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# The Structure and Composition of a Tropical Dry Forest Landscape After Land Clearance; Azuero Peninsula, Panama

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*Characterization of preexisting flora is an essential preliminary step for successful land rehabilitation projects. This descriptive study was undertaken in a fragmented, dry tropical forest region in Panama. Five different habitat types were selected: active pasture, 2-yr and 5-yr abandoned pastures, forested riparian zones, and a forest fragment. Species richness, density, basal area, dispersal modes, and phenology of trees as well as their uses were determined. Diversity of preexisting seed resources as well as natural regeneration was poor after 2- and 5-yr postcattle removal, suggesting that at an early successional stage, enrichment planting is necessary. Guazuma ulmifolia and Cordia alliodora dominated the pastoral landscape, representing 63% of all inventoried trees in*

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*the active pasture. More than half the trees within pastures (76%) had some use, with shade for cattle as the most common reason for leaving trees in the landscape. The largest trees and the greatest diversity were found within the less managed forested riparian zones because of inaccessibility and water conservation. The pastoral landscape is largely shaped by farm management as well as ecological selection process which will in turn affect successional processes.*

*KEYWORDS Guazuma ulmifolia, pasture, riparian forest, reforestation, regeneration, succession, Tabebuia*



## INTRODUCTION

Dry tropical forests were the most common forest type along the Pacific coast of Central America until cattle ranching transformed the landscape in the early part of the last century (Janzen, 1983; Calvo-Alvarado, McLennan, Sanchez-Azofeifa, & Garvin, 2009). In Central America, pastures remained productive for decades (Reiners, Bouwman, Parson, & Keller, 1994; Aide, Zimmerman, Rosari, & Marcano, 1996; Thomlinson, Serrano, Lopez, Aide, & Zimmerman, 1996; Holl, 1999; Harvey & Haber, 1999), most notably in dry regions where soil fertility was higher (Murphy & Lugo, 1986). Eventually, high cattle stocking rates, repeated burning, and the removal of native vegetation resulted in severe soil erosion followed by a decline in land productivity (Heckadon-Moreno, 1984; Janzen, 1988). Cattle ranching is no longer a viable option for many landholders and with the recent increase in land prices along the coast, selling is a desirable option (Ankersen, Regan, & Mack, 2006; Kull, Ibrahim, & Meredity, 2010). Consequently, there is an opportunity to rehabilitate one of the least known and most threatened tropical ecosystems because many new landowners place a high value on diversity, forest cover, and ecosystem health (Ankersen et al., 2006; Kull et al., 2010). Most of these landowners are purchasing land for vacation, recreational purposes, or the development of resorts.

Natural history descriptions of the flora and fauna within these regions are essential for a baseline understanding of the successional trajectory of old pastures. Old pastures on the Azuero peninsula in Panama may follow several developmental pathways. The land may remain a savanna in a permanent state of arrested forest succession where grass perpetuates the fire disturbance regime (Hopkins, 1983; Olivares & Medina, 1992); land owners may convert the land to teak (*Tectona grandis* L.f.) plantations (Sloan, 2008), or the land may be rehabilitated into a native forest ecosystem that provides ecological and economic services.

Natural regeneration may be the most cost-effective and realistic strategy for rehabilitating pastures to one with productive uses (Lugo, 1988, Aide, 2000; Hooper, Condit, & Legendre, 2002). Other more intensive strategies, such as reforestation with exotic or native nurse tree plantation systems, although highly effective (Parrotta, 1992; Guariguata, Rheingans, & Montagnini, 1994; Ashton, Gamage, Gunatilleke, & Gunatilleke, 1997; Montagnini, 2001; Wishnie et al., 2007) are more costly. This choice depends on economics; past management history; and the current distribution, diversity, abundance, autecology, and phenology of relic trees and fragments.

The dominant type of dispersal is critical to the colonization of abandoned sites. Many tree species in dry tropical forests (40–70%) have been reported to be dispersed by animals (Janzen, 1988; Castilleja, 1991; Gentry, 1995; Vieira & Scariot, 2006). Animal-dispersed species, especially large-seeded species, may be lost through time in landscapes devoid of forest fragments (Nepstad, Uhl, & da Silva, 1996). With the exception of howler monkeys, which usually stay within riparian zones, large seed-dispersing mammals (e.g., agoutis, tapirs, spider monkeys) are noticeably absent from this study site. Janzen (1988) observed that wind-dispersed species dominated the regenerating cohort in 10-yr-old abandoned pastures suggesting that animal-dispersed species are lost through time in dry tropical systems. Pasture trees that persist in the landscape are generally species that are fire-tolerant and readily resprout (Janzen, 1983; Swaine, 1992; Hooper et al., 2002; Griscom, Griscom, & Ashton, 2009).

