Agroforestry Systems (2006) 68:15–26
DOI 10.1007/s10457-005-5831-5

Live fences and landscape connectivity in a neotropical agricultural landscape

Mario Chacón León and Celia A. Harvey*
*Department of Agriculture and Agroforestry, Apdo. 7170, Centro Agrónomico Tropical de Investigación y Ensenañza (CATIE), Turrialba, Costa Rica; *Author for correspondence (e-mail: charvey@catie.ac.cr; phone: 506-558-2596; fax: 506-556-2576)*

Received 7 March 2005; accepted in revised form 6 December 2005

Key words: Agroecosystems, Cattle production systems, Costa Rica, Fragmented landscapes, Landscape structure, Linear elements

Abstract

Live fences are common elements in neotropical agricultural landscapes and could play important roles in the conservation of biodiversity by enhancing landscape connectivity, however, little is known about their abundance and spatial arrangement. The objectives of this study were to characterize the abundance and spatial patterns of live fences in a fragmented landscape dominated by pastures in Río Frío, Costa Rica, to determine their contribution to landscape structure and connectivity and to examine their role as tools for landscape conservation planning. Live fences accounted for 45.4% of all fences in the landscape and occurred with a mean density of 50.5 linear meters per hectare. Although live fences covered only a small total area of the landscape (< 2%), they had an important effect on landscape structure and connectivity, increasing total tree cover, dividing pastures into smaller areas, creating rectilinear networks that cross the landscape and providing direct physical connections to forest patches. Simulations showed that the conversion of all existing wooden fences to live fences would greatly enhance landscape connectivity by more than doubling the area, density and number of direct connections to forest habitats, and reducing the average distance between tree canopies. Our study demonstrates that live fences play key roles in defining the structure and composition of neotropical agricultural landscapes and merit consideration in both conservation efforts and agricultural policies designed to enhance landscape connectivity and promote biodiversity conservation.

Introduction

One of the main challenges facing tropical conservation biologists is how to conserve biodiversity within the highly deforested and fragmented landscapes that dominate most tropical regions. In Central America, where the majority of the land is currently dedicated to either cattle or agricultural production and land pressure is intensifying due to a rapidly growing population (Harvey et al. 2005a), conservation organizations are increasingly exploring options for designing and managing agricultural landscapes to meet both productive and conservation goals. To date, these strategies have included the protection of on-farm forest fragments, the reforestation or natural regeneration of degraded areas, and the promotion of agroforestry and silvopastoril systems (Pimentel et al. 1992; Bennett 1999; McNeely and Scherr 2003; Schroth et al. 2004). A driving force behind all of these initiatives is the recognition that neotropical agricultural landscapes may retain considerable plant and animal diversity if they retain sufficient tree cover and maintain a certain level of connectivity (Estrada et al. 2000; Daily et al. 2001; Ricketts et al. 2001; Petit and Petit 2003).

One element that could hold potentially aid in providing habitats and maintaining landscape connectivity within agricultural regions are the live fences that farmers use to divide pastures, protect crops from animal entry, or mark farm boundaries. Live fences are narrow linear strips of planted trees, generally consisting of a single row of a few densely planted species that are established and managed by farmers (Sauer 1979; Budowski 1987; Harvey et al. 2005b). In many neotropical regions, live fences form complex rectilinear networks that cross the agricultural landscape, interrupting the monotony of fields and pastures and increasing both horizontal and vertical complexity of the landscape (Budowski 1987; Budowski and Russo 1993).

In contrast to the vast literature on the value of hedges, windbreaks and other linear woody elements as habitats, safe sites, resources and biological corridors for plant and animal species in temperature regions (e.g., Forman and Baudry 1984; Burel 1996; Baudry et al. 2000a; Marshall and Mooonen 2002), remarkably little information is available on the conservation value of the live fences that occur in tropical landscapes. However, a handful of emerging studies indicate that, like their temperate counterparts, live fences may play a role in maintaining both plant and animal biodiversity in agricultural landscapes (e.g., Harvey et al. 2004). For example, studies in a pastoral landscape in Veracruz, Mexico have reported a total of 98 bird species (or roughly 54% of the bird species detected in adjacent forests; Estrada et al. 2000), 14 bat species (Estrada et al. 1994), and 11 species of non-flying mammals using live fences (Estrada et al. 1994), and indicate that these species use the live fences for shelter, perching, foraging, and, in some cases, as corridors to cross the agricultural landscape. Similarly, a study in an agricultural landscape of Rivas, Nicaragua found 34 bird species, 18 bat species, 24 dung beetle species, and 22 butterfly species occurring in live fences in active pastures (Harvey et al., in review). Although these studies highlight the potential importance of live fences in landscape conservation strategies, it is difficult to assess their potential contribution to conservation efforts without detailed information on the abundance or spatial arrangement of live fences in tropical agricultural landscapes.

The objectives of this study were to characterize the abundance and spatial arrangement of live fences in a pastoral landscape in Río Frío, Costa Rica and to determine their contribution to landscape structure and connectivity. We also explore how the conversion of existing wooden (i.e. not living) fences to live fences would change the structure and connectivity of the agricultural landscape and highlight the potential value of live fences as conservation tools in regional landscape conservation planning.

Methods

Study site

The study was conducted in an area of 4483 ha in Río Frío, Sarapiquí, Province of Heredia, in the northern Atlantic region of Costa Rica (10°36′, 84°04′). The area is located at 100–300 m a.s.l., with an average annual rainfall of 4120 mm, average relative humidity of 88% and average temperature of 23.4 °C (Miranda 1991). The site falls within the Wet Tropical Forest life zone (Holdridge 1967). The Río Frío landscape was deforested beginning in the 1950's and the current landscape is dominated by pastures (which cover 45% of the landscape), with small forest polygons (average size of 8.1 ha; Chacón 2003), riparian forests (average area of 9.2 ha; Chacón 2003), palmito plantations (*Bactris gasipaes* Kunth ex HBK) and home gardens embedded within this matrix (Figure 1). The overall landscape is highly heterogeneous and fragmented, with forest patches and riparian forests covering less than 25% of the landscape.

