Assessing Forest Structure, Biodiversity, and Ecosystem Functions between Public and

Private Tropical Dry Secondary Forests, a case study in Guanacaste, Costa Rica

A Dissertation

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Dedication

For Rebecca Montgomery,

whose compassion, encouragement, and

passion for plant ecology have been a continual source of inspiration.

I know it is not possible to be a better adviser.

Abstract

For this dissertation, I was interested by how human decisions may affect forest
ecology and, in turn, how those ecological effects may feedback to influence social
systems. Humans are the dominant force driving global environmental changes, yet we
are still working towards quantifying how humans affect ecosystem functions,
environmental services, and biodiversity across varying environmental and human land
use gradients. I conducted a case study in Guanacaste, Costa Rica to evaluate ecological
differences in public and private tropical dry secondary forests and assessed what factors
influenced private landowners' decisions to allow forest regeneration on their farms. For
the forest study, I found that public and private forests did not differ significantly in
integrative metrics of forest structure or biodiversity. Yet there were tree species
compositional differences with tell-tale signs of a human signature: highly prized timber
species were more abundant in public forest, suggesting high-grading in private forests
and the most abundant species in private forests was a species favored and consumed by
cattle, *Guazuma ulmifolia.* In the farmer land-use study, I found that landowners
appreciated the multiple benefits and services that their forests provided for them and for
society; however, landowners noted that market prices were the main factor affecting
their farm land use decisions regarding production expansion or contraction. Finally, I
was interested in conducting a combined assessment of ecological and human use traits
that may differentially affect ecosystem functions in private versus public lands. I
expected that the patchy forest characteristics on private lands would favor plant species
that have low seed mass, fast relative growth rate, and high leaf N. I acquired functional
plant trait data for the majority of tree species in the forest inventory analysis from
international databases. I also created a human use plant trait summary for traits I
expected to be less evident in private forests ('harvest traits' e.g. timber) and traits that I
expected to be more evident private forests ('on farm use traits' e.g. ornamentals, living
fences). Seed mass was the only trait that was significantly different between public and

private forests: public forests had higher seed mass relative to private. Likely, this is due to differences in animal dispersal vector behaviors between continuous and patchy forest. I also found a trend of 'on farm use traits' more evident in private forests, so the species that people select to use on their farms may be more abundant in nearby naturally regenerating forests. I found differences in species composition, seed mass, and 'on farm use traits' between public and private forests that appear to be caused by differences in management yet, overall, these differences to not appear to influence ecological function between public and private forests.

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CHAPTER 1

Introduction

Forests supply multiple environmental services, provide habitat for flora and fauna, and support people's livelihoods; forests are fundamental to ensuring resilience of many social-ecological systems. In the tropical dry forests of Guanacaste, Costa Rica, public and private forests landscape structure differs; the public forests are generally large in extent and contiguous while private forests are more fragmented (Best 2002; Butler and Leatherberry 2004). In the tropics, tropical dry forests have been disproportionally cleared and settled relative to other tropical forest ecosystems because the soils and climate are favorable for agricultural endeavors (Janzen 1988; Sanchez-Azofeifa et al. 2005). Thus, secondary forests are particularly critical for sustaining tropical dry forests (Heather P. Griscom and Ashton 2011; Janzen 1988). Here, I used an interdisciplinary approach to assess ecological and management differences between publicly and privately owned secondary tropical dry forests in Guanacaste, Costa Rica. I conducted a forest inventory survey in private forests and compared that survey with one previously conducted survey on public lands (Powers et al. 2009). At farms where I completed the private forest inventory survey, I also conducted in-person interviews with landowners.

In Chapter 1, I examine whether differences in forest ownership led to systematic differences in forest structure, biodiversity, and tree species composition across a gradient of soil fertility and forest age. To accomplish this, I identified the species of individual trees $\geq$ 10 cm diameter at breast height in 66 private 0.1 ha forest plots arrayed across forest age and soil fertility gradients and compared them to an existing dataset of 82 plots from public lands in tropical dry forests in Guanacaste, Costa Rica collected by Powers and colleagues (2009) using the same methodology. Using these data, I compared forest structural measurements of biomass, basal area, and stem density. I assessed species diversity between public and private forests by comparing species accumulation curves, the Shannon-Wiener Diversity index, and species composition.

In Chapter 2, I assess what factors influence landowners' willingness to allow secondary forest regeneration on their farms. I conducted 30 in-person interviews with

the landowners whose farms were included in the private forest inventory survey. All interviews were conducted in Spanish by the principle investigator and lasted between 45 minutes and 4 hours; interviews were structured with a questionnaire; I used a mixed questionnaire design with 70% closed, 12% open, and 18% Likert scale questions. Questionnaire themes centered on general farm information, farm management, landowners' forest values, tree species used on their properties, and landowners' views on the Costa Rican payments for environmental services program. Twenty-five of the 30 interviews were recorded and transcribed; for interviews that were not recorded, the PI took extensive notes. I quantitatively assessed most questions from the questionnaire and qualitatively assessed key open-ended questions to find emergent themes (Glaser 1992). I focused theanalyses on how land tenure, farm size, livelihoods, and landowner motivations affected secondary forest regeneration.

In Chapter 3, I was interested in assessing these secondary tropical dry forests as a social-ecological system; I wanted to advance understanding of how ecosystem functions such as secondary forest recovery are affected by differences in human land use and management between public and private forests. As a first step towards understanding how ecosystem functions may vary between public and private, I assessed plant functional traits, which served as a proxy for ecosystem function. I build a functional plant trait database from both the literature and international plant trait databases (e.g. TRY and Seed Information Database (SID)). I was also interested in the human dimensions of tropical dry forest tree species use. People select species for various uses based on plant traits; for example, tree species used for sawmill timber generally have a combination of plant traits such as high wood density and tall, straight trunks while ornamental species are often selected for their showy floral or foliar traits. The way in which landowners use species with particular sets of plant traits likely affects whether those species should be expected be more or less abundant in private forests; native species used for timber that are not widely commercially planted (i.e. most native species save for *Pachira quinata*), for example, may be less abundant in private forests while species used as ornamentals or living fences, may be more abundant in private forests.

Thus, I created a human use plant trait database in which I summarized positive and negative human use plant traits separately.

CHAPTER 2

A comparison of forest structure and biodiversity in public and private secondary tropical dry forests of Guanacaste Province, Costa Rica

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Introduction

Secondary forests that have naturally regenerated after human disturbances compose approximately half of tropical forestlands and will likely contribute an increasing important component of pan-tropical forest cover as mature forests continue to be cleared for agriculture and subsequently abandoned (Gibbs et al. 2010; Perz and Skole 2003; S. J. Wright 2005). Given the current and expected increases in tropical secondary forest extent, these forests are fundamental to conservation (R. L. Chazdon 2008). A rich literature has developed examining tropical secondary forest recovery that demonstrates that secondary forests provide valuable environmental services such as carbon sequestration, water purification, and biodiversity protection (Robin L. Chazdon 2003; Guariguata and Ostertag 2001; Marin-Spiotta, Silver, and Ostertag 2007). However, the biodiversity conservation value of regrowth forests has been strongly debated (S. J. Wright and Muller-Landau 2006a; Laurance 2007; S. J. Wright and Muller-Landau 2006b; Gardner, Barlow, et al. 2007). Wright and Muller-Landau (2006a; 2006b) argue that the predicted biodiversity crisis (Pimm et al. 1995) will be circumvented due to high rates secondary forest recovery after land abandonment due to rural outmigration. Conversely, others contend that there is not enough evidence to predict that the trend of rural outmigration and secondary forest regeneration will continue nor that the biodiversity value of regrowth forests will be sufficient to avoid the biodiversity crisis (DeFries et al. 2010; Gardner, Barlow, et al. 2007; Gardner, Hernández, et al. 2007; Harvey et al. 2008; Laurance 2007).

Who owns tropical secondary forests and do management differences among ownerships affect secondary forest biodiversity conservation and ecosystem service provisions? Secondary forests on private lands compose a significant and increasing proportion of tropical forests: currently, 46% of forestlands in Central America are privately owned and, globally, the upward trend of private forest ownership is expected to continue (Agrawal, Chhatre, and Hardin 2008; FAO 2010; T. M. Hayes 2006). The

cause of this global trend is unknown and further research is necessary to ascertain which FAO Forest Resource Assessment (FRA) forest type categories (primary, naturally regenerated, planted for production, planted for protection) are increasing for private ownership (FAO 2010). Differences in species composition and diversity between public and private ownerships may be related to a variety of factors: for example, public and private forests may differ in the types of sites available for forest regeneration, in the species available and/or able to colonize regenerating patches, in performance of species in regenerating patches, and in the management of regenerating forests (Pickett, Cadenasso, and Grove 2005; Turner, Gardner, and O'neill 2001). These factors can operate independently and interactively.

For forest regeneration to initiate, a site with the potential to support forest species must be available for colonization. Differential site availability for forest regeneration is likely non-random with respect to biophysical variables such as soil quality and topography as well as socioeconomic variables such as road and market accessibility (Lambin, Geist, and Lepers 2003). The spatial pattern of landscape-scale 'disturbances' or 'developments' (depending on the disciplinary framing) is non-random: over time, lands that have attributes such as high soil fertility and plane topography are often systematically selected for mechanized cultivation (T. P. Evans and Moran 2002). At the scale of an individual private farm parcel, areas of a farm with high soil quality, plane topography, and road access are likely more tenable for agricultural production than areas on a farm without those characteristics. Approximately one of every six or seven hectares cleared in the tropics regenerates due to land abandonment caused by factors such as poor agricultural productivity or changing market demands (S. J. Wright 2005). Forest regeneration may be more likely in areas of low soil fertility because sites favorable for high agricultural productivity are less likely to be taken out of production as evidenced by forest recovery patterns subsequent to market pressure abatement (Arroyo-Mora et al. 2005; Brown 2003). In addition, public and private owners usually operate on distinct

temporal scales: private land management often tracks changing market demands, so the frequency of disturbance events is likely different (Siry, Cubbage, and Newman 2009).

Secondary forest on public vs. private lands may have differential species availability. Propagule pools may be dissimilar between ownerships due to variation in pollinator and dispersal vectors based on landscape connectivity. Publicly owned forests are often composed of contiguous forest cover and are generally large in extent (FAO 2010; T. Hayes and Ostrom 2005; Sunderlin et al. 2008; Suzuki 2003; White and Martin 2002). Conversely, forest fragmentation has emerged as a considerable issue on private lands (Best 2002; Butler and Leatherberry 2004), suggesting that private forests have higher fragmentation and less connectivity. Forest fragmentation has ecological effects (Debinski and Holt 2000; Hill et al. 2011; Laurance and Curran 2008). For example, both plant and pollinator species abundance, richness, and composition are affected by forest fragmentation (Viana et al. 2012). Pollinator abundance can decrease with increasing distance between patches, affecting pollinator-dependent plant populations (Carvalheiro et al. 2010). Differences in the presence and abundance of livestock between public and private forests may also differentially affect plant species; seed dispersal by cattle is most evident in tropical dry forests and cattle preferentially consume species from the plant family Fabaceae, although other plant families are dispersed as well (Miceli-Méndez, Ferguson, and Ramírez-Marcial 2008). Finally, wild animal abundance and behavior may also differ between public and private ownerships as a result of differences in forest landscape pattern (Van Dyck and Baguette 2005); there is evidence that large seed recruitment in forest fragments is minimal because movement of large animals is restricted in fragmented forests (Cramer, Mesquita, and Bruce Williamson 2007; Melo et al. 2009).

Once trees are established, public and private forests may have differential species performance based on resource availability (e.g. soil fertility, soil moisture holding capacity). Differential species performance relates to differential site availability in that, at the landscape and farm parcel scale, agricultural areas tend to be non-randomly

selected with respect to soil fertility. Moreover, differential species performance in public vs. private lands could be affected by species life history traits. Tree species that employ low investment reproductive and growth strategies such as rapid growth and plentiful, small seeds that are wind dispersed (i.e. many early seres or disturbance adapted species) could be more prevalent on private lands because these plant traits are better suited to compete in an agricultural forest matrix (Mesquita, Delamônica, and Laurance 1999; Marcelo Tabarelli, Peres, and Melo 2012).

Differences in management between public and privately held lands can affect forest landscape patterns (Brown 2003; Stanfield, Bliss, and Spies 2002; Turner, Wear, and Flamm 1996). Divergent forest cover patterns created by differential management regimes on public and private lands may affect ecological processes such as forest regeneration. On private lands, interactions between croplands and forestlands likely occur at higher probabilities: for example, private forests may be at a higher risk to exotic species introductions and chemical runoff from adjacent croplands (Marcello Tabarelli and Gascon 2005). Finally, management differences between public and private forests could influence vegetation dynamics. For example, rates of high-grading valuable timber species from forests could differ between public and private lands and differentially affect regeneration dynamics (Clark and Covey 2012; Ruiz, Fandino, and Chazdon 2005).

Tropical secondary forests provide a substantial ecosystem service in the form of storing carbon in woody biomass (Pan et al. 2011; Peter B. Reich 2011). Recognizing the social value of this ecosystem service to increase resilience to climate change, the Costa Rican program for environmental services (PES) specifically mentions the role of forest in mitigating greenhouse gases through carbon sequestration (Forestry Law 1999) and the PES program pays private landowners providing this service. Thus, understanding whether private forests provide the same level of ecosystem service in terms of carbon stocks is important. I expect that private and public forests likely have similar carbon stocks since these are largely a function of structural attributes of forests. Across a range of secondary forests that differ in historical land use, structure recovers rapidly

(Guariguata and Ostertag 2001; Marin-Spiotta, Silver, and Ostertag 2007; Robin L. Chazdon 2003; Letcher and Chazdon 2009). Thus, forest structural measurements such as stem density, basal area, CWMWD, and biomass are likely similar in public and private forests.

Almost forty years ago, Gomez-Pompa and Vasquez-Yanes (1972) observed that we are in the "era of secondary vegetation" as a result of human drivers of land cover and land use changes. Yet, studies of tropical secondary forests remain relatively sparse (Gardner, Hernández, et al. 2007; Gardner, Barlow, et al. 2007; Robin L. Chazdon et al. 2009). In the 21st century, given the trends of old-growth deforestation, agricultural expansion, and secondary forest regeneration on abandoned lands, patterns suggest that secondary forests on *privately* owned land could be the 'forests of the future'. While there have been studies conducted in private forests in Costa Rica (Nicotra, Chazdon, and Iriarte 1999; Mayfield and Daily 2005; Morse et al. 2009; Bouroncle and Finegan 2011) an explicit comparison of biodiversity, forest structure, and carbon stocks from private and publicly owned forests is novel. Here, I use an extensive dataset of forest inventory plots arrayed across soil and successional gradients in both private and public lands in Guanacaste, Costa Rica. Our primary objectives were to compare public and private forests in terms of biodiversity, forest structure, and biomass. I tested the hypotheses that (i) tree biodiversity measured by the Shannon-Wiener Diversity index and species richness was lower in private forests; (ii) that public and private forests had comparable structure as measured by stem density, basal area, CWMWD, and biomass. Finally, I examined whether tree species composition was distinct between public and privately owned naturally regenerated secondary tropical dry forests

Methods

Site description and land-use history

Our study was conducted in tropical dry forests of Guanacaste, Costa Rica. Mean annual temperature is ~25° C and dry season length ranges from 5 to 6 months (Gillespie, Grijalva, and Farris 2000; Holdridge 1967). Public forest data were from forest plots located in Palo Verde National Park National Park, Área de Conservación Tempisque (10.358N, 85.358W) and Área de Conservación Guanacaste (10.848N, 85.628W) (Powers et al. 2009). In 2011, I collected data on the structure and composition of secondary forests located on private lands near Palo Verde National Park National Park and Área de Conservación Guanacaste (ACG). I did not use plot location as a predictor variable in subsequent statistical analyses to avoid multicollinearity in predictor variables: location was correlated with the two Principle Components Analysis (PCA) axes that summarized soil variables (Figures 1 and 2). Land use in Guanacaste was dominated by extensive, hacienda-style, ranches with low productivity (Edelman, 1985). The most recent wave of deforestation from ~1950s-1980s was closely tied to Costa Rica's integration into the international beef market (Calvo-Alvarado et al. 2009; Edelman 1985). Countervailing land-use policies took hold in early 1970s with the establishment of a national park system and forestry laws that restricted forest cutting on private lands (Brockett and Gottfried, 2002). Área de Conservación Guanacaste and Palo Verde National Park National Parks were created in the years following the national policy shift (S. Evans 1999).

I chose private farms based on three primary criteria (1) sufficient forest cover to complete a forest inventory plot with a forest edge buffer of at least 15 m ($\geq$2 ha forest patch), (2) landowner consent, and (3) accessibility. In Área de Conservación Guanacaste, there are distinctive forest patches characterized by a high abundance of *Quercus oleoides,* therefore within ACG I sampled both forests with and without abundant *Q. oleoides*. In addition, I stratified our sampling scheme using forest stand age estimated based on three distinct measures: local expert knowledge, satellite imagery, and

δ^{13} carbon isotope analyses. I used a time-series of georectified Landsat images from 1986, 1996, 2000, and 2007. Further, δ^{13} carbon isotope analyses of soil provided additional verification of our stand age estimates as the stable isotope signature of organic carbon in the soil reflects the relative contribution of C_4 dominated grasslands to C_3 dominated tree communities (Bernoux et al. 1998). A concerted effort was made to sample stand ages equally between public and private lands in and around Palo Verde National Park and for both the diverse tropical dry forest and oak-dominated forest types in and around ACG: the resulting distributions of forest age between these categories are similar (Figure 3). The geographic locations of all inventory plots were recorded with a Garmin GPS. In total, our combined dataset consists of 66 private and 82 public forest plots.

Plot sampling

Plot sampling procedures in private forests followed those used for the public forest inventory dataset (Powers et al. 2009) and are reported here in brief. In each 50 x 20 m (0.1 ha) plot, trees were sampled in nested subplots depending on diameter at breast height. Every tree $\geq$ 10 cm DBH was measured and identified to species. When I encountered a species that I could not identify in the field, I collected a sample for subsequent identification. In total I sampled 5,662 individuals $\geq$ 10 cm DBH. There were two species that I was unable to identify, which represented 0.04% of the species inventory. In 50 2x4 m subplots within each plot, I recorded the diameter at breast height but did not identify saplings <10 cm DBH and at least 1.3 m in height. I also noted the presence/absence of cattle in 50 1-m^2 subplots; domesticated ungulates were noted by presence/absence of feces, hoof prints, or well-defined cow paths. The public forest sampling protocol did not include presence/absences of ungulates; however, Palo Verde National Park National Park uses cattle as a management tool to reduce the fire-promoting introduced pasture grass *Hyparrhenia rufa* (Stern, Quesada, and Stoner 2002) while Área de Conservación does not. For trees $\geq$ 10 cm DBH, I collected wood density samples with an increment borer from three different individuals per species if the

species had not been previously sampled in the public forest plot survey (Powers and Tiffin 2010). Wood density determinations followed Powers and Tiffin (2010).

Biomass calculations

Aboveground biomass (AGB) in trees was estimated using an allometric equation for tropical dry forests that include species-specific wood density and DBH (J. Chave et al. 2005). Tree height, DBH, wood density, and forest community type are all important predictor variables of AGB. Tree height, however, is often difficult to measure in tropical forests that contain different canopy levels and a multitude of tree species. Chave et al. (2005) found that, by including forest community type, a reliable estimate of ABG was possible without tree height. For saplings <10 cm DBH and ≥ 1.3 m I used the community weighted mean wood density (CWMWD) calculated using species abundance per plot in place of species-specific wood density to calculate AGB.

