance and species richness of birds using live fences was related to live fence management. A comparison of bird communities in unpollarded live fences with large trees and wide crowns and recently pollarded live fences with smaller trees in Río Frío, showed that the pollarded live fences had only 55% of the species and 33% of the number of individuals found in the unpollarded fences. A total of 1141 birds of 81 species were observed in unpollarded live fences compared to only 407 birds of 45 species in the frequently pollarded fences with similar sampling effort of 33.5 h across fence types. In addition, bird species richness was positively correlated with the mean diameter, height and crown width of individual live fences (Fig. 3).

4. Discussion

Live fences were abundant and conspicuous features of all four agricultural landscapes studied and had important productive and ecological functions: acting as barriers to animal movement and sources of fodder, firewood and fruits, while also serving as habitat, providing resources and acting as corridors for wildlife conservation. Although the specific characteristics of live fences varied amongst farms within sites and amongst sites, they formed an integral part of the extant farming systems within which they were embedded. The prevalence of live fences within rural landscapes and their joint utility for both farm production and biodiversity conservation suggests that they merit much greater attention in sustainable land management strategies.

As has been found in comparable studies of hedges in temperate regions (e.g. Baudry et al., 2003; Thenail and Baudry, 2004), differences in farm management amongst the sites reported here, had a marked influence on both the composition of live fences and their structure within the landscape. For example, live fences were least common in the Rivas landscape because the mixed farming system there involved rotation of land from pasture to cropping with consequent requirements for moving fence lines, making the permanent live fences a less flexible option than dead posts. Differences were also evident amongst types of cattle production systems within sites. At Río Frío, for example, live fences were more abundant, but also more heavily managed and consequently smaller and less densely planted, in dairy farms with more intensive land use than on other cattle farms. This pattern emerges because the dairy farmers divided their land into a larger number of smaller paddocks (21.2 paddocks per farm compared to 3.5 in less intensively managed farms), rotated animals more frequently, and used the live fences (often with electric fencing, rather than barbed wire) to create these subdivisions (Fig. 1). In addition, dairy farmers pollarded their live fences more frequently than the other farmers to prevent shading of the improved grasses that they used, resulting in lower tree densities within the live fences.

Differences in species composition were also apparent across sites, reflecting differences in ecological and physical conditions, as well as differences in how farmers established and managed their live fences. In all four landscapes, the dominant species within live fences were those that had been actively planted by farmers, and appear from comparison with the literature (Budowski, 1987; Cordero and Boshier, 2003) to have been well adapted to the particular climatic conditions at each site. *Bursera simaruba* and *P. quinata*, for example, known to favor drier conditions, predominated in the dry Cañas and Rivas sites, while the *Erythrina* species grow better in the more humid conditions characteristic of Río Frío but all three species were found at the intermediate Matiguás site and *G. sepium*, tolerant of a wide range of conditions, was among the dominant species at all four sites. Differences in live fence structure also reflect differences in farm management, and particularly the frequency and intensity of pollarding.

4.1. Productive and ecological roles

Farmers actively managed live fences to facilitate farm and cattle management, pollarding live fences regularly to avoid the tree crowns from shading the adjacent pasture and replanting trees in live fences that have gaps or old trees, and these activities were a standard part of the management of cattle farms in the region. The high degree of integration of live fences within cattle farming systems and the familiarity of farmers with live fence establishment and management concurs with previous literature that highlights the productive roles of live fences within existing farming systems (e.g. Sauer, 1979; Budowski, 1987, 1988).

Live fences also played potentially important roles in wildlife conservation. As farmers establish and manage live fences to facilitate farm and cattle management, they inadvertently increase the total tree cover within the farming landscape, creating alternative habitats, stopover points, and resources for wildlife. The present research showed that a large number of animal species visited live fences, using them as perching sites, shelter, or foraging sites, and in some cases, as corridors to cross the otherwise open agricultural land. Many of the dominant tree species within live fences are known to provide food from their flowers, fruits and nectar or to act as foraging sites for wildlife, so their presence is likely to be beneficial for at least some animal species. Most of the animal species that benefit, however, are likely to be generalist species that can adapt to open agricultural landscapes. These results add to the growing literature on the importance of on-farm tree cover for the conservation of both plant and animal species within rural landscapes (e.g. Estrada et al., 1998; Estrada and Coates-Estrada, 2001; Harvey and Haber, 1999;

Harvey et al., 2004), and indicate that that the ways in which farmers manage the tree cover within their farms may have important ramifications for wildlife.

The physical presence of live fences on cattle farms may also benefit wildlife conservation by enhancing the structural connectivity of tree cover. By establishing live fences around pasture and farm borders, farmers create intricate networks of tree cover that divide the landscape into smaller areas, increase the spatial distribution of tree cover across the landscape and connect otherwise isolated forest patches or riparian forests, with potential benefits to conservation. Since live fences are durable features (with individual live fences lasting at least 50 years), once established, they are likely to enhance the structure, composition and functionality of rural landscapes for at least several decades. Although the presence of live fences changes the structure and composition of the agricultural landscape and may enhance the degree of landscape connectivity for some animal species, additional studies of animal movement within live fences are required to determine the degree to which live fences increase the functional connectivity of agricultural landscapes and which species may benefit or otherwise from their presence.