The region is dedicated to cattle production, with the majority of the farms specialized in dairy production (52.1%), and remainder devoted to meat (18.3%), dual-purpose production (16.9%) or a combination of cattle production with agriculture (16.9%; Villacís et al. 2003). Farms are generally small (mean of 22.1 ± 3.1 ha) and are intensively managed, with daily rotation of cattle across paddocks and a mean stocking rate of 3.1 animal units per hectare. Common pasture grasses

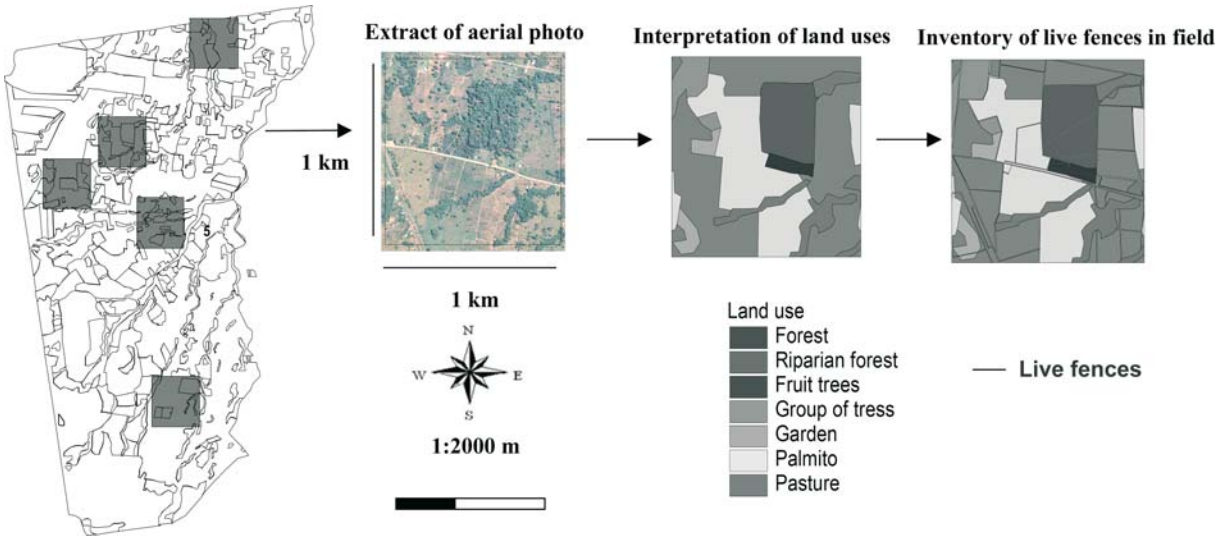

Figure 1. A summary of the process used to explore the effect of live fences on landscape connectivity in Río Frío, Costa Rica. Five sites (each 1 × 1 km) were randomly selected in the landscape and the aerial photographs of these sites were interpreted and validated in the field. Fences were mapped based on field surveys and added to the GIS database for analyses of landscape structure, composition and connectivity.

include *Ischaemum ciliare* (Retz) and *Brachiaria arrecta* (Stent.). Dairy cow breeds include crosses of Jersey, Holstein and Brown Swiss, while beef breeds include crosses of Indobrasil and Brahman. Live fences occur in all cattle farming systems, and are actively managed by farmers to serve as barriers to animal movement and to delimit farm boundaries (see Harvey et al. 2005b for additional details).

Using an aerial photo of the study area from 1998 (scale 1:40,000, pixel size of 3 × 3 m), we randomly selected five blocks of 100 ha (each 1 km by 1 km; total area of 500 ha) for the inventory of live and wooden fences (Figure 1). On average, these sites were located 2.68 km apart. The land use within each site was identified from the aerial photo, verified by field visits, and digitalized in ArcView 3.3.

We inventoried each of the five 100 ha sites in the field for the presence of both live and wooden fences. For the purpose of this study, we defined 'live fences' to be fences that were composed of a linear row of trees (with either barbed or electric wire attached to them), that separated farms, individual pastures or agricultural plots, and had a tree density of at least 20 trees in 100 linear meters. 'Wooden fences' were defined as fences consisting primarily of wooden posts, connected by either electric or barbed wire, that were located on farm, pasture and field boundaries; several of these wooden fences included a few individual trees but at very low densities (usually < 1 tree per 100 m). The beginning and end points of individual fences were defined as where the fence crossed with another fence (creating a node), or where the fence joined another habitat (forest patch, riparian forest, or other land use) or landscape feature (e.g., a road or house).

Within each 100 ha site, we located all fences (both live and wooden and regardless of age or structure) in the field, georeferenced them using a GPS unit (Garmin GPS 12 XL), measured their length and recorded the number of wooden fence posts present. In addition, we recorded the habitats at the beginning and end of each fence, as well as the habitats occurring on each site of the fence. The location of each fence was included in a GIS data base, from which it was also possible to determine whether each fence connected to other live fences (and if so, what type of node it created), and whether it connected directly to a forest patch or riparian forest. In live fences, we collected additional data on the total number of trees and the tree species present. We randomly chose five planted trees per live fence and measured for diameter at breast height and crown radius (defined as the perpendicular distance from the fence to the widest point of the canopy). All field data were introduced as a thematic layer within ArcView 3.3.

Simulations of changes in landscape structure and connectivity due to the presence of live fence

We conducted two simulations to evaluate the contributions of live fences to landscape structure and connectivity (Figure 2). First, to determine the current contribution of live fences to the structure and connectivity of the landscape, we compared the current landscape with a simulated scenario in which all existing live fences were eliminated. Second, we compared the current landscape to another simulated scenario in which all existing wooden fences were converted to live fences to determine the potential contribution of live fences if all fences in the landscape consisted of living trees. In this simulation, all wooden fences were assigned an average crown radius of 1.8 m (reflecting the average crown width of live fences in the study area). Each of these simulations was performed for each of the five 100 ha blocks separately.