Characterizing the landscape also involves understanding the rationale for why farmers leave certain trees. The number and diversity of pasture trees is a function of farmers' perceptions. Isolated trees or trees within riparian zones are selectively removed or conserved based on their perceived beneficial and detrimental characteristics. In Central America, farmers frequently leave trees or plant trees in the form of live fences, isolated trees, and riparian forests (Budowski, 1981; Guevara, Purata, & Van der Maarel, 1986; Harvey & Haber, 1999; Estrada, Cammarano, & Coates-Estrada, 2000, Harvey et al., 2005). Isolated trees are left in the landscape to provide shade and fodder, construction material, firewood, and fence posts (Budowski, 1981; Guevara et al., 1986; Harvey & Haber, 1999; Barrance, Flores, Padilla, Gordon, & Schreckenberg, 2003; Cordero & Boshier, 2003; Leon & Harvey, 2006; Garen et al., 2009) while trees within riparian zones are conserved to provide shade and cool water for the cattle (Garen et al., 2009). These riparian zones are typically thin, degraded stripes of vegetation, representing the most common forest habitat remaining in a pasture matrix (Graham & Blake, 2001).

Pasture trees also have important ecological values, some of which are recognized by farmers. Trees help prevent soil erosion (Nair, 1991; Bird et al., 1992), they increase water quality by reducing sediment and nutrient run-off (Fennessey & Cronk, 1997), and they serve as seed sources for timber species (Uhl, Clark, Clark, & Murphy, 1981; Guevara & Laborde, 1993). In addition, trees attract animal seed-dispersers into the pastures by functioning as foraging, nesting, perching, and/or roosting sites (Guevara et al., 1986; Nepstad, Uhl, & Serrao, 1991; Gerhardt & Hytteborn, 1992; Guevara, Meave, Moreno-Casasola, & Laborde, 1992; Guevara & Laborde, 1993; Estrada, Coates-Estrada, & Meritt, 1993; Silva, Uhl, & Gregory, 1996; Aide, 2000; Griscom, Kalko, & Ashton, 2007). Landowners must balance the benefits of keeping trees on their land with other concerns, such as tree competition with forage grass (Harvey & Haber, 1999; Barrance et al., 2003) and water flow.

Pastures have been inventoried in dry regions in Columbia (Cajas-Giron & Sinclair, 2001) and Honduras (Gordon, Hawthorne, Sandoval, & Barrance, 2003), but these studies focused on tree uses. Other studies in dry tropical ecosystems have conducted inventories in secondary forests (Taylor, 1963; Holdridge, 1967; Janzen, 1983; Murphy & Lugo, 1986; Sabogal, 1992; Mizrahi, Prado, & Jimenez-Osornio, 1997; Colon, 2006), riparian forests (Taylor, 1963; Elizondo & Jiménez, 1988; Meave & Kellman, 1994; Glander, Nisbett, & Richard, 1996; Pither & Kellman, 2002), chronosequences of successional stages (Ruiz, Fandino, & Chazdon, 2005; Lebrija-Trejos, Bongers, Perez-Garcia, & Meave, 2008; Marin, Mulualem, Gonzalez-Rivas, & Oden, 2009; Powers, Becknell, Irving, & Perez-Aviles, 2009), or active pastures (Esquivel, Harvey, Finegan, Casanoves, & Skarpe, 2008). Few studies have compared secondary forest, riparian forest, active pasture, and recently abandoned pastures in terms of species richness and basal area as well as their usefulness in the landscape.

For the following study, we selected five types of habitat (active cattle pasture, riparian forest within an active pasture, secondary forest fragment, and recently abandoned pasture of two ages). The active pasture, riparian forest, and forest fragment provided data on the existing capital of the landscape, in terms of a seed source; while the 2-yr abandoned pasture and 5-yr abandoned pasture provided data on expected successional pathway trends in terms of species density, basal area, and diversity. Active pastures and riparian forest were common habitat types within this landscape whereas forest fragments (>20 ha) and abandoned pastures were rare. However, a research laboratory purchased land in the area which consisted of a 70-ha secondary forest and two parcels of active pasture protected from cattle and fire at two different time periods. This particular study site was also the location of a long-term study site on forest restoration (Griscom et al., 2005, 2007, 2009).

The aim of our study was twofold: (a) to characterize and compare the floristics of different habitats and successional stages by quantifying the following response variables: species richness, stem count, basal area, and phenology; and (b) to determine the rationale for selectively leaving certain species in the landscape by conducting interviews of farmers in the area. This characterization will enable us to better assess the rehabilitation potential of one farm, which can serve as a model for how to proceed with the restoration of other similar pastures in the area.