A final potential value of the live fences is that by providing both a durable and renewable source of fencing on farms, they reduce the need for farmers to harvest fence posts from the few remaining forested areas. In each of the sites, farmers mentioned that their decisions to use live fences, in part, stemmed from the difficulty and high cost of obtaining dead wooden fence posts, due to the limited forest resources on their farms and in the surrounding agricultural landscape. If the use of live fencing reduces the pressure on the remaining forest patches even to a small degree, this could have important conservation benefits at the landscape scale. Further research to quantify this is merited.

An important caveat regarding the conservation value of live fences is that it will depend on their composition, structural diversity and location, as has been found for windbreaks and hedges in temperate regions (e.g. Osborne, 1983; Baudry, 1988). These attributes of fences are influenced by management decisions taken by farmers for productive, rather than conservation, reasons. The data presented here illustrate a positive relationship between live fence size and bird species richness, with fences with trees with large crowns harboring almost double the number of species than recently pollarded live fences. Additional studies are needed to understand the effect on conservation value of tree species composition, management and live fence location, particularly proximity to forest, as they are all likely to affect how well live fences serve as wildlife habitat.

4.2. *Opportunities for integrating live fences into conservation planning within agricultural landscapes*

Although live fences are typically ignored in land use and conservation planning, the results reported here show that they represent an important component of tree cover within rural landscapes in Central America and may fulfill important ecological roles, in addition to their more obvious contribution to the farming systems of which they are a part. Given the ease of integrating live fences within current farming systems, the small area that they occupy, and the familiarity of farmers with their management, they could serve as a tool for conservation efforts within rural landscapes. If appropriately designed and managed, live fences could help increase on-farm woody habitat and resources for wildlife, as well as enhancing landscape connectivity, without much reduction in farm production or complication of farm management.

One opportunity to capitalize on the ecological roles of live fences would be to increase the total number and extent of live fences in these landscapes by converting the wooden fences to live fences. In landscapes such as Rivas, Nicaragua, where only half of the current fences are living, there is an important opportunity to increase on-farm tree cover by converting wooden fences to live fences. The division of pastures into smaller paddocks and the concurrent adoption of rotational grazing, might also improve cattle productivity (Humphreys, 1991). The conversion of existing dead wooden fences to live fences in Río Frío would result not only in greater tree cover, but also in greater overall landscape connectivity and more connections between live fences and riparian forests, with potential benefits for biodiversity conservation (Chacon and Harvey, 2005). In this scenario, converting all existing wooden fences to live fences would increase the total length of live fences by 21.2%, double the density of live fences, more than double the number of live fences that directly connect to riparian forests, and dramatically reduce the distance between tree crowns within the landscape, potentially making it easier for arboreal animals to cross the landscape.

Another important goal of conservation strategies should be to improve the structural and floristic diversity of existing live fences. Currently most live fences are dominated by only a handful of species, most of which are deciduous for at least part of the year. While many of these dominant species temporarily provide flowers, nectar and fruit for visiting animals, the dominance of only a handful of tree species within live fences limits the potential year-round attractiveness of live fences to wildlife. If live fences could be established with a greater number of tree and shrub species, preferably of different architectures and with species that provide fruits, foliage and flowers to wildlife year-round, their conservation value would likely be enhanced, as has been demonstrated for windbreaks and hedges in temperate regions (Arnold, 1983; Capel, 1988; Hinsley and Bellamy, 2000). A complementary strategy might include the abandonment of live fences in some less productive parts of the farm, resulting in taller, larger and most likely, more diverse live fences that provide additional perching and foraging sites for wildlife.

A third opportunity in the use of live fences for conservation planning is to strategically place them so that they connect remnant patches of natural habitat and provide tree cover in open areas that currently lack cover. Ensuring that individual live fences connect to other live fences and/or forests or riparian forests is a simple but effective way of increasing landscape connectivity for at least some wildlife species, as has been shown in temperate regions (Fritz and Merriam, 1993; Yahner, 1983; Petit and Burel, 1998; Bennett, 1999), and may enhance the overall connectivity of agricultural landscapes for some species (Baudry et al., 2003). However, the strategic promotion of live fences needs to be integrated with the retention or creation of sufficient forest cover for the live fences to connect up, implying the need for landscape scale planning to meet conservation goals.

A final opportunity for enhancing the contribution that live fences make to conservation lies in the adoption of management practices that are more conservation-friendly, such as staggered pollarding across a farm, reduction in the frequency of pollarding, and/or adoption of partial (as opposed to complete) pollarding. These strategies would favor biodiversity conservation by reducing the overall impact of pollarding on the amount of tree cover available within a given area, and by ensuring that at least some live fences continue to offer perching, roosting, or feeding sites throughout the year. In addition, less frequent and less rigorous pollarding would allow the colonization of live fences by epiphytes, vines and lianas, which in turn could provide additional resources for wildlife.