Soil sampling

Soil sampling procedures followed those outlined in Powers et al. (2009), so I report here in brief. For soil chemical analyses, I collected 10 samples per plot to a depth of 10 cm; six samples were evenly dispersed along the central line of the plot and one sample was collected at each of the four plot corners. I removed leaf litter before sampling and homogenized the ten samples per plot. Soils were air dried for 2 weeks, sieved, and shipped to the University of Minnesota Research Analytical Laboratory (St. Paul, MN) for further processing. Samples were analyzed for the following total elements following a hot nitric acid digest and quantification via inductively coupled plasma spectroscopy (ICP): Al, B, Ca, Cr, Cu, Fe, K, Mg, Mn, Na, Ni, P, and Zn. Total soil carbon (C) and nitrogen (N), and their stable isotopic signatures were quantified at the Stable Isotope Facility at the University of California at Davis. An oven dry weight correction was applied to all samples.

Statistical Methods

Soils

  To summarize linear patterns of covariation in the soils dataset and reduce the quantity of variables for use in subsequent statistical analyses, I used a Principle Components Analysis (PCA). PCA is an appropriate multivariate analysis for soil chemical variables because these variables are highly correlated and I was interested in assessing independent factors that summarized those underlying correlations (Tabachnick and Fidell 2007). I chose a correlation-based PCA to normalize differences in the scale of soil measurements (Clarke and Warwick 1994).I log transformed all soil variables except Al, which was normally distributed. I used PCA ordination scores for the first two PCA axes (hereafter PCA1 and PCA2) for each forest plot as predictors in a hierarchical multiple linear regression (MLR). PCA1 and PCA2 scores were also used as explanatory variables in a subsequent nonmetric multidimensional scaling (NMS) ordination in order to examine the role of soil fertility gradients on species composition. The PCA scores for each plot were calculated by multiplying the PCA loadings by the original matrix (i.e. soil by forest plot matrix). This approach has also been used in other studies (Powers and Peréz-Aviles 2013).

Forest structure and Shannon-Wiener diversity index

  I was interested in understanding the predictive capacity of ownership and soil fertility; however, it is well known that forest stand age is correlated with both forest structure and biodiversity (Guariguata and Ostertag 2001). Therefore, I conducted a hierarchical multiple linear regression (MLR) in which forest age was input in step 1 of the MLR followed by the soils PCA1 and PCA2 in step 2 and ownership in step 3 (Tabachnick and Fidell 2007). The dependent variables in our model were ABG, basal area, stem density (trees $\geq$10 cm DBH), small stem density (trees < 10 cm DBH and > 1.3 m in height), CWMWD, and Shannon-Wiener diversity index. Ownership was coded as a dummy variable and forest stand age was log transformed to meet MLR assumptions of linearity, normality, and homoscedasticity. The independent variables, forest stand age,

PCA1, PCA2, and ownership, were tested for colinearity and found not to be correlated (IBM Corp. Released 2011).

Species richness

I used the Estimates software program v. 8.2 (Gotelli and Colwell 2001; Robert K. Colwell, Mao, and Chang 2004) to calculate individual-based species rarefaction curves using species abundance data per 10 x 10 m subplot (N=660 private and N=820 public subplots). Tropical forests are especially species-rich so sampling effort often does not capture the full species pool. It is also important consider that the relative abundance or the pattern of species abundance or rarity in samples can differ. I chose individual replication when comparing species richness between public and private forests because this method explicitly accounts for species relative abundance among samples. Further, I selected the rarefaction curve because it provides a smooth curve that is the statistical mean of individuals randomly sampled from the species pool (Chao et al. 2004; R. K. Colwell et al. 2012; Gotelli and Colwell 2001).

Species composition

To assess tree species compositional differences between public and private ownerships, I used a nonmetric multidimensional scaling ordination (NMS) in PC-ORD v. 6.07 (B. McCune and Mefford 2011). NMS is a multivariate ordination technique often used with species abundance datasets using the Sørensen distance measure. The Sørensen distance measure is used because a species composition data matrix is typically sparse and Sørensen uses proportions instead of totals, so this distance measure is not unduly influenced by an abundance of zeros in the data; additionally, Sørensen is not does not have distributional assumptions. The NMS algorithm iteratively tests a randomly populated Euclidian distance matrix until the final matrix closely resembles the rank order of the interpoint distances of the original basic input data, which is the species composition and abundance matrix. The only statistical assumption that must be met is that the correlation between the original data set and the randomly generated Euclidian data set must be monotonic; in other words, the relationship must either be flat or have a

positive slope. A stress measure is provided to assess the assumption of monotonicity. I excluded species singletons and doubletons from the dataset a priori. This is a standard approach since tropical forests species data sets often have many rare species; rare species do not provide information on patterns of species composition between groups and can complicate patterns (Peck 2010). Our main matrix consisted of species abundances per plot; I also included a second matrix with the following explanatory variables to aid in interpretation: ownership, PCA1, PCA2, and forest age. For each continuous variable, the parametric Pearson's correlation coefficient and the nonparametric tau coefficient are given to assess the relationship between the specific variable and each of the NMS axes. Unlike PCA, NMS variation is calculated as after-the-fact variation by correlating distances between the original matrix and the Euclidian matrix with the same distance measure used for the original matrix, in this case Sørensen, and is done to circumvent issues of not representing the ecological gradients precisely (B. McCune and Mefford 2011; Økland 1999; Peck 2010).

I used a second approach, the Classification Method (CLAM), to examine tree species compositional differences between public and private ownerships (Robin L. Chazdon et al. 2011). Species abundance data between habitat types are often not sampled evenly; the CLAM model diminishes unequal sampling bias between groups and also reduces bias associated with inadequate sampling of rare species between each group (i.e. public and private forests). CLAM separately categorizes species generalists and species that are too rare to classify so that data need not be removed a priori. I calculated both a simple majority threshold of 0.5 and a super majority threshold of 0.677 each with a significance level p=0.005 to assess whether a species was more prevalent in public or private forests at those two threshold levels.

Species composition due to forest age, soil, and ownership

I was interested in partitioning the variance in tree compositional differences due to forest age, soil, and ownership. Soil variables are often correlated so I used a subset of the log of soil variables that were highly correlated and standardized them using a Z-

score to create a soil composite as conducted in Powers and colleagues (2009). I conducted Mantel and partial Mantel tests in PC-ORD v. 6.07 (B. McCune and Mefford 2011); a Mantel test examines the hypothesis that there is no correlation between two matrices while a partial Mantel tests examines the hypothesis that when a third matrix is input as a covariate there is no correlation between matrices. In other words, I assessed if there was a significant correlation between a matrix of age, soil composite, and ownership, and a matrix of tree composition. I used a partial Mantel tests to examine whether ownership was significantly correlated with composition when soil composite was entered as a covariate matrix. Mantel and partial Mantel tests assess correlation and probability values using the Monte Carlo permutation method and the resultant standardized Mantel statistic (r), which ranges between -1 and 1 and is equivalent to the Pearson correlation.

Results

Soils

I found two major axes in the principal components analysis that explained a considerable amount of the variation in the ordination; PCA1 explained 47.2% of the variation while PCA2 explained 15.5% of the variation. All soil chemical variables were strongly and negatively correlated with PCA1 except for Mn (Table 1). In general, soil fertility increased as PCA1 scores decreased. Manganese was the only element that had a higher correlation with PCA2 than PCA1.

As expected, there was considerable overlap between private and public plots in soil chemical properties (Figure 1). However, I identified three subsets of plot clusters with non-overlapping characteristics. First, I observed a subset of public forest plots that was clearly distinguished from private plots and was characterized by low PCA1 scores and low PCA2 scores, indicating relatively high K, P, Na, and Ni; these were high soil fertility plots. This subset of public plots was especially high in N, P, K, C, Ca, Mg, and Na. On PCA2 there was an additional split between public and private forest plots, specifically among plots with high PCA1 scores and hence low soil fertility. The subset of public plots on PCA2 had relatively high Mn and low N, P, K, Ca, and Na; all of these plots had an abundance of *Quercus oleoides*. The subset of private forest plots on PCA 2 had low Mn, Al, B, Cu, Fe, and Zn; this subset of plots represented both diverse tropical dry forest species as well as plots dominated by *Q. oleoides*. On private lands, therefore, *Q. oleoides* dominated plots occurred on soils that were relatively more fertile. Overall, these results reflect a regional gradient in soil fertility; the highest soil fertility sites were public forests in Palo Verde National Park while the lowest soil fertility sites were public forests in *Área de Conservación Guanacaste* characterized by abundance of *Q. oleoides*.

Hypothesis 1: Tree species diversity

I expected the Shannon-Wiener diversity index to be predicted by stand age, soils, and ownership. The best model included stand age and the two soil variables: PCA1 and

PCA2 (Table 2 and Table 3). Ownership was not a significant predictor but private forest had lower Shannon-Wiener diversity index values than public. Shannon-Wiener diversity index increased with stand age and with PCA2, which correlated positively with Mn, B, Fe, Zn, and Al (Table 1). Shannon-Wiener diversity index was negatively correlated with PCA1, signifying that it increased with increasing soil fertility. Variability explained was 21%, 2%, and 3% for stand age, PCA1, and PCA2, respectively.

Individual-based species rarefaction curves showed no strong differences between private and public ownerships (Figure 2). Public rarefaction curves were slightly higher than private but had overlapping confidence intervals. However, neither curve reached an asymptote, suggesting that sampling efforts did not capture the full range of species in either public or private forests.

Hypothesis 2: Forest Structure

Overall, stand age was the strongest predictor of forest structure explaining from 10-20% of the variation in the response variables (Table 2 and Table 3). Soil characteristics were significant predictors for a few response variables but explained less of the variation (2-8%). Ownership was a significant predictor only for community weighted mean wood density. Below, I examine each response variable in more detail.

I expected forest structural measurements to be similar between ownerships and primarily predicted by stand age. Basal area and aboveground biomass were best predicted by stand age alone. As expected, basal area and aboveground biomass increased with stand age (Becknell, Kissing Kucek, and Powers 2012). The best model of stem density of$\geq$10 cm DBH included both stand age and PCA2 as predictors (Table 3); stem density increased with stand age and with PCA2. PCA2 explained 8% of the variability and forest age explained 11%. Sapling stem density (<10 cm DBH and $\geq$ 1.3 m height) was not predicted by any of the independent variables I chose for the model (R^2=0.050, $F_{1,142}$=1.864, p=0.120).

I expected community weighted mean wood density (CWMWD) to be similar along the forest age gradient and between ownerships; further, I predicted that soil characteristics would affect CWMWD as soil fertility was found to be negatively correlated with CWMWD in over 2,000 neotropical tree species (Jérôme Chave et al. 2006). The best model of CWMWD included ownership and PCA1; ownership explained 10% of the variability while PCA1 explained 6%. Publically owned forest had higher CWMWD and CWMWD was positively correlated with PCA1 scores: less fertile soils had higher CWMWD, which paralleled Chave and colleagues findings (2006).

Although CWMWD was significant higher in public forests, the mean difference between public and private CWMWD was small (public mean=0.655, private mean=0.616). I were primarily interested in CWMWD differences between public and private forests because species-specific wood density measurements improve aboveground biomass calculations (J. Chave et al. 2005; Jerome Chave et al. 2009). To test the impact of the 0.039 g/cm^3 difference in CWMWD on biomass, I created two dummy data sets each with 148 plots with identical features saves for the wood density values. The mean biomass difference calculated between the dummy data sets was not significantly different (public=140 Mg/ha and private=131 Mg/ha, two-tailed t-test, t-statistic=0.893, df 294, p=0.373). Thus, in terms of aboveground biomass, the statistically significant CWMWD difference between public and private forests did not translate into a biologically significant difference in either our biomass calculations or biomass calculations in the dummy data sets.

Tree Composition

I explored tree species composition between public and private forests using Nonmetric Multidimensional Scaling (NMS). After confirming that solutions were consistent between five distinct NMS ordinations run with different random number seeds, I chose to interpret one of the five ordinations. I chose two axes to interpret, which represented 29% and 17% of the after-the-fact variation for axes 1 and 2, respectively (Figure 3). The final stress for the ordination was 17.3: a value below 25 for species data

sets is considered to be a good stress value (Peck 2010). I interpreted these axes using a number of predictor variables including stand age, soils and ownership.

NMS Axis 1, hereafter NMS1, was correlated with PCA1 ($r= -0.5$) and stand age ($r= 0.41$). Thus as NMS1 scores increased, plots were both older and more nutrient rich. NMS Axis 2, hereafter NMS2, was correlated equally with stand age and PCA2 ($r=-0.48$). Therefore, as NMS2 scores increased plots were younger and had lower PCA2 scores; low PCA2 scores were correlated with, Ca, Cr, K, Mg, Na, Ni, and P in decreasing order. The lower quadrants of NMS2 were correlated with high PCA2 scores so correlated with Mn, Al, B, Cu, and Fe in decreasing order (Table 3). A visual examination of the NMS ordination graph suggested that species compositional differences between public and private forests separated to some extent on NMS2. There was a cluster of public forest plots in the lower NMS2 quadrants, especially the lower right quadrant that diverged from the compositional pattern created by the majority of public and private forest plots (Figure 3). For private forests plots, there was also a cluster in the upper quadrants.

To assess the specific tree species that were more prevalent in public and private forests, I conducted a CLAM analysis, a multinomial model that classifies species abundances between two groups. The CLAM analysis revealed that nineteen species were more prevalent in public forests (11%), twelve species were more abundant in private forests (7%), fifty-three showed no distributional bias (32%) and eighty-two species were too rare to classify (49%). Tree species categorized as more prevalent public or private are listed in Table 3. Species that were most prevalent in public forests included: *Rehdera trinervis* and *Luehea speciosa*. The most prevalent private forest species included *Guazuma ulmifolia, Quercus oleoides,* and *Byrsonima crassifolia*.

Tree Composition due to age, soil, and ownership

To partition the variance in species composition between age, soil, and ownership, I conducted Mantel tests (public and private plots N=148). The Mantel statistics for age

(r=0.151), soil composite (r=0.189), and ownership (r=0.121) were all statistically significant after a Bonferroni correction factor was applied (p>0.002). Since the results from the PCA showed that some of the public and private plots clustered distinctly with respect to soil chemical properties, I also conducted a partial Mantel test to explore whether ownership was still significantly correlated with species composition after the effects of soil were removed: I found that ownership had a Mantel statistic of r=0.127 and was significant (p>0.002). Forest age and soil chemical characteristics are known to affect species composition (Guariguata and Ostertag 2001; John et al. 2007). Here I show that ownership had a significant effect on species composition as well.

Discussion

In many tropical areas, secondary forest regeneration occurs on agricultural fields fallowed as a result of soil degradation or shifts in market demands (S. J. Wright 2005); many of these lands are privately owned. However, few studies have compared the biological diversity and ecosystem service provisions between public and private forests (Gardner, Hernández, et al. 2007). Our research shows that public and private tropical dry secondary forests in Guanacaste, Costa Rica differ edaphically. First in the high soil fertility area of Palo Verde National Park and the surrounding lands, private forests had poorer soils relative to public; this suggests that private landowners cultivate areas of high soil fertility and allow forests in areas with lower soil fertility. Second, in the low soil fertility area of ACG and the surrounding lands, private forests had higher soil fertility. The public forests located in ACG were especially poor in critical plant nutrients N, P, K. Because of the poor soil quality in ACG, areas surrounding ACG with slightly more fertile soils may have been disproportionally selected for pasture and agricultural lands with the effect that large areas of forest on those lands remained intact. When the park system was being set up in Costa Rica, this core area of intact forest was valuable for conservation. I found no difference between public and private forests in integrative measures of aboveground biomass, forest structure, and simple diversity measures; this suggests that if these are conservation values of interest in Guanacaste, public and private tropical dry forests in this area provide similar value. While there was an overlap in species composition, I found strong evidence that there were also differences in species composition between public and private forest in Guanacaste. This suggests that if particular species (e.g. high-value timber species) are of interest for conservation in Guanacaste in this area, public and private forests offer different conservation value for these tropical dry forests. Further, private forests appear to be important for *Quercus* dominated communities in Guanacaste.

Public and Private Edaphic Conditions

Spatial heterogeneity of soil quality affects land use (T. P. Evans and Moran 2002). In our study, there was considerable overlap in edaphic variables as well as some differences between public and private forests. The southern region of our study area in and around Palo Verde National Park National Park had the highest levels of soil fertility: this region has a large agricultural area characterized by deep fertile soils from *Tempisque* River deposits (Hartshorn 1983). Within this region, private forests had relatively lower soil fertility compared with public forests. This result suggests that landowners non-randomly cultivate the portions of their land that have higher soil fertility with the effect that private forests are on the less fertile soils. This bias towards forests occupying land that has one or a combination of factors such as low soil fertility, poor drainage, rocky soils, and steep slopes has been found in other studies (Frimpong et al. 2006; Scull and Harman 2004). In the northern region of our study area, public forests in *Área de Conservación Guanacaste* (ACG) were particularly poor in soil nutrients and characterized by very low levels of N, P, K, Ca, Na and high Mn. Public forests in ACG may have the lowest soil quality because these soils likely did not support very rich agricultural or pasture lands. Thus, when ACG bought this land, the farmland value may have been less than the value of the land for conservation. Conservation areas are often disproportionally situated in areas with poor soil quality, complex topography, and/or high elevations (Pressey 1995; Scott et al. 2001).

Private Forests and Carbon

Carbon markets and policies such as Reducing Emissions from Deforestation and Degradation (REDD+) have developed to curb greenhouse gas inputs from deforestation and forest degradation by creating an environmental services payment scheme for conserving carbon stocks. Global policies such as REDD+ must consider forest ownership, management rights, and benefits (Sandbrook et al. 2010); indeed, the transition from REDD to REDD+ included an attentive reformulation of the role of forest tenure (Agrawal, Nepstad, and Chhatre 2011). Thus, calculating aboveground biomass

and measuring related forest structural attributes in public and private forests is timely. Ownership effects were not evident in integrative measurements of forest structure or aboveground biomass. Likely, this is because secondary forests recover structural complexity swiftly (Guariguata and Ostertag 2001) and the relatively small variability in plant traits as a result of compositional differences probably average out in stand-level metrics. For ownership, the only integrative variable that was significantly different between public and private forests was CWMWD. Public forests were 0.04 g/cm^3 or 3% higher than private forests and the difference was driven by species compositional and abundance differences between ownerships. However, the slight CWMWD difference did not translate into a significant difference in aboveground biomass between ownerships. This result is analogous to results across multiple tropical forest sites that showed no correlative trend in aboveground biomass and CWMWD (Stegen et al. 2009). These results are noteworthy because it suggests that, in terms of carbon stocks in aboveground forest biomass, the conservation value of public and private forests in Guanacaste is equivalent on a per area basis. The extent to which these results reflect patterns in other tropical dry forests is unknown. Tenure regimes are dynamic and anthropogenic effects on land use ebb and flow in tandem with societal and market shifts. Results likely depend on the interaction between institutional tenure arrangements, national forest policies, markets, infrastructure, climatic regimes, and soil fertility gradients.

