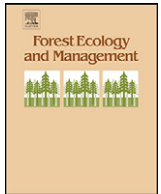




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## Forest Ecology and Management

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# Conservation value of dispersed tree cover threatened by pasture management

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### ARTICLE INFO

#### Article history:

Received 14 June 2010

Received in revised form 2 November 2010

Accepted 3 November 2010

#### Keywords:

Cattle production

Farmer decision-making

Local knowledge

Natural regeneration

Tree diversity

### ABSTRACT

Trees dispersed in pastures are a prominent feature of many Central American landscapes, particularly in cattle producing regions where farmers retain trees to serve as shade, fodder, timber and firewood. The presence of dispersed trees in pastures is often considered as important for the conservation of biodiversity by providing habitat and enhancing landscape connectivity. However, despite their critical productive and environmental roles, little is known about tree distribution within pastures or how farmers' management decisions influence the trees themselves and their impact on farm productivity and biodiversity conservation. Here, we present a synthesis of (a) the abundance, composition, and size of dispersed trees in four important cattle producing regions of Costa Rica (Cañas and Río Frío) and Nicaragua (Rivas and Matiguás), based on inventory of 18,669 trees on 1492 ha of pasture, (b) the local knowledge, management and use of trees by cattle farmers, and (c) opportunities for ensuring sustainable management of dispersed trees in pasture-dominated landscapes. Dispersed trees were common in all four landscapes, with mean frequency ranging from 8.0 trees ha<sup>-1</sup> in Cañas to 33.4 trees ha<sup>-1</sup> in Matiguás. A total of 255 tree species were found in pastures across the four landscapes. The total number of tree species per landscape varied from 72 in Rivas to 101 in Cañas and Río Frío, with mean species richness per farm ranging from 22.9 in Río Frío to 45.9 in Matiguás. In all four landscapes, a handful of tree species dominated the pastures, with the ten most abundant species in each landscape accounting for >70% of all trees recorded. Most of these common tree species provide fruits or foliage eaten by cattle, or are important timber or firewood species, and are deliberately retained by farmers for these uses. In all four landscapes, farmers had a detailed knowledge of tree attributes affecting pasture and animal productivity, and influenced tree cover through pasture management activities and occasional tree cutting. Current farm management practices are gradually decreasing the diversity of trees in pastures, and in some cases also tree density, reducing their contribution to farm productivity and biodiversity conservation. To reverse this trend, incentives are required to encourage cattle farmers to retain and enhance tree cover in pastures, through the adoption of pasture management practices that favor the regeneration and persistence of a diverse range of tree species.

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## 1. Introduction

In many regions of Central America, cattle production has transformed forested areas into agricultural landscapes dominated by pastures and crop fields. More than 9 million hectares of the region are currently used for cattle production (Szott, 2000), and this is likely to grow as the agricultural frontier expands into forest areas. Cattle production has already led to widespread deforestation of Tropical Dry Forests in the region and less than 1.7% of intact forest remains (Calvo-Alvarado et al., 2009). Within a few decades, it

**Table 1**  
Biophysical and productive characteristics of the four agricultural landscapes in Costa Rica and Nicaragua in which dispersed trees were studied.

Landscape	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua
Biophysical characteristics				
Area (ha)	13,051	15,987	11,621	10,108
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
% of landscape covered by pasture	48.4	47.0	56.7	68.2
Farming systems				
Main production system	Beef	Dairy (some beef and dual-purpose)	Mixed (dual-purpose cattle + agriculture)	Dual purpose cattle (with some agriculture)
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
Cattle breeds	Crosses of Indobrasil, Brahman, and Gyr breeds	Dairy: crosses of Jersey, Holstein, and Brown Swiss Beef: 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	<i>Brachiaria brizantha</i> , <i>Brachiaria decumbens</i> , <i>Hypparrhenia rufa</i>	<i>Ischaemum ciliare</i> , <i>Brachiaria arrecta</i>	<i>Hypparrhenia rufa</i>	<i>Panicum maximum</i> , <i>Paspalum virgatum</i> , <i>Hypparrhenia rufa</i>
Level of farm intensification (herbicide, pesticide + concentrate use)	Extensive	Intensive (some extensive)	Extensive	Extensive
Publications with additional details on farming systems	Restrepo (2002), Villanueva et al. (2003), and Esquivel et al. (2004)	Villacís (2003) and Villacís et al. (2003)	López et al. (2004)	Ruiz et al. (2005)

is likely that most of the region will have been affected by cattle production to some extent (Wassenaar et al., 2007), with significant impact on biodiversity and the provision of ecosystem services (Harvey et al., 2005a).

Although rural landscapes, and pasture-dominated landscapes in particular, are generally viewed as biological wastelands, they often retain a high tree cover interspersed within the pasture matrix, including small forest remnants, riparian forests, live fences and dispersed trees in pastures. The presence of dispersed trees in pastures is a particularly conspicuous feature of these landscapes, with trees occurring in different cattle production systems, elevations, ecological life zones, soil types, and culturally distinct regions across Central America (Guevara et al., 1994; Harvey and Haber, 1999; Gordon et al., 2003; Love and Spaner, 2005). Dispersed trees are commonly retained in pastures because of their value as shade, fodder, timber and firewood (Harvey and Haber, 1999; Cajas-Girón and Sinclair, 2001). However, these trees also play important roles in conserving biodiversity, by providing habitat, resources and nesting sites for animals, increasing overall tree cover within the landscape and thereby enhancing landscape connectivity (Guevara et al., 1998; Fischer and Lindenmayer, 2002; Harvey et al., 2006; Medina et al., 2007), and ameliorating microclimatic conditions within the pasture matrix for forest-dependent species (Sekercioglu et al., 2007). Dispersed trees therefore play both productive and environmentally protective roles within the agricultural landscape, and can contribute to both sustainable development and conservation initiatives.

While there is growing interest in the potential importance of dispersed trees as keystone elements of agricultural landscapes (Manning et al., 2006), to date, relatively little is known about the diversity and abundance of dispersed trees in Central America and how these are changing over time. There have been a few isolated studies of dispersed trees in cattle production systems in the region (e.g., Harvey and Haber, 1999; Gordon et al., 2003; Love and Spaner, 2005), but none have looked at the range of products and ecological functions that dispersed trees provide, or compared tree diversity and abundance across different regions. In addition, there is little information available about how cattle farmers make decisions to retain, eliminate or modify on-farm tree cover, and how these decisions impact the density and composition of dispersed

trees within the pasture matrix, and, in turn, their environmental and productive functions. This contrasts with the literature on dispersed tree cover in Europe and Australia (e.g., Peterken, 1996; Manning et al., 2006), where the value of on-farm tree cover is well-established and agrienvironmental schemes aimed at conserving tree cover as a means of maintaining the ecological integrity of rural landscapes exist (e.g., Mattison and Norris, 2005; Gibbons et al., 2008). Understanding more about the existing on-farm tree cover and the ways in which farmers shape and manage this tree cover is critical for incorporating dispersed trees into both sustainable farm management initiatives and efforts to conserve the region's rich biodiversity.