For each of the three landscapes (the current landscape, the simulated landscape without live fences, and the simulated landscape with wooden fences converted to live fences), we made the following measurements of landscape structure and composition: (1) total area of live fences (defined as the area covered by the tree crowns of live fences, calculated as a rectangular area of the average crown width per individual live fence multiplied by the live fence length); (2) live fence length; (3) the number of live fence polygons (where a polygon represents an isolated live fence or a set of connected live fences); (4) the total area of pastures; and (5) the number and size of pasture polygons. Details on these variables appear in Table 1.

We assessed the effect of live fences on structural connectivity by calculating the number and proportion of live fences that connect to other live fences and/or forest patches, as well as the number of nodes (= intersections between two or more fences) and type of nodes (connecting two, three or four fences) created by live fences (*sensu* Forman and Baudry 1984; Forman 1995). We also calculated the average distance between individual tree crowns in the landscape (considering tree crowns of live fences, forest patches, and riparian forests), as a measure of landscape connectivity. Connectivity studies usually only calculate the average

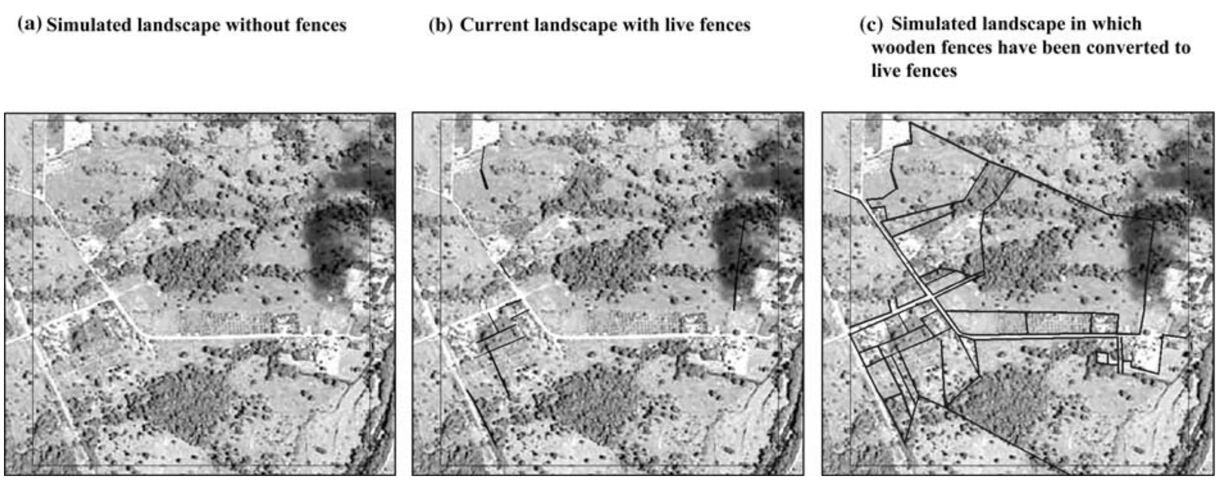

Figure 2. An example of one of the five study sites (each 1 km × 1 km) in Río Frío, Costa Rica in which the contribution of live fences to landscape structure and connectivity was explored. The central image shows the current arrangement and density of live fences (marked by black lines) in one site, based on field work; the image on the left shows the same landscape without live fences and the image on the right shows a simulated landscape in which all existing wooden fences have been converted to live fences (marked by black lines).

Table 1. List of variables used to explore the contribution of live fences to landscape structure and composition in Río Frío, Costa Rica.

Variable	Explanation of why variable was used
Pasture area (ha)	Since pastures are considered 'hostile' habitats to many forest species (Forman 1995), the greater the area under pasture, the lesser its value for conservation.
Number of pasture polygons present	The number of pasture polygons in the landscape indicates the grain size of the landscape. Landscapes with a higher total number of polygons are considered more heterogeneous than those with fewer polygons (Forman 1995).
Live fence length (km)	The total length of live fences indicates the potential habitat available for organisms that can use live fences.
Average area of pasture polygons (ha)	The average size of pastures is an indication of the grain size of the landscape. Landscapes with smaller pasture polygons are considered more heterogeneous than those with larger polygons (Forman 1995).
Total area under crowns of live fences (ha)	The area under live fences is usually area that would otherwise be pasture. An increase in the area of live fences (at the expense of pasture) is therefore thought to be beneficial for conservation efforts.
Number of live fence polygons	The number of live fence polygons is an indication of both the number of live fences present and their degree of connectivity. The number of live fence polygons can increase either when additional live fences are added, or when existing live fences are physically separated from each other. Conversely, the number of polygons can be reduced if live fences are eliminated or if the existing live fences become more connected.
Total number of nodes and number of nodes of type 1, 2, 3 and 4	Nodes are the points of contact between the fences. An increase in the number of nodes per hectare is an indication that the live fences are better connected. The literature mentions three possible node types (Forman 1995; Barr and Gillespie 2000) that are commonly found in the field and that serve to quantify the number of connected live fences: type 1 nodes are nodes that connect two individual live fences; type 2 nodes connect 3 individual fences and type 3 nodes connect 4 individual live fences in the shape of a cross. A higher proportion of nodes of type 3 and 4 indicates a higher complexity in the connection of live fences in the landscape and therefore a higher number of connected live fences (Forman 1995).
Number of direct physical connections between live fences and polygons of forests or riparian forests	A greater number of physical connections between live fences and forest fragments or riparian forests is likely to enhance the chances for animal movement from live fences to forests, or vice versa (Lack 1988; Charrier et al. 1997; Joyce et al. 1999)
Average distance between the central points of each riparian forest and dense forest polygons (m)	The average distance between forest polygons is an often-used description of the connectivity of the landscape (Forman 1995). Landscapes are considered to be well connected if the distances between the existing forest polygons are small.
Average distances between the central points of live fences and forest polygons or riparian forest polygons (m)	The average distance between live fences and forest polygons is another indication of live fence connectivity. As the average distance decreases, the landscape is considered more connected. This calculation is obtained by calculating the distance from the central point of each live fence to that of all other live fences and forest polygons, and calculating the mean distance across the entire landscape.