Forest Tree Species Biological Diversity and Composition

Forest composition is a fundamental component of understanding tropical forest dynamics. Species identity can affect ecosystem functions such as recruitment, survival, and productivity (Nadrowski, Wirth, and Scherer-Lorenzen 2010). Additionally, species display varying tolerances to changing climatic conditions so tracking and predicting tree species compositional shifts can forecast future changes in forest processes and resultant environmental services (Feeley et al. 2011). Broad indices such as the Shannon-Weiner diversity index do not assess tree composition: forests can have identical Shannon-Weiner diversity index values and yet show strong compositional differences. In our

study, I found no difference between private and public forests in Shannon-Weiner diversity or in estimates of species richness. However, I found strong differences in tree composition between public and private forests using two separate approaches. In the NMS, tree composition patterns showed distinct clusters of public and private forest plots in ordination space (Figure 3). Using CLAM, I found nineteen species more prevalent in public forests and twelve species more prevalent in private forests. These species could be categorized as public or private for a variety of reasons (Figure 1); for example, high-grading (differential management) may occur more often in privately owned forests, causing public forest to have a higher relative abundance of valuable timber species. I found that species more prevalent in public forests included those well-known in international hardwood markets such as *Swietenia macrophylla* (mahogany) and *Cedrela odorata* (cedar). Indeed, overharvesting *S. macrophylla* has led to it being listed in the Americas with the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Rodan and Campbell 1996). Other studies in tropical dry forests have attributed a notable lack in valuable timber species abundance to high-grading (Ruiz, Fandino, and Chazdon 2005) and references therein). However, private forest species also included two regionally important timber species, *Cordia alliodora* and *Enterolobium cyclocarpum*.

Rehdera trinervis was the most abundant public forest species and was 17 times more abundant in forest on public than private lands; other studies at *Area de Conservacion Guanacaste* have also found abundant levels of *R. trinervis* in secondary forests (Heinrich and Hurka 2004; Kalacska et al. 2004; Powers et al. 2009). *R. trinervis* has strong wood and so overharvest within private forests may occur. Similarly, *Manilkara chicle* was more prevalent in public forests; *M. chicle* is a timber species prized for its durable wood (Dugelby 1998; Kalacska et al. 2004).

Species compositional differences can be due to a number of factors. I used Mantel test to partition the variance affecting species composition using age, soil, and ownership each as separate predictor variables with species composition. Mantel tests

showed that age, soil, and ownership each explained a significant proportion of the variation in species composition. Moreover, using a partial Mantel test, I found that ownership was still significant even when the effect of soil was removed. This further underscores our result that species composition in public and private forests differs.

Dissimilarities in species availability, performance, and management between public and private forests may differentially affect tree species composition. Differential species availability between public and private forests as a result of dispersal vector availability could affect tree species abundance. For example, cattle-forest interactions have been noted as potential drivers of particular species abundance within tropical dry forests (Janzen 1985; Miceli-Méndez, Ferguson, and Ramírez-Marcial 2008). The most abundant species in private forest was *Guazuma ulmifolia. Guazuma* fruits are favored, consumed, and dispersed by domesticated ungulates (Janzen 1985), suggesting that cattle may play an important role determining species-specific abundances within private forests. In private forests, I found that 68% of plots had evidence of cattle presence. Palo Verde National Park uses cattle in park management to reduce the fire fuel load so including public and private forest plots in the Palo Verde National Park region could confound results (Powers et al. 2009; Stern, Quesada, and Stoner 2002). When all public and private plots in the Palo Verde National Park region were removed, *G. ulmifolia* was still the second most abundant species in private forests. Another possibility for species compositional dissimilarities between ownerships is differential species performance as a result of resource availability (David Tilman 1999). On the low end of the soil fertility gradient, private forest plots had soils with relatively higher N, P, and K. Species in these plots may be more abundant due to the relatively higher soil quality. *Quercus oleoides, Byrsonima crassifolia, Apeiba tibourbou,* and *Curatella americana* were more abundant on private lands. These trees generally co-occur in areas of low soil fertility (McClellan, unpublished data).

Conclusion

Private forests are fundamental to conservation goals, however, few research campaigns collect data within private tropical forests: there is a strong bias in the literature towards public, protected forests (McDade et al. 1994; Fazey, Fischer, and Lindenmayer 2005; Gardner, Hernández, et al. 2007; Harvey et al. 2008; Robin L. Chazdon et al. 2009; Rudel 2012). Demands on tropical landscapes to provide food, feed, and fuel will continue to increase with the likely effect that mature forest cover will continued to decline (Fargione et al. 2007; Cowling et al. 2008; Carpenter et al. 2009; Gibbs et al. 2010; Foley et al. 2011; D. Tilman et al. 2011). Given their limited and diminishing extent, mature forests cannot provide the bulk of forest-derived environmental services on which societies depend. Thus, although mature forests have irreplaceable biodiversity value (Gibson et al. 2011), they are not a conservation panacea. Globally, only 12% of forests are protected for biological diversity and most are within the borders of protected parks (FAO, 2010). Thus, protected parks are an important but inadequate system through which to conserve global forest biodiversity and environmental services (Andam et al. 2008; Gaston, Pressey, and Margules 2002; T. Hayes and Ostrom 2005; Mora and Sale 2011; Suzuki 2003).

Secondary forests compose an increasingly important component of tropical forestland and often occur on private lands (S. J. Wright 2005; Robin L. Chazdon et al. 2009; FAO 2010; Gibbs et al. 2010). For example, forest regeneration in Guanacaste, Costa Rica from 1986 to 2005 demonstrated a highly skewed distribution with respect to ownership: ninety percent of forest recovery occurred on private lands (Calvo-Alvarado et al. 2009). Our result from tropical dry forests in Guanacaste suggests that private and public forest protect biodiversity and environmental services equally: the Shannon-Wiener diversity indices and species accumulation curves were similar and carbon stocks were also comparable. On the other hand, an ownership signature emerged in the tree species compositional variation between public and private forests. These compositional differences likely result from (i) non-random placement of public and private lands with

respect to soil fertility (ii) non-random location of regenerated forests on private lands with regards to soils and (iii) different management activities such as timber harvesting, cattle grazing, and remnant species selection. These results suggest species-specific sensitivities to ownership; thus conservation programs for encouraging sensitive species regeneration such as outplanting should be encouraged. In concert, our results echo suggestions towards flexibility in land policies (Fromond, Simila, and Suvantola 2008) and suggest that I need a broader conservation dialog that includes social institutions, societal production needs, and conservation values to assess the tradeoffs inherent in land use and conservation strategies (Carpenter et al. 2012).

Table 1 Principle Components Analysis (PCA) of soil chemicals from public and private forests

Pearson's product-moment correlation coefficient (r) for each element for a principle components analysis (PCA) of mineral soil samples collected in public and private tropical dry forest plots in Guanacaste, Costa Rica. This table shows PCA1 and PCA2, which explain 47.2% and 15.5% of the variation respectively.

Soil Variable	PCA1	PCA2
Al	-0.666	0.359
B	-0.596	0.525
Ca	-0.858	-0.335
Cr	-0.678	-0.352
Cu	-0.761	0.321
Fe	-0.715	0.539
K	-0.589	-0.388
Mg	-0.831	-0.319
Mn	-0.413	0.634
Na	-0.627	-0.473
Ni	-0.568	-0.388
P	-0.665	-0.361
Zn	-0.777	0.349
C	-0.706	0.047
N	-0.725	0.038

Table 2 Descriptive statistics comparing biodiversity and forest structure

Descriptive statistics for public and private tropical dry forests in Guanacaste, Costa Rica. Response variables include Basal Area, Aboveground Biomass, Stem Density (>10 cm DBH, Shannon-Wiener diversity index, and community weighted mean wood density (≥10 cm DBH, Shannon-Wiener diversity index, and community weighted mean wood density (CWMWD).

Response Variable	Ownership	N	Min	Max	Mean	Mean SE	Mean SD
Basal area (m^2 ha^{-1})	Public	82	1.84	48.08	24.20	1.01	9.17
	Private	66	2.42	58.36	23.91	1.52	12.35
Aboveground biomass (Mg ha^{-1})	Public	82	10.38	429.92	173.23	9.19	83.24
	Private	66	11.36	416.18	148.63	10.33	83.95
Stem density (stems ha^{-1})	Public	82	10.00	830.00	411.34	18.03	163.30
	Private	66	20.00	880.00	346.67	20.66	167.82
Shannon-Wiener diversity index	Public	82	0.00	3.12	2.03	0.08	0.73
	Private	66	0.00	3.16	1.80	0.09	0.71
CWMWD (g cm^{-3})	Public	82	0.48	0.80	0.65	0.01	0.07
	Private	66	0.29	0.79	0.62	0.01	0.08

Table 3 Multiple Linear Regression (MLR) comparing biodiversity and forest structure

Results of three distinct hierarchical multiple linear regressions (MLR) comparing biodiversity and forest structure between public and private tropical dry forests in Guanacaste, Costa Rica. Shannon-Wiener diversity index, Stem Density (stems/ha $\geq$10 cm DBH), and community weighted mean wood density (CWMWD) (g/cm^3). For Shannon-Wiener diversity index R^2 = 0.255 for Step 1 and ΔR^2 = 0.05; Stem Density, R^2 = 0.124 for Step 1 and ΔR^2 = 0.08 for Step 2; CWMWD, R^2 = 0.000 for Step 1, ΔR^2 = 0.039 for Step 2, and ΔR^2 = 0.086 for Step 3 (*p<0.05, **p<0.01, ***p<0.002, ****p<0.0001).

Model		B	SE B	p-value
Step 1 Shannon-Wiener diversity index	Constant	0.323	0.233	
	Age	1.195	0.169	0.505***
Step 2 Shannon-Wiener diversity index	Constant	0.467	0.233	
	Age	1.088	0.169	0.459***
	PCA1	-0.038	0.019	-0.141*
	PCA2	0.086	0.033	0.181**
Step 1 Stem Density	Constant	123.4	58.43	
	Age	192.7	42.36	0.352
Step 2 Stem Density	Constant	137.7	57.53	
	Age	182.0	41.77	0.333***
	PCA1	1.359	4.801	0.022
	PCA2	31.24	8.228	0.283***
Step 1 CWMWD	Constant	0.631	0.028	
	Age	0.005	0.021	0.018

Continue Table 3

Step 2 CWMWD	Constant	0.618	0.029	
	Age	0.014	0.021	0.058
	PCA1	0.006	0.002	0.199
	PCA2	0.002	0.004	0.034
Step 3 CWMWD	Constant	0.646	0.028	
	Age	0.010	0.020	0.040
	PCA1	0.007	0.002	0.252**
	PCA2	-0.003	0.004	-0.060
	Ownership	-0.048	0.013	-0.314***

Table 4 Relative abundance of species more prevalent in public and private tropical dry forests

Relative abundance (x 1000) of tree species identified in a multinomial CLAM analysis as species more prevalent in either public or private forest at a simple majority of 0.5 in secondary tropical dry forests in Guanacaste, Costa Rica. Species in public and private prevalent lists are listed numerically from highest abundance to lowest in public and private, respectively. Species with an asterisk are more prevalent at a super majority of 0.667.

More prevalent in public	Relative abundance (X1000)		More prevalent in private	Relative abundance (X1000)	
species	Public	Private	Species	Public	Private
Rehdera trinervis*	121	7	Guazuma ulmifolia	56	114
Luehea speciosa	59	26	Quercus oleoides	68	112
Manilkara chicle*	21	0	Cochlospermum vitifolium	39	57
Ateleia herbert-smithii*	19	0	Byrsonima crassifolia*	4	54
Sebastiania pavoniana*	16	2	Cordia alliodora	16	47
Lysiloma divaricatum	14	7	Luehea candida	6	40
Exostema mexicanum*	11	0	Chomelia spinosa	9	24
Brosimum alicastrum	11	4	Curatella americana*	1	17
Astronium graveolens	9	2	Ocotea veraguensis	6	13
Lonchocarpus parviflorus*	9	0	Apeiba tibourbou*	2	12
Cedrela odorata*	9	0	Acrocomia vinifera	1	6
Sapranthus palanga*	5	0	Bixa orellana*	0	5
Swietenia macrophylla*	5	0			
Acosmium panamense	5	1			
Coccoloba guanacastensis*	4	0			
Cordia collococca	4	0			
Mabea occidentalis	4	0			
Karwinskia calderonii	3	0			
Pithecellobium dulce	3	0			
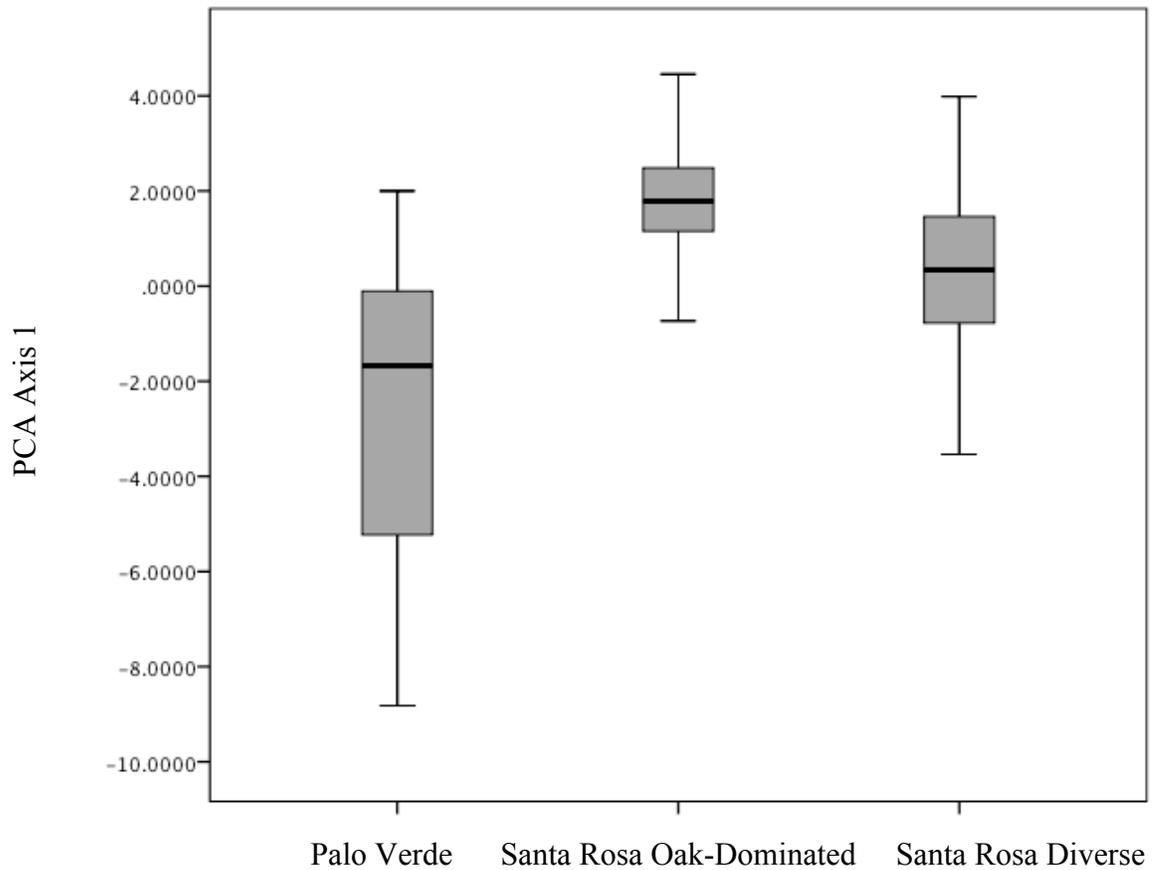
Figure 1 Plot location and type compared with Principle Components Analysis (PCA) Axis 1.

This figure depicts plot locations: the southern region sample region was in and around Palo Verde National Park National Park and the northern region was in and around Área de Conservación Guanacaste (ACG). The northern region had two different forest types, Santa Rosa oak-dominated and Santa Rosa diverse. Since the soil PCA axis 1 is correlated with plot location, I did not include location in the predictor variables so as to avoid multicollinearity.
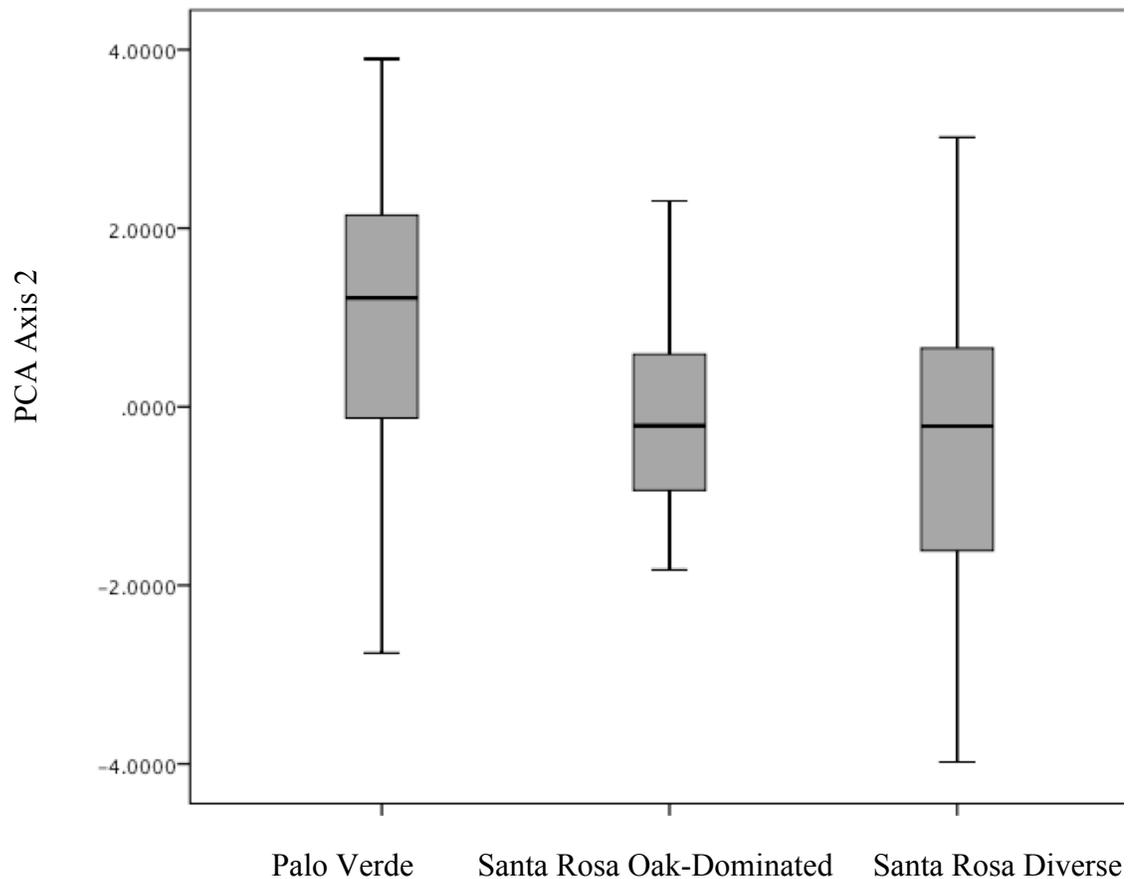
Figure 2 Plot location and type compared with Principle Components Analysis (PCA) Axis 2.