The general objective of the research reported here was to assess the status of dispersed trees within agricultural landscapes in Central America and farmers' knowledge and management practices relating to them. Specifically, we focus on understanding (a) the abundance, species composition and size of dispersed trees in pastures in four important cattle production regions of Costa Rica and Nicaragua, (b) farmer local knowledge, use and management of dispersed trees, and (c) what opportunities exist for the sustainable management of dispersed trees in pasture-dominated landscapes. Our analysis is based on a set of integrated studies which consisted of socioeconomic surveys of cattle farms, inventories of dispersed trees in pastures, acquisition of local knowledge of farmers about trees, and the monitoring of farm management, including information on dispersed tree harvesting, management and use.

## 2. Methods

We studied dispersed trees in four cattle-producing regions where pasture was the predominant land use: Cañas and Río Frío in Costa Rica and Matiguás and Rivas in Nicaragua (Table 1). Both the Cañas and Rivas landscapes are typical of the cattle production systems in the seasonally dry Pacific slope of Central America, where the original Tropical Dry Forest has been largely converted to pasture (Calvo-Alvarado et al., 2009), with extensively managed cattle systems for beef in Cañas and dual-purpose (beef and dairy production) in Rivas. The Matiguás landscape is located in the transitional zone between Tropical Dry Forests and humid forests, and

**Table 2**

A summary of the data collected on dispersed trees in pastures in four agricultural landscapes of Central America.

Data collected	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua	Total
# of farmers interviewed in socioeconomic survey	53	71	57	100	281
# of farms on which dispersed trees were inventoried	16	16	12	15	59
# of farms on which farm productivity was monitored during one year	15	16	15	15	61
Total area of pastures surveyed for dispersed trees (ha)	800.7	117.9	248.6	324.6	1491.8

is characterized by dual-purpose cattle production. The Río Frío landscape, in contrast, is a dairy farming region on the wet Atlantic slope of Costa Rica and is the most intensively managed landscape, with high fertilizer use and introduced grass species (Table 1).

In each landscape, we selected an area of approximately 10,000–16,000 ha as representative of the region, using aerial photos and satellite images. All four landscapes have been highly modified by cattle production, and were dominated by pasture (48–68% of the land), with only small forest patches and degraded riparian forests remaining.

We collected data on dispersed trees through 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 on-farm tree cover was collected; (2) a complete inventory of the floristic composition, density and size of dispersed trees present in a sample of 12–16 cattle farms in each landscape; (3) the acquisition of local knowledge that farmers held about dispersed trees; and (4) the monitoring of farm management, including information on the management and pollarding of dispersed trees in 12–16 farms in each landscape during one year. 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. A similar integrated study was conducted for live fences in the same farms and landscapes (Harvey et al., 2005b).

### 2.1. Farm survey

In order to characterize the dispersed tree cover present in cattle production farms, we conducted a survey on farm use and management with 53–100 farmers per landscape (281 in total), randomly selected from a list of all farmers in each study area. The objective of the semi-structured questionnaire was to characterize farm types, understand land use patterns and farm management practices, and collect detailed information on the presence of dispersed trees in pastures, the number of tree species present, and associated management practices. Additional details on the farm survey are available in Restrepo (2002), Villacís (2003) and Gómez et al. (2004). All information from farm surveys was compiled in a data base, and summarized using descriptive statistics.

### 2.2. Inventory of dispersed trees

We collected detailed data on the abundance, composition and size of dispersed trees in pastures by conducting a complete census of all dispersed trees present in a subset of 12–16 randomly selected farms in each of the four landscapes (total of 59 farms, including 1492 ha of pastures). Within each of these farms, all dispersed trees in pastures with a stem diameter at breast height  $\geq 10$  cm were identified, and data collected on tree species, diameter at breast height (dbh), total height and crown diameter (measured as the widest point of the tree canopy). Dispersed tree abundance, density and species richness were summarized at both farm and landscape scales. Histograms were used to summarize the distribution of tree diameter sizes in each landscape. To compare tree

density and species richness across different landscapes, we used one-way ANOVA. For each landscape, we generated species rarefaction curves, using Monte Carlo simulations with 1000 iterations, in the statistical program EcoSim (Gotelli and Entsminger, 2009).

### 2.3. Farmer knowledge and management of dispersed trees

In each of the landscapes, we also acquired farmers' knowledge about dispersed trees in pastures. Detailed and repeated, semi-structured interviews were followed by recording knowledge using well established knowledge based systems methods (Sinclair and Walker, 1998; Walker and Sinclair, 1998). Knowledge was elicited through interviews with 20–25 purposively selected informants in each landscape, covering locally defined strata that grouped people according to what knowledge they were expected to have (e.g., gender, age and wealth). Interviews focused on farmers' knowledge about tree species, biological and physical characteristics of trees, tree uses (e.g., firewood, timber and fodder), ecological interactions between trees, pastures and cattle, and other aspects of local importance. All interviews were tape-recorded, transcribed and entered into a formal knowledge base using the Agroecological Knowledge Toolkit software (AKT5, version 4.01; Dixon et al., 2001). This knowledge was then validated with a larger stratified, random sample of farmers (45–69 per landscape) that had not been involved in the original acquisition. A more detailed description of the methods is available for each landscape (Río Frío and Cañas: Muñoz et al., 2004; Matiguás: Martínez, 2003; and Rivas: Joya et al., 2004). Additional information on dispersed tree management was collected through monthly visits to the 12–16 sample farms per landscape, with a particular emphasis placed on whether farmers had harvested trees for firewood or changed pasture management practices that affect tree abundance or composition. In each landscape, the main activities that affect on-farm tree cover were identified and farmers asked to explain the reasons for decisions taken to remove, retain, plant or manage trees or natural regeneration in pastures.