Each of these variables was calculated for the three different scenarios in each of the five 1 km^2 (= 100 ha) sites: (1) a simulated landscape without live fences; (2) a landscape with the actual live fences; and (3) a simulated landscape with all wooden fences converted to live fences.

distance between polygons of a similar habitat class (e.g. only forests; Turner et al. 2001), however we considered distances between tree cover of forests, riparian forests and live fences because live fences are important habitats and stepping stones for some organisms as they move across the agricultural landscape (Bennett 1999; Millán de la Peña et al. 2003).

We compared the structural and connectivity measurements for the current landscape and the two simulated landscapes using ANOVA's (followed by Duncan multiple comparison tests) to determine differences across the different landscapes (Sokal and Rohl 1994). All statistical analyses were conducted in Infostats v.1.

Results

General characterization of fences

A total of 377 fences, spanning almost 56 km, were inventoried in the 500 ha, of which 45.4% were live fences and 55.5% were wooden fences. A total of 20,497 trees and 15,995 wooden posts were counted. Most live fences were between 100 and 200 m long (mean of 147.8 m), densely planted (mean of 87.6 trees per 100 m), and consisted of small trees (mean dap of 8.9 cm) with narrow tree crowns less than four meters wide (Table 2). Live fences contained a total of 19 different tree species; however the dominant species were Madero negro (*Gliricidia sepium* (Jacq.) Kunth ex Walp.) and Poró (*Erythrina costaricensis* Micheli), which accounted for 47% and 43% of the trees, respectively. Most live fences had little or no natural regeneration below due to cattle grazing and clearing by farmers.

Wooden fences had similar dimensions to those of live fences, but occurred in a slightly higher density in the landscape (mean of 99.8 m of wooden fence per ha vs. mean of 50.5 m of live fence per ha) and totaled 30,643 m in length (Table 2).

Effects of live fences on landscape structure, composition and connectivity

In the current landscape, live fences occupy a mean of 1.3 ± 0.5 ha per 100 ha (i.e. a mean of 1.3% of the total area), and account for a mean of 11 polygons (Table 3). If all of the wooden fences were converted to live fences, the mean area under live fences would more than double, but the number of live fence polygons would decrease (to 3.60 polygons/100 ha) because as more live fences are added to the landscape, more of the live fences become connected (by nodes) and the number of

Table 2. Characteristics of the live fences and wooden fences found in 5 sites (each 1 km by 1 km) in Río Frío, Costa Rica. Numbers in parenthesis represent standard errors.

Variable	Sites					
	1	2	3	4	5	$\bar{X}$ ± E.E
Live fences						
Number of live fences	73	28	42	12	16	171
Total length of live fences (m)	8216	4213	8899	2605	1330	5053 ± 15
Live fence density in the landscape (m/ha)	82.2	42.1	89	26.1	13.3	50.5 ± 15.1
Mean length of individual live fences (m)	112.5 ± 9.6	150.5 ± 13.8	211.9 ± 19.5	217.1 ± 26.1	83.2 ± 11.3	147.8 ± 7.9
Mean dbh of trees in live fences (cm)	9.6 ± 0.5	8.2 ± 0.8	9.1 ± 0.6	8.1 ± 0.9	7.02 ± 0.8	8.9 ± 0.3
Mean crown radius (m)	2.09 ± 0.1	1.78 ± 0.2	1.5 ± 0.2	1.5 ± 0.2	1.4 ± 0.2	1.9 ± 0.1
Tree density (individuals/100 m)	90.0 ± 10	87.9 ± 10.8	107.1 ± 8.8	44.8 ± 7.3	56.7 ± 7.3	87.6 ± 5.3
% isolated live fences (connected to dead fences)	2.7	14.3	9.5	25.0	31.3	16.56 ± 5.17
Wooden fences						
# wooden fences	25	54	26	27	74	206
Total length (m)	3414	7502	3445	7511	8769	30,642
Dead fence density in the landscape (m/ha)	49.1	161	53.3	99.4	136.2	99.8 ± 22.1
Mean length of wooden fences (m)	136.6 ± 14.2	138.6 ± 13	132.5 ± 15.4	278.2 ± 28.5	118.5 ± 11.7	148.8 ± 7.8
Density of wooden posts (posts/100 m)	51 ± 5	41 ± 2	52 ± 3	42 ± 3	48 ± 2	46.4 ± 1.3

Table 3. Characteristics of composition, structure and connectivity in the current and simulated landscapes in Río Frío, Costa Rica. All data represent the mean values (± standard error) of the five study sites. Different letters in the same row indicate significant differences between the three landscape scenarios ($p < 0.05$). F and p values are for one-way ANOVAs.