## METHODS

### Site Description

This study was conducted in the Los Santos province on the Azuero peninsula, Panama (7° 15′ 30″ N, 80° 00′ 15″ W). The hilly, relatively steep topography was the last land to be cleared in the province. Valuable timber—*Cedrela odorata* L., *Dalbergia retusa* Hemsl, and *Pachira quinata* (Jacq.) Dugand—was selectively logged in the early part of the 1900s. In the 1940s and 1950s, the land was cleared for cattle ranching. Conversion to pasture accelerated in 1978 following construction of the road between the towns of Pedasí and Tonosí (Heckadon-Moreno, 1984). Cattle grazing is currently the dominant land use in the region but many large parcels are being sold off to landowners who are interested in alternative management options—such as vacation homes, recreation, and environmental restoration.

The study site receives an average of 1,700 mm of rainfall. This precipitation range falls into the dry tropical forest ecosystem classification, although temperature, elevation, and evapotranspiration are other important considerations of the Holdridge life zone classification (Holdridge, 1967). The dry season is pronounced with 5 months out of the year receiving no rain (December through March). Rain begins in late April and ends in late November. The annual average temperature is 25°C. The undulating terrain, ranging in elevation from 10 to 100 m, is a mosaic of pastures planted with African grasses *Hyparrhenia rufa* (Nees) Stapf and *Panicum maximum* Jacq., forested riparian zones, isolated trees, and live fences.

The following mosaic of habitats were selected because they were part of a long-term restoration project and in close proximity to each other (thus, controlling for more heterogeneity in the landscape): an active pasture, riparian forests within the active pasture, a protected secondary forest, a 2-yr abandoned pasture, and a 5-yr abandoned pasture. The active pasture and riparian forest were part of an 85-ha cattle farm that had been ranched for 50 yr. The active pasture was grazed by a herd of 50 to 70 Brahman cattle from mid-July until mid-March.

The secondary forest and abandoned pasture sites were part of an adjacent 100-ha property. Prior to1985, the property had been grazed by cattle and burned for approximately 30 yr. The forest had never been cleared for pasture but had most likely been grazed by cattle in the understory, burned, and selectively logged.

## Sampling Design

Several different sampling methods were used to inventory tree species (>5 cm dbh) within this landscape due to constraints of each forest type. Within the 85-ha active pasture, linear riparian zones were inventoried in transects while open active pasture were inventoried as circular plots. Four forested riparian fragments within active pastures were randomly selected from eight riparian forested areas in the active pasture. Riparian fragments were inventoried by randomly selecting two points along the stream (at least 20 m apart) and establishing two rectangular subplots (10-m width by 100-m length) parallel to the bank of the stream. Eight circular plots of 50-m radius were randomly selected with the active pasture. Plots were located within different watersheds.

Within the 100-ha property, four 100 $m^2$ plots, at least 100 m apart, were randomly selected within a 2-yr abandoned pasture, a 5-yr abandoned pasture, and a secondary forest. All plots were replicated within a habitat type but not at the landscape scale because protected forest fragments and recently abandoned pasture were unusual for this area. In each of the three habitat types, individuals greater than 10-cm dbh were identified and measured for basal area. Stem count was also calculated.

Three individuals for each of the 20 most common wind and animal-dispersed species in the pasture were randomly selected from 100 individuals and permanently tagged for monitoring phenology. Once a month for 2 yr, the absence or presence of flowers and fruit were recorded. Presence was determined if greater than 20% of the canopy were fruiting or flowering. Phenology was monitored to determine fruit availability and to identify species that provided fruit when little else was available.

Semi-structured interviews were carried out with 36 landholders selected at random from a list of 926 farms registered with the Ministry of Agrarian Reform (Summer, 2003). The landowners were selected from the registration list for the corregimientos of Oria Arriba and Los Asientos in the province of Los Santos. All the landowners had secure land rights and were devoted to cattle ranching. Most of the farmers interviewed relied on their farm as their primary, though not always exclusive, source of income. Interviews included a walking tour of the farm. The objective was to determine common uses of trees in farms and rationale for keeping trees in the landscape.

## Analysis

Importance value indices (Curtis & McIntosh, 1951) for each species at all sites were calculated as the sum of relative density, relative frequency, and relative basal area. The qualitative similarity between habitats was calculated with Jaccard's Index (Krebs, 1989) as follows:

$$C_j = a/(a + b + c)$$

where C is the index, "a" represents the number of tree species present in both habitats, "b" represents species present only in the first habitat, and "c" represents species present only in the second habitat. The presence of a species in a habitat was scored as 1, and its absence was scored as 0. EstimateS (Version 8.0, Chaos Estimate) was used to statistically estimate species richness in the different habitat types. Stem density and basal area could not be statistically analyzed as plot size varied in different habitat types. However, these variables were standardized as per hectare to allow for comparisons between habitats.