## 3. Results

### 3.1. Abundance, species composition and size of dispersed trees

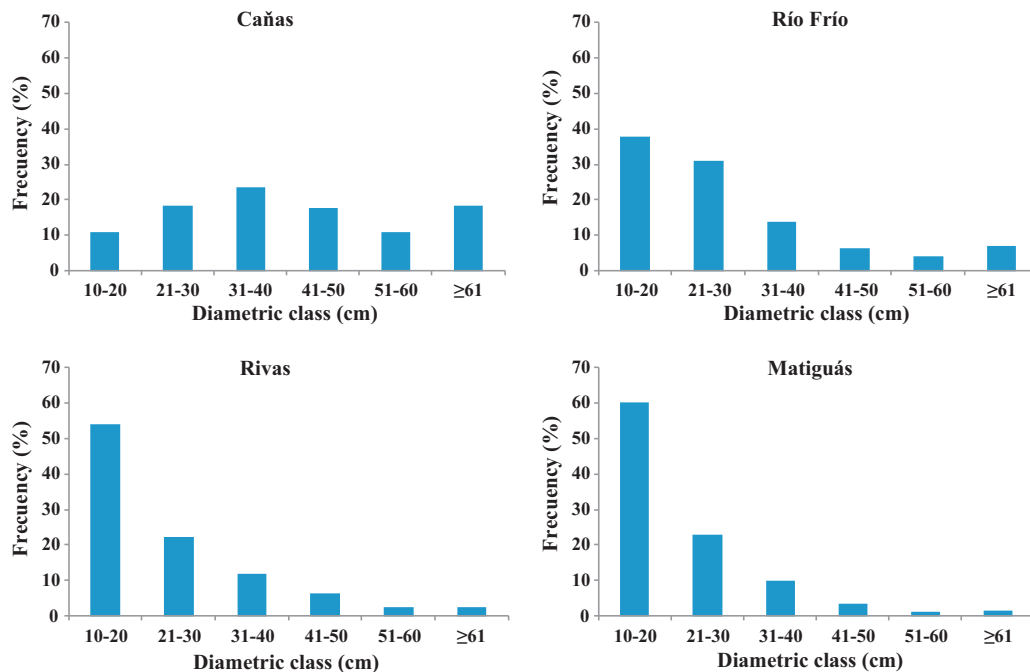
Dispersed trees in pastures were a conspicuous feature in all four landscapes, occurring in all of the farms surveyed. A total of 18,669 trees were inventoried in the 59 farms across all the landscapes, representing 255 species (241 identified and 9 unidentified).

Dispersed trees occurred at low frequencies in all four landscapes, ranging from a mean of 8.0 trees ha<sup>-1</sup> in Cañas, Costa Rica, to 33.4 trees ha<sup>-1</sup> in Matiguás, Nicaragua (Table 3). There were significant differences in tree density across the four landscapes, with Matiguás having a higher tree density than Rivas and Cañas ( $F = 7.08$ ,  $p < 0.001$ ). The Río Frío landscape had the second highest tree density and had significantly more trees than Cañas.

There were also differences across landscapes in the size distribution of trees present (Fig. 1). In the Nicaraguan landscapes, the diameter distribution was skewed towards trees with small diameters, with 54% of the trees in Rivas and 60.1% of the trees in Matiguás having diameters less than 20 cm, but more than 10 cm. The Río Frío

**Table 3**  
Main characteristics of the dispersed trees present in pastures in four agricultural landscapes of Central America, based on complete inventories of all dispersed trees in 12–16 farms per landscape. Means in the same row with the same letter are not significantly different according to a one-way ANOVA test, followed by Duncan at  $p < 0.001$ .

Variable	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua
# dispersed trees inventoried	5896	2482	2297	7994
Mean density of dispersed trees $ha^{-1}$ ( $\pm SE$ )	7.97 $\pm$ 1.00c	23.10 $\pm$ 3.40ab	16.94 $\pm$ 5.14bc	33.4 $\pm$ 6.07a
Total # spp. recorded	101	101	72	100
Mean # spp. of dispersed trees/farm ( $\pm SE$ )	34.31 $\pm$ 3.81b	22.88 $\pm$ 1.85c	25.50 $\pm$ 3.90bc	45.93 $\pm$ 4.65a
Mean dap ( $\pm SE$ ) in cm	44.32 $\pm$ 0.33a	30.86 $\pm$ 0.52b	24.18 $\pm$ 0.30c	18.56 $\pm$ 0.13d
Mean height ( $\pm SE$ ) in m	11.13 $\pm$ 0.08b	13.78 $\pm$ 0.14a	9.28 $\pm$ 0.07c	8.21 $\pm$ 0.05d
Mean canopy size ( $\pm SE$ ) in $m^2$	91.03 $\pm$ 2.16a	74.47 $\pm$ 4.63b	51.17 $\pm$ 1.11c	35.59 $\pm$ 1.46d



**Fig. 1.** Distribution of tree diameters of dispersed trees found in cattle production landscapes in (a) Cañas, Costa Rica; (b) Río Frío, Costa Rica; (c) Rivas, Nicaragua and (d) Matiguás, Nicaragua. Data are based on 5896 trees in Cañas, 2482 trees in Río Frío, 2297 trees in Rivas, and 7994 trees in Matiguás. Data represent the % of trees found in each diameter class.

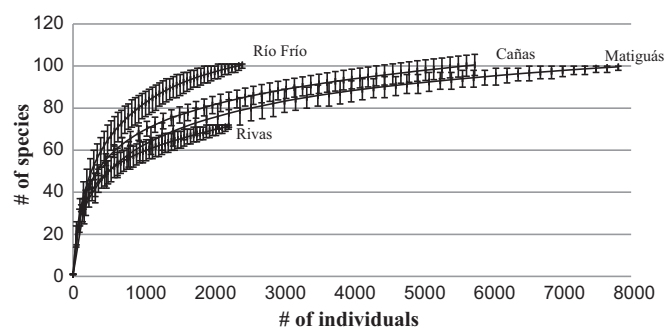
landscape also had a predominance of smaller-diameter trees, but the distribution was less skewed, due to the presence of some remnant trees of the original forest cover which had large diameters. The distribution of tree diameters in the Cañas landscape was distinct from the other landscapes due to the sizeable number of trees with medium to large diameters (52.2% of trees had diameters of 30–60 cm and 18.3% had diameters exceeding 60 cm) and few trees with small diameters. The overall mean tree diameter in Cañas was larger than that of other landscapes ( $F = 2032.55$ ;  $p < 0.0001$ ), and both Costa Rican landscapes had larger tree diameters than the Nicaraguan landscapes.

There were also differences in tree height across the landscapes. Trees were the tallest in Río Frío, followed by Cañas, and both Costa Rican landscapes had taller trees than either of the Nicaraguan landscapes ( $F = 770.9$ ,  $p < 0.0001$ ). The trees in Cañas and Río Frío also had much larger crowns than trees in the Nicaraguan landscapes ( $F = 164.04$ ,  $p < 0.0001$ ).

At the landscape level, the total species richness was quite high, with between 72 and 101 tree species recorded per landscape and an overall total of 255 species across the four landscapes. Species rarefaction curves for all landscapes were reaching a plateau suggesting that sampling larger numbers of individuals would not have resulted in many more species being recorded (Fig. 2). The landscapes can be compared at a sample size of 2000 individuals, showing that the Tropical Wet Forest landscape (Río Frío) had greater overall tree diversity than the other three landscapes.