Variables	Landscape without live fences	Current landscape with live fences	Landscape with dead fences converted to live fences	$F_{2,\ 12}$	p-value
Pasture area (ha)	66.5 ± 5.4a	65.4 ± 5.5a	62.8 ± 5.4a	0.12	0.8894
Number of pasture polygons	3.4 ± 0.7a	13.6 ± 5.6a	32.4 ± 3.9ab	13.82	0.0008
Area of pasture polygons	31.8 ± 1.1a	13.3 ± 6.8ab	2.1 ± 0.3b	3.50	0.0636
Live fence area (ha)	0a	1.3 ± 0.5b	3.4 ± 0.2c	28.46	0.0001
Number of live fence polygons	0a	11 ± 2.0b	3.6 ± 0.7a	17.86	0.0003
Total length of live fences (km/100 ha)	0a	5.0 ± 1.5b	11.1 ± 4.5b	4.86	0.0284
Live fence density (linear m/ha)	0a	50.5 ± 15.1b	111.0 ± 45.3b	37.93	< 0.0001
# of nodes of type 2	0a	8.0 ± 3.2a	30.6 ± 5.71b	17.51	0.0003
# of nodes of type 3	0a	10.8 ± 4.9b	32.0 ± 3.3c	22.62	0.0001
# of nodes of type 4	0a	1.0 ± 0.7a	2.8 ± 1.32a	2.58	0.1168
# of total nodes (nodes/100ha)	0a	35.8 ± 10.5b	72.6 ± 10.6c	17.86	0.0003
Mean number of direct connections between live fences and polygons of dense forests and riparian forests	0a	9.4 ± 2.1b	21.8 ± 2.7c	30.92	< 0.0001
Mean distances between live fences and forest polygons or riparian forest polygons (m)	527.4 ± 55.3a	487.8 ± 51.0a	71.6 ± 24.0b	30.60	< 0.0001

polygons is reduced. At the same time, the average number of paddocks would almost triple, while pasture size would be considerably reduced (due to the division of large pastures into smaller paddocks).

Live fences presently occur with a mean density of 50.5 m of live fences per hectare of land, have a mean of 35.8 nodes (per 100 ha) and have a mean of 9.4 live fences (per 100 ha) that connect directly to either forest fragments or riparian forests. If all of the existing wooden fences were converted to live fences, the live fence density and the number of direct connections would be more than double. At the same time, the number of live fence nodes would increase and the types of nodes would change, with a greater number of nodes that connect three or four live fences, which are considered to represent a greater degree of connectivity (Table 3).

Currently, the tree cover in forest patches and riparian forests is located at an average distance of 527.4 ± 55.3 m. If the existing tree crowns within live fences are included in these calculations, the average distance between tree crowns (of either forests, riparian forests or live fences) is reduced to 487.8 ± 5 m. This distance between tree crowns would be further reduced if all wooden fences were converted to live fences to only 71.6 ± 24.4 m ($F_{2.12} = 30.60$; $p < 0.0001$).

Discussion

Although live fences occupy less than 2% of the total landscape area, they have a disproportionately large effect on landscape structure and composition. In Río Frío, the presence of live fences increased the amount of on-farm tree cover, divided pastures into smaller areas, increased the number of polygons within the landscape, and created a more heterogeneous and fine-grained landscape. In addition, live fences also enhanced the structural connectivity of the agricultural landscape by creating intricate rectilinear networks across the landscape, providing direct physical connections to riparian forests and forest patches, and reducing the distance that arboreal organisms need to cover to get from one tree crown to the next.

The fact that live fences play a decisive role in structuring neotropical agricultural landscapes is perhaps not surprising, given that numerous studies have pointed to the importance of linear features (such as hedges and windbreaks) in determining landscape patterns in agricultural regions in temperate (e.g., Baudry et al. 2000a; Schmucki et al. 2002; Thenail and Baudry 2004; Burel and Baudry 2005) and subtropical regions (Baudry and Zhenrong 1999). However, to our knowledge this is the first study to quantify the contribution of live fences to landscape structure and connectivity within a neotropical agricultural landscape. A comparison of the characteristics of the live fences in the Río Frío landscape to hedge and windbreak networks elsewhere (Table 4) further highlights the similar roles of the linear elements in shaping landscape patterns. The mean density of live fences within the Río Frío (50.5 m per hectare of farmland) falls within the range of hedgerow and windbreak densities reported from temperate regions, and live fences occur in similar lengths as hedges, but are usually narrower than their temperate counterparts. The overall degree of connectivity of the live fence network is similar to that found in temperate regions: for example, whereas our landscape had a mean of 35.8 ± 10.5 nodes of connection per square kilometer, the national average of hedgerow node connections in Great Britain is 37 per square kilometer (Barr and Gillespie 2000).

The presence of live fences in neotropical agricultural landscapes and their effects on landscape structure are likely to be beneficial for conservation efforts due to the ability of live fences to provide habitat, shelter and resources for some plant and animal species (Estrada et al. 2000; Estrada and Coates-Estrada 2001; Harvey et al. 2004). Ongoing studies in the Río Frío study area have already reported a total of 92 bird species, 23 bat species, 12 dung beetle species and 16 butterfly species using the live fences for shelter, resources or movement (Joel Saenz, unpublished data; Lang et al. 2003). In addition, the physical connectivity afforded by live fences could potentially facilitate the movement of some animals (particularly small arboreal species) in the landscape by reducing the distances that organisms need to cross to move from one tree crown to the next and by physically connecting the remaining forest polygons. This potential corridor function of live fences, hedges and windbreaks has been well demonstrated for bats (Verboom and Huitema 1997), birds (Dmowski and Koziakiewicz 1990; Haas 1995), terrestrial mammals (Bennett et al. 1994) and insects (Petit and Burel 1993; Charrier et al. 1997; Millán de la Peña et al. 2003) in temperate regions, and casual observations suggest that this may also be true for some arboreal species, such as birds (Santivañez 2005) and monkeys (Estrada et al. 2006) in the Río Frío landscape.

Our data shows that the potential impact of live fences on landscape connectivity could be easily increased by converting the existing wooden fences to live fences. This change would dramatically increase the physical connectivity of the landscape, more than doubling the total length and density of live fences, doubling the number of direct connections to forest fragments, increasing the number of nodes within the live fence network, and decreasing the amount of open area that organisms have to cross to reach forest fragments to a sixth of the current distance. In the Río Frío area, farmers are already gradually converting wooden fences to live fences due to the limited supply and high costs of wooden posts and are planting new live fences (Harvey et al. 2005b), however it would be possible to enhance the rate of conversion by providing incentives or policies that promote these changes, such as environmental payment services (Pagiola et al. 2005). Replacing wooden fences with live fences could be easily achieved without requiring changes in farm land allocation patterns or farm management strategies, and would significantly enhance the structural connectivity of the landscape with potential benefits for biodiversity conservation.