This figure depicts plot locations: the southern region sample region was in and around Palo Verde National Park National Park and the northern region was in and around Área de Conservación Guanacaste (ACG). The northern region had two different forest types, Santa Rosa oak-dominated and Santa Rosa diverse. Since the soil PCA axis 2 is correlated with plot location, I did not include location in the predictor variables so as to avoid multicollinearity.
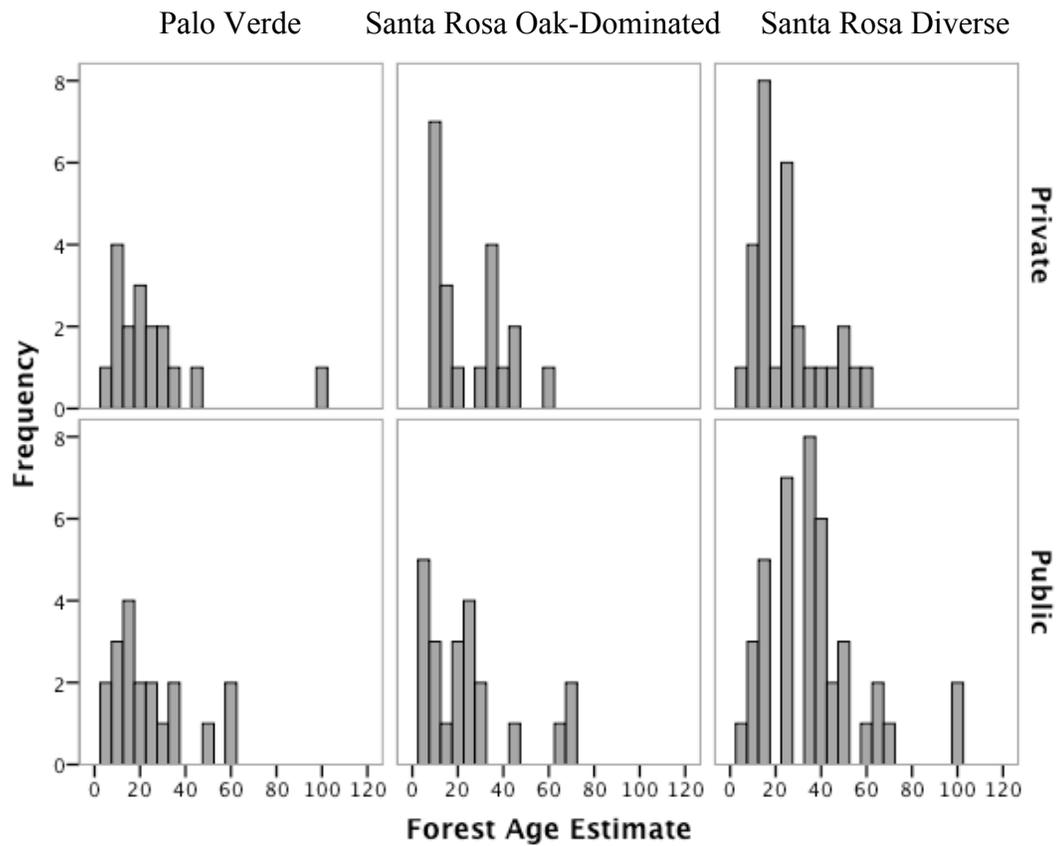
Figure 3 Histogram of forest stand age estimates between public and private plots.

This histogram depicts the distribution of forest stand age estimates between both public and private categories for Palo Verde, Santa Rosa oak-dominated, and Santa Rosa diverse plots.
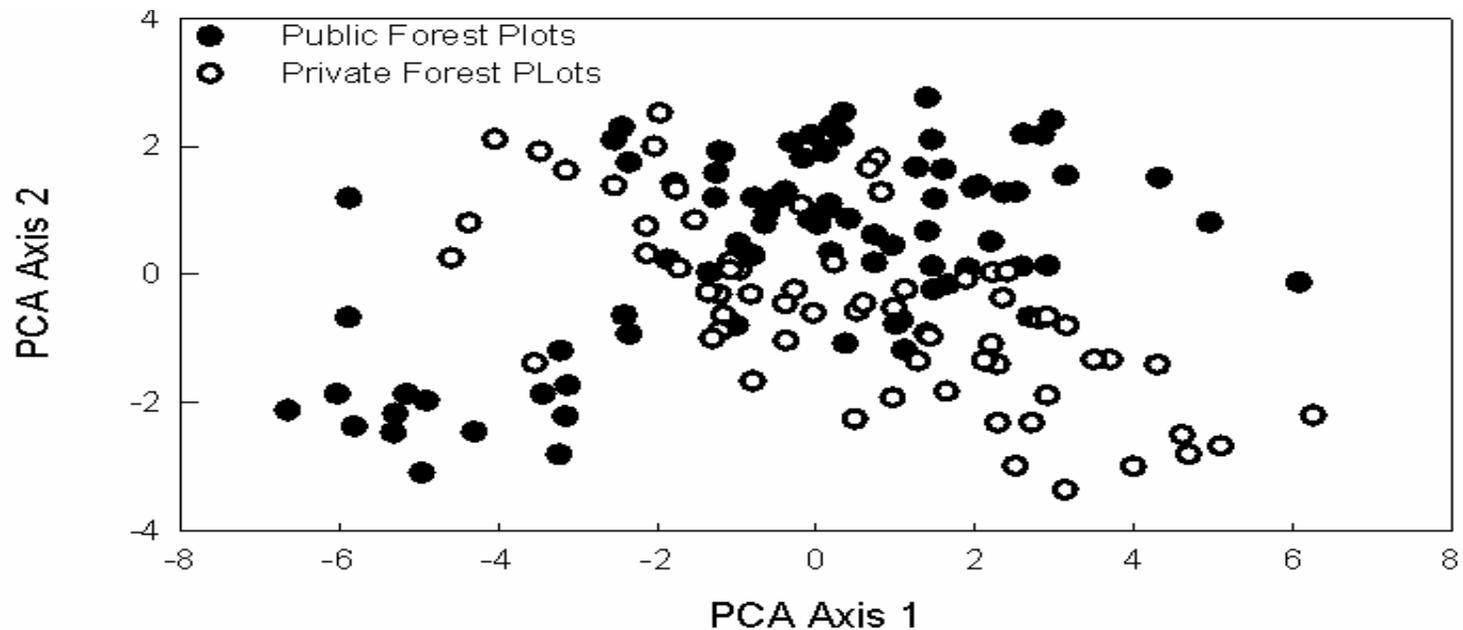
Figure 4 Principle Components Analysis (PCA) ordination of soil properties in public and private forest inventory plots

Mineral soil principle components analysis (PCA) between public and private tropical dry forest plots in Guanacaste, Costa Rica. PCA1 and PCA2 explained 47.2% and 15.5% of the variation, respectively. PCA1 was strongly and negatively correlated with all soil nutrients except Mn. As PCA1 decreased, soil fertility became richer. On the low end of soil fertility, a divergence between public and private soil variables were observed; the public subset had high Mn and low N, P, K, Ca, and Na, whereas the private subset of forest plots had low Mn, Al, B, Cu, Fe, and Zn. Open circles are private forest plots, closed circles are public forest plots.
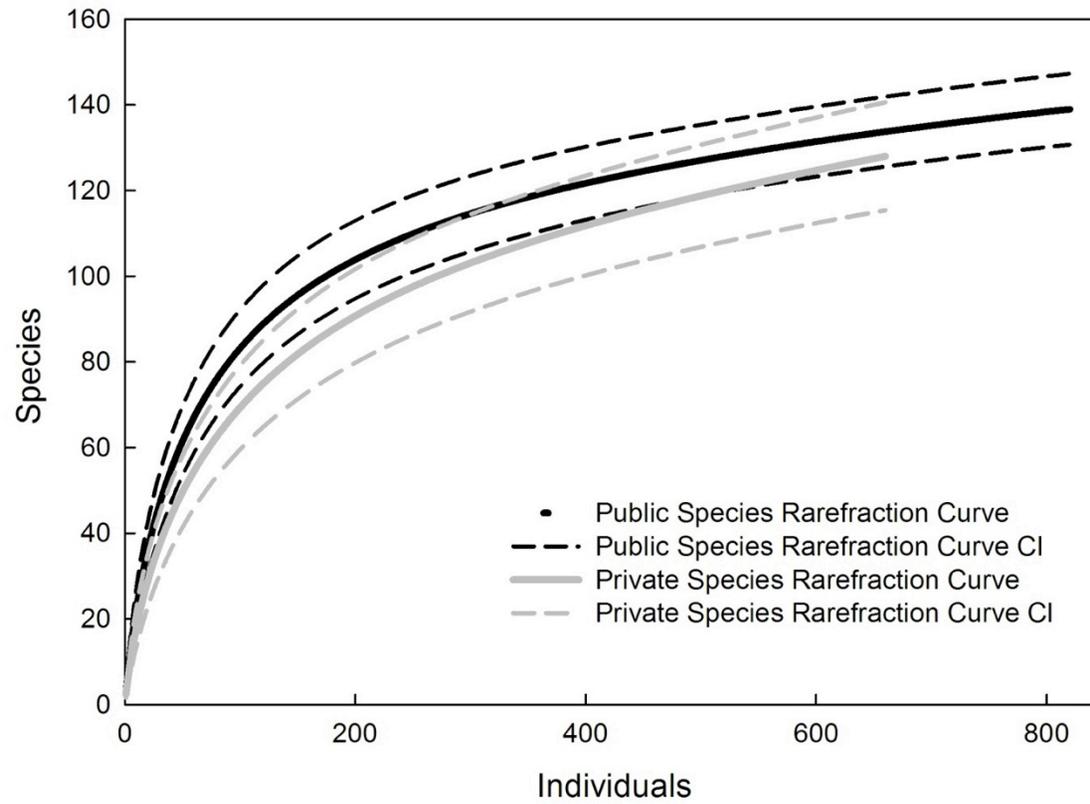
Figure 5 Public and private forest individual-based species rarefaction curves

Individual-based species rarefaction curves for public and private tropical dry forests in Guanacaste, Costa Rica.
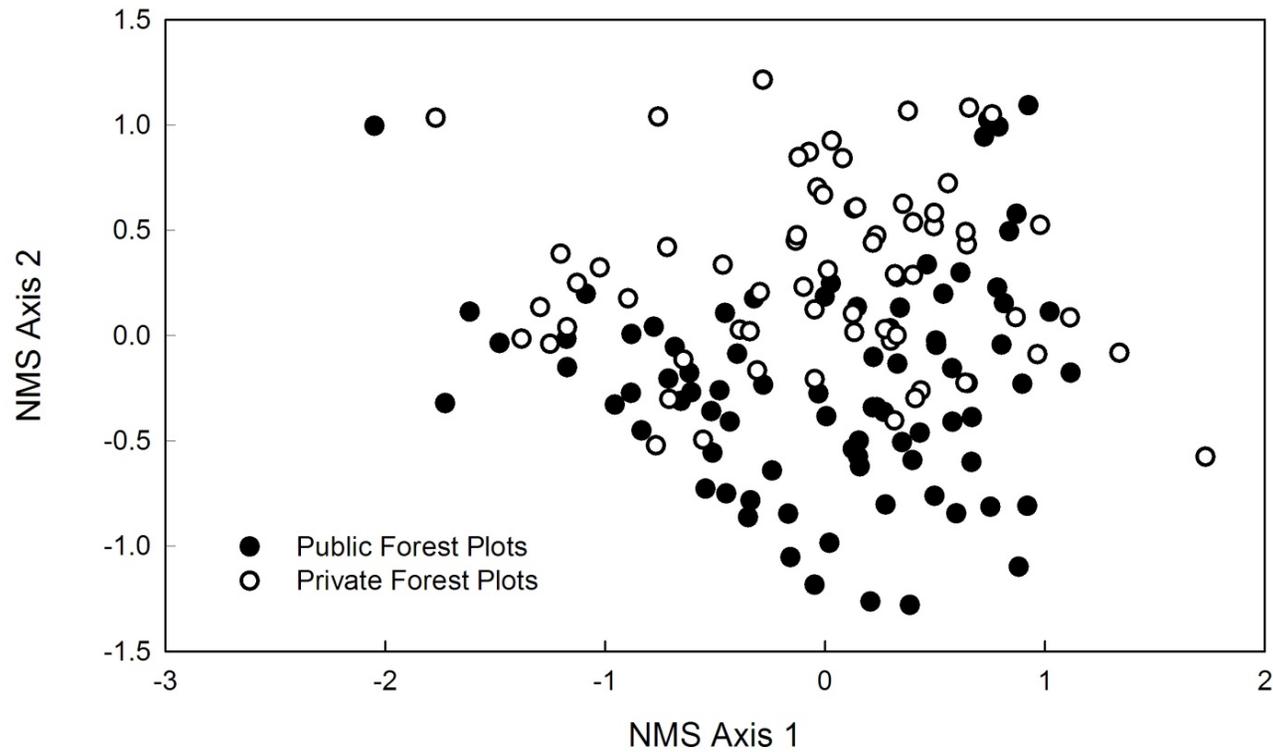
Figure 6 Nonmetric multidimensional scaling (NMS) ordination graph of public and private forest tree species composition.

Nonmetric multidimensional scaling (NMS) ordination of tree species composition in public and private tropical dry forests in Guanacaste, Costa Rica. The ordination graph shows axis 1 (NMS1) and axis 2 (NMS2), which represent 29% and 17% of the after-the-fact variation for each axis respectively. The stress score was 17.3. Open circles are private forest plots, closed circles are public forest plots.

CHAPTER 3

Landowner forest management decisions: the tension between productive land use and forest regeneration

Introduction

Ultimately, in countries where private forests compose a significant proportion of forestland, private landowners are the *de facto* stewards of forest-based environmental services and biodiversity. Thus it is important to understand what factors influence landowners' forest decisions. Landowners' decisions are structured by the land use rights and regulations described by a tenure system. Within the context of those land use rights and regulations, landowners' motivations drive their livelihood strategies. Thus, landowner decision making around forest dynamics can be affected by land tenure (Bonilla-Moheno et al. 2013; Ekbia and Evans 2009; Moran and Ostrom 2005; Robinson, Holland, and Naughton-Treves 2011), landowner motivations (Brehm, Eisenhauer, and Stedman 2013; Schelhas and Pfeffer 2005; Wyman and Stein 2010), and landowner livelihoods (Arriagada et al. 2009; Tacconi 2007; Zumbado-Morales 2010). Here I explore how each of these themes may affect landowners' decisions to allow secondary forest to regenerate on their farms in Guanacaste province, Costa Rica. Landowners' decisions may also influence forest ecological attributes such as biodiversity or forest structure, yet most studies do not consider attributes beyond forest cover (Meyfroidt and Lambin 2011). Thus, I assess landowners' use of tropical dry forest tree species on their farms and relate these results to a parallel ecological study of forest inventory data collected on the same properties (Ch. 2).

Land Tenure

Land tenure defines lawful forest use decisions thus it has long been an active area of scholarship as a driver of forest dynamics (Brockett and Gottfried 2002; Dorner and Thiesenhusen 1992; Ostrom 1950; Zhang and Pearse 1997). Tenure systems organize natural resource use rights and stipulate which subsets of society have access to those rights (Food and Agriculture Organization of the United Nations 2002); natural resources are the basis of most societies' economies, so the architecture of tenure systems shapes that of societies (Geisler 1993). In Costa Rica, landowners' forest use decisions have been decreed by distinct land tenure policies through time. Prior to the 1970s forest policies in Costa Rica encouraged deforestation; land-titling requirements stipulated that settlers clear half their land to create 'improved' lands (i.e. useful for crops and pasture) (Augelli 1987; Brockett and Gottfried 2002). These frontier tenure policies led to forest resource overexploitation and subsequent forest policy reassessment (Brockett and Gottfried, 2002).Overtime, restricted natural resource policy eventually resulted in a quarter of Costa Rica's land base governed under public tenure for conservation (de Camino Velozo et al. 2000). Private landowners' forest use rights were again redefined in 1996 with the Costa Rican Forestry Law 7575 (Brockett and Gottfried, 2002; Daniels et al., 2010); private landowners effectively lost management rights to any portion of their land that Forestry Law 7575 defined as forest—two hectares or more of land with at least 70 trees per hectare that measured 15 cm diameter at breast height and contained mixed species of various ages (Forestry Law 1999). Furthermore, if landowners allowed secondary forest regeneration to reach the lawful forest definition, they would lose management rights to that portion of their land as well, creating a perverse incentive to remove early forest successional growth (Morse et al. 2009; Sierra and Russman 2006). Thus, not only are tenure systems dynamic, but the bundle of divisible land use rights are also dynamic such as the right to purchase, sell, manage, and exclude others (Schlager and Ostrom 1992). With the loss of private forest management rights, Robalino and Pfaff (2013) suggest that landowners were offered compensation through Payments for

Environmental Services (PES) contracts that paid for the benefits their forests provided to society to encourage landowners to accept the change in forest policy. Market-based PES programs, in theory, are designed to tip the scales towards landowners' deciding to preserve forests that would otherwise be cut or prevented from regeneration; however, evidence that exists shows that these effects are slim (Daniels et al. 2010).

Landowner Motivations

Landowners continually navigate the tension between production and protection in tandem with changing policies and incentives. Landowners' decisions are structured not only within the framework of land use policies, regulations, and market incentives but also under cultural and social ideologies (Schelhas and Pfeffer 2005). Costa Ricans have undergone considerable cultural and social change since the latter half of the 20th century (Biesanz, Biesanz, and Biesanz 1999) and the shift from a largely agricultural economy to a tourism-based economy buoyed Costa Rican emerging conservation ideology (Campbell 2002; S. Evans 1999; Schelhas and Pfeffer 2005). Additionally, landowners' motivations may be linked with nonfinancial benefits that forests provide; in Southern Costa Rica, for example, landowners showed emergent cultural forest values by highlighting forests as providing clean air, oxygen, and water for human use, and preserving wildlife as a heritage value (Schelhas and Pfeffer 2005). These values may affect landowners' forest management decisions.

Landowner Livelihoods

Private forests provide environmental services such as carbon sequestration and biodiversity protection (Robin L. Chazdon et al. 2009), but farm livelihoods can depend on development of farm products that may be at odds with forest conservation (Foley et al. 2011; Gibbs et al. 2010). In Guanacaste, landowners pursue a mix of livelihood strategies each associated with a specific land use type and these can have disparate effects on forests. Dominant land use types include extensive ranching and crop production systems (Arroyo-Mora et al. 2005). Although ranching was the single largest

driver of deforestation in Guanacaste, pastures in Guanacaste are rarely devoid of native trees and dispersed trees provide nuclei for forest regeneration following pasture abandonment (Esquivel-Mimenza et al. 2011; Turner et al. 1998) On the other hand, croplands, dominated by sugar cane and rice, tend to be consistent features of Guanacaste's landscape through time and so do not support secondary forest development (Arroyo-Mora et al. 2005; Daniels et al. 2010). Landowners may also have tourism ventures on their farms: the Costa Rican Institute of Tourism and Agrarian Development Institute (IDA) began promoting agro-ecotourism in the mid-1990s, which generated interest among landowners eager to cash in on the lucrative tourism sector (Bagdonis et al. 2009). Agro-ecotourism ventures offer tourists farm-based activities such as ranch tours or farm-stays. Agro-ecotourism, in line with ecotourism philosophies, is expected to promote conservation through managing the farm in accordance with ecological principles or by investing in conservation areas (Zumbado-Morales 2010). The landowners' benefit by broadening their farms economic range. However, successful agro-ecotourism requires significant investment in infrastructure, expertise, and marketing, which could be a high barrier for many landowners (Zumbado-Morales 2010).