The adoption of live fence management strategies that are more conservation friendly will likely require a combination of farmer training and education about the importance of live fences for biodiversity conservation, provision of technical information on how to design and manage live fences for conservation benefits, and possibly the use of payments or incentives that compensate for any additional time or resources that the adoption of these strategies may entail, or that reward farmers for their conservation efforts. It is important to keep in mind that although farmers are already establishing and managing live fences on their own accord, they do so for productive purposes, not to meet conservation goals, and some of the changes proposed above to enhance conservation value may complicate farm management practices, require additional labour or money, or occupy pasture areas that would otherwise be available for cattle grazing. Clearly, proposed changes in live fence design and management must be considered within a farming systems framework (Le Coeur et al., 2002).

Cattle farmers in some places were already gradually converting dead fences to live fences, because of the scarcity of trees for dead wooden posts and some farmers were interested in diversifying their live fences, particularly to include timber or fruiting species, suggesting that the changes in live fence establishment and management proposed to enhance conservation value here may be reasonably easy for farmers to adopt. Furthermore, the recent decision of the Costa Rican government to include live fences as a land use that is eligible for payment for the environmental services they provide (Forestry Law Number 7575, decree number 30962-MINAE; La Gaceta, 1996) means that a funding mechanism is already in place that could be used to motivate farmers to manage live fences in pursuit of conservation goals. At present, however, not enough funding is available within this scheme to include all farmers who are interested. The widespread application of this type of payment in Costa Rica, and the adoption of similar payment schemes in other Central American countries, could bring attention to the important roles live fences already play within agricultural landscapes and raise their profile within conservation and sustainable land use programs.

5. Conclusions

The research presented here highlights the important productive and ecological roles of live fences within rural landscapes in Central America, and indicates that the establishment and judicious management of live fences within farms not only serves agronomic functions, but may also help contribute to conservation goals. Like forest fragments, riparian forests, dispersed trees and other on-farm tree cover, live fences may provide habitat, resources and landscape connectivity for a subset of plant and animal species, while at the same time providing services to the farmers who establish them. Given their compatibility with existing farming systems and the small areas they occupy, live fences offer a means of increasing tree cover in fragmented agricultural landscapes that can be readily adopted by farmers. Consequently, they merit much greater attention in the development of sustainable land management and conservation strategies for rural landscapes in Central America.

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Appendix 1

Summary of all tree and palm species (dbh > 10 cm) recorded in live fences in Cañas, Río Frío, Rivas and Matiguás study sites. Data are organized in decreasing order of abundance

Scientific name	Family	Common name in the study sites		Number of trees recorded in live fences				Total	% of all trees
		Costa Rica	Nicaragua	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua		
Bursera simaruba (L.) Sarg.	Burseraceae	Jiñote, Indio pelado	Jinocuabo	11363	98	32	1735	13228	43.84
Pachira quinata (Jacq.) W.S. Alverson	Bombacaceae	Pochote	Pochote	5787		18	245	6050	20.05
Erythrina costaricensis Micheli	Fabaceae/ Mimosoideae	Poro			2880			2880	9.55
Gliricidia sepium (*Jacq.*) Steud.	Fabaceae/ Papilionoideae	Madero Negro	Madero negro	401	425	108	189	1123	3.72
Spondias purpurea L.	Anacardiaceae	Jocote	Jocote dulce	826	31	5	61	923	3.06
Ficus werckleana Rossberg	Moraceae	Chilamate		801				801	2.65
Guazuma ulmifolia Lam.	Sterculiaceae	Guácimo	Guácimo de ternero	202		175	300	677	2.24
Tabebuia rosea (Bertol.) DC. In A. DC.	Bignoniaceae	Roble	Roble	419	1	58	81	559	1.85
Cordia alliodora (Ruiz & Pav.) Oken	Boraginaceae	Laurel	Laurel	63	107	90	112	372	1.23
Erythrina spp.	Fabaceae	Elequeme	Elequeme	1		117	153	271	0.90
Cordia dentata Poir.	Boraginaceae		Tiguilote			177		177	0.59
Myrospermum frutescens Jacq.	Fabaceae/ Papilionoideae	Guachipelín arco	Chiquirin	3		139		142	0.47
Acacia collinsii Saff.	Fabaceae/ Mimosoideae	Cornizuelo	Cornizuelo			138		138	0.46
Spondias mombin L.	Anacardiaceae	Jobo	Jobo	23		31	79	133	0.44
Tabebuia ochracea (A.H. Gentry) A.H. Gentry	Bignoniaceae	Cortez ama	Corteza	115			9	124	0.41
Byrsonima crassifolia (L.) Kunth in Humb.; Bonpl. & Kunth	Malphigiaceae	Nance	Nancite	82		39	2	123	0.41
Caesalpinia eriostachys Benth.	Caesalpiniaceae	Saino		123				123	0.41
Simarouba glauca DC. (=*Simarouba amara* Aubl. in Nicaragua)	Simaroubaceae	Aceituno	Acetuno	1		111		112	0.37
Enterolobium cyclocarpum (Jacq.) Griseb.	Fabaceae/ Mimosoideae	Guanacaste	Guanacaste	21		24	62	107	0.35
Citrus sinensis (L.) Osbeck (=*Citrus* × *aurantium* L. in Nicaragua)	Rutaceae	Naranja	Naranja dulce	10	65	1	2	78	0.26
Delonix regia (Bojer ex Hook.) Raf.	Fabaceae/ Caesalpiniodae	Malinche	Malinche	41		31	3	75	0.25
Caesalpinia violacea (Mill.) Standl.	Fabaceae/ Caesalpiniodae		Arco			72		72	0.24
Ehretia latifolia DC.	Boraginaceae	Tiolote		72				72	0.24
Dracaena fragrans (L.) Ker Gawl.	Liliaceae	Caña India			70			70	0.23