Many of tree species reported in pastures were present in low numbers: of the 255 species identified, 160 were represented by ten individuals or less (across the four landscapes), including 45 species that were represented by only a single tree. This pattern of overall high species richness at the landscape level and a dominance of a few very common species (with the majority of species occurring in very low abundances) was evident in all four landscapes.

Tree species richness at the individual farm level ranged from 22.9 tree species per farm in Río Frío to 45.9 tree species per farm



**Fig. 2.** Species rarefaction curves for dispersed trees in pastures in four agricultural landscapes based on Monte Carlo simulations. Error bars represent 95% confidence intervals.

**Table 4**

A summary of the ten most abundant tree species occurring as dispersed trees in pastures in each of the four agricultural landscapes, and their respective uses.

Cañas (n = 5896)		Río Frío (n = 2482)		Rivas (n = 2297)		Matiguás (n = 7994)	
Species	% of trees	Species	% of trees	Species	% of trees	Species	% of trees
<i>Tabebuia rosea</i> <sup>a</sup>	12.8	<i>Cordia alliodora</i> <sup>a</sup>	25.9	<i>Cordia alliodora</i> <sup>a</sup>	22.7	<i>Guazuma ulmifolia</i> <sup>b,c,d</sup>	35.8
<i>Guazuma ulmifolia</i> <sup>b,c,d</sup>	12.6	<i>Psidium guajava</i> <sup>b,c,d</sup>	22.5	<i>Guazuma ulmifolia</i> <sup>b,c,d</sup>	15.2	<i>Cordia alliodora</i> <sup>a</sup>	12.9
<i>Cordia alliodora</i> <sup>a</sup>	12.0	<i>Pentaclethra macroloba</i> <sup>a</sup>	4.7	<i>Tabebuia rosea</i> <sup>a</sup>	7.1	<i>Tabebuia rosea</i> <sup>a</sup>	5.9
<i>Acrocomia aculeata</i> <sup>d,e</sup>	10.3	<i>Citrus sinensis</i> <sup>e</sup>	4.7	<i>Byrsonima crassifolia</i> <sup>e</sup>	6.6	<i>Enterolobium cyclocarpum</i> <sup>a,c,d</sup>	5.7
<i>Byrsonima crassifolia</i> <sup>e</sup>	7.4	<i>Citrus limon</i> <sup>e</sup>	3.1	<i>Gliricidia sepium</i> <sup>b,c,d</sup>	6.4	<i>Samanea saman</i> <sup>a,c,d</sup>	5.0
<i>Tabebuia ochracea</i> <sup>a</sup>	4.5	<i>Cocos nucifera</i> <sup>e</sup>	2.6	<i>Cordia dentata</i> <sup>e</sup>	3.8	<i>Platymiscium parviflorum</i>	3.9
<i>Pachira quinata</i> <sup>a</sup>	3.1	<i>Billia columbiana</i> <sup>a</sup>	2.3	<i>Myrospermum frutescens</i> <sup>b</sup>	3.6	<i>Gliricidia sepium</i> <sup>b,c,d</sup>	3.8
<i>Andira inermis</i> <sup>a</sup>	2.9	<i>Guazuma ulmifolia</i> <sup>b,c,d</sup>	2.0	<i>Acrocomia vinifera</i> <sup>d</sup>	3.1	<i>Lonchocarpus minimiflorus</i> <sup>a</sup>	2.0
<i>Piscidia carthagenensis</i>	2.7	<i>Bactris gasipaes</i> <sup>e</sup>	2.0	<i>Enterolobium cyclocarpum</i> <sup>a,c,d</sup>	3.0	<i>Cordia bicolor</i> <sup>ab</sup>	2.0
<i>Acosmium panamensis</i> <sup>a</sup>	2.4	<i>Zanthoxylum kellermanii</i>	1.9	<i>Swietenia humilis</i> <sup>a</sup>	2.9	<i>Tabebuia ochracea</i> <sup>a</sup>	1.9
Total	70.7	Total	71.7	Total	74.4	Total	78.9

<sup>a</sup> Timber species.<sup>b</sup> Firewood species.<sup>c</sup> Foliage for cattle consumption.<sup>d</sup> Fruits consumed by cattle.<sup>e</sup> Fruits for human consumption.

in Matiguás. Farms in Matiguás had the highest overall number of tree species, followed by Cañas ( $F = 5.47$ ,  $p = 0.002$ ).

Although many tree species were found in pastures, a handful of tree species dominated (Table 4). The most common tree species was *Guazuma ulmifolia*, a tree species which produces fruits that cattle eat (Cajas-Girón and Sinclair, 2001), which accounted for over 20% of all of the trees recorded across the four landscapes and was abundant in all four landscapes. The other two very common tree species were *Cordia alliodora* (a timber species that regenerates easily in pastures; Somarrriba and Beer, 1987) which accounted for 15% of trees registered and was common in all four landscapes, and *Tabebuia rosea* (another timber species) which was common in all landscapes except the wetter environment of Río Frío and totaled 7.5% of all trees. In each landscape, the ten most common species accounted for >70% of all of the trees registered.

Nearly all trees retained on pasture were of species of well-established utility for timber, firewood, fruit or forage, with many of them serving multiple functions (Table 5). In all four landscapes, timber species accounted for >42% of all dispersed trees. The presence of firewood species was more variable across landscapes, with greater dominance in the Matiguás landscape, intermediate densities in Rivas and Río Frío, and very few present in Cañas, reflecting the importance of fuel wood as an energy source for heating and cooking in these landscapes. Over a quarter of all trees in each landscape were species that provided fodder for cattle, and in Matiguás, fodder species (particularly *G. ulmifolia*) accounted for 53% of all trees. With the exception of Río Frío, more than a quarter of the trees recorded in each landscape were of species that produced fruit eaten by cattle.

The species composition of the trees present in pastures reflected the different ecological conditions. The two dry forest landscapes (Rivas, Cañas) and the humid forest landscape (Matiguás) shared the same basic set of common species, with *G. ulmifolia*, *C. alliodora* and *T. rosea* representing the three most abundant species in each landscape. In contrast, the species composition

of Río Frío was distinct, with species typical of wetter conditions (such as *Pentaclethra macroloba*) predominating. Río Frío was also unique in the very high abundance of fruit trees especially *Psidium guajava* and *Citrus* species which represented 22% and 8% of the trees in this landscape, respectively.

### 3.2. Utility and management of dispersed trees within farming systems

According to interviews with farmers, most of the trees present in pastures were either relicts of the original forest that were left when the forests were cleared, or trees that had arisen from natural regeneration within the pastures. Very few dispersed trees were planted by farmers, with the exception of an occasional fruit tree, such as *Citrus* species.