Landowners livelihood strategies often include off-farm income; off-farm employment opportunities in diverse Latin American countries have been shown to promote forest regrowth both by drawing labor away from the farm and expanding social network connections for future off-farm opportunities (Rudel et al. 2005; Sunderlin et al. 2005; Zbinden and Lee 2005). Finally, Payments for Environmental Services program is also an option for landowner revenue, although it was designed to compete with moderately profitable land uses so the compensation is relatively modest (Sven 2005). In summary, landowners have a diverse mix of livelihood strategies and these strategies affect forests differentially.

Landowner Forest Tree Species Management

Private landowners' management decisions may affect secondary forest ecological attributes such as floristic diversity, yet the majority of social science studies do not consider forests beyond 'forest cover'(Meyfroidt and Lambin 2011). Forest cover is relatively simple to measure, which likely accounts for its ubiquity in the literature; however, an equivalent area of 'forest cover' can differ in terms of forest structure, tree species biodiversity, and tree species composition. Moreover, tropical secondary forest regeneration patterns may result in more forest cover on private lands relative to public: secondary forests often regenerate on abandoned agricultural lands and many times these lands are privately owned. Thus a large quantity of secondary forestland may be affected by landowners' forest tree species management.

It is important to understand how institutions, laws, landowner motivations and livelihoods influence land use decisions because these multifaceted, often uncoordinated decisions across different landowners influence the forested landscape pattern (Williams 2003). The social science literature concerning forest regeneration in the tropics has focused on communally managed forests (Nagendra and Southworth 2010; Nagendra 2007; Poudel 2012; Wollenberg et al. 2007). Yet, privately owned forestlands are a significant component of the landscape. In Central America, for example, 2% of forests are communally owned and managed while 47% of forestlands are privately owned (FAO, 2010). Here, I explore how land tenure, landowner motivations, and livelihoods are associated with landowners' decisions to allow forest to regenerate on their lands. I also evaluate how landowners' value forests and what tree species they tend to favor on their farms.

Methods

Site description

Our study site was in the tropical dry forest biome of Guanacaste, Costa Rica. Mean annual temperature is 25° C and dry season length ranges from 5 to 6 months (Gillespie, Grijalva, and Farris 2000; Holdridge 1967). Globally, tropical dry forests are the most endangered biome so forest regeneration in dry forest regions is particularly critical for this ecosystem type. Guanacaste is the largest province in Costa Rica yet has the lowest population, only 7.6% of Costa Ricans live in Guanacaste (Instituto Nacional de Estadística y Censos (INEC), Costa Rica 2013); the provincial city is Liberia and 19.2% of the provincial population dwells within city borders. The largely agricultural-based economy has shifted to a service oriented tourism-based economy; in 1950, for example, 80% of the population worked in agricultural industry while in 2000 only 8% remained in the agricultural sector (Calvo-Alvarado et al. 2009). Historic land use in Guanacaste was dominated by extensive, hacienda-style ranches (Edelman, 1985).Both During the latter half of the 20th century, both deforestation and secondary forest regeneration in Guanacaste was tied to Costa Rica's integration into and subsequent fall out of the international beef market (Calvo-Alvarado et al. 2009; Edelman 1985). However, drivers of forest changes in Guanacaste have shifted with time and changing contexts (Calvo-Alvarado et al. 2009; Daniels et al. 2010).

Sample

I used an ecological survey to guide respondent recruitment (McClellan et al. Ch. 2); primary goal was to match public and private forests arrayed across soil and forest age gradients. I used a Geographical Information Systems (GIS) approach with both GIS layers of public/private lands ("Costa Rica Atlas" 2008) and a time series of georectified Landsat satellite images (1986, 1996, 2000, and 2007) to locate private farms around *Area Conservacion Guanacaste* (ACG) and *Area Conservación Arenal Tempisque* (ACAT) that had forest that matched this public park land forest in terms of forest age

and soil type. Although I made a concerted effort to sample evenly among small, medium, and large farms, small farms rarely had the quantity of forest required to conduct the ecological research component (>2 ha forest patch to accommodate a 50x20 m plot with a forest buffer area). Therefore, the final sample included primarily medium (~100-500 hectares) and large sized (>500-9,000) farms surrounding public forests in the tropical dry forest zones of Guanacaste Province. Furthermore, land area nearby the public forests in our ecological study zone was predominantly medium to large sized ownership parcels. The sampling strategy focused on visiting the private farms with forests I had identified in satellite images and asking managers for landowner contact information. The final sample included 30 landowners who had secondary tropical dry forests on their property.

Landowner Interviews

All interviews were conducted in-person by the PI and lasted from 45 minutes to 4 hours, generally in the respondent's home. Other individuals such as family members or a land manager were occasionally present during interviews and contributed to the conversation. Interviews were conducted based on a questionnaire with 108 questions and in Spanish, the PI's second language.

Questionnaire themes were structured to parallel a conversation and allow more sensitive topics towards the end of the interview (Alreck and Settle 2004; Schwarz 1996). Themes focused on (i) general farm information and infrastructure; (ii) farm management; (iii) landowner forest values rankings; (iv) tree species commonly utilized on farms in Guanacaste; (v) Costa Rica's Payment for Environmental Services (PES) program; and (vi) demographic information. I employed a mixed question design with 70% closed, 12% open, and 18% Likert scale questions, (Alreck and Settle 2004; Krosnick and Presser 2010). I conducted two pilot interviews with non-study landowners in Guanacaste to evaluate the questions and then modified the questionnaire appropriately.

I took summary notes of responses and, for 25 out of 30 interviews, digitally recorded interviews both to cross-check data and provide context regarding key findings. For eight open-ended questions, I coded the 25 transcribed interviews and classified landowner responses by key themes. Although these questions were open-ended, they were also specific, such as: 'what factors most influence your land management choices? These directed questions generally resulted in short responses, which I coded by hand. I focused on the key themes for the first round of coding but also iteratively assessed transcriptions to allow emergent themes (Glaser 1992).

Analysis

Quantitative data were non-normal, skewed, and kurtotic thus, for subsequent analyses, I used a variety of non-parametric statistical tests based on variable type. I used Kendal's tau to assess correlations between interval data, Chi-sq test for nominal variables, and Mann-Whitney U for interval data to compare differences between groups (IBM Corp. Released 2011). All significant p-values were corrected using the Holm's correction for multiple comparisons (Holm 1979). I chose the Holm's correction instead of Bonferroni because the Bonferroni has poor statistical power for assessing type II errors (i.e. rejecting an incorrect null hypothesis) (Nakagawa 2004). Asking directly for annual income often results in respondent refusal (Alreck and Settle 2004), so I provided respondents with a printed table of annual income ranges in Costa Rican colones each labeled with sequential letters from the Spanish alphabet. I also asked about the percent annual income derived from crops, cattle, tourism, and off-farm income. To obtain an estimate of annual income from each category, I selected the mean dollar amount for each annual income range and multiplied by percent category each respondent reported to get estimated annual income from crops, cattle, tourism, and off-farm endeavors. One respondent made $0 annually while two respondents made above $400,800; for those two categories I used $0 and $400,800 instead of the mean. All annual income information is reported here in United States dollars. Since the majority of our data were highly skewed

and kurtotic, I identified and labeled variables with significant skew and kurtosis (Table 5). I determined significance at alpha=0.05 critical values for each sample size (a) is positive skew, b=negative skew, c=platykurtic; d=leptokurtic; e=normal this serves to simplify and highlight the variability but I also include values for interested readers.

Results and Discussion

The landowner sample was largely composed of wealthy mid to large size farm owners. Landowners reported that the main factors affecting their decisions for crop and pasture land use were associated with the market factors, especially market prices. Ranching, agriculture, agrotourism, and off-farm income provided varying percentages of landowners' income portfolios. Off-farm income was a consistently important source of livelihood for many of the landowners; forty-five percent of landowners depended on off-farm income for 55% or more of their total annual income. Landowners' forest management decisions focused on conservation or non-interference of natural forest regeneration processes (i.e. no management). Most landowners had contracts with Costa Rica's national Payments for Environmental Services program; however, forest additionally (PES avoided deforestation) was low. Landowners recognized and valued their forests for the benefits provided to them (e.g. on-farm water protection) and to society at large (e.g. carbon sequestration). For tree species management, most landowners' mentioned a similar suite of dry forest tree species that they used for on-farm management such as live fence posts or conventional fence posts. Further, valuable timber species were mentioned most frequently as being used for remnant trees, encouraged to grow, or rare.

Landowner sample

Although the interview sample size was small, the amount of land was not insignificant and these landowners' owned a sizeable extent of Guanacaste's forest cover. This reflects the fact that the sample included multiple mid-sized and large farms. Land ownership patterns in Guanacaste typify the legacy of colonialism with a highly skewed distribution of farm size (Brockett 1990; Edelman 1992; Edelman 1985). Farm size, furthermore, is generally correlated with numerous socioeconomic variables such as wealth (Barbosa 2009; Brockett 1990); landowner median and mean total annual estimated income—USD 57,000 and 148,368, respectively—was well above the Costa

Rican gross national income per capita of USD 8,475 (United Nations 2013). The thirty landowners owned a total of 43,099 farm hectares in Guanacaste province. Olson and colleagues (2001) calculated that the potential extent of tropical dry forest in Costa Rica is 755,900 hectares; Portillo-Quintero and Sánchez-Azofeifa (2010) used that potential extent of tropical dry forest as a baseline and reported that 27,900 of the 179,500 remaining hectares of tropical dry forest Costa Rica was protected. Therefore, privately owned land area represents 5.7% of the potential land area extent in which tropical dry forests could grow in Costa Rica. In comparison, the total forest cover protected through public tenure represents only 3.7% of the potential tropical dry forest land extent (Portillo-Quintero and Sánchez-Azofeifa 2010). Of course, private farms have multiple land use objectives, so it is unlikely that all private lands would be forested; however, landowners' in this study reported that the total forest allowed to regrow from non-forest to forest during their tenure was 4,692 hectares and that forest area is 17% of the total protected forest area in Costa Rica (Portillo-Quintero and Sánchez-Azofeifa 2010); in addition, landowners reported that their total forest cover was >8,000 ha, so they manage a considerable amount of forest cover.

Landowners' management decisions

Multiple factors affect management decisions but market prices was the most important factor. Since our research questions centered on what factors influenced landowners' decisions to allow forest regeneration, I sampled privately owned farms that had secondary tropical dry forests. Twenty-four percent (7/30) of landowners maintained forest cover during their tenure; in other words, the quantity of forest cover they reported in the interview was equal to the quantity of forest cover evident at the beginning of their tenure. Seventy-two percent (21/30) had allowed forest to regenerate during their tenure in other words the total forest cover had increased during their tenure. In general, forest cover changes occur as a consequence of agricultural or pasture expansion or contraction so I asked landowners an open-ended question on what factors most influenced their crop

and pasture land use choices. The most common responses centered on markets and, more specifically, market prices.

> *"The market price is in charge. For example, I have a ranch, but the price of cattle lately has been so low, that I would prefer to rent it [for cattle] instead of keep cattle on it. So, it's about market prices, supply and demand."* (Interview #11)

Landowners' faced constraints that affected their management decisions; these included issues such as the size of the farm, pasture, or cultivated area available to them. Landowners noted water availably constraints due to the strong seasonality of rainfall or the lack of irrigation infrastructure. Three landowners had made the switch from extensive cattle ranching for meat production to dairy farming for milk production; they discussed issues related to market conditions such as the increased frequency of revenue for diary and poor returns for beef production. The fact that markets and market prices were the most important factors influencing land use management decisions is not surprising; these are working lands that landowners depend on to generate a proportion of their incomes, so their decisions are strongly affected by markets and market prices.

Livelihoods

Off-farm income

Landowners depended on their farms to support their livelihood to various degrees. The range of annual income among landowners was substantial, ranging from $0 to >$400,800. Approximately seventy percent (20/29) of respondents relied on off-farm income to some extent. A smaller but still considerable twenty-four percent (7/29) of landowners depended on off-farm income for 90-100% of their total income. Although increasing off-farm income is sometimes correlated with forest regeneration in other studies (Hecht and Saatchi 2007; Morse et al. 2009; Rudel, Perez-Lugo, and Zichal 2000), off-farm income was not significantly correlated with the number of hectares of forest allowed to grow during landowner tenure in this study, although the trend was

positive. Further, based on the skew and kurtosis values, off-farm income was a consistently important source of income for many landowners (Table 5), suggesting that farm income did not provide a sufficient income to be the sole source of livelihood for most landowners. Said another way, 45% of landowners (13/29) depended on off-farm income for 55% or more of their total income.

Ranching

Guanacaste is the historical heartland of cattle ranching in Costa Rica and many landowners depended on ranching for a proportion of their annual income, although more landowners depended on off-farm income compared to ranching (Table 5). All landowners had pasture even if they did not own cattle (Table 5). A few landowners rented their pasture for cattle foraging while others maintained pasture for horses. Estimated annual income from ranching was positively correlated with early forest successional growth (*charral*). Ranch production systems are often associated with early successional growth (Perz and Walker 2002) (Serrão and Toledo 1990); however, early vegetation does not necessarily develop into secondary forest as it can be cleared for other land uses.

Eighty-seven percent of landowners (26/30) had ranching operations; however, nineteen percent (5/26) of those reported no income from ranching.

> *"Here is the situation. Look, beef here is sold for less than half of what it is sold for in the USA, and the cattle feed costs more than double what it does in the USA. You just can't do it."* (Interview #17)

In other studies, scholars have argued that ranching in Guanacaste has a strong cultural legacy and cattlemen enjoyed prestigious status, suggesting that some landowners may maintain cattle ranches as hobby farms, particularly those who own small to mid-size farms (range of 30-200 ha) (Brockett and Gottfried 2002; Brockett 1990; Edelman 1985; S. Evans 1999; Schelhas and Sánchez-Azofeifa 2006). However, in this study, the nineteen percent who reported no income from ranching owned farms between the ranges

of 130-9000 ha and had cattle head that ranged from 10-750. Another explanation for operating at a loss is simply that cattle ranching is not profitable in the current international trade system (Anderson 2010) but sunk costs and a lack of profitable alternatives induce landowners to remain through the economic troughs. Cattle ranching was profitable from the 1960s until the mid-1980s when it was heavily subsidized in Costa Rica; and although it is not currently profitable, cattle ranching is still considered a viable land use option as it requires low labor and nutrient/water inputs compared to alternative land uses such as agriculture (Roebeling and Hendrix 2010).

Since extensive ranching systems require less water distribution, fewer inputs, and can be managed on poorer quality soils compared to crop systems, it remains an attractive land use option (Schelhas and Sánchez-Azofeifa 2006). Especially considering the peculiar predicament that landowners face as a result of Costa Rica's strict private forest land use laws; if natural forest regenerates on their property, the landowner has effectively 'lost' that portion of his land to alternative future land uses, barring pursuit of a bureaucratic permitting process (Consejo Nacional de Áreas de Conservación 2010). Thus, it is possible that landowners maintain pasture to avoid that loss.

> *"You cannot touch the forest because of the laws of Costa Rica. It is very difficult for them to give you a permit to cut trees down, and you do not live off of that [the forest]. If you are committed to the environment and want to conserve the environment, then you buy [land], but it is not profitable. If you are a rancher you can have cattle, if you have irrigation and a river you can have corn or sugarcane, and the value then becomes much greater."* (Interview #27)

Farming

Approximately half (14/29 or 48%) of landowners derived between 2-100% of their annual income from crops while fifty-one percent (15/29) did not earn an income from crops. Farms with significant farming operations had water infrastructure to support croplands; the three farms that had the highest proportion of croplands were in close proximity to rivers. Rice and sugar cane, crops that both require significant water inputs,

were the most important crops in terms of extent with a total of 7,400 ha and 5,703 ha, respectively.

Agrotourism

Agrotourism was not widely prevalent in our sample; eighty-six percent (25/29) of landowners reported no tourism activities on their properties. Yet, although only fourteen percent (4/29) derived income from tourism, it was an important source of income for two of the landowners: tourist activities represented 80% of their annual income and these landowners had high total annual income ranges of $200,400-$255,600 and $400,800 and above, respectively. Further, the number of tourists visiting these farms annually was 33,000 and 28,000, respectively. It is likely that only two landowners derived significant income from tourist activities because of the high financial start-up investments required. One of the farms had a canopy tour while the other had a canopy tour, horseback riding tours, and hotel facilities: the infrastructure, equipment, advertising budget, and personnel required for these ventures is likely cost-prohibitive for the majority of landowners.

"This [tourism venture] is what most produces for me." (Interview #10)

The Costa Rican service sector, which includes tourism, leads the national economy, accounting for 63% of GDP and employing 64% of the population (Bagdonis et al. 2009). These results accord with a study of 68 Costa Rican agrotourism farms of which only 10% had high and constant visitation levels (Zumbado-Morales 2010). As found in this study, agrotourism does not appear to be a chosen livelihood for many landowners likely because it requires substantial investments.

Payments for Forest Environmental Services

Payments for Environmental services (PES) programs were proposed as a mechanism through which landowners could be compensated for the ecosystem goods and services they provide to society (Daily 1997; Millennium Ecosystem Assessment

2005). Forest protection and regeneration provide a suite of environmental services such as carbon sequestration and water purification (Robin L. Chazdon et al. 2009). The PES program in Costa Rica is the poster child of the Payments for Environmental services approach, so there are numerous studies evaluating program cost, involvement, and efficacy (Daniels et al. 2010; Pagiola 2008; Rojas 2003; Sánchez-Azofeifa et al. 2007; Wunder, Engel, and Pagiola 2008). The first line of interest in assessing a PES program is whether or not landowners are aware of the program. For example, in northeastern Costa Rica, Arriagada and colleagues (2009) found that non-participant landowners cited lack of information as the primary cause for non-participation. Conversely, I found that the majority of landowners (26/30 or 87%) had heard of the PES program from a variety of sources, including newspaper (25%), foresters (18%), the Ministry of Ranching and Agriculture (18%), the Liberia Agricultural Center (11%), neighbors (11%), and other sources (20%).

Not only did landowners know about the PES but they were actively engaged in the program or seeking out future contracts. Forty percent (12/30) of respondents either had a PES contract in the past or had a contract at the time of the interview, another seven percent (2/30) had applied for a contract, and twenty-seven percent (8/30) were interested in applying for a contract. For the 40% of landowners who had a contract, the range of the forest area included in the program varied from 13-1,500 hectares with a total of 5,118 hectares included in PES. The landowners with a PES contract had a property size range from 300-8,200 hectares with median of 700 and a mean of 1,936 hectares. Seventy-three percent (22/30) of landowners were either interested in applying for a contract, had applied, or had a contract while twenty-seven percent (8/30) were not interested. Those who were not interested in obtaining a PES contract cited a number of reasons such as inadequate land or forest resources (3/8), inadequate compensation (1/8), reluctance to forfeit land use decision making (1/8), procedural difficulty involved in obtaining a contract (1/8), and reluctance to participate in government programs (1/8). Earlier studies of participation in Costa Rica found that farm size, absentee ownership,

and reliance on off-farm income are significant positive predictors of PES program participation (Arriagada et al. 2009; Legrand, Froger, and Le Coq 2013; Morse et al. 2009). Since our sample consisted primarily of landowner with large parcels, it is not unexpected that many landowners had PES contracts.