While our study clearly illustrates both the current and potential effects of live fences on landscape structure and connectivity, there are several important caveats to their use as conservation tools. First, live fences are likely to provide habitat, resources and/or corridors for only a subset of the original species, due to their small size (mean crown diameter of 3.8 m and mean length of only 148 m), frequent disturbance by pollarding, and low tree species richness, as well as their high exposure to the pasture matrix and disturbance by cattle. Studies in temperate regions have indicated that bird and mammal use of other linear habitats, such as windbreaks and hedges, is a function of their height, width, species richness, and management regime (e.g., Yahner 1982a, b; Osborne 1983; Capel 1988; Dover and Sparks 2000; Hinsley and Bellamy 2000), and it is likely that these same principles apply in neotropical live fences. A related study of bird diversity within the Río Frío live fences, for example, found that bird species richness and abundance were positively correlated to live fence height, crown width and tree diameters (Lang et al. 2003).

Table 4. Structural characteristics of hedgerow and live fence networks in different agricultural landscapes.

Study area	Type of linear element	Mean length (m)	Mean width (m)	Density (m/ha)	#connections/ha	# of hedgerow or live fence nodes/km^2	Reference
Godmanchester, Southern Quebec, Canada	Hedgerows in clay plain landscapes	–	5.0 – 12.0	18.7 ± 4.2	< 0.005[a]	–	Schmucki et al. (2002)
	Hedgerows in mixed deposit landscapes	–	5.0 – 12.0	15.3 ± 4.2	0.12 ± 0.10[a]	–	
	Hedgerows in glacial deposit landscapes	–	5.0 – 12.0	25.2 ± 2.3	0.52 ± 4.14[a]	–	
Mont-Saint-Michel Bay, Britanny, France	Hedgerows	73	1.0	201.0	–	–	Baudry et al. (2000b)
Department of Côtes d'Armour, Britanny, France	Hedgerows	–	–	64.0–205.0	0.68–3.77[b]	–	Millán de la Peña et al. (2003)
Meerhout, Flanders, Belgium	Hedgerows	71.87	7.52	146.3	–	–	Deckers et al. (2004)
Peer, Flanders, Belgium	Hedgerows	–	–	36.7	0.46[b]	–	Deckers et al. (2005)
Central Jutland, Denmark	Hedgerows	138.0	–	25.0	–	46.6	Kristensen and Caspersen (2002)
Great Britain (nation-wide)	Hedgerows	–	61% are <2 m	24.0	–	37.0	Barr and Gillespie (2000)
Río Frío, Costa Rica	Live fences	147.8 ± 7.9	1.9 ± 0.1	50.5 ± 15.1	0.09 ± 0.02[a]	38.5	This study

[a]The number of connections to woodland or forest per hectare.
[b]The number of connections among live fences or hedges per hectare.

Second, the fact that live fences enhance the structural connectivity of the landscape does not necessarily mean that animal species will be able to move through the live fences from one forest patch to the next. The ability of animals to use live fences as travel paths or corridors will depend on the one hand, on the specific ecological and behavioral attributes of the animal species (such as their ability to cross gaps, sensitivity to disturbed areas and dispersal and foraging patterns), and, on the other, on the characteristics of individual live fences (Bennett 1999). Structural and floristic characteristics of the live fences (such as their height, width, plant species diversity), as well as their location within the landscape (particularly the adjacent habitats, spatial configuration in the landscape, and proximity to remnant habitats), are likely to strongly influence the degree to which live fences are used by plant and animal species (Burel 1992, 1996; Bennett 1999; Dover and Sparks 2000; Hinsley and Bellamy 2000). Additional studies are therefore required to determine what types of fences and spatial arrangements are needed to enhance the functional connectivity of neotropical landscapes, which species are benefited by their presence, and whether there are thresholds of live fence densities that determine the persistence of different animal species within the agricultural landscape.

A third important caveat is that the degree of landscape connectivity afforded by live fences may vary seasonally and annually, as farmers pollard live fences to reducing shading of pasture, as trees lose leaves in the dry season, or as farmers change the density or arrangement of live fences on their farms over time. In Río Frío, farmers pollard live fences at least once a year to prevent the trees from growing too high and developing large crowns (Harvey et al. 2005b). Since bird species richness in live fences is positively correlated with crown size (Lang et al. 2003), this annual reduction of live fence crowns is likely to limit their use as habitat during certain months in the year. However, as the main live fence tree species have the capacity to quickly resprout following pollarding, most trees regain a full crown within 3–4 months of pollarding (Budowski 1987). In areas with strong dry seasons (such as the Pacific lowlands of Costa Rica and Central America), the value of live fences is also likely to be reduced in the dry season as some of the live fence species lose their leaves for 1–4 months, reducing habitat availability during that time. Farmers may also change the densities or spatial arrangement of live fences within their farms over time, due to changes in farm management strategies and/or agricultural policies (as has been reported for hedges elsewhere: Baudry and Zhenrong 1999; Schmucki et al. 2002; Kantelhardt et al. 2003; Thenail and Baudry 2004; Burel and Baudry 2005); consequently, the importance of live fences and their contribution to landscape connectivity is likely to be temporally dynamic.

Conclusions

Live fences play key roles in defining the composition and structural connectivity of agricultural landscapes and merit consideration in both conservation efforts and agricultural policies designed to enhance landscape connectivity and promote biodiversity conservation within agricultural landscapes. These policies should ensure that existing live fences are retained, promote the establishment of live fences in areas where they are lacking, encourage the replacement of wooden fences with live fences, and strategically locate live fences to enhance landscape connectivity across the agricultural matrix. Even relatively small changes in the number of live fences can significantly modify landscape structure and connectivity and potentially lead to the increased conservation of biodiversity within agricultural landscapes at both local and landscape scales.