In all four landscapes, farmers reported using dispersed trees as a source of timber, fence posts, firewood, and fodder for cattle (both leaves and also fruits) but the degree to which farmers depend on these products varied across landscapes (Table 6). For example, while all farmers in both Nicaraguan landscapes used trees in pastures as a source of timber, a smaller percentage of Costa Rican farmers reported this use. Similarly, the Nicaraguan farmers reported a much higher use of dispersed trees for firewood than their Costa Rican counterparts. In all landscapes (except Río Frío, which was dominated by intensified dairy farms with specialized grasses), roughly one third of cattle farmers also used trees as a source of fodder or fruits for cattle, particularly in the dry season when grass was in limited supply.

Cattle farmers had detailed knowledge about dispersed trees in pastures, including knowledge of the tree species present, their respective uses, and their interactions with other farm components, such as cattle and grass. In each landscape, farmers recognized between 70 and 84 different tree species as occurring in pastures, the majority of which are species that can be used for timber, firewood, fodder or fruits (Table 7).

**Table 5**

Percent of dispersed trees in each landscape that provide timber, firewood, fodder or fruits for cattle consumption, based on tree inventories (5896 trees in Cañas, 2482 trees in Río Frío, 2297 trees in Matiguás, and 7994 trees in Matiguás).

Tree uses	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua	Total (across the four landscapes)
Timber species	49.7	42.5	48.8	46.4	47.2
Firewood species	1.5	23.4	12.2	48.9	26.0
Fodder for cattle	28.7	27.1	33.0	53.1	39.4
Fruits for cattle consumption	27.5	3.2	26.6	48.9	33.4

Note: many tree species have more than one use, so percentages do not add to 100.

**Table 6**  
Percent of farmers who use dispersed trees and live fences on their farms as a source of timber, fence posts, firewood and fodder for livestock (data based on surveys with farmers).

Variable	Cañas, Costa Rica (n = 53)	Río Frío, Costa Rica (n = 71)	Rivas, Nicaragua (n = 91)	Matiguás, Nicaragua (n = 97)
Timber	52.8	69.0	100.0	100.0
Fence posts	71.7	74.6	71.0	90.7
Firewood	58.5	42.3	74.5	81.4
Fodder and fruits for livestock	35.8	11.3	35.6	26.8

There were some interesting differences in farmer knowledge across the four landscapes, with Nicaraguan farmers identifying many more firewood species and timber species than their Costa Rican counterparts (most likely due to greater dependence on these resources in the Nicaraguan landscapes). Similarly, the Nicaraguan farmers used a greater number of forage species for cattle than the Costa Ricans.

In all four landscapes, farmers had a fairly sophisticated understanding of the interactions between tree cover, grass production and cattle production, including both the positive and negative interactions, and made decisions about which trees to leave in pastures (and in what densities) based on an attempt to balance both positive and negative impacts of trees (Table 8). Farmers reported that trees are important as shade for cattle (reducing animal heat stress and maintaining a favorable microclimate) and as a source of fruits and foliage for cattle during the dry season when grass is grass availability is low. According to farmers, the most commonly consumed tree species are *G. ulmifolia*, *Samanea saman*, *Gliricidia*

*sepium*, *Enterolobium cyclocarpum*, and *Psidium guajava*, and farmers often specifically leave these trees in pastures to provide fodder and fruits for cattle (though they rarely actively manage fruit tree densities in their pastures, or collect or store fruits to feed cattle in the dry season).

However, farmers were also aware of the potential negative effects of trees on grass production (through shading and competition) and the potential risk of some fruit trees that can be toxic to cattle. Farmers reported that the effects of trees on grass production depend on particular attributes of tree species, such as their height, crown size and foliage density. In all four landscapes, farmers classified trees on the basis of their shade, distinguishing those that are most compatible with pasture production (tall, sparse, and small crowns) from those that exert a strong negative impact (dense and low crowns), and took this classification into consideration when deciding which trees to leave in pastures. In addition, farmers had a detailed knowledge of which tree species can have a negative effect on cattle, causing intoxication or abortion, if consumed in excess.

**Table 7**  
Summary of the main tree species that are used as timber, firewood and fodder by farmers in four cattle production landscapes (derived from local knowledge studies).

Variable	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua
<b>Timber species</b>				
Total number of tree species mentioned	83	84	70	81
# of timber species	15	12	37	30
Most commonly known timber species	<i>Guazuma ulmifolia</i> , <i>Samanea saman</i> , <i>Enterolobium cyclocarpum</i> , <i>Pachira quinata</i> , <i>Lysiloma divaricatum</i> , <i>Diphysa americana</i> , <i>Cedrela odorata</i>	<i>Cordia alliodora</i> , <i>Pentaclethra macroloba</i> , <i>Minuartia guianensis</i> , <i>Cedrela odorata</i> , <i>Swietenia humilis</i>	<i>Swietenia humilis</i> , <i>Pachira quinata</i> , <i>Enterolobium cyclocarpum</i> , <i>Diphysa robinoides</i> , <i>Gliricidia sepium</i> , <i>Cordia alliodora</i> , <i>Anacardium excelsum</i> , <i>Tabebuia rosea</i>	<i>Pachira quinata</i> , <i>Cordia alliodora</i> , <i>Swietenia macrophylla</i> , <i>Hymenaea courbaril</i> , <i>Samanea saman</i> , <i>Enterolobium cyclocarpum</i> , <i>Gliricidia sepium</i>
<b>Firewood species</b>				
# of firewood species	11	12	26	38
Most commonly used firewood species	<i>Andira inermis</i> , <i>Tabebuia chrysantha</i> , <i>Diphysa robinoides</i> , <i>Guazuma ulmifolia</i> , <i>Cordia alliodora</i> , <i>Gliricidia sepium</i> , <i>Cupania guatemalensis</i> , <i>Byrsonima crassifolia</i> , <i>Dipterodendron costaricensis</i> , <i>Caesalpinia eriostachys</i>	<i>Chrysophyllum caimito</i> , <i>Pentaclethra macroloba</i> , <i>Inga edulis</i> , <i>Inga punctata</i> , <i>Psidium guajava</i> , <i>Spondias</i> spp., <i>Gliricidia sepium</i> , <i>Melicoccus bijugatus</i> , <i>Byrsonima crassifolia</i> , <i>Citrus</i> spp., <i>Chimarrhis parviflora</i>	<i>Calycophyllum candidissimum</i> , <i>Cordia dentata</i> , <i>Eucalyptus</i> spp., <i>Guazuma ulmifolia</i> , <i>Diphysa robinoides</i> , <i>Gliricidia sepium</i>	<i>Guazuma ulmifolia</i> , <i>Calycophyllum candidissimum</i> , <i>Gliricidia sepium</i> , <i>Leucaena shannoni</i> , <i>Cordia alliodora</i> , <i>Cassia grandis</i> , <i>Lysiloma auritum</i> , <i>Acacia pennatula</i> , <i>Genipa americana</i> , <i>Manilkara zapota</i> , <i>Psidium guajava</i>
<b>Forage for cattle</b>				
# tree species that produce forage (leaves or fruit) for cattle	3	3	10	15
Species that are most commonly used for cattle forage	<i>Bursera simaruba</i> , <i>Guazuma ulmifolia</i> , <i>Gliricidia sepium</i>	<i>Erythrina costaricensis</i> , <i>Gliricidia sepium</i> , <i>Samanea saman</i>	<i>Guazuma ulmifolia</i> , <i>Samanea saman</i> , <i>Gliricidia sepium</i> , <i>Leucaena leucocephala</i> , <i>Enterolobium cyclocarpum</i>	<i>Samanea saman</i> , <i>Senna atomaria</i> , <i>Gliricidia sepium</i> , <i>Enterolobium cyclocarpum</i> , <i>Bursera simaruba</i>
<b>Fruits for cattle consumption</b>				
# of trees that produce fruits eaten by cattle	11	7	12	4
Tree species whose fruit cattle eat	<i>Andira inermis</i> , <i>Samanea saman</i> , <i>Genipa americana</i> , <i>Enterolobium cyclocarpum</i> , <i>Albizia guachapele</i> , <i>Guazuma ulmifolia</i> , <i>Spondias mombin</i> , <i>Mangifera indica</i> , <i>Byrsonima crassifolia</i> , <i>Brosimum lactescens</i> , <i>Citrus pardisii</i>	<i>Andira inermis</i> , <i>Enterolobium cyclocarpum</i> , <i>Psidium guajava</i> , <i>Guazuma ulmifolia</i> , <i>Spondias purpurea</i> , <i>Syzygium malaccense</i> , <i>Brosimum lactescens</i>	<i>Acrocomia vinifera</i> , <i>Cassia grandis</i> , <i>Crescentia alata</i> , <i>Enterolobium cyclocarpum</i> , <i>Guazuma ulmifolia</i> , <i>Samanea saman</i> , <i>Spondias purpurea</i> , <i>Mangifera indica</i> , <i>Spondias mombin</i> , <i>Psidium guajava</i> , <i>Mastichondendron capiri</i> , <i>Brosimum alicastrum</i>	<i>Citrus</i> spp. (several varieties), <i>Spondias mombin</i> , <i>Annona purpurea</i>