Appendix 1 (*Continued*)

Scientific name	Family	Common name in the study sites		Number of trees recorded in live fences				Total	% of all trees
		Costa Rica	Nicaragua	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua		
Cedrela odorata L.	Meliaceae	Cedro	Cedro	35		1	28	64	0.21
Samanea saman (Jacq.) Merr. (=*Albizia saman* (Jacq.) F. Muell. in Nicaragua)	Fabaceae/ Mimosoideae	Cenízaro	Genizaro	8		4	44	56	0.18
Cochlospermum vitifolium (Willd) Spreng.	Bixaceae	Poro poro	Comajoche	48		4	1	53	0.18
Cassia grandis L.	Fabaceae/ Caesalpiniodae	Carao	Carao	10		10	29	49	0.16
Azadirachta indica A. Juss., Mém.	Meliaceae		Neem			48		48	0.16
Eugenia salamensis (Standl.) Mc Vaugh	Myrtaceae	Fruta de pava	Guacuco	45		3		48	0.16
Pisonia aculeata L.	Nyctaginaceae		Espino negro			43		43	0.14
Trichilia Americana (Sessè & Moç.) T.D. Penn.	Meliaceae		Piojillo				43	43	0.14
Acacia spp.	Fabaceae/ Mimosoideae	Acacia	Acacia	6			35	41	0.14
Lonchocarpus minimiflorus Donn. Sm.	Fabaceae/ Papilionoideae		Chaperno			21	19	40	0.13
Lysiloma divaricatum (Jacq.) J.F.	Fabaceae/ Mimosoideae	Quebracho	Quebracho	5		22	13	40	0.13
Maclura tinctoria (L.) Steud.	Moraceae	Mora	Mora	27		7	4	38	0.13
Calycophyllum candidissimum (Vahl) DC.	Rubiaceae	Madroño Negro	Madrono	5		31	1	37	0.12
Cordia bicolor A. DC.	Boraginaceae		Muneco			9	28	37	0.12
Psidium guajava L.	Myrtaceae	Guayaba	Guayaba	4	29	4		37	0.12
Spondias spp.	Anacardiaceae		Jocote			37		37	0.12
Genipa americana L.	Rubiaceae	Waitil	Jagua	7		7	21	35	0.12
Karwinskia calderonii Standl.	Rhamnaceae		Guiliguiste			35		35	0.12
Platymiscium parviflorum Benth.	Fabaceae/ Papilionoideae		Coyote				35	35	0.12
Hymenaea courbaril L.	Fabaceae/ Caesalpiniodae	Guapinol	Guapinol	27		4	3	34	0.11
Annona reticulata L.	Annonaceae	Anono	Anona	20		11		31	0.10
Casearia corymbosa Kunth in Humb., Bonpl. & Kunth	Flacourtiaceae	Cerito	Cerrillo	1		30		31	0.10
Jatropha curcas L.	Euphorbiaceae	Tempate		30				30	0.10
Acosmiun panamense (Benth.) Yakovlev	Fabaceae/ Papilionoideae	Guayacan		28				28	0.09
Andira inermis (W. Wright) Kunth ex DC.	Fabaceae/ Papilionoideae	Almendro	Almendro	26		1		27	0.09
Tabebuia chrysantha (Jacq.) G. Nicholson	Bignoniaceae		Cortes			27		27	0.09
Tapirira myriantha Triana & Planch	Anacardiaceae	Manteco		27				27	0.09
Bauhinia ungulata L.	Fabaceae/ Caesalpiniodae		Casco de venado			25		25	0.08