Acknowledgements

We thank J. Saenz (UNA) for allowing use of unpublished data on the animal species visiting live fences, C. Brenes (CATIE) for help with GIS, F. Casanoves (CATIE) for help with statistical analyses, A. Perez (CATIE) for assisting with field work, and colleagues from the FRAGMENT project (especially F.L. Sinclair, M. Ibrahim and P. Hernandez) for discussions on this research. This research was conducted as part of the FRAGMENT project "Developing methods and models for assessing the impacts of trees on farm productivity and regional biodiversity in fragmented landscapes", funded by the European Community (INCO-Dev ICA4-CT-2001-10099). The authors are solely responsible for the material reported here; this publication does not represent the opinion of the Community and the Community is not responsible for any use of the data appearing herein. Additional funding for M. Chacón was provided by FINNIDA and MICIT.

References

Barr C.J. and Gillespie M.K. 2000. Estimating hedgerow length and the pattern characteristics in Great Britain using Countryside Survey data. J. Environ. Manage. 60: 23–32.

Baudry J., Bunce R.G.H. and Burel F. 2000a. Hedgerows: an international perspective on their origin, function and management. J. Environ. Manage. 60: 7–22.

Baudry J., Burel F., Thenail C. and Le Couer D. 2000b. A holistic landscape ecological study of interactions between farming activities and ecological patterns in Brittany, France. Landsc. Urban Plan. 50: 119–128.

Baudry J. and Zhenrong Y. 1999. Landscape patterns changes in two subtropical Chinese villages as related to farming policies. Crit. Rev. Plant Sci. 18(3): 373–380.

Bennett A.F. 1999. Linkages in the Landscape – The Role of Corridors and Connectivity in Wildlife Conservation. IUCN, Gland.

Bennett A.F., Henein K. and Merriam G. 1994. Corridor use and the elements of corridor quality: chipmunks and fencerows in a farmland mosaic. Biol. Conserv. 68: 155–165.

Budowski G. and Russo R.O. 1993. Live fence posts in Costa Rica: a compilation of farmer's beliefs and technologies. J. Sustain. Agr. 3(2): 65–87.

Budowski G. 1987. Living fences in tropical America, a widespread agroforestry practice. In: Gholz H.L. (ed.), Agroforestry: Realities, Possibilities and Potentials. Martinus Nijhoff Publishers, pp. 169–178.

Burel F. 1992. Effect of structure and dynamics on species diversity in hedgerow networks. Landscape Ecol. 6(3): 161–174.

Burel F. 1996. Hedgerows and their role in agricultural landscapes. Crit. Rev. Plant Sci. 15(2): 169–190.

Burel A. and Baudry J. 2005. Habitat quality and connectivity in agricultural landscapes: the role of land use systems at various scales in time. Ecological Indicators 5: 305–313.

Capel S.W. 1988. Design of windbreaks for wildlife in the Great Plains of North America. Agric., Ecosyst. Environ. 22/23: 337–347.

Charrier S., Petit S. and Burel F. 1997. Movements of *Abax parallelepipedus* (Coleoptera, Carabidae) in woody habitats of a hedgerows network landscape: a radio-tracking study. Agric., Ecosyst. Environ. 61: 133–144.

Chacón M. 2003. Tree cover and live fences in a fragmented landscape in Río Frío, Costa Rica. M.Sc. Thesis. CATIE, Turrialba, Costa Rica, pp. 107

Daily G.C., Sanchez-Azofeifa G.A. and Ehrlich P.R. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecol. Appl. 11(1): 1–13.

Deckers B., Hermy M. and Muys B. 2004. Factors affecting plant species composition of hedgerows: relative importance and hierarchy. Acta Oecol. 26: 23–37.

Deckers B., Kerselaers E., Gulinck H., Muys B. and Hermy M. 2005. Long-term spatio-temporal dynamics of a hedgerow network landscape in Flanders, Belgium. Environ. Conserv. 32: 20–29.

Dover J. and Sparks T. 2000. A review of the ecology of butterflies in British hedgerows. J. Environ. Manage. 60: 51–63.

Dmowski K. and Koziakiewicz M. 1990. Influence of a shrub corridor on movements of passerine birds to a lake littoral zone. Landscape Ecol. 4: 98–108.

Estrada A., Coates-Estrada R. and Merritt D.A. 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. Ecography 17: 229–241.

Estrada A., Cammarano P.L. and Coates-Estrada R. 2000. Bird species richness in vegetation fences and in strips of residual rain forest vegetation at Los Tuxtlas, Mexico. Biodivers. Conserv. 9: 1399–1416.

Estrada A. and Coates-Estrada R. 2001. Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. Ecography 24: 94–102.

Estrada A., Sáenz J., Harvey C., Naranjo E., Muñoz D. and Rosales-Medina M. 2006. Primates in agroecosystems: conservation value of some agricultural practices in Mesoamerican landscapes. In: Estrada A., Garber P. and Pavelka M. (eds), Study of Mesoamerican Primates: Distribution, Ecology, Behavior and Conservation. Kluwer Academic Publisher, New York, USA, pp. 437–470.

Forman R.T.T. and Baudry J. 1984. Hedgerows and hedgerow networks in landscape ecology. Environ. Manage. 8(6): 495–510.

Forman R.T.T. 1995. Landscape Mosaics-the Ecology of Landscape and Regions. Cambridge University Press, Cambridge, Great Britain, pp. 632

Haas C.A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. Conserv. Biol. 9: 845–54.

Harvey C.A., Tucker N. and Estrada A. 2004. Live fences, isolated trees and windbreaks: tools for conserving biodiversity in fragmented tropical landscapes?. In: Schroth G.A., Fonseca B., Harvey C.A., Gascon C., Vasconcelos H.L. and Izac A.M.N. (eds), Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, D.C., pp. 261–289.