## RESULTS

### Dominant Species

The most important species varied between habitat types although the Leguminosae family had the most number of species regardless of habitat type. In the secondary forest, *Calycophyllum candidissimum* (Vahl) DC. (Importance Value by Inventory [IVI] = 15.37) and *Tabebuia rosea* (Bertol.) DC. (IVI = 13.99) had the greatest importance values; whereas in the riparian forest, *Guazuma ulmifolia* (Lam; IVI = 16.87) and *Hura crepitans* L. (IVI = 10.87) had the greatest importance values (Table 1). In the active pasture, *Guazuma ulmifolia* (IVI = 0.5) and *Cordia alliodora* (Ruiz & Pav.) Oken (IVI = 0.33) had the greatest importance values. *Guazuma ulmifolia* and *C. alliodora* represented 63% of the tree species in active open pasture. In the abandoned pasture of 2 and 5 yr, very few species were represented and *Guazuma ulmifolia* dominated, representing 92 and 37% of the stems, respectively. By comparison, in the riparian zones, *Guazuma ulmifolia* represented 22% of the total stems. The only habitat type where *G. ulmifolia* was rarely encountered was within the secondary forest.

### Dispersal Modes

Within the secondary forest, wind-dispersed species were slightly more common than animal-dispersed species in terms of species number (55%) and individuals (57%), in part due to the dominance of two wind-dispersed species, *Calycophyllum candidissimum* and *Tabebuia rosea*. The most common animal-dispersed species in the secondary forest fragment were small understory trees, *Genipa americana* Linn. and *Pouteria campechiana* (Kunth) Baehni, both of which have large fleshy fruits dispersed by bats and monkeys. Within the riparian zones, 64% of the individuals (and 52% of the species) were animal-dispersed.

In the active pasture, wind and cattle were the dominant seed dispersal modes due to the abundance of *Guazuma ulmifolia* and *Cordia alliodora*. Fifty-five percent of the total stems inventoried were dispersed by animals

**TABLE 1** Plant Species Importance Values by Inventory Location

| Plant species | Dispersal | Use | Plant family | SF | RZ | AP | 5-AP | 2-AP |
|---|---|---|---|---|---|---|---|---|
| *Acacia collinsii* | Animals | | Leguminosae | 1.279 | | 0.03 | | |
| *Albizia adinocephala* | Wind | | Leguminosae | 0.83 | 0.83 | | | |
| *Albizia guachapele* | Wind | SH, FO | Leguminosae | | 2.24 | | | |
| *Allophyllus psilospermus* | Animals | | Sapindaceae | 0.616 | | | | |
| *Annona purpurea* | Animals | SH, FO | Annonaceae | | 1.75 | 0.03 | | |
| *Apeiba tibourbou* | Wind | SH | Tiliaceae | 0.629 | | | 3.392 | |
| *Astronium graveolens* | Wind | TI, SH | Anacardiaceae | 3.194 | 3.569 | 0.03 | | |
| *Bauhinia* sp. | Wind | | Leguminosae | 0.794 | | | | 0.417 |
| *Bursera simaruba* | Animals | LF, FI, M | Burseraceae | 2.714 | 3.062 | 0.06 | 0.338 | |
| *Byrsonima crassifolia* | Animals | SH, FI, FR | Malphigiaceae | | | 0.06 | | |
| *Calycophyllum candidissimum* | Wind | TI, SH, LF, FI | Rubiaceae | 15.37 | 2.952 | 0.03 | | |
| *Cecropia peltata* | Animals | FO | Cecropiaceae | | 5.73 | 0.07 | | |
| *Cedrela odorata* | Wind | TI, SH, LF | Meliaceae | 1.731 | 1.94 | 0.09 | 0.339 | |
| *Ceiba pentandra* | Wind | SH | Bombaceae | | | 0.07 | | |
| *Chlorophora tinctoria* | Animals | | Moraceae | | 3.858 | | | |
| *Chomelia spinosa* | Animals | | Rubiaceae | 0.966 | | | 3.004 | |
| *Coccoloba laseri* | Animals | SH | Polygonaceae | 0.415 | | 0.1 | | |
| *Cochlospermum vitifolium* | Wind | TI, SH, LF, FO | Cochlospermataceae | 3.565 | 2.16 | | 5.438 | 0.418 |
| *Cojoba rufescens* | Animals | | Leguminosae | 0.363 | | | | |
| *Cordia alliodora* | Wind | TI | Boraginaceae | 2.109 | 4.427 | 0.33 | 0.339 | |
| *Cordia panamensis* | Animals | | Boraginaceae | 0.782 | 2.33 | | 0.677 | |
| *Dalbergia retusa* | Wind | TI, SH | Leguminosae | 3.139 | 0.91 | | 1.693 | |
| *Diphysa robinioides* | Wind | TI, SH | Fabaceae | | 1.27 | 0.17 | | |

(*Continued*)