**Table 8**  
Summary of key aspects of farmers' knowledge about interactions amongst trees, grass production and cattle production in each of the four study landscapes.

Variable	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua
Characteristics of trees that are compatible with grass production	Low shade production	Low shade production No superficial roots	Fine leaves Tall trees Sparse tree crown Trees that provide nutrients	Tall tree Dispersed branches Straight growth Little shade
Tree species considered compatible with grass production	<i>Gliricidia sepium</i> , <i>Pachira quinata</i> , <i>Bursera simaruba</i>	<i>Erythrina</i> spp., <i>Gliricidia sepium</i> , <i>Psidium guajava</i>	<i>Swietenia macrophylla</i> , <i>Tabebuia rosea</i> , <i>Cordia alliodora</i> , <i>Gliricidia sepium</i>	<i>Platymiscium parviflorum</i> , <i>Cedrela odorata</i> , <i>Tabebuia rosea</i> , <i>Cordia alliodora</i> , <i>Swietenia</i> spp., <i>Pachira quinata</i>
Tree characteristics that are NOT compatible with grass production	Dense shade	Dense shade Superficial roots	Wide leaves Low trees Big crowns	Dense shade Low trees
Tree species considered NOT compatible with pasture production	<i>Andira inermis</i> , <i>Ficus</i> spp., <i>Enterolobium cyclocarpum</i> , <i>Guazuma ulmifolia</i>	<i>Pentaclethra macroloba</i> , <i>Dipteryx panamensis</i> , <i>Ficus</i> spp.	<i>Ficus</i> spp., <i>Enterolobium cyclocarpum</i> , <i>Samanea saman</i>	<i>Enterolobium cyclocarpum</i> , <i>Samanea saman</i> , <i>Gliricidia sepium</i> , <i>Guazuma ulmifolia</i>
Importance of tree cover for cattle	Protects cattle from heat	Protects animals from heat stress	Protects cattle from heat Creates favorable microclimate in which cattle eat more Increases milk production	Maintains a cool environment Provides fodder for cattle
Publications with additional details	Muñoz (2003) and Muñoz et al. (2004)	Muñoz (2003) and Muñoz et al. (2004)	Joya et al. (2004)	Martínez (2003)

For example, in Cañas, some farmers claimed that the excessive consumption of *S. saman* fruits can cause cattle to abort; in Río Frío some farmers attributed the same effect to *Cecropia* spp. and *G. sepium* (Muñoz et al., 2004).

In all four landscapes, farmers used their local knowledge about tree uses and attributes to make decisions about the density and composition of dispersed trees present in pastures. In general, farmers mentioned that they try to balance their demand for tree products and services against the negative impacts of too much shade on grass production, choosing to maintain low tree densities to avoid over shading the grass. Farmers repeatedly mentioned that the main reason for maintaining low tree densities was to minimize impacts on grass productivity, but they articulated little detailed knowledge about how shade tolerant different grass species were or how high tree densities could become before grass production was affected.

### 3.3. Farmer management practices that influence tree density, composition, and size

In all landscapes, all farmers conducted management practices that reduce the tree cover within pastures (Table 9). The most frequent management practice was the weeding of pastures, which entails clearing natural regrowth and weeds from pastures either using herbicides or manual methods, and was generally done two to four times a year. While some farmers selectively retained saplings

of useful tree species when weeding pastures, the majority cleared all non-grass vegetation, thereby eliminating any regenerating tree saplings. In the dry forest landscapes, some farmers (4% of farmers in Cañas, 18% in Rivas) used fire to clear pastures and encourage grass regrowth.

Farmers also reduced dispersed tree cover through the harvesting of trees for timber or fence posts; however this was generally sporadic, depending on farmer demand for products. Most timber harvesting was for home use, but a small percent of farmers (1.4% in Cañas, 6.9% in Rivas, and 11% in Matiguás) also sporadically sold timber from their pastures to earn money. Changes in land use (to and from fallow) were more common in the Nicaraguan landscapes than the Costa Rican landscapes, as the Nicaraguan farmers had more integrated crop and livestock systems and often use fallow areas to recuperate degraded land for agricultural production. In contrast, Costa Rican farmers tended to dedicate their production entirely to cattle or have distinct separate areas for cattle production and agriculture, and therefore made little use of fallows.

Although changes in dispersed tree cover on pastures were frequent, they tended to occur on a small scale, affecting individual trees or groups of trees near to one another, rather than entire pastures. During our one year surveys, we did not register any large scale changes in on farm tree cover, with the exception of the conversion of a small area of natural regeneration to pasture in Nicaragua.