Harvey C.A., Alpizar F., Chacón M. and Madrigal R. 2005a. Assessing linkages between Agriculture and Biodiversity in Central America: Historical overview and Future perspectives. Mesoamerican and Caribbean Region, Conservation Science Program. The Nature Conservancy (TNC), San Jose, Costa Rica, pp. 140

Harvey C.A., Villanueva C., Villacís J., Chacón M., Muñoz D., López M., Ibrahim M., Taylor R., Martínez J.L., Navas A., Sáenz J., Sánchez D., Medina A., Vilchez S., Hernández B., Pérez A., Ruiz F., López F., Lang I., Kunth S. and Sinclair F.L. 2005b. Contribution of live fences to the ecological integrity of agricultural landscapes. Agric., Ecosyst. Environ. 111: 200–230.

Harvey C.A., Medina A., Sanchez D., Vilchez S., Hernandez B., Saenz J., Maes J.M., Casanoves F. and Sinclair F.L.

Patterns of animal diversity associated with different forms of tree cover retained in agricultural landscapes. Ecol. Appl. (in review).

Hinsley S.A. and Bellamy P.E. 2000. The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. J. Environ. Manage. 60: 33–49.

Holdridge L.R. 1967. Life Zone Ecology. Centro Científico Tropical, Costa Rica, pp. 206.

Joyce K.A., Holland J.M. and Doncaster C.P. 1999. Influences of hedgerow intersections and gaps on the movement of carabid beetles. Bull. Entomol. Res. 89: 523–531.

Kantelhardt J., Osinski E. and Heissenhuber A. 2003. Is there a reliable correlation between hedgerow density and agricultural site conditions? Agric., Ecosyst. Environ. 98: 517–527.

Kristensen S.P. and Caspersen O.H. 2002. Analysis of changes in a shelterbelt network landscape in central Jutland, Denmark. J. Environ. Manage. 66: 171–183.

Lack P.C. 1988. Hedge intersections and breeding bird distribution in farmland. Bird Study 35: 133–136.

Lang I., Gormley L., Harvey C.A. and Sinclair F.L. 2003. Composición de la comunidad de aves en cercas vivas de Río Frío, Costa Rica. Agroforestería en las Américas 10(39–40): 86–92.

Marshall E.J.P. and Moonen A.C. 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agric., Ecosyst. Environ. 89: 5–21.

McNeely J.A. and Scherr S.J. 2003. Ecoagriculture: Strategies to Feed the World and Save Wild Biodiversity. Island Press, Washington D.C pp.323.

Millán de la Peña N., Butet A., Delettre T., Morant P. and Burel F. 2003. Landscape context and carabid (Coleoptera: Carabidae) communities of hedgerows in western France. Agric., Ecosyst. Environ. 94: 59–72.

Miranda J.M. 1991. Evaluación de gramíneas y leguminosas: establecimiento y producción en época máxima y mínima de precipitación en la zona de Río Frío. Tesis Ing. Agr. San José, Costa Rica, pp. 95

Osborne P. 1983. Bird numbers and habitat characteristics in farmland hedgerows. J. Appl. Ecol. 21: 63–82.

Pagiola S., Agostini P., Gobbi J., De Haan C., Ibrahim M., Murgueito E., Ramirez E., Rosales M. and Ruiz J.P. 2005. Paying for biodiversity conservation services. Mt. Res. Dev. 25(3): 206–211.

Petit S. and Burel F. 1993. Movement of *Abax ater* (Col. Carabidae): do forest species survive in hedgerow networks? Vie Mileiu 43: 119–124.

Petit L.J. and Petit D.R. 2003. Evaluating the importance of human-modified lands for neotropical bird conservation. Conserv. Biol. 17(3): 687–694.

Pimentel D., Stachow F., Takacs D., Brubaker H., Dumas A., Meaney J., O'Neil J., Onsi D. and Corzilius D. 1992. Conserving biological diversity in agricultural/forestry systems. Bioscience 42(5): 354–362.

Ricketts T.H., Fay J.P., Ehrlich P.R. and Daily G.C. 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. Conserv. Biol. 15(2): 387–388.

Santivañez J.L. 2005. Efecto de la estructura, composición y conectividad de las cercas vivas en la comunidad de aves de Río Frío, Costa Rica. Tesis Mag. Sc. Turrialba. CATIE, Costa Rica, pp. 136.

Sauer J.D. 1979. Living fences in Costa Rican agriculture. Turrialba (IICA) 29(4): 225–261.

Schmucki R., De Blois S., Bouchard A. and Domon G. 2002. Spatial and temporal dynamics of hedgerows in three agricultural landscapes of Southern Quebec, Canada. Environ. Manage. 30(5): 651–664.

Schroth G., Fonseca G.A.B., Harvey C.A., Gascon C., Vasconcelos H.L. and Izac A.M.N. 2004. Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, D.C., pp. 523.

Sokal R.R. and Rohlf F.J. 1994. Biometry: The Principles and Practice of Statistics in Biological Research. W. H. Freeman, pp. 880

Thenail C. and Baudry J. 2004. Variation of farm spatial land use pattern according to the structure of the hedgerow network (bocage) landscape: a case study in northeast Brittany. Agric., Ecosyst. Environ. 101: 53–72.

Turner M.G., Gardner R.H. and O'Neill R.V. 2001. Landscape Ecology in Theory and Practice. Pattern and process. Springer Verlag, New York, Inc. USA, pp. 401.

Verboom B. and Huitema H. 1997. The importance of linear landscape elements for the pipstrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. Landscape Ecol. 12(2): 117–125.

Villacís J., Harvey C.A., Ibrahim M. and Villanueva C. 2003. Relaciones entre la cobertura arbórea y el nivel de intensificación de las fincas ganaderas en Río Frío, Costa Rica. Agroforestería en las Américas 10(39–40): 17–23.

Yahner R.H. 1982a. Avian use of vertical strata and planting in farmstead shelterbelts. J. Wildl. Manage. 46(1): 50–60.

Yahner R.H. 1982b. Avian nest densities and nest site selection in farmstead shelterbelts. Wilson Bull. 94: 156–175.