**TABLE 1** (Continued)

| Plant species | Dispersal | Use | Plant family | SF | RZ | AP | 5-AP | 2-AP |
|---|---|---|---|---|---|---|---|---|
| *Enterolobium cyclocarpum* | Animals | TI, SH, FO | Fabaceae | | 8.911 | 0.08 | | |
| *Erythroxyllum* sp. | Animals | | Erythroxylaceae | 0.355 | | | | |
| *Eugenia coloradoensis* | Animals | SH, LF | Mytaceae | | 0.83 | 0.03 | | |
| *Genipa americana* | Animals | SH, LF, FO | Rubiaceae | 7.8 | 2.24 | | | |
| *Guazuma ulmifolia* | Animals | SH, FO, FI | Sterculiaceae | 0.64 | 16.87 | 0.5 | 9.48 | 11.71 |
| *Hura crepitans* | Ballistic | SH | Euphorbiaceae | | 10.87 | 0.07 | | |
| *Licania arborea* | Animals | SH | Chysobalanceae | | | 0.04 | | |
| *Lonchocarpus felipei* | Wind | TI, SH | Leguminosae | | 1.97 | 0.03 | | |
| *Lonchocarpus velutinus* | Wind | TI, SH | Leguminosae | 0.344 | | | | |
| *Luehea speciosa* | Wind | SH, FO | Tiliaceae | | | | 1.356 | |
| *Machaerium microphyllum* | Wind | | Leguminosae | | | | 1.016 | |
| *Manilkara achras* | Animals | TI, SH | Sapotaceae | | 1.41 | | | |
| *Pachira quinata* | Wind | TI,SH, LF | Bombaceae | | 0.88 | | | |
| *Platymiscium pinnatum* | Wind | TI, SH | Leguminosae | | | 0.03 | | |
| *Pouteria campechiana* | Animals | TI | Sapotaceae | 5.857 | 1.98 | 0.05 | | |
| *Sapium glandulosum* | Animals | SH | Euphorbiaceae | 1.04 | 3.602 | 0.06 | | |
| *Sciadodendron excelsum* | Animals | SH, LF | Araliaceae | | 5.102 | 0.07 | | |
| *Spondias mombin* | Animals | SH, FO | Anacardiaceae | 0.77 | 5.161 | 0.09 | | |
| *Sterculia apetala* | Animals | SH | Sterculiaceae | | | 0.04 | | |
| *Swartzia simplex* | Animals | | Leguminosae | | 0.83 | | | |
| *Tabebuia guayacan* | Wind | TI | Bignoniaceae | 0.379 | | | | |
| *Tabebuia rosea* | Wind | TI, SH | Bignoniaceae | 13.99 | 2.33 | 0.06 | | |

*Note*. Importance values were calculated as the sum of relative density, relative frequency, and relative basal area. Tree uses are denoted as the following: SH = shade, FO = fodder, TI = timber, FR = fruit, FI = firewood, LF = live fence, M = medicine. Inventories were conducted in secondary forest (SF), forested riparian fragment (RZ), active pasture (AP), 5-yr abandoned pasture (5-AP), and 2-yr abandoned pasture (2-AP).