**Table 9**  
Summary of the annual frequency of activities that increase or decrease on-farm tree cover in each of the four study landscapes and the number of farmers who conduct these activities annually (n = 15 per site).

Activities that affect dispersed trees in pastures	Cañas, Costa Rica		Río Frío, Costa Rica		Rivas, Nicaragua		Matiguás, Nicaragua	
	Frequency	# of farmers	Frequency	# of farmers	Frequency	# of farmers	Frequency	# of farmers
<b>Decrease</b>								
Weeding of pastures and elimination of naturally regenerating saplings	4	13	3	15	2	15	2	15
Tree harvesting for firewood, timber or fence posts	1	10	1	9	3	13	2	11
Changes in land use from forests or fallows, to pastures	0	0	0	0	1	1	0	0
<b>Increase</b>								
Changes in land use from pastures or crop fields to fallow	0	0	0	0	1	1	1	2

#### 4. Discussion

Dispersed trees were a common feature of all four of the agricultural landscapes studied and were an integral part of the cattle production system, providing both essential services (such as shade) and products (such as firewood, timber, fruit and fodder). Across the four landscapes, dispersed trees were present in low densities (8.0–33.4 trees ha<sup>-1</sup>), included trees of a wide range of sizes, represented many tree species (72–101 per landscape; 255 species total), and were dominated by a subset of common species that were important timber, fodder or fruit species.

##### 4.1. Impacts of farm management on dispersed trees

The current densities, size and composition of dispersed trees in pastures reflect the combination of both historical and current management decisions made by cattle farmers about which trees to harvest or eliminate, which trees to keep, and what densities to maintain. In all four landscapes, cattle farmers had detailed knowledge of the tree component present in their pastures. They were able to recognize the vast majority of tree species (>80%), and recall details about their uses, attributes (e.g., canopy size and shape and tree height), fodder value and effects on adjacent pasture. This concurs with studies of farmers' knowledge about fodder trees in contrasting cultural contexts as far apart as Asia (Thapa et al., 1997) and Africa (Roothaert and Franzel, 2001) as well as elsewhere in Latin America (Cajas-Girón and Sinclair, 2001; Love and Spaner, 2005; Barrance et al., 2009), where farmers have been found to select trees for retention or planting based on detailed knowledge of both fodder quality (Thorne et al., 1999) and attributes conferring low competitiveness with crops or pasture (Thapa et al., 1997). The importance of trees in providing shade and a favorable microclimate for cattle, articulated by farmers in all four landscapes in the present study, is corroborated by animal science research showing lower rectal temperatures and respiratory rates and hence higher welfare and production under tree shade (Valtorta et al., 1997). The value of tree leaves and fruits for cattle diets in the seasonally dry Neotropics, especially during the dry season when herbaceous grass forage is low in both quantity and quality, has been similarly documented elsewhere (Cajas-Girón and Sinclair, 2001). Farmers did not provide detailed information on thresholds of tree cover at which negative impacts outweighed positive effects or shade tolerance of pasture species. This suggests that scientific advice on how tree densities, spatial arrangements and pasture composition affect pasture production (Dagang and Nair, 2003) might improve farmers' management of cattle productivity from pastures with dispersed tree cover.

In addition to determining the tree densities within pastures, farmers exerted selective pressure over the composition of dispersed trees. In all four landscapes, despite an overall high tree species richness (72–101 tree species per landscape) the composition of trees in pastures was heavily skewed towards a subset of species, with the top ten tree species in each landscape representing more than 70% of all trees. In particular, the pastures were dominated by a suite of useful tree species (particularly timber and fodder species) which were actively retained by farmers, as well as pioneer species that regenerate easily in pastures. Farmers were well aware of the functions of individual tree species and selectively retained those that are useful to them – keeping these trees when they clear new pastures, or allowing saplings of these species to remain in pastures. Conversely, they generally removed regenerating saplings of tree species that have no known uses or species that produce very heavy shade, biasing the composition towards useful species. The composition of trees in pastures is further skewed by the presence of cattle, as tree species whose seeds are eaten by cat-

tle (e.g., *G. ulmifolia*, *P. guayava*, and *E. cyclocarpum*) are dispersed across the pasture matrix and present in high numbers.

##### 4.2. Differences in dispersed tree cover across the four landscapes

There were some differences in tree cover across the four landscapes that reflect the combination of different management strategies, land use history, farming systems and socioeconomic conditions of individual landscapes. For example, the Cañas landscape had a much greater abundance of tall trees with large diameters and sweeping crowns than the other landscapes, suggesting that the Cañas farmers have retained more relict trees than farmers in other regions. There were also few smaller diameter trees suggesting that regeneration was suppressed by pasture management. In contrast, much smaller trees were predominant in the Nicaraguan landscapes (shorter and with smaller stem diameters and crowns), suggesting that many of the trees were younger and that natural regeneration and regrowth, at least of tree species favored by farmers, can persist under current management. More frequent and intensive firewood collection may partially account for the smaller trees present in Nicaraguan than Costa Rican pastures but differences in temporal land use patterns are likely to also be important. In the Rivas landscape, most farmers rotate pastures and crop production and remove all tree cover from cropped plots. After a period of crop cultivation the plots revert to pastures, and these areas slowly regain tree cover through natural regeneration (López et al., 2004). In the Matiguás landscape, the region was heavily deforested and cleared for pasture production in the 1960s, but many pastures were subsequently abandoned during the guerilla movement of the 1980s, during which period many trees reestablished in abandoned pastures (CIERA, 1985; Rocha, 2002).

Farmer dependence on trees as a source of fuel wood varied amongst landscapes. In the Nicaraguan landscapes, where most of the rural population still depends on firewood (McCrary et al., 2005), more than 74% of the farmers in each landscape reported regularly using branches of dispersed trees as fuel wood. In contrast, few farmers mentioned the use of firewood in the Costa Rican landscapes and this use was sporadic for individual barbecues, rather than for daily cooking. This difference in the use of firewood as a main cooking source was also apparent from the local knowledge acquired: Nicaraguan farmers knew over twice as many firewood tree species and their attributes than their Costa Rican counterparts.