Bauhinia pauletia Pers.	Fabaceae/ Caesalpiniodae		Espino blanco			23		23	0.08
Thouinidium decandrum (Bonpl.) Radlk.	Sapindaceae	Escobillo	Melero	1		22		23	0.08
Crescentia cujete L.	Bignoniaceae	Jícaro	Jícaro casero	22				22	0.07
Dalbergia retusa Hemsl.	Fabaceae/ Papilionoideae	Cocobolo	Nambar	16		5		21	0.07
Diphysa Americana (Mill.) M. Sousa	Fabaceae/ Papilionoideae		Guachipín			20	1	21	0.07
Inga spectabilis (Vahl) Willd.	Fabaceae/ Mimosoideae	Guaba			21			21	0.07
Machaerium biovulatum Micheli	Fabaceae/ Papilionoideae		Siete cuero			21		21	0.07
Psidium friedrichsthalianum (O. Berg) Nied. in Engl. & Prantl	Myrtaceae	Cas			20			20	0.07
Ocotea veraguensis (Meisn.) Mez, Jahrb. Königl.	Lauraceae	Canelo		19				19	0.06
Swietenia humilis Zucc.	Meliaceae		Caoba			19		19	0.06
Ficus cotinifolia Kunth	Moraceae	Higuerón		17				17	0.06
Leucaena leucocephala ssp. *glabrata* (Rose) Zárate	Mimosaceae		Leucaena			12	4	16	0.05
Piscidia carthagenensis Jacq.	Fabaceae/ Papilionoideae	Siete cueros		16				16	0.05
Pterocarpus rohrii Vahl	Fabaceae/ Papilionoideae		Sangregrado				15	15	0.05
Stemmadenia obovata (Hook. & Arn.) K. Schum.	Apocynaceae		Cachito			14		14	0.05
Abarema macradenia (Pittier) L. Rico	Fabaceae/ Mimosoideae	Arenillo		12				12	0.04
Persea americana Mill.	Lauraceae	Aguacate	Aguacate	5	6		1	12	0.04
Schizolobium parahyba (Vell.) S.F. Blake	Fabaceae/ Caesalpiniodae	Gallinazo	Gavilán	4		8		12	0.04
Acrocomia aculeata (Jacq.) Lodd. ex Mart. (*Acrocomia mexicana* Karw. ex Mart. in Nicaragua)	Arecaceae	Coyol	Coyolito	11		1		12	0.04
Coccoloba caracasana Meisn. In A. DC.	Polygonaceae	Papaturro		2		9		11	0.04
Abarema barbouriana (Standl.) Barneby & Grime	Fabaceae/ Mimosaceae	Aguacatillo de monte			10			10	0.03
Pentaclethra macroloba (Willd.) Kuntze	Fabaceae/ Mimosaceae	Gavilán			10			10	0.03
Annona cherimola Mill.	Annonaceae		Chirimoya				10	10	0.03
Anacardium occidentale L.	Anacardiaceae	Marañon	Marañon	2		7		9	0.03
Annona purpurea Moç. & Sessé ex Dunal	Annonaceae	Soncoyo	Soncoya	6			3	9	0.03
Swietenia macrophylla King, Hooker's	Meliaceae	Caoba		9				9	0.03
Inga vera Willd.	Fabaceae/ Mimosaceae		Cuajiniquil				9	9	0.03
Chomelia spinosa Jacq.	Rubiaceae	Mala caute	Malacaguiste	1		7		8	0.03
Gmelina arborea Roxb. ex Sm. in Rees	Verbenaceae.	Melina	Melina	8				8	0.03
Cecropia peltata L.	Cecropiaceae		Guarumo				7	7	0.02
Sapium thelocarpum (=*S. macrocarpum*) Müll. Arg.	Euphorbiaceae	Palo leche		1			6	7	0.02

Appendix 1 (*Continued*)

Scientific name	Family	Common name in the study sites		Number of trees recorded in live fences				Total	% of all trees
		Costa Rica	Nicaragua	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua		
Sapranthus violaceus (Dunal) Saff.	Annonaceae		Palanco			7		7	0.02
Citrus × *limon* (L.) Osbeck	Rutaceae	Limón ácido			5		1	6	0.02
Eucalyptus saligna Sm.	Myrtaceae	Eucalipto			6			6	0.02
Licania arborea Seem.	Chrysobalanaceae	Alcornoco	Hoja tostada	6				6	0.02
Sciadodendron excelsum Griseb.	Araliaceae		Lagarto			5	1	6	0.02
Astronium graveolens Jacq.	Anacardiaceae	Ron ron	Quitacalzón	2			3	5	0.02
Calophyllun brasiliense Cambess.	Clusiaceae	Cedro maría	María		5			5	0.02
Casearia aculeata Jacq.	Flacourtiaceae	Mata Cartago		5				5	0.02
Ceiba pentandra (L.) Gaertn.	Bombacaceae	Ceiba	Ceiba	1		1	3	5	0.02
Citrus paradisi	Rutaceae	Toronja		5				5	0.02
Ficus spp.	Moraceae	Ficus		1	4			5	0.02
Ficus citrifolia Mill.	Moraceae		Chilamate				5	5	0.02
Mangifera indica L.	Anacardiaceae	Mango	Mango	4			1	5	0.02
Manilkara zapota (L.) P. Royen	Sapotaceae	Nispero	Nispero	4			1	5	0.02
Leandra dichotoma (G. Don) Cogn.	Melastomataceae		Capirote				5	5	0.02
Anacardium excelsum (Bertero & Balb. ex) Kunth Skeels	Anacardiaceae	Espavel	Espavel	3		1		4	0.01
Crescentia alata Kunth in Humb.; Bonpl. & Kunth	Bignoniaceae		Jicaro			3	1	4	0.01
Curatella americana L.	Dilleniaceae		Hoja chigue			4		4	0.01
Tabebuia donnell-smithii J.N. Rose	Bignoniaceae	Cortez blanco		4				4	0.01
Lacmellea panamensis (Woodson) Markgr.	Apocynaceae	Lagarto			4			4	0.01
Sapindus saponaria L.	Sapindaceae	Jaboncillo	Patacon	2			2	4	0.01
Stryphnodendron microstachyum Poepp. & Endl.	Fabaceae/ Mimosoideae	Vainillo			4			4	0.01
Senna atomaria (L.) H.S. Irwin & Barneby	Fabaceae/ Caesalpiniodae		Vainillo				4	4	0.01
Tamarindus indica L.	Fabaceae/ Caesalpiniodae	Tamarindo	Tamarindo	1		1	2	4	0.01
Zanthoxylum setulosum P. Wilson	Rutaceae	Lagartillo		4				4	0.01
Albizia guachapele (Kunth) Dugand	Fabaceae/ Mimosaceae		Gavilán			1	2	3	0.01
Coccoloba floribunda (Benth.) Lindau	Polygonaceae		Papaturro			3		3	0.01
Cojoba arborea (L.) Britton & Rose	Fabaceae/ Mimosaceae	Lorito			3			3	0.01
Diospyros salicifolia Humb. & Bonpl. ex Willd.	Ebenaceae		Chocoyito			3		3	0.01
Ilex skutchii Edwin ex T.R. Dudley & W.J. Hahn	Aquifoliaceae	Espino blanco		3				3	0.01
Ilex spp.	Aquifoliaceae	Azulillo		3				3	0.01
Luehea candida (Moç. & Sessè ex DC.)	Tiliaceae		Guácimo de molenillo			3		3	0.01
Sapranthus palanga R.E. Fr.	Annonaceae	Palanco		3				3	0.01