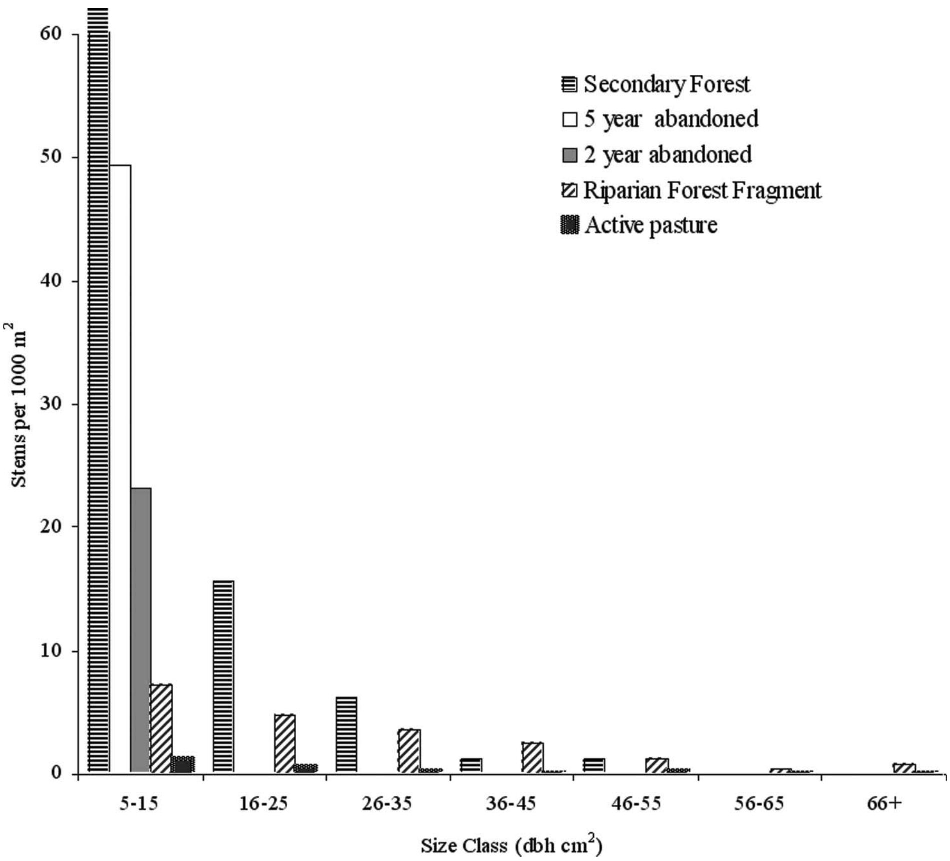


**FIGURE 1** Size class distributions of trees >5-cm dbh within an active, 85-ha cattle pasture, forested riparian fragments, 5-yr abandoned pasture, 2-yr abandoned pasture, and a secondary forest.

(representing 15 species) and 44% by wind (representing 11 species). In the abandoned pasture of 5 yr, 41% percent of the total stems inventoried were dispersed by animals (representing four species) and 58% by wind (representing seven species). In the abandoned pasture of 2 yr, 92% percent of the total stems inventoried were dispersed by animals (representing one species, *G. ulmifolia*) and 8% by wind (representing two species; Table 1).

## Stem Count and Basal Area

The forest fragment had a greater stem count (900/ha) than any of the other habitat types, including the forested riparian zone (180 stems/ha; Table 2). However, basal area in the forest fragment (13 $m^2$/ha) was similar to riparian zones (15.3 $m^2$/ha), both of which were greater than the other habitat types ($p < .05$). In terms of size classes, within the 2- and 5-yr abandoned pasture, 100% of the trees were less than 15-cm dbh (Figure 1). Seventy-two percent

**TABLE 2** Stem Count, Basal Area, Diversity, and Dispersal Mode by Habitat Type

| Forest type | Stem count (1 ha) | Basal area ($m^2$/ha) | Species richness | Abiotic disp. | Biotic disp. |
|---|---|---|---|---|---|
| Secondary forest | 900 (117) | 17.7 (7) | 30 | 0.57 | 0.42 |
| Riparian forest | 180 (74.9) | 14.3 (5.4) | 38 | 0.35 | 0.64 |
| 5-yr abandoned | 494 (286) | 1.88 (1.36) | 14 | 0.58 | 0.41 |
| 2-yr abandoned | 231 (177) | 1.00 (.87) | 7 | 0.08 | 0.92 |
| Active pasture | 12.0 (8.3) | 1.26 (1.06) | 32 | 0.44 | 0.55 |

*Note*. One standard error of the mean is given in parentheses. Species richness was estimated by EstimateS Version 8.0. Dispersal mode percentages were calculated from the total number of stems found in each habitat type.



of the trees were less than 15-cm dbh within the secondary forest. Forested riparian zones and active pastures had the largest diameter trees with only 35 and 43% of the trees in the smaller diameter size class (<15-cm dbh).

## Species Richness

Of all habitat types, riparian zones had the greatest estimated number of species ($N = 38$) according to the rarefraction curves of EstimateS (Table 2). A total of 31 species in 16 plant families were identified in the riparian zones. However, species richness varied greatly between forested riparian zones. The most species rich riparian forest had 21 species, whereas the most species poor riparian forest had 8 species. The species poor riparian zones were dominated by *Guazuma ulmifolia*.

Within the secondary forest a similar number of species were identified (29 species in 15 plant families). Number of species in the forest was estimated to be 30 species, similar to the active pasture. Active pastures were represented by 25 tree species. The active pasture and the riparian zone were the most similar according to Jaccard's Index (Table 3). Only 12 species in eight plant families were inventoried in the 5-yr abandoned pasture and three plant species were identified in the 2-yr abandoned pasture. Five-yr pastures were estimated to have 14 species and 2-yr pastures were estimated to have 7 species.

## Phenological Data

All recorded wind-dispersed species (except for *Cedrela odorata* L.) flowered during the dry season (December-February; Figure 2). The most common month for flowering was February, in the middle of the dry

**TABLE 3** Tree Species Similarity Between Habitats Using Jaccard's Index

| | 2-yr abandoned | 5-yr abandoned | Active pasture | Riparian zone |
|---|---|---|---|---|
| 2-yr abandoned | | | | |
| 5-yr abandoned | 0.2 | | | |
| Active pasture | 0.04 | 0.12 | | |
| Riparian zone | 0.07 | 0.22 | 0.51 | |
| Secondary forest | 0.16 | 0.33 | 0.31 | 0.43 |

*Note*. Values range from 0 to 1 where 1 represents 100% overlap and 0 represents no overlap of species in two habitats.