##### 4.3. The future of dispersed trees in agricultural landscapes

Many of the tree species found in the pastures are already present in very low numbers, with 63% of the tree species being represented by ten individuals or less. Consequently, the loss of even a few of these trees to harvesting for timber, firewood or posts, or to natural senescence, would be expected to reduce local tree diversity in pastures. In addition, in all of the landscapes, but particularly in Cañas, there are still remnant trees of the original forest, which will likely die over the next few decades due to old age. Whereas some of these tree species may be able to regenerate within the active pastures, others are likely to have limited regeneration because of competition with pasture grasses, compacted soils, and unfavorable microclimatic conditions, or grazing and trampling by cattle (Esquivel et al., 2008). In addition, even those tree species that are able to regenerate within pastures may be subsequently eliminated by the frequent manual weeding of pastures, application of herbicides, or use of fire which are differentially applied across the landscapes studied. Consequently, as result both of natural senescence and farmers management strategies, it is probable that the floristically diverse tree cover within pastures will be further simplified and increasingly dominated by



tree species that farmers favor and actively retain together with pioneer species that can regenerate easily in pastures. Combinations of natural senescence, clearing and low recruitment have led to loss of paddock trees in Australian grazing regions (Gibbons and Boak, 2002; Fischer et al., 2009), British woodland pastures (Kirby et al., 1995) and the dehesas of Spain and Portugal (Pulido et al., 2001), indicating that maintaining diverse dispersed tree cover in agricultural landscapes is of global concern.

Over the long term, the failure to maintain a diverse, structurally complex tree component within pastures could have significant negative impacts both on farm productivity and on biodiversity conservation. For example, reductions in tree density and overall tree cover would likely reduce the shade available for cattle (increasing their potential exposure to heat stress and reducing weight gain), decrease the availability of fodder and fruits to sustain cattle during the dry season, and also reduce the availability of timber, firewood and fence posts for farmer use. Similarly, if there are fewer large trees present, fewer species typical of the original forests, and less overall tree cover in pastures, the animal species that currently depend on these tree resources are also likely to decline or become rarer due to a lack of habitat, nesting and foraging sites, and unfavorable microclimatic conditions (Benton et al., 2003; Vesk and MacNally, 2006; Sekercioglu et al., 2007). In addition, particularly in the two Tropical Dry Forest landscapes (Rivas and Cañas) where little forest remains, the loss of on-farm tree diversity could have significant repercussions for efforts to conserve the last remaining Central American Dry forests which are already highly threatened (Calvo-Alvarado et al., 2009).

The presence of a diverse tree cover on pastures documented here indicates the relevance of an integrated landscape approach to conservation that combines sustainable farm management with the conservation of on-farm tree cover (including dispersed trees, riparian forests, forest fragments and live fences), forest protection and management, and restoration of degraded areas, to reconcile both farm production and conservation goals (Fischer et al., 2005; Vandermeer and Perfecto, 2007; Harvey et al., 2008). Trees on pastures, if at sufficient density and of sufficient diversity, may enhance connectivity of forest habitat for some species in fragmented landscapes (Manning et al., 2006; Medina et al., 2007). Without an explicit recognition of the value of diverse on-farm tree cover, and the risks associated with its potential decline, it is unlikely that any long-term improvement will be achieved or that current tree diversity on pasture will be maintained, and the ability of these agricultural landscapes to provide ecosystem services in the long term may be reduced.

It is clear from the extant farmer knowledge and management practices documented here, that there is scope to work with farmers to adapt current management practices to encourage natural regeneration of trees in pastures and to maintain a diverse and viable tree component. This could be achieved through changes in cattle rotation practices to allow some areas to regenerate before cattle return, more extensive pasture management, careful use of appropriate cattle stocking densities, adoption of alternative grazing regimes, selection of sapling or seedlings for protection against cattle grazing, reduced use of herbicides and fires, implementation of fire breaks, use of temporary fencing around individual mature trees to allow them to serve as seed sources and foster natural regeneration of rarer species, and abandonment of some areas to fallow (during which trees can regenerate), all of which have been shown to enhance natural regeneration of trees in pastures elsewhere (e.g., Spooner et al., 2002; Esquivel et al., 2008; Fischer et al., 2009). Since not all tree species will be capable of regenerating within pastures – either due to unfavorable conditions or lack of nearby seed sources – direct enrichment planting or seeding may also be necessary for certain tree species (Esquivel et al., 2008). The rapid regrowth of Tropical Dry Forest in areas of Guanacaste, Costa

Rica, where pastures have been abandoned due to low cattle prices (Calvo-Alvarado et al., 2009), highlights the potential for forest recovery, and suggests that facilitating tree regrowth on pastures is an achievable goal, if appropriate management strategies are put in place. Efforts to maintain and enhance on-farm tree cover are likely to be more effective if they take into account local knowledge, species preferences, and specific farming practices so that they are tailored to local ecological and socioeconomic circumstances.

The retention of trees in pastures is likely to have ecological benefits that extend beyond the farm itself such as, potential contributions to watershed management, soil conservation and climate mitigation (Pagiola et al., 2007; Verchot et al., 2007). This opens up possibilities for combining incentives (e.g., payment for ecosystem services, carbon credits, reforestation credits, and tax breaks) and conservation policies to achieve sustainable management of on-farm tree cover. Under Costa Rican law, farmers are already eligible to receive payments for ecosystem services for the establishment of silvopastoral systems in pastures, but preference has historically been given to conserving or managing remaining forest patches (Calvo-Alvarado et al., 2009). Recent efforts to establish payments for ecosystem services specifically to encourage trees within pastures have proven successful in changing farmer management practices and increasing on-farm tree cover (Pagiola et al., 2007), but the long-term sustainability of these payment schemes is uncertain.

## 5. Conclusions

Our study suggests that, in Central America, as in other regions (e.g., Gibbons and Boak, 2002; Fischer et al., 2005; Barrance et al., 2009), dispersed trees merit more attention as potential keystone features of agricultural landscapes that play critical productive and ecological roles. While our analysis focused on the patterns of dispersed trees within four regions of Costa Rica and Nicaragua, the general principles identified here are likely to apply generally to other landscapes in Central America and elsewhere where cattle grazing is the dominant land use and where on-farm tree cover is affected by pasture management practices.

Dispersed trees are common in cattle production landscapes in Central America and play valuable productive and environmentally protective roles, but current farm management practices are likely to lead to a reduction in tree diversity, and in more intensively managed pastures and landscapes where relict trees predominate, also a reduction in tree density. Farmers know a lot about the trees on their pastures and selectively manage regeneration of species that they favor because of their utility as shade, fodder, fuel wood and timber. On the one hand, this farmer knowledge represents a resource that can be built upon to communicate and encourage greater tree diversity on pastures, but, on the other hand, may constrain tree composition to a few favored species. Financial incentives for farmers are likely to be required to maintain, let alone, enhance, tree density and diversity on pastures and it is imperative that payments for ecosystem services are set high enough to exceed opportunity costs for farmers, and thereby encourage management decisions that favor retention of diverse tree cover.

## Acknowledgements

We thank the 281 farmers for sharing their local knowledge and experiences with dispersed trees and farm management, and for facilitating access to their farms. We also thank D. Tobar with help in preparing figures and M. Daniels for help identifying scientific literature. 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 Fight Framework Programme (INCO-DEV ICA4-CT-2001-10099). The authors are solely responsible for the material published 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.

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