The Forestry Law 7575 was created in part for the expressed purpose of compensating landowners for environmental services provided and, since PES transaction costs are equivalent regardless of farm size, larger farms generally provide more forest cover per conservation dollar (Morse et al. 2009). However, an active argument in the conservation literature asserts that if conservation incentives are spent preserving forests that would have been preserved even without those incentives, the limited pool of conservation funds are not being used efficiently: conservation funds should be spent on forest additionality, or forest cover that would not be preserved without conservation incentives (Andam et al. 2008; Robalino and Pfaff 2013). Large land holders tend to participate in Costa Rica's PES more frequently than small to mid size landowners (Zbinden and Lee 2005). If additionality is low for large landowners, perhaps conservation investments should target small to mid size farm landowners in high deforestation risk areas. Costa Rica does have organizations of small to mid-size land owners such as the Commission for Forest Development in San Carlos (CODEFORSA) and the national PES program also supports small farmers in Guanacaste through the Guanacaste Association for Forestry Development (AGUADEFOR) (de Camino Velozo et al. 2000) yet programs such as these do not appear to be commonly available in communities of small landowners in Guanacaste (McLennan and Garvin 2012).

PES contracts in Costa Rica are not an economically viable long-term strategy for landowners that have the option of other land uses under current or future market conditions. A PES contract currently lasts a maximum of ten years and does not generate significant income; further, once a forest develops, the landowner loses all management rights to that portion of their land. Thus PES additionality should be expected to be low.

Additionality in our study was low: of the forty percent (12/30) of landowners who had a
PES contract, ninety percent (10/11, one refusal) reported that they would have allowed
forest to regenerate without conservation incentives. The total number of hectares
landowners' reportedly had in PES contracts was 6,018 and only one landowner, who had
a PES contract of 300 hectares, reported that he would have used the land for productive
purposes, therefore, only five percent of the total 6,018 hectares can be considered forest
additionality. An important caveat to this discussion, however, is that Costa Rican forest
policy diverges considerably from most national forest policies in its comprehensive
commitments to forest conservation. The PES payment stipulation was written in the
same law that revoked private landowners' tenure rights to their forests; thus, even if
additionally is low, the overall effect of Forestry Law 7575 in conserving private forests
cannot be overlooked (Robalino and Pfaff 2013).

Forest value

A corollary issue related to Forestry Law 7575 that has not received much
attention in the literature is that, if an 'official forest' develops, the landowner forfeits
their tenure land use rights for that portion of their property. Thus, they lose all future
income from productive land uses or future development. Forestry Law 7575, therefore,
may have effectively lowered the baseline economic value of land that contains 'official
forest'. The forest value for both forest already on the farm and forest allowed to
regenerate during a landowner's tenure—either through a PES contract or not—may
reduce the value of the land. In this line of thought, I wanted to test the hypothesis that a
hectare of property containing forest would have a lower purchase price than a hectare of
property with pasture. I asked landowners to estimate the purchase cost of one hectare of
pasture vs. one hectare of forest of a parcel in close proximity to their farm. I requested
they predict prices in close proximity to their farm under the assumption that local
estimates made by local actors would be more accurate. I further asked them to explain
the justification behind their estimates. Although farmland is a significant part of the

Guanacaste landscape, I did not include croplands because cropland value is highly dependent on irrigation appraisal (Edelman 1992). The monetary values landowners' reported were highly variable and some landowners responded "less" or "more" instead of specifying a number, so I classified values categorically as forest cost equal to, less than, or more than pasture cost. There was no statistically significant difference between the three groups (χ^2=0.609, df 2, p= 0.739). Of the twenty six landowners who responded, 38% said the cost was equal, 33% said a hectare of forest was worth less than a hectare of pasture, and 29% said that forest was worth more relative to pasture. The following landowner comments represent diverse perspectives on property value related to forest cover:

(property with forest more valuable)

> *"Because [the forest] is a resource that is more difficult to replace, it is a more valuable resource in the sense of its biological riches. The forest is more beautiful."* (Interview #23)

(property with forest less valuable)

> *"Forests do not generate anything, or very little, in economic terms, in terms of money. In terms of the environment, we can't put a price to its value, but no one pays for it either. The closest thing to it is this program you talk about "payments for environmental services."* (Interview #7)

> *"Pasturelands feed cattle, but the forest creates oxygen and no one is paying for that."* (Interview #18)

There were several key themes garnered from the open-ended question in which landowners spoke of Guanacaste land values. Landowners described a buyer dichotomy; buyers on one side were described as 'locals', 'producers', and 'developers' while those on the other side were described as 'North American', 'foreigner', and 'someone with resources'. Landowners said that land value depended on who was buying and what land uses they intended.

"Depends on the client, some will say "No. That does not work for me because it has a lot of trees." But someone else, especially a North American, a gringo, will say "How beautiful—it's got so many trees". (Interview #6)

McLennan and Garvin (2012) found that Guanacaste landowners' land use strategies in some coastal communities had changed to encourage foreign land investments by allowing forest to regenerate on their farms. In an effort to attract foreign direct investment, the Costa Rican government has promoted residential tourism and Guanacaste's coast, nicknamed "Costa Rica's Gold Coast", has seen the lion's share of that growth; Costa Rican foreign direct investment in real estate increased from 5% in 2003 to 34% in 2007 (van Noorloos 2011).

Landowner motivations

Landowners value forest for both economic reasons and less calculable but no less tangible reasons such as enjoyment or sense of responsibility (Bengston, Asah, and Butler 2011). Based on eleven statements meant to assess a variety of forest values, there was little variation in landowner responses: the majority of landowners 'agreed' with all of the forest value statements (Table 6). Overall these results suggest that landowners recognize and appreciate the many benefits their forests provide for them and society. In crop and pasture land use decisions, however, landowners reported that markets and market prices most influenced their choices (see previous section); Thus, although landowners' appreciate forests for the benefits and services those forests provide, land use decisions are driven by market economics.

Forest Management

The Costa Rican context of restricted forest land use on private lands appeared to affect landowners' forest management; most landowners' revealed that they either left the forests alone or that they managed their forests only for conservation. Others have found that Landowner forest management decisions are often framed in terms of market factors such as timber prices (Koontz 2001) or non-monetary benefits such as recreation (Butler

and Leatherberry 2004). In Costa Rica, however, it is illegal to cut or sell timber from naturally regenerated private forests, to hunt (Forestry Law 1999), and forests are generally not used for recreation by locals. Based on a direct question about what factors most influence forest management decisions, the most dominant response was that they did not manage forests or that they managed forests specifically for conservation.

> *"The goal of forest management is to become carbon neutral. Aside from the fact that we believe in the forest, we acknowledge the contribution of the forest to the atmosphere. So our decision making is focused on protecting it from fire, to help with its conservation… to collaborate with the environment… the natural environment. That is to say, factors in our decision making for forest include measures for damage prevention. We work to prevent, prevent, prevent so that there is no damage."* (Interview #20)

Landowners mentioned over six diverse factors that influenced their forest management choices, most often noted were wood provisional benefits for construction and fence posts or, more generally, valuable timber. Some expressed enjoyment of the trees and wildlife the forests attract as factors that motivated their forest management. Others mentioned water protection and climate change mitigation. Two landowners mentioned biophysical management issues; for example, the quantity of rainfall in the wet season affected the extent of forest fire precautions undertaken in the dry season. Another noted that the land area prohibitive to tractor use, he allowed to regenerate into forest. Finally, a few landowners also mentioned the change in conservation ideology in Costa Rica. One landowner referred to this as "the global current…we are all going toward protecting the forest, we are thinking green. And it's logical." (Interview #6)

Management decisions that affect forest ecosystems

Road access, water access, and fire management are all important factors in Guanacaste farm management. In this study access to a paved road to transport farm products was not cited as a factor limiting farm production; likely this is due to the fact that all farms were in relatively proximity to a major and well-maintained highway, the Pan-American. Water access is an important issue in Guanacaste due to the 5-6 month

dry season; landowners with access to a water canal earned significantly more of their income from crop production. Fire management is also an important issue due to the lengthy dry season. Historically, fire was used as a method for cleaning pasture; landowners in this study most frequently mentioned employing chemicals/herbicides to clean pasture, although some said that fire is still used. I discuss road access, water access, and fire management in more detail below.

Road Access

Road access and quality is generally a significant driver of deforestation (Kaimowitz and Angelsen 2008; Laurance and Curran 2008; Sader and Joyce 1988). However, in my study, most landowners with lower quality dirt road access to their property did not perceive that this decreased their production capacity while those with paved road access did not think that this increased their capacity. Most landowners (21/30 or 70%) had dirt road access to their farm and the closest paved road ranged from 1-17 km distance from the main farm gate. However, most landowners who had dirt road access were not far from a relatively well-kept major paved road, the Pan-American Highway (mode =1 km, mean=6.67, median=6 km). Of landowners with dirt road access to their farm, eighty-one percent (17/21) said that dirt road access did not limit the number of cattle they had or number of hectares of crops they decided to plant while nineteen percent (4/21) stated that the road access did affect their decisions. Thirty percent (9/30) of landowners had immediate access to a paved road and eighty-eight (8/9) of these respondents said that this did not increase the number of cattle they maintained or number of hectares of crops they decided to cultivate on their farm while eleven percent (1/9) said that it did.

Water Access

Limited rainfall during the 5-6 month dry season and significant rainfall in the wet season poses a substantial management issue for landowners in Guanacaste (Edelman 1992). Based on a hypothetical question about water availability, almost half reported

that they would increase their cattle herd if they had more water available, and over seventy percent said that they would cultivate additional cropland (Table 6 section B). Likely, the average price disparity between extensive cattle ranching and crop production is driving this difference. Almost all (28/30 or 93%) landowners had some access to water for farm production during both the dry and wet seasons, however, landowners that had access to an irrigation canal earned both a significantly higher percentage of their income from crop production and higher estimated income from crop production (Mann-Whitney U test U=2 and 9, p-value 0.001 and 0.000, respectively). Water access, however, may be limited not because of lack of water availability but due to other factors such as the cost of electricity required to pump water.

Fire Management

An issue of particular significance for landowner operations in tropical dry forest regions is fire management (Miles et al. 2006). Historically, fire was used to clear forest, remove early successional growth from pasture, and incite pasture grass growth. However, native tropical dry forest species have not evolved to cope with the imposed fire management regime so these species are negatively impacted (H. P. Griscom et al. 2011). The past few decades has brought about a shift in pasture burning regulations and norms; currently, burning crop residue or pasture is illegal in Costa Rica without a permit, yet illegal burning does occur (Allen 2001). In Guanacaste, using fire as a management tool to clear forest and pasture is stigmatized, so I expected landowners to be hesitant to admit to using fire on their farms. To reduce bias in socially acceptable responses, I asked parallel, open-ended questions about self-reported fire use and fire use by landowners on other farms in Guanacaste (as suggested by, Alreck and Settle, 2004). Landowners mentioned a total of 7 methods for cleaning pasture: the most mentioned methods in order of importance were chemicals/herbicides, weed-eaters, machetes, and tractors (fire was only mentioned as a use by other landowners). Chainsaws, cattle, and sickles were also noted as methods for cleaning pasture but with less frequently. The

trend towards landowners admitting that others used fire to clean was not significant after a Holm's correction. Fire is a particularly destructive threat to tropical dry forests worldwide (Miles et al. 2006) and even infrequent fire use during the dry season can cause substantial forest destruction. The use of fire may be difficult to 'put out', as one landowner noted, *"there are a lot of people who like to start fires in the summer."* (Interview #11).

Tree Species

Landowners in Guanacaste employ particular tree species for different uses on their farms, and their selection of particular tree species can affect forest regeneration dynamics (Schlawin and Zahawi 2008). I asked landowners both which species they tended to use and why they favored those species. I found that species used as conventional or living fences, left as remnant trees, and encourage to grow were generally used due to those species trait characteristics. For example, conventional fence species were chosen for their durability while living fence post species were chosen for those species ability to coppice. Landowners' often mentioned valuable timber species as species that they kept as remnant trees, encouraged to grow, and noted as rare species.

Fences

Landowners in this study used both conventional and living fences; they selected conventional fence species based on durability and local abundance while they chose living fence species that were able to resprout and locally available. A noticeable management practice in Guanacaste landscapes are the presence of living fences; in lieu of posts, some farms feature closely spaced trees that serve as living fences. The species are usually chosen for their ability to coppice; this capability to resprout from a branch facilitates building and managing live fences. A study of naturally regenerated secondary forests in Puerto Rico found that their forest inventory included a large number of individuals of *Tabebuia heterophylla,* a species used for live fences (Marin-Spiotta, Silver, and Ostertag 2007). Both living fences and conventional posts are used for

fencing in Guanacaste. In this study, all landowners used conventional post fences on their farms. Fifty-seven percent (16/28) of landowners used primarily conventional post fences while seven percent (2/28) used both in equal proportion. Eighteen percent (5/28) used only conventional fence posts while another eighteen percent used only living fence posts. The species used most frequently for live fence posts are listed below (Figure 2). As expected, the majority of landowners chose species based on their ability to resprout from branches; in addition, landowners frequently mentioned that they chose species that were available on their farm or locally abundant.

Fence posts can be harvested both from timber or harvested nondestructively by cutting mature tree branches. Species used for fence posts are likely chosen for their durability—for example, high wood density and decomposition resistance. Species with these qualities are also often used for timber, although highly prized or expensive timber is not used for fence posts (Cordero and Boshier 2003). As anticipated, landowners chose fence post species based on durability, availability, and abundance.

> "*They say that the níspero [Manilkara chicle] was the iron of the old days. In past centuries it was used like iron. To build bridges. Water could not destroy it, it's indestructible like iron, the níspero is.*" (7)

Remnant Trees

Remnant trees were often chosen because they were valuable timber species. Specific remnant tree species are often left on the landscape depending on landowner land use and management goals. When forests are cleared to create pasture, for example, certain species are selected as remnants (Harvey et al. 2011). Landowners choose these tree species for a number of reasons; for example, remnant species may have high timber quality or provide shade/fodder for cattle (Esquivel-Mimenza et al. 2011). Remnant trees also promote tree diversity of secondary forests that regenerate subsequent to land abandonment (Schlawin and Zahawi 2008; Turner et al. 1998). When asked what tree species they tended to leave as remnants. The four species most noted were all valuable

timber species (Figure 2). Sixty-two percent (18/29) also mentioned a species commonly consumed and dispersed by cattle, *Guazuma ulmifolia*; in the parallel ecological study (Ch. 2) in which I compared public and private tropical dry forests, I found that *G. ulmifolia* was the most abundant species in private forests. Moreover, the species landowners' mentioned accord with a pasture tree inventory conducted on 16 cattle farms in Guanacaste: Esquivel and colleagues (2011) found that 50% of the trees in pasture were timber species, 27% were fruit bearing species, and 27% were forage species. Remnant trees attract seed dispersers such as birds and bats and enhance tree species diversity (Guevara, Purata, and Van der Maarel 1986; Harvey et al. 2006). In Costa Rican lowland wet forests, Schlawin and Zahawi (2008) found that tree sapling diversity, density, and girth were greatest within a 10 m buffer circumambient to the trunk. In our study, landowners' commonly reported that they chose particular remnant species because those species provided timber. Landowners also mentioned selecting remnants that provided shade and fodder for their cattle; however, this was not universal, one landowner said that he kept pastures free of tree species, because cattle would eat almost anything in the dry season when fodder is scarce, including seeds that are harmful for their digestive systems. Some landowners also mentioned that they selected particular species as remnants to conserve that species and a few said that they chose specific remnant species as ornamentals.

> *"I have guacimo [Guazuma ulmifolia] because it provides good shade and is an excellent food source for cattle…and not only for cattle but for deer and for birds."* (13)

> *"We leave trees that could be used for wood or … to conserve, more than anything to conserve the forest. If they are large trees and if they are trees that provide fruits, then we take that into account, they are not cut down. We let them grow depending also on the type of species, because, for example, the alcornoque [Licania arborea] can be hardly found here… they are in danger of extinction so we leave them."* (16)

Tree Species Landowners Encourage

In addition to preserving specific remnant species when forests are cleared for pasture, landowners may actively encourage species that germinate and develop on their farms. A species may be encouraged on a farm because of its management use; for example, a particular species may be used for erosion control or encouraged because of timber value (Cordero and Boshier 2003). The species landowners' mentioned most frequently as ones they encouraged were valuable timber species (Figure 2) for their economic value. Landowners also mentioned that they encouraged trees that provided shade and fodder for their cattle. Some mentioned that they encouraged tree species from which they could harvest fence posts. Some landowners said that if it were an endangered species, they would encourage it on their farms.

Rare Tree Species

In this study, a particular interest was native dry forest tree species that were once common but are currently rare. Similar to results above, the top species noted were timber species (Figure 2). Unlawful logging in Costa Rica supplies between 25-35% of commercial timber and is especially prevalent on private lands (Miller 2011). Tropical dry forests have many valuable native tree species and high-grading appears to be widespread in this biome (Fredericksen et al. 2000). Gonzalez-Rivas and colleagues (2005) found that, in Nicaraguan tropical dry forests sampled in 1994 and resampled in 2000, species used for timber and firewood had declined. In the parallel ecological study in Ch. 2, integrative metrics of biodiversity such as the Shannon diversity index and species accumulation curves did not differ significantly between public and private forests. However, species composition was distinctive: highly valuable tropical timber species, *Swietenia macrophylla* (mahogany) and *Cedrela odorata* (Spanish cedar) were significantly more abundant in public forests, suggesting high-grading within private forests. Overwhelmingly, during conversations about tree species, landowners noted that specific species had declined as a result of timber extraction. Many landowners also

considered agriculture and pasture expansion responsible for species rarity. Some cited tree species susceptibility to fire. Landowners mentioned that the ecological attributes of these species may impede recovery; for example, species that are not easily dispersed and/or that grow slowly. Finally, landowners cited poor timber management practices in that trees were not replanted nor were mature trees left to re-seed.

Conclusions

Privately owned tropical forests contribute to environmental services production and biodiversity preservation. Landowners' forest management decisions have corollary effects for society at large, so factors that affect those decisions are consequential. Yet private tropical forests and the landowners who manage them have not received sufficient attention in the literature. Assessment of land tenure and the bundle of rights that a specific tenure system describes are a necessary first step to understanding the context of private forest management. Costa Rica national forest policy is unusual compared to other countries in that all forests—as defined by Forestry Law 7575—are protected for conservation regardless of whether those forests are publicly or privately owned. Given this national conservation forest policy, it makes sense that the factors landowners' mentioned with greatest frequency as affecting their forest management decisions were either no management or management strictly for conservation. Conversely, landowners' noted that their agricultural and pasture land use decisions were primarily affected by market prices. Agricultural and pasture extensification across the tropics and in Guanacaste generally come at the expense of forests (Brockett and Gottfried 2002; Gibbs et al. 2010) so, at first glance, it appears contradictory that market prices most affected landowners' farm land use management decisions while conservation considerations most affected forest land use decisions; but given the national forestry laws, it makes sense. I also assessed landowners motivations related to a broad range of forest values to try to understand whether those values affected landowners forest management; landowners acknowledged and appreciated the benefits forests provided to themselves and society; however, since the majority of landowners' 'agreed' with all forest value Likert statements, there was not sufficient heterogeneity to develop understanding around how those forest values may have affected landowners' decisions.