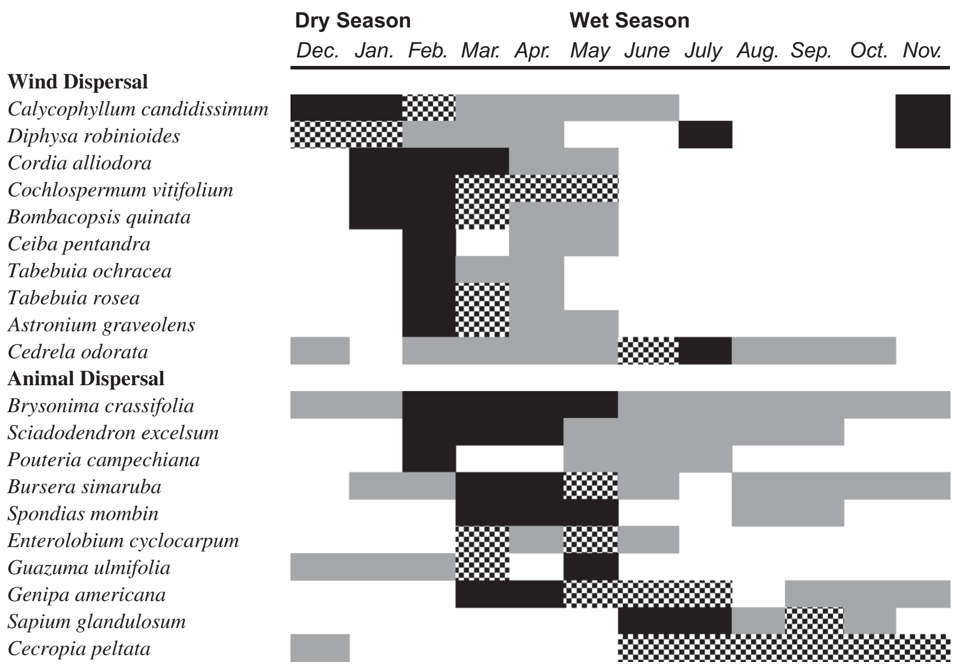


**FIGURE 2** Flower and fruiting patterns of the 10 most common wind-dispersed and the 10 most common animal-dispersed tree species throughout the year within an active pasture in Panama (black-filled boxes = presence of flowers, gray-filled boxes = presence of fruits, gray-black checkered boxes = presence of fruits and flowers).



season. Animal-dispersed species were more variable with the majority of flowering beginning in February and lasting through May. However, most animal-dispersed tree species flowered from March through May when wind-dispersed species were in fruit. Animal-dispersed species were then in fruit during the rainy season (May through November), when wind-dispersed species were no longer fruiting. Only four animal-dispersed species had fruit during the dry season— *Bursera simaruba* (L.) Sarg., *Byrsonima crassifolia* (L.) Rich., *Cecropia peltata* (L.), and *G. ulmifolia*.

### Interviews

The majority of species in the pasture inventories (76%) had at least one use recognized by local farmers. Trees were reported to provide shade and supplemental fodder for cattle, and to supply construction material, live fence posts, and firewood. The most common use of pasture trees was to provide shade for cattle (29 species, 64% of the species). Tree shade was reported to be essential for the health and survival of the cattle during the 5-month dry season. Many trees also had timber value (16 species, 35% of the species). However, timber is usually used directly by landowners for construction, rather than sold into timber markets. Occasionally, farmers retain or actively plant high value timber species (e.g.. *Cedrela odorata* and *Cordia alliodora*) to diversify their income. With the exception of *Cordia alliodora*, all of the timber species inventoried in pastures had other uses. Like timber, trees harvested for firewood (four species, 9% of the species) had at least two additional purposes. Live fence posts were represented by 23% of the species (eight species total) while fodder was associated with 18% of the species (nine species; Table 1). Edible fruit (*Bysonima crassifolia*, *Hymenaea courbaril* L., *Manilkara achras* [Mill] Fosberg, medicine (*Bursera simaruba*, *Hymanaea courbaril*), and fish poison (*Hura crepitans* L.) accounted for less than 10% of inventoried species. Half of the species had multiple uses (51% of the species). Trees with at least three different uses were the following: *Bursera simaruba*, *Byrsonima crassifolia*, *Calycophyllum candidissimum* (Vahl) DC., *Cedrela odorata*, *Cochlospermum vitifolium* Willd (Spreng), *Enterolobium cyclocarpum* Jacq. Griseb, *Genipa americana*, *Guazuma ulmifolia*, and *Pachira quinata* (Table 1).