Sideroxylon capiri (Pittier) T.D. Penn.	Sapotaceae	Tempisque		3				3	0.01
Sloanea terniflora (Moc. ex Sesse ex DC.) Standl.	Elaeocarpaceae	Terciopelo	Tercio pelo	3				3	0.01
Tabebuia impetiginosa (Mart. ex DC.) Standl.	Bignoniaceae	Cortez Negro		3				3	0.01
Lawsonia inermis L.	Lythraceae		Receda				3	3	0.01
Tectona grandis L. f.	Verbenaceae.		Teca				3	3	0.01
Aspidosperma excelsum Benth.	Apocynaceae	Guaniquíl			2			2	0.01
Calotropis procera (Aiton) W.T. Aiton	Asclepiadaceae		Huevo de yanque			2		2	0.01
Couepia polyandra (Kunth) Rose	Chrysobalanaceae	Olosapo		2				2	0.01
Eucalyptus torelliana F. Muell.	Myrtaceae	Eucalipto					2	2	0.01
Nephelium lappaceum L.	Sapindaceae	Mamón chino			2			2	0.01
Muntingia calabura L.	Elaeocarpaceae		Capulín				2	2	0.01
Leucaena shannonii Donn. Sm.	Fabaceae/ Mimosaceae		Frijolillo				2	2	0.01
Roupala montana Aubl.	Proteaceae	Carne asado	Zorrillo	1			1	2	0.01
Acacia farnesiana (L.) Willd.	Fabaceae/ Mimosaceae	Aromo	Aromo			1		1	0.00
Apeiba tibourbou Aubl.	Tiliaceae	Peine de mico	Peine de mico	1				1	0.00
Bixa orellana L.	Bixaceae		Achiote				1	1	0.00
Brosimum alicastrum Sw.	Moraceae	Ojoche Negro	Ojoche	1				1	0.00
Caesalpinia exostemma DC.	Fabaceae/ Caesalpiniodeae		Manteco			1		1	0.00
Citrus × *aurantium* L.	Rutaceae		Naranja agria			1		1	0.00
Conostegia spp.	Melastomataceae	Lengua de vaca		1				1	0.00
Gyrocarpus americanus Jacq.	Hernandiaceae		Talalate			1		1	0.00
Laetia thamnia L.	Flacourtiaceae	Quita calzón		1				1	0.00
Melicoccus bijugatus Jacq.	Sapindaceae		Mamon			1		1	0.00
Morella cerifera (L.) Small	Myricaceae	Cerillo		1				1	0.00
Platymiscium spp.	Fabaceae/ Papilionoideae	Cachimbo		1				1	0.00
Schoepfia schreberi J.F	Olacaceae		Melon			1		1	0.00
Semialiarium mexicanum (Miers) Mennega	Hippocrateaceae	Guacharo		1				1	0.00
Senna papillosa (Britton & Rose) H.S. Irwin & Barneby	Fabaceae/ Caesalpiniodeae	Candelillo		1				1	0.00
Spondias dulcis Parkinson	Anacardiaceae	Yuplón			1			1	0.00
Virola koschnyi Warb.	Myristicaceae	Fruta dorada			1			1	0.00
Vitex cooperi Standl.	Verbenaceae.	Manu platano			1			1	0.00
Zygia longifolia (Humb. & Bonpl. ex Willd.) Britton & Rose	Fabaceae/ Mimosoideae	Sotacaballo			1			1	0.00
Cupania guatemalensis (Turcz.) Radlk.	Sapindaceae		Cola de pava				1	1	0.00
Ormosia macrocalyx Ducke	Fabaceae/ Caesalpiniodeae		Coralillo				1	1	0.00
Tabernaemontana amygdalifolia Jacq.	Apocynaceae		Huevo de gato				1	1	0.00
Caesalpinia coriaria (Jacq.) Willd.	Fabaceae/ Caesalpiniodeae		Nacascolo				1	1	0.00
Tetragastris panamensis (Engl.) Kuntze	Burseraceae		Kerosene				1	1	0.00

Appendix 1 (*Continued*)