Landowner livelihood strategies associated with specific land uses can differentially affect forests. Of the landowner livelihood strategies assessed here, off-farm income and ranching were consistently important sources of income for landowners. Income from crops and agrotourism were less consistently evident across the landowner sample. For croplands, this likely this is due to water infrastructure limitations. For agrotourism, only two landowners earned a significant proportion of their total annual income from agrotourism; likely, this is due to the costly investments required for developing and maintaining a high-volume on-farm tourism venture. In this study, landowner livelihood strategies were not significantly correlated with the quantity of forest allowed to regenerate during landowners' tenure. Off-farm income in other Latin American has been shown to promote forest conservation (Rudel et al. 2005; Sunderlin et al. 2005; Zbinden and Lee 2005). Extensive ranching operations were the primary cause of deforestation in Guanacaste through the 1970s, yet ranchlands often maintain some forest patches and remnant trees, which promote forest regeneration when market pressures abate (Calvo-Alvarado et al. 2009; Esquivel-Mimenza et al. 2011; Turner et al. 1998). Other studies in Guanacaste have found that croplands, once established, rarely revert to forest (Arroyo-Mora et al. 2005; Daniels et al. 2010). While not specific to forest regeneration, in a study of agrotourism ventures in Costa Rica, Zumbado-Morales (2010) found that 80% of ventures contributed to conservation (either through on-farm conservation areas or via monetary donations to conservation organizations).

Another objective of this study was to assess whether landowner decision making may affect not only forest cover but also forest biodiversity. In Ch. 2, an ownership signature emerged in the tree species compositional differences between public and private forests that seemed related to landowners' tree species management. For example, the highly prized timber species, Mahogany (*Swietenia macrophylla)* and Spanish Cedar *(Cedrela odorata),* were underrepresented in private forests. In Ch. 3 landowners noted those species as species rare as a result of timber extraction, agricultural expansion, and

susceptibility to fire. Thus, landowners commonly manage a suite of specific tree species (Table 11) and this may affect the tree species abundances in private forests (e.g. Ch. 2).

Landowner decisions regarding forest management are affected by Costa Rican tenure and associated land use rights (Brockett and Gottfried 2002; Calvo-Alvarado et al. 2009; Edelman 1985). Livelihood options and landowner motivations in Guanacaste have shifted with changing economic markets; the national importance of the agricultural sector has waned while the services sector, which includes tourism, now dominates the national economy. The restrictive private forest land use laws and the spike in real estate sales associated with the Guanacaste tourism boom may also influence landowner decision making around forest regeneration; further research is necessary to explore this avenue. Conservation ideologies in Costa Rica have changed in line with overarching cultural and economic shifts. Landowners are a part of these shifting trends and their forest management decisions affect conservation outcomes; as one landowner described this change as, "the [changing] global current…we are all going toward protecting the forest, we are thinking green. And it's logical." (Interview #6).

Table 5 Descriptive statistics for measured landowner variables

I determined significance at alpha=0.05 critical values for each sample size (a) is positive skew, b=negative skew, c=platykurtic; d=leptokurtic; e=normal this serves to simplify and highlight the variability but I also include values for interested readers.

	N	Minimum	Maximum	Median	Mean	Std. Deviation	Skew	Kurtosis	Skew and Kurtosis Codes
Farm and Forest Variables									
Farm (ha)	30	14	9000	318	1157	2305	2.79	6.10	ad
Forest Allowed to Regenerate During Tenure (ha)	29	-150	1500	20	157	389	3.14	9.34	ad
Early Forest Succesional Growth/ *Charral* (ha)	30	0	325	0	43	84	2.29	4.68	ad
Pasture (ha)	30	2	5350	160	378	964	5.05	26.68	ad
Plantation (ha)	30	0	90	0	10	25	2.5	5.08	ad
Total Crop (ha)	30	0	7030	2	446	1596	3.75	13.22	ad
Number of Cattle	29	0	5600	100	349	1026	5.13	27.03	ad
Closest Paved Road to Farm Entrance (km)	30	0	17	3	5	5	0.9	-0.27	a
Percent Forest Allowed to Grow During Tenure	29	-86	56	5	11	25	-1.65	7.63	bd
Percent Pasture	30	1	89	45	0	0	-0.00	-0.97	e
Percent Plantation	30	0	16	0	0	0	2.65	7.10	ad
Percent Crop	30	0	78	1	0	0	2.61	6.72	ad
Number of Employees	30	0	850	4	53	172	4.11	17.39	ad
Number of Family Member Employees	30	0	5	1	1	1	1.52	3.26	ad

Continue Table 5

Variable	N	Minimum	Maximum	Median	Mean	Std. Deviation	Skew	Kurtosis	Skew and Kurtosis Codes
Landowner Social Variables									
Organizations	30	0	8	2	2	2	0.88	0.68	a
Workshops	29	0	50	0	5	10	4.00	18.49	ad
Owner Tenure of Property (years)	30	3	71	28	26	16	0.68	0.42	e
Family Tenure of Property (years)	18	37	411	84	112	87	2.58	8.47	ad
Farm Management Experience (years)	30	3	80	34	38	19	0.45	-0.48	e
Landowner Age (years)	30	37	89	56	60	13	0.46	-0.61	e
Landowner Income									
Percent Annual Income Crops	29	0	100	0	19	31	1.61	1.31	a
Percent Annual Income Ranching	29	0	100	20	28	33	1.21	0.32	a
Percent Annual Income Tourism	29	0	80	0	6	21	3.53	11.40	ad
Percent Annual Income Off-farm	29	0	100	40	44	40	0.19	-1.68	c
Estimated Total Annual Income ($)	28	0	400800	57000	148368	156159	0.70	-1.21	c
Estimated Annual Income Crops ($)	29	0	236970	0	31956	62009	2.10	3.79	ad
Estimated Annual Income Ranching ($)	29	0	200400	8550	29246	48963	2.35	5.58	ad
Estimated Annual Income Tourism ($)	29	0	320640	0	18413	66448	4.05	16.81	ad
Estimated Annual Income Off-farm ($)	27	0	394200	14850	67621	105418	1.85	2.96	ad
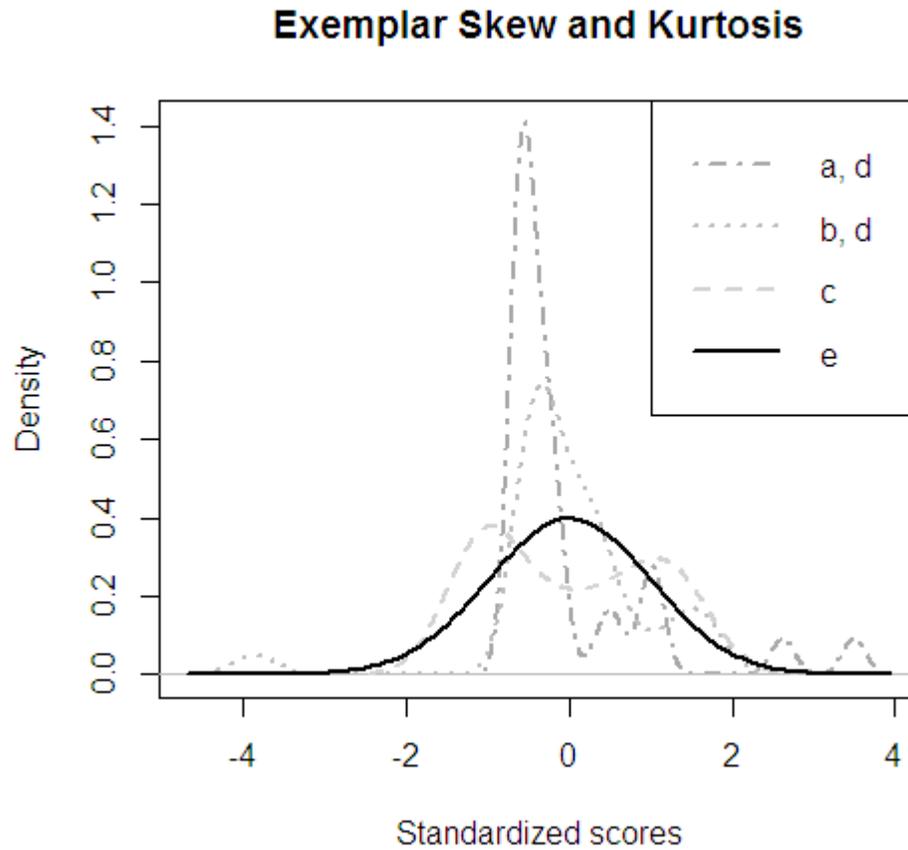
Figure 7 Exemplar Skew and Kurtosis

Normal Gaussian distribution displayed with standardized Kernel density plots for each non-normal combination of skew and kurtosis from Table 5: a, d = positive skew, leptokurtic; b, d = negative skew, leptokurtic; c=platykurtic; d=leptokurtic.

Table 6 Likert statements.

Landowners' ranked each statement according to a Likert scale of agree, neutral, and disagree. Percentages and sample size are reported for each Likert statement. Sections A and B describe different questionnaire themes: A forest benefits and services and B on-farm water use.

Section	Likert Statement	N	Percentage Agree	Percentage Neutral	Percentage Disagree
A1	I allow forest to grow on my farm to protect water reserves on my farm.	30	100	0	0
A2	I allow forest to grow on my farm to provide fodder for my cattle.	26	73	8	19
A3	I allow forest to grow on my farm to provide shade for my cattle	26	81	8	12
A4	I allow forest to grow on my farm to protect my crops with windbreaks.	16	56	6	38
A5	I allow forest to grow on my farm so that I can enjoy the birds and other wildlife.	30	90	3	7
A6	I allow forest to grow on my farm so that I can enjoy beautiful views on my farm.	30	90	3	7
A7	I allow forest to grow on my farm so the air feels fresher.	30	93	3	3
A8	I allow forest to grow on my farm to help protect the water in Guanacaste	30	97	3	0
A9	I allow forest to grow on my farm to help protect the wild fauna and flora.	30	93	0	7
A10	I allow forest to grow on my farm to protect the environment.	28	89	7	4
A11	I allow forest to grow on my farm so that the landscapes in Guanacaste are more beautiful.	30	87	7	7
B1	If I had more water available on my farm, I would use more land for cattle ranching.	28	47	10	37
B2	If I had more water available on my farm, I would cultivate more land.	29	73	7	17

Table 7 Four most mentioned tree species per tree use category

Use category	Genera species	Spanish Common Name	Percentage Frequency Mentioned
Fence post	*Gliricidia sepium*	madero negro	97
	Manilkara chicle	níspero	33
	Quercus oleoides	encíno	23
	Sideroxylon capiri	tempisque	20
Live fence	*Gliricidia sepium*	madero negro	73
	Bursera simaruba	indio desnudo	53
	Pachira quinata	pochote	30
	Spondias purpurea	jocnote iguanero	27
Remnant	*Enterolobium cyclocarpum*	guanacaste	90
	Samanea saman	cenízaro	73
	Gliricidia sepium	madero negro	70
	Cedrela odorata	cedro amargo	67
Encourage	*Enterolobium cyclocarpum*	guanacaste	67
	Gliricidia sepium	madero negro	67
	Tabebuia ochracea	cortez amarillo	50
	Cordia alliodora	laurel	50
	Pachira quinata	pochote	50
Rare	*Swietenia macrophylla*	caoba	70
	Dalbergia retusa	cocobólo	67
	Cedrela odorata	cedro amargo	63
	Astronium graveolens	ron ron	63

CHAPTER 4

A trait-based approach to assessing ecosystem functions in public and private tropical dry forests in Guanacaste, Costa Rica

Introduction

People have immense impacts on Earth's systems (Millennium Ecosystem Assessment 2005; Millennium Ecosystem Assessment 2003; Rockström et al. 2009; Vitousek et al. 1986) and these impacts, such as large-scale deforestation, create feedbacks that influence social systems (e.g. climate change) (Millennium Ecosystem Assessment 2005; Millennium Ecosystem Assessment 2003). Environmental services, the benefits and services nature supplies, are fundamental to ensuring resilient social-ecological systems under changing environmental conditions (Carpenter 2002; Daily et al. 2009; Folke et al. 2004).Yet, it is a substantial challenge to understand and predict ecosystem functions (S. Lavorel and Garnier 2002) and a step further to translate ecosystem functions into quantifiable environmental services (Díaz et al. 2007; Diaz et al. 2011). Ecosystem functions such as secondary forest regeneration are impacted by the spatial and temporal patterns of human land use. A first step towards understanding how ecosystem functions may vary between land uses is to assess functional plant ecology through plant traits.

Functional plant ecology uses plant functional traits, physiological and morphological plant characteristics that affect survival (P. B. Reich et al. 2003), as proxies to assess ecosystem functions (Cornelissen et al. 2003; S. Lavorel and Garnier 2002; Sandra Lavorel et al. 2013; Weiher et al. 1999; Westoby 2007). Ecosystem functions are often difficult to measure (so-named 'hard' traits) so 'soft' plant functional traits are used as proxies: for example, it is a challenge to measure seed dispersal in space but seed mass is easy to measure and can be proxy for dispersal distance. An assessment of plant functional traits can shed light on how ecosystem functions may differ along human land use gradients (Garnier et al. 2007; Mayfield et al. 2013). People use land in a non-random way with respect to physical geography gradients (e.g. soil, slope) and temporal scales of land use change (e.g. market pressures)) (T. P. Evans and Moran 2002; Laurance, Goosem, and Laurance 2009; Rudel 2002). Non-random land use has resulted

globally in a pattern of biotic homogenization with a 'few winning' species dominating the landscape (McKinney and Lockwood 1999; Olden et al. 2004). For example, in northern Atlantic and southern Amazon forest, Tabarelli and colleagues (2012) found that a few native pioneer and edge-adapted species flourished, conceivably due to pioneer associated functions such as fast growth and easy dispersal that can be predicted by plant traits such as wood density and seed mass. Diverse ecosystems provide functional redundancy, creating a buffer against environmental changes through time; thus, biodiversity loss diminishes that safeguard and may reduce social-ecosystem system resilience under changing environmental conditions (Isbell et al. 2011; P. B. Reich et al. 2012).

Functional plant traits respond to abiotic and biotic gradients with predictable trends (Hulshof and Swenson 2010; Peter B. Reich and Oleksyn 2004; Westoby and Wright 2006) and non-random land use may create a landscape that favors a particular combination of plant traits (J. L. McCune and Vellend 2013; McGill et al. 2006). Functional traits are often correlated and the correlation structure describes fundamental plant trait tradeoffs indicative of plant life history strategies (Grime 2006; Sandra Lavorel et al. 2011; P. B. Reich et al. 2003). High fecundity, broad dispersal, and fast growth, for example, describe the 'fast economics' plant strategy (Peter B. Reich, Walters, and Ellsworth 1997; I. J. Wright et al. 2004). This plant strategy has a competitive advantage in early successional conditions and areas that undergo frequent disturbance (i.e. most human land uses), so species with the fast economic plant strategy are particularly successful, which leads towards biotic and functional homogenization. I expect that plant traits indicative of the fast economic plant strategy will have a competitive advantage in private forests because private forests are highly fragmented and land uses in the agricultural matrix are likely more subject to changes than land uses within the public parks. Thus, I expected that the species-weighted average functional plant traits, or community weighted mean plant traits, as well as the species considered most prevalent in private forest would tend towards the fast economic plant strategy. In addition,

drought-avoidant (deciduous) species and nitrogen-fixing legume species may have an advantage in early seres or high disturbance prone tropical dry forests: deciduous species can avoid extreme negative plant water status through leaf drop and nitrogen-fixing species can fix atmospheric nitrogen, enabling growth in poor soil fertility conditions. I expected species more prevalent in private forests to possess these traits. Understanding how plant traits respond to contrasting human land use conditions furthers ecosystem function predictions in time of rapid global changes (Carpenter et al. 2012; Chapin 2003; De Deyn, Cornelissen, and Bardgett 2008; Díaz et al. 1999; Folke et al. 2004).

Not only may human land use influence ecosystem functions between public and private lands, but also tree species selected for specific uses may affect ecosystem functions. People select certain plant species for specific uses because of the plant functional traits of those species. Species selected for sawmill timber, for example, are chosen for a combination of plant traits such as moderate to high wood density, resin color, and tree architecture (e.g. straight boles) (Cordero and Boshier 2003). Wood density is negatively correlated with relative growth rate (RGR) (Jerome Chave et al. 2009) so highly prized tropical timber species often have slow growth rates (Jiménez Madrigal 1993). Therefore, tree species harvested for these traits may become less abundant, which may influence ecosystem functions. People also select ornamental plants for their showy floral or foliar displays (Adams, Bamford, and Early 2012); in a household study in Los Angeles, participants were asked what types of trees they preferred and given such options as native, fruit, beautiful, fast growing, requiring little maintenance, etc the majority (80%) selected "beautiful" (Pataki et al. 2013). In rural areas, people also select species based on plant traits. In Central American tropical dry forest ecosystems, for example, *Guazuma ulmifolia, Bixa orellana, Gliricidia sepium,* and *Bursera simaruba* are recommended for soil erosion control (Cordero and Boshier 2003), presumably because of those species root structure and/or relatively fast growth rates. In another example, farmers in Costa Rica prefer to use species for live fence posts that have the ability to coppice (Budowski and Russo 1993) McClellan, Ch. 3).

Tropical dry forests have been preferentially chosen for human land use intensification (Bullock, Mooney, and Ernesto 1995; Janzen 1988; Miles et al. 2006): only a fraction the historic global extent remains (Miles et al. 2006). Thus, understanding community reassembly through secondary succession in these forests is important (H. P. Griscom et al. 2011; Murphy and Lugo 1986). Forest regeneration dynamics in the tropics may be differentially affecting forest landscape pattern in public and private lands: secondary forest regeneration often occurs on abandoned agriculture or pastures lands (S. J. Wright 2005), many of which are privately owned. In Costa Rica, naturally regenerated forests on both public and private lands are protected by law for conservation (Forestry Law 7575, 1996) so, technically, forest land use between public and private lands should be the same. However, tropical dry forest regeneration patterns on public vs. private lands in Guanacaste, Costa Rica have resulted in different forest landscape patterns: public parks have larger areas of continuous forest while private forests have a higher number of small forest patches (Arroyo-Mora et al. 2005) and 90% of the forest regrowth that has occurred in the last few decades has been on private lands (Calvo-Alvarado et al. 2009). In Ch. 2, I found species compositional differences between public and private tropical dry forests. I hypothesized that these composition differences may be related, in part, to differential management on private versus public lands. Here, I blend functional ecology with community ecology to explore potential functional trait differences between plant communities in regenerating tropical dry forests located on public and private lands. I hypothesize that community weighted mean (CWM) life-history and functional plant traits in private forest will reflect the 'few winners' model; for life-history traits, private forests will have higher instances of traits associated with long distance dispersal and high fecundity (e.g. wind dispersed, low seed mass) and dominant functional traits in privately owned forests will reflect the fast economic plant strategy i.e. rapid growth, high investment in leaf N, and low investment in structural carbon (e.g. high SLA, high leaf N, low C, low C:N ratio). Species that avoid drought and associate with N-fixing bacteria may have a competitive advantage in edge and patchy

forest habitats more characteristic of private lands; thus, I expect to find more deciduous and more leguminous-type compound leaves in private forests. Finally, private forests are likely to have a lower value of plant traits that reduce species' abundances (e.g. sawmill timber) and a higher value of plant traits associated with rural farm use that may increase species' abundances (i.e. erosion control, living fences) (Table 7).