## DISCUSSION

Tree diversity within pastures is shaped by management and ecological constraints. These processes in turn determine the ability of abandoned pastures to regenerate. The majority of trees at this study site on the Azuero peninsula had some recorded use and most species had multiple uses. Farmers selectively leave certain tree species in pastures but most species will eventually be harvested for construction after they reach a certain size. Within the active pasture, almost 50% of the trees were less than 15-cm dbh. Two and 5 yr later after cattle had been removed from the pastures (and the land sold), all trees were less than 15-cm dbh, suggesting timber harvesting prior to sale. *Enterolobium cyclocarpum* (Jacq.) Griseb.—a common, large remnant tree in pastures—is increasingly used for construction because the locally preferred timber species (*Cedrela odorata*) has become scarce.

A few species of remnant trees dominated active and abandoned sites. Within active pastures, *Guazuma ulmifolia* and *Cordia alliodora* represented 63% of all inventoried trees. *Guazuma ulmifolia* also had the highest importance value in a secondary forest in Nicaragua (Sabogal, 1992). After pastures had been abandoned for 3 to 4 yr, *G. ulmifolia* was one of the few trees remaining, as well as successfully regenerating. *Guazuma ulmifolia* and *C. alliodora* were both abundant in active and abandoned pastures because they are particularly resilient to fire and grazing. They have no reproductive barriers, as *G. ulmifolia* is dispersed by cattle and is a prolific basal stem sprouter, and *C. alliodora* is dispersed by wind and readily sprouts from roots. These two species are also used by farmers either for livestock shade and fodder (*G. ulmifolia*; Janzen, 1982; Sabogal, 1992; Cajas-Giron & Sinclair, 2001), or timber (*C. alliodora*; Cajas-Giron & Sinclair 2001).

Of the farmers we interviewed, shade for cattle was the most common reason for leaving trees in the landscape. Interestingly, this trend varies by region. In Los Santos, where this study took place, 71% of farmers reported leaving trees for food and shade; whereas in the very dry tropical region of Rio Hato in Panama, no farmers left trees for cattle (Garen et al., 2009). Several farmers informed us that in years of drought when pasture grass is scarce, their cattle have almost exclusively survived on the fruit and leaves of *G. ulmifolia*. *Guazuma ulmifolia* was partially deciduous, losing 50–75% of its leaves during the dry season. According to farmers, this species does not deplete water resources within riparian zones as fast as other species, such as *Hura crepitans*. Thus, farmers selectively leave *G. ulmifolia* within areas close to water, which explains why this species was the most commonly encountered along some streams. Almost all farmers reported leaving trees within riparian zones to protect water sources (Garen et al., 2009).

The dominance of *Guazuma ulmifolia* is expected to decrease as succession proceeds as it is a light-demanding species. In Costa Rica, Kalacska et al. (2004) found that although *G. ulmifolia* was one of the two most common species in the early successional stage, its importance declined through time. We also recorded very few *G. ulmifolia* trees within the secondary forest fragment. Instead, *Calycophyllum candidissimum* had the greatest importance value, similar to inventories conducted in forests of Santa Rosa, Costa Rica (Janzen, 1983). This may be because it was selected for within forest fragments as it has multiple uses (construction, firewood, live fence). The second most common species, *Tabebuia rosea*, is also a useful timber species.

Less managed, relic forests were found within forested riparian zones bordering perennial streams. These areas had an even size class distribution, the largest relic trees (>45-cm dbh) and the greatest species richness. Riparian forests were often never cleared either because farmers desired shade trees, water protection (Garen et al., 2009), or because they were located at the base of steep, inaccessible slopes. The more accessible forested streams are likely to be more intensively managed. Farmers often girdle tree species (e.g., *Hura crepitans*) due to perceived competition with cattle for water during the dry season.

The Pacific coast of Panama has potential, despite its highly disturbed appearance. From this study, we have achieved a better understanding of the missing or unbalanced arboreal elements of the landscape. Forested fragments, especially along inaccessible riparian zones, are critical to successful restoration projects as these areas are where the greatest diversity of tree species may be found. Recently abandoned pastures were extraordinarily low in tree numbers and species with *Guazuma ulmifolia* dominating the landscape even after 5-yr postabandonment. These areas will require more intensive restoration efforts to accelerate forest succession. Enrichment planting with other fleshy-fruited tree species would increase diversity of the flora and fauna. Seeds could be collected from mature forests and riparian zones and planted in species poor sites. A few species were especially important because they fruit in the dry season when resources are limited (e.g., *Bursera simaruba* and *Cecropia peltata*). In some cases, such as with the 2-yr abandoned pasture with no diversity of remnant trees, plantations of native species are recommended to increase diversity.



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