Scientific name	Family	Common name in the study sites		Number of trees recorded in live fences				Total	% of all trees
		Costa Rica	Nicaragua	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua		
Spathodea campanulata P. Beauv.	Bignoniaceae		Llamarada del 13				1	1	0.00
Cassia fistula L.	Fabaceae/ Caesalpiniodeae		Caña fístula				1	1	0.00
Ficus elastica Roxb.	Moraceae		Palo de hule				1	1	0.00
Unidentified spp. #1	Moraceae		Matapalo				3	3	0.01
Unidentified spp. #2	Myricaceae		Palo de cera				3	3	0.01
Unidentified spp. #3	Loganiaceae		Jicarillo				2	2	0.01
Unidentified spp. #4	Fabaceae		Zopilote				7	7	0.02
Unidentified spp.				38			3	34	0.11
No. of species				84	27	71	70	161	
Total no. of trees				20967	3812	1958	3464	30170	100

Appendix 2

Summary of bird, bat, dung beetle and butterfly species recording using eight live fences in Cañas, Costa Rica (C) and Rivas, Nicaragua (R). Known sampling methods and effort are described in Section 2, forest species are indicated by asterisks

Birds	Bats	Butterflies	Beetles
Aimophila rufescens (Swainson, 1827) C	*Artibeus hartii** (Thomas) C	*Adelpha serpa* ssp. *massilia* (Felder & Felder, 1987) R	*Agamophus lampros* (Bates) C
Aimophila ruficauda (Bonaparte, 1853) C, R	*Artibeus intermedius** (Allen) R, C	*Agralius vanillae* (Linnaeus, 1758) C	*Ateuchus rodriguezi* (PreudhomedeBorre) R, C
Amazilia rutila (DeLattre, 1843) C, R	*Artibeus jamaicensis* (Leach) R, C	*Anartia fatima* (Godart, 820) R, C	*Canthidium guanacaste* (Howden & Gill) C
Amazilia tzacatl (De La Llave, 1833) C	*Artibeus lituratus* (OlferS) R, C	*Anartia jatrophae* (Linnaeus, 1763) C	*Canthidium perceptible* (Howden & Young) R
*Amazona albifrons**(Sparman, 1788) C, R	*Artibeus phaeotis* (Miller) R, C	*Callicore pitheas* (Latreille, 1811) R	*Canthidium subdopuncticolle* (Howden & Young) R
Aratinga canicularis (Linnaeus, 1758) R, C	*Artibeus watsoni* (Thomas) R	*Cissia calixta* (Butler, 1877) C	*Canthidiun* sp57 C
Aratinga nana (Vigors, 1830) R	*Balantiopteryx plicata* (Peters) C	*Cissia similis* (Butler, 1886) R, C	*Canthon cyanellus* (LeConte) C
Archilochus colubris (Linnaeus, 1758) C	*Carollia brevicauda* (Schinz) C	*Chlosyne hippodrome* (Geyer, 1837) C	*C. cyanellus sallei* (Harold) R
Arremonops conirostris (Bonaparte, 1851) C	*Carollia perspicillata* (Linnaeus) R, C	*Dipthera festiva* (Fabricius) C	*Canthon deyrollei* (Harold) R

Brotogeris jugularis (Müller, 1776) R, C
Buteo magnirostris (Gmelin, 1788) C
Calocitta formosa (Swainson, 1827) C R
Campylorhynchus rufinucha (Lesson, 1838) C, R
Colinus leucopogon (Linnaeus, 1766) C
Columba flavirostris (Wagler, 1831) C, R
Columbina inca (Lesson, 1847) C, R
Columbina minuta (Linnaeus, 1766) C
Columbina passerina (Linnaeus, 1758) C
Contopus sp. C
Crotophaga sulcirostris (Swainson, 1827) C, R
Cyanocorax morio (Wagler, 1829) C
*Chiroxiphia linearis** (Bonaparte, 1838) C
Chloroceryle americana (Gmelin, 1788) C
Chlorostilbon canivetii (Lesson, 1823) R
Dendroica petechia (Linnaeus, 1766) R, C
Eumomota superciliosa (Sandbach, 1837) C
Heliomaster constantii (DeLattre, 1843) R
*Hylophilus decurtatus** (Bonaparte, 1838) C
Icterus galbula galbula (Linnaeus, 1758) C
Icterus pustulatus (Wagler, 1829) C
Leptotila verreauxi (Bonaparte, 1855) R, C
Melanerpes hoffmannii (Cabanis, 1862) R
Morococcyx erythropygius (Lesson, 1842) R
Myiarchus crinitus (Linnaeus, 1758) R
Myiarchus nuttingi (Ridgway, 1883) C, R
Myiarchus tuberculifer (Orbigni and Lafresnaye, 1837) C, R
Myiarchus tyrannulus (Müller, 1776) C
Myiodynastes maculatus (Müller, 1776) C
Myiozetetes similis (Spix, 1825) R
Pheucticus ludovicianus (Linnaeus, 1766) R
Piaya cayana (Linnaeus, 1766) R, C
Pitangus sulphuratus (Linaeus, 1766) R, C