Methods

Plant Trait Database

I conducted a forest inventory survey of 66 0.1 hectare private plots in 2011 (McClellan et al., Ch. 2) to compare to an existing dataset of 82 public forest plots (Powers et al. 2009). Site locations are described elsewhere (Ch. 2) but, in brief, all sites were located in tropical dry forests of Guanacaste, Costa Rica. These forests have a 5-6 month dry season and mean annual temperature of approximately 25° C (Gillespie, Grijalva, and Farris 2000; Holdridge 1967). Public forest inventory plot data was collected from Palo Verde National Park National Park, *Area de Conservación Arenal Tempisque* (ACAT) and *Área de Conservación Guanacaste* (ACG) by Powers and colleagues (2009). In 2011, I established forest inventory plots on private forest lands near ACAT and ACG that matched forest stand age and soil characteristics of public forest plots (Powers et al. 2009). At ACG there are two distinct tree communities, one community is oak-dominated and associated with poor soil fertility while the other community is a more diverse tropical dry forest community associated with richer soils. For subsequent analyses, I excluded oak-dominated forest inventory plots because low fertility soil is a strong driver of plant functional traits and so could mask other plant treatment effects. For the forest inventory plots, all individual trees $\geq$ 10 cm at Diameter at Breast Height (DBH) were measured and identified to species. Forest inventory plots were arrayed across soil and age gradients. After excluding the oak-dominated plots, there were 66 public forest plots and 46 private forest plots. In total 4,053 individual trees representing 160 species were identified to species in these public and private forests.

I conducted a Classification Method (CLAM) analysis to identify which species were more prevalent in public or private forests (Robin L. Chazdon et al. 2011). The CLAM analysis also identified which species were too rare to classify and which species were generalists (i.e. had no distributional bias between public and private forests). CLAM algorithm allows either a simple majority comparison between groups (i.e. 0.5)

and a super majority comparison between groups (0.667). The algorithm iteratively classifies species so Chazdon et al (2011) suggest using a p-value of 0.005 to avoid statistical errors associated with multiple tests. I assessed both simple and super majority public and private species at the recommended probability value. Species classified as more prevalent in public and private for both the simple and super majority thresholds are listed in Table 11.

I collected biological plant trait data from a variety of plant trait databases and literature sources for 103 species. I was unable to compile data for 57 species but all of those species had fewer than 5 individuals in the entire dataset. The total number of individual stems not included was 1.1% of the private trees and 1.9% of the public trees. Since I calculate the community weighted mean per plot, I also assessed the percentage of stems missing per plot. A total of 61 plots had a fraction of missing stems. In the majority of the 61 plots (93%), missing stems accounted for less than 10% of all stems while 7% of the plots with missing stems had between 10-14% missing.

To populate my species plant trait database, I used two primary sources; TRY (Kattge et al. 2011) (www.try-db.org) and Seed Information Database (SID) (data.kew.org/sid/). For each of the 103 species, I build a database of leaf physical and chemical traits, seed traits, floral traits, and root associated traits (mycorrhizal evidence, N fixation capacity). The TRY database can have multiple data points per species per plant trait so I preferentially chose data that came from an ecological site similar to our tropical dry forest biome conditions in Guanacaste, Costa Rica. If similar sites were not available, I averaged the plant trait data. I also garnered plant trait data for our species from The National Biodiversity Institute (INBio) (http://www.inbio.ac.cr) and the United States Department of Agriculture Germplasm Resources Information Network (GRIN) (www.ars-grin.gov). Plant trait databases are often sparse, so I also searched the literature through Google scholar for all plant traits that were unavailable from the databases listed above. The final plant trait database only included traits for which I was able to find data for the majority of the 103 species. Every plant trait source in the database was recorded.

I was also interested in how people use tropical dry forest tree species. I used an extension manual, Trees of Central America, as a starting point for building my human use plant trait database (Cordero and Boshier 2003). The extension manual and accompanying website (www.arbolesdecentroamerica.info) provided categorical use data for 204 Central American tree species for 20 types of uses (Table 9). For the species in my dataset not included in the Trees of Central America extension manual, I searched published literature. For the human use plant traits, I created human use trait summaries that were relevant for tropical dry forest use (Cordero and Boshier 2003). After an exhaustive search of the literature for each human use trait for each species, if no data was found, I assumed it was not used for specific human use trait. Human use plant traits can have a negative or positive effect on species abundance. For example, some human use plant traits are destructive (e.g. sawmill timber) while other human use plant traits may promote species abundance (e.g. tree species used for cattle fodder). So I split human use plant traits into two categories relevant for land uses in Guanacaste and summed across those categories. The 'Human Use Plant Trait Destructive Harvest', hereafter 'harvest traits', included sawmill, construction, furniture, handicrafts, trees in pasture, and fence posts. The 'Human Use Plant Trait On Farm Use', hereafter 'on farm use traits', included animal consumption, shade trees, live fence posts, and ornamentals. Each data source was recorded.

I acknowledge that there are limitations to our assessment in that I did not collect site-specific plant trait data and cannot account for intraspecific variation that may be evident (Hulshof and Swenson 2010). However, site-specific plant trait data are not often available through plant trait databases so plant trait values from multiple sites and species populations are commonly averaged but have been shown to vary from site-specific data (Cordlandwehr et al. 2013). When possible, I selected plant trait data from sites similar to the tropical dry forests in Guanacaste.

Given that plant trait databases are often sparse, imputation methods for missing plant trait data are becoming more available (Shan et al. 2012; Stekhoven and Buhlmann

2011). I chose the missForest package in R because this algorithm effectively handles continuous and categorical multivariate data and performed strongly when data had interactions. Further, missForest does not have distributional assumptions so it is appropriate to use with non-parametric data (Stekhoven and Buhlmann 2011). The missForest algorithm can impute up to 30% of a dataset. Our plant trait database had missing values that represented 8% of the full dataset.

Statistical Analyses

Plant traits are known to correlate (e.g. leaf economics spectrum) so I chose to assess plant trait differences between species classified by CLAM as more prevalent in public and private groups using a multivariate analysis of variance (MANOVA) to account for potential interactions among co-varying biological plant traits and human use plant traits (Garnier et al. 2007). Variables included in the MANOVA are listed in Table 7. I chose a non-parametric MANOVA since much of my data was categorical and thus did not meet normality assumptions for parametric analyses.. Statistical analyses were conducted using the adonis function in the vegan package in R (Oksanen, 2011; R Core Development Team 2013).

I also assessed the mean of each plant trait per plot weighted by species abundance (i.e. community weighted mean (CWM) using the FD package in R (Laliberté and Legendre 2010). For categorical variables, I assessed the dominant mode per plot (i.e. if the dominant leaf habit in the plot was simple and not compound leaves, the plot was categorized as simple). For discrete variables, I compared public and private groups using the chi-sq test. I used t-tests to compare the CWM of continuous plant traits between public and private forests after checking normality, homoscedasticity, and transforming data when necessary. Since I conducted multiple t-tests, I used the Holm's correction factor to avoid type II errors.

Results

Plant traits associated with species in public versus private forests

To assess species more prevalent in public and private tropical dry forests, I used the CLAM multinomial model, which classified the 160 species into four categories: 20 species (13%) as more prevalent in public forests, 12 species (8%) were more prevalent in private forests, 46 species (29%) showed no distributional bias, and 82 species (51%) were too rare to classify. This analysis differs from that conducted in Ch. 2 in that all oak-dominated plots were excluded from analyses: I did not include oak-dominated plots in this analysis because the oak-dominated plots had low soil fertility (Ch. 2) and soil fertility is a significant driver of plant traits. In prior analyses in which I included oak-dominated plots, the only signature revealed was linked to soil fertility (results not shown here); I was interested in assessing plant functional traits between public and private forest beyond the low soil fertility oak-dominated signature so I excluded those plots. Thus, this CLAM analysis is a subset of the plots used for the CLAM analysis conducted in Ch. 2. The subsequent analyses in this chapter differ from that of Ch. 2, moreover, because the focus of this analysis is on functional plant traits.

For the CLAM analysis, *Rehdera trinervis* was the most abundant species in public forests while *Guazuma ulmifolia* was the most abundant in private forests; these results are equivalent to results from the full forest plot dataset conducted in Ch. 2 (Table 11). Also analogous to Ch. 2 results, high-priced timber species, *Swietenia macrophylla* and *Cedrela odorata,* were classified as indicative of public forests. Although I excluded oak-dominated plots, co-occurring species in oak-dominated communities are also found in the more diverse tropical dry forest communities, so *Quercus oleoides*, *Byrsonima crassifolia* and *Curatella americana* emerged in this CLAM analysis as well. A notable difference between the CLAM analyses from Ch. 2 and here is that *Quercus oleoides* is classified here as more prevalent in public forests where as in Ch. 2 results it was

classified as more prevalent in private forests. In this CLAM analysis and in the CLAM analysis in Ch. 2, *Byrsonima crassifolia* and *Curatella americana* were more prevalent in private forests. I discuss possible explanations in sections to follow.

I found marginally significant differences in plant functional traits between species identified in the simple majority (0.5) CLAM threshold as more prevalent in public versus private forests using MANOVA ($F_{1,30}$=3.06, *P*=0.049). I also conducted t-tests or chi-square tests on continuous and discrete variables, respectively, to assess individual trait behaviors between species classified as more prevalent in either public or private. Wood density was higher in public forests but the effect was not significant after Holm's correction was applied (Table 8). Seed mass showed a trend of being higher in public compared to private forests but, again, this was not significant (Table 8). Neither 'harvest use traits' or 'on farm use traits' were significantly different between species CLAM classified as more prevalent in public versus private forests, although the trends were in the direction expected. The chemical, physical, and physiological leaf plant traits assessed were not significantly different between species more prevalent in public versus private (Table 9). The effect sizes for all variables were small.

Community Weighted Mean (CWM) plant traits

The discrete variables of leaf habit, seed dispersal, and leaf compoundness, which were summarized by the dominant trait per plot, were not significantly different between public and private forests (Table 12). For CWM seed mass, public forests had significantly larger seed mass than private forests (Table 13). The summary 'harvest use traits' were not different between public and private forests while the summary of 'on farm use traits', although not significant, did show a trend towards a higher value on private lands. CWM wood density was not significantly different between public and private forests. CWM SLA was not significantly different between public and private forests; SLA did show a slight trend with public forests having a lower CWM SLA than private forests but the mean differences was small and likely not biologically important.

Finally, neither CWM leaf N or leaf C:N differed significantly different between public and private forests.

Discussion

Plant traits associated with tree species that were more prevalent in public and private forests

In Ch. 2 I found species compositional differences within public and private tropical dry forest in Guanacaste, Costa Rica (Table 4). Here, I was interested in understanding how species that are indicative of public versus private forests may differ in traits related to dispersal and growth. Since low soil fertility strongly influences plant traits, I did not include oak-dominated forest inventory plots in the analyses for this chapter (Table 11). As functional plant traits are correlated (Grime 2006; P. B. Reich et al. 2003; I. J. Wright et al. 2004), I expected that a MANOVA, which can assess correlations on multiple dimensions, would reveal differences between suites of plant traits of species classified as more prevalent in public or private forests (Garnier et al. 2007).

I found that the MANOVA of functional plant traits for the species more prevalent in public or private forests was marginally significant but did not remain so after the Holm's correction. With the individual plant trait analyses, wood density showed a slight trend of being higher in public forests; likely this due to the fact that there are multiple timber species classified as more prevalent in public forest and timber species tend to have medium to high wood density (Jerome Chave et al. 2009). When the stricter CLAM majority threshold of 0.667 was used, a higher percentage of the species more prevalent in public forests were timber species so, as I found in Ch. 2, public parks provide a valuable conservation service for these species. Seed mass also showed a trend towards being higher for the species more prevalent in public forests. Suggesting that species indicative of public forest may be dispersal limited.

Quercus oleoides was classified differently in these CLAM results here compared to those from Ch. 2. In the Ch. 2 analysis, in which oak-dominated plots were included,

all sympatric species in the oak-dominated community were classified as indicative of private forests. I interpreted this as an effect of soil fertility differences: relative to public forests, oak-dominated private forests had higher soil fertility, so private soils could support more abundant levels of sympatric oak species relative to public. Here, with the oak-dominated plots removed, *Quercus oleoides* was classified as more prevalent in public instead of private forests while *Byrsonima crassifolia* and *Curatella americana*, as in Ch.2, remain classified as species more prevalent in private forests. Likely, this is due to a dispersal limitation related to differences in seed mass: seed mass for *Quercus oleoides* is 401.5 mg while *B. crassifolia* and *C. americana* have seed masses of 2.94 mg and 18.9 mg, respectively. Oak acorn dispersal in tropical dry forests may be limited because the majority of mammals that interact with this *Q. oleoides* are actually seed predators; the only mammal species that may disperse acorns is the scatter-hording agouti (*Dasyprocta punctata*), yet agouties rarely venture into pasture and do not cache in pasture (Klemens, Deacon, and Cavender-Bares 2011); thus, patchy private forests in a matrix of pasture are likely less attractive habitat for agouties. Other research has found that forest fragmentation can differentially affect large and small seeded tree species; Cramer et al. (2007) found that the large-seeded, mammal dispersed species, *Duckeodendron cestroides*, was strongly dispersal-limited in fragmented Amazonian forests relative to the small-seed species *Bocageopsis multiflora,* which was dispersed by multiple bird species.

Community Weighted Mean (CWM) plant traits

The relative abundance of plant traits represented in the biotic community provides a measure of community functional diversity that can inform ecosystem functioning (Díaz et al. 2007) . Here, I assessed the community weighted mean of functional plant traits for forest inventory plots in public and private forests. I expected that private forest would have lower values of 'harvest traits' and higher values of 'on

farm use traits', and be consistent with the 'few winners' model (Table 7). I did not find evidence to support these hypotheses.

The CWM summary of 'harvest traits' did not differ between public and private forests; the average value for 'harvest traits' of public tropical dry forest species, which was plot-based assessment of species used for sawmill, construction, furniture, handicrafts, trees in pasture, and fence posts, was not higher in public compared to private forests. This seems surprising given that the CLAM analyses revealed multiple timber species as more prevalent in public forests. I had expected that 'harvest traits' would be higher in public forests because species that have those traits are more likely to be harvested in private forests. The CLAM algorithm, which found highly valuable timber species as indicative of public forests, compared all species abundances between public and private forests. If a species had a 0.5 relative abundance (i.e. a simple majority) in public forests, it was classified as indicative of public forests. Species with 'harvest traits', are likely not abundant in either public or private forests; prior to being protected, public parks had been logged for valuable timber species such as *Swietenia macrophylla* (mahogany) (Quesada and Stoner 2004). Moreover, although harvesting timber from private forests was deemed illegal by Forestry Law 7575, an estimated 25-35% of timber is sourced illegally in Costa Rica and most of those trees come from private forests (Miller 2011). Perhaps if species with 'harvest traits' have low abundances, the signal of 'harvest traits' was not strong in the CWM. Conversely, the 'on farm use traits', although not significant, showed a trend towards higher values for 'on farm use traits' in private forests; thus, private forests had more species with traits that people valued for use on their farms (i.e. animal consumption, shade trees, live fence posts, and ornamentals). Other studies have noted a higher abundance of species used for living fences in nearby naturally regenerated forests (Marin-Spiotta, Silver, and Ostertag 2007).

Seed mass was the only variable that remained significant after the Holm's correction. Seed mass was higher in public compared to private forests; I expected this to be the case as many dispersal agents for large tropical dry forest seeds have become extinct (Janzen and Martin 1982) and, since forest fragmentation affects animal dispersal behavior (Cramer, Mesquita, and Bruce Williamson 2007; Markl et al. 2012; Van Dyck and Baguette 2005), animals that now serve the that ecological dispersal role may be less likely to occupy patchy forests in a matrix of agriculture or pasturelands characteristic of private lands (Klemens, Deacon, and Cavender-Bares 2011). It seems counterintuitive, therefore, that animal dispersal was not significantly higher in public forests. I also expected wind-dispersal to be the dominant mode in private forests but I did not find evidence to support those hypotheses. If data on the specific animal dispersal agent group (e.g. birds versus mammals) were available, a more complete analysis could have been undertaken. Species dispersal data for tropical dry forests tree species, however, are not readily available so studies often classify seed dispersal at a higher level of categorization, such as animal or wind, lumping together animal species whose behavior may differ across land uses. This is an important limitation for my comparison of public and private forests because animal dispersers do not navigate the landscape equivalently (Fenner 2000; Wehncke, Valdez, and Domínguez 2004). Bird species, for example, may not have the same limitations as large mammals and rodents in fragmented systems (Fenner 2000).

Specific leaf area (SLA) is a key plant trait because it displays both interspecific and functional group variation, responds to environmental gradients, and scales with leaf N, leaf P, leaf lifespan, and mass based photosynthetic rate (Poorter et al. 2009; I. J. Wright et al. 2004). SLA is also a strong positive correlate of relative growth rate (RGR) (Peter B. Reich, Walters, and Ellsworth 1997; Veneklaas and Poorter 1998). I expected that plant traits associated with generalist and disturbance-adapted species (e.g. high SLA) would be over-represented in private forests. I found that there was a slight trend towards CWM SLA being higher in private (110 cm^2g^{-1}) compared to public forests (104

cm^2g^{-1}) but, that trend was not significant. Moreover, a difference in SLA of 6 cm^2g^{-1} is not a large given that SLA ranges can be vast: for example, Reich et al. (1997) assessed 6 biomes with a total of 280 herbaceous, shrub, and tree plant species and found a minimum SLA range of 35 ± 6 cm^2g^{-1} and a maximum range of 267 ± 62 cm^2g^{-1}. Tropical dry forest species display a particularly wide variation in SLA; Hulshof and colleagues (2013) suggested that environmental heterogeneity evident in tropical dry forest biomes across spatial scales such as soil moisture and slope gradients and temporal scales such as the strong seasonally in precipitation regimes encourage variability in functional plant traits across these gradients. Moreover, if SLA was higher in private forests as a proxy for fast relative growth rate, I would also expect leaf N to be significantly higher in public forests (Wright et al. 2006) and leaf N in my sample was not different between public and private forests. Likewise, the other leaf traits, evergreen/deciduous, simple/compound, leaf C, and leaf C:N, did not differ significantly between public and private forests. Perhaps soil moisture gradients associated with differences in leaf habit are heterogeneous across both public and private lands. Further, legume species are common in public forests (Powers and Tiffin 2010)and there are many non-legume, compound leaved species in tropical dry forests.

CWM wood density was also not significantly different between public and private forests. This result was different from Ch. 2 in which I found that public forests had significant higher CWM wood density. The difference, however, was small (public mean=0.655 mg/mm^3, private mean=0.616 mg/mm^3), not biologically important, and did not translate into a difference in standing biomass between public and private forests. In Ch. 2 CWM wood density was calculated primarily from wood density samples taken in the sample plots while CWM wood density for Ch. 4 was calculated from plant trait databases. The average values for CWM wood density from the plant trait database were similar to those from samples collected in Guanacaste (mean public=0.637 mg/mm^3 and mean private = 0.614 mg/mm^3). The difference in significance is likely a function of distinct sample sizes; in Ch. 2 I was interested in calculating biomass so I measured both

trees ($\geq$ 10 cm DBH) and saplings (i.e. <10 cm DBH and at least 1.3 m). Saplings were not identified to species but a plot level CWM wood density was assigned to each sapling. The substantially number of saplings likely made the small mean difference in CWM wood density statistically significant. Here, I