Carollia subrufa (Hahn) R
*Chiroderma villosun** (Peters) C
Desmodus rotundus (E. Geoffroy) R
Eptesicus brasiliensis (Desmarest) C
Eptesicus furinalis (ĎOrbigny) C
Glossophaga commissarici (Gardner) R, C
Glossophaga soricina (Pallas) R, C
*Micronycteris minuta** (Gervais) C
Myotis nigricans (Schinz) R
Noctilo albiventris (Desmarest) C
Noctilo leporinus (Linnaeus) C
Phyllostomus discolor (Wagner) R, C
Phyllostomus hastatus (Pallas) R, C
Platyrrhinus helleri (Peters) R
*Pteronotus davy** (Gray) C
Pteronotus parnellii (Gray) C
Rogeessa tumida (Allen) C
Saccopteryx bilineata (Temmink) R, C
*Saccopteryx lectura** (Schreber) R, C
Sturnira lilium (Geofroy) R, C
Uroderma bilobatum (Peters) R, C

Dryadula phaetusa (Linnaeus, 1758) R, C
Dryas iulia (Fabricius, 1775) R, C
*Eueides isabella** (Gramer, 1781) R, C
Euptoieta hegesia hoffmanni (Comstack, 1944) C
Eurema daira (Godort, 1819) R, C
Eurema elathea (Gramer, 1775) C
Eurema nise (Gramer, 1775) C
Eurema proterpia (Fabricius, 1775) R, C
Eurytides epidaus epidaus (Doubleday, 1849) C
Eudesmia cf. *menea* (Drury) C
Hamadrias arinome ariensis (Godman and Salum, 1883) C
Hamadryas februa (Godart, 1824) R
Hamadryas feronia farinulenta (Fruhstorfer, 1916) C
Hamadryas glauconome (Bates, 1864) R
Hamadryas guatemalena (Bates, 1864) R
Heliconius charitonius (Linnaeus, 1767) R
Heliconius hecale zuleika (Hewitson, 1854) R
Heraclides thoas nealces (Rothschild & Jordan) R, C
Junonia evarete (Gramer, 1782) C
Mechanitis polymnia (Bates, 1863) C
Mocis repanda (Wilson, 1979) C
*Morpho peleides** (Butler, 1872) R
*Myscelia cyaniris** (Doubleday, 1848) R
Myscelia pattenia (Butler and Druce, 1875) R
Opsiphanes cassina chiriquensis (Boisduval, 1870) C
Opsiphanes tamarindi (Felder, 1861) R
Papilio cresphontes (Gramer, 1777) R
Philaethria dido (Linnaeus, 1763) C
Phoebis sennae (Linnaeus, 1758) R, C
Protographium epidaus (Doubleday) R
Pyrgus oileus (Linnaeus) C
Siproeta stelene (Fruhstorfer, 1907) R
Taygetis andromeda (Gramer, 1779) R

Canthon euryscelis (Bates) R
Canthon indigaceus (LeConte) C
Canthon meridionalis (Halffter & Halffter) R, C
Canthon mutabilis (Lucas) C
Copris lugubris (Boheman) R, C
Coprophanaeus corythus telamon (Howden & Young) R
Deltochilum lobipes (Bates) R
Dichothomius yucatanus (Bates) C, R
Dichotomius annae (Harold) R, C
Dichotomius centralis (Harold) R, C
Hister sp. R
Malagoniella astyanax (Olivier) R
Omorgus suberosus (Fabricius) R
Onthophagus acuminatus (Harold) R, C
Onthophagus batesi (Howden & Cartwright) R, C
Onthophagus championi (Bates) R, C
Onthophagus hopfneri (Harold) R, C
Onthophagus landolti (Harold) R, C
Onthophagus marginicollis (Solis) R, C
Onthophagus praecellens (Bates) C
Phanaeus demon (Laporte) R, C
Phanaeus eximius (Bates) C
Phanaeus wagneris (Harold) R
Pseudocanthon perplexum (LeConte) R
Sisyphus mexicanus (Harold) R, C
Uroxys sp. C

Appendix 2 (*Continued*)

Birds	Bats	Butterflies	Beetles
Polioptila albiloris (Sclater and Salvin, 1860) C		*Taygetis kerea* (Butler, 1879) R	
Polyborus plancus (Miller, 1777) C		*Urbanus simplicius* (Stoll) C	
Psarocolius montezuma (Lesson, 1830) R			
Quiscalus mexicanus (Gmelin, 1788) R			
*Ramphastos sulfuratus** (Lesson, 1830) C			
Sturnella magna (Linnaeus, 1758) C			
Thryothorus modestus (Cabanis, 1861) R			
Thryothorus pleurostictus (Sclater, 1860) R			
Tityra semifasciata (Spix, 1825) R, C			
Todirostrum cinereum (Linnaeus, 1766) R			
Tolmomyias sulphurescens (Spix, 1825) R			
*Trogon melanocephalus** (Gould, 1835) C, R			
Turdus grayi (Bonaparte, 1838) C			
Tyrannus forficatus (Gmelin, 1789) C			
Tyrannus melancholicus (Vieillot, 1819) C			
Vermivora peregrina (Wilson, 1811) C			
Volatinia jacarina (Linnaeus, 1766) C			
No. of spp. total: 59	No. of spp. total: 30	No. of spp. total: 44	No. of spp. total: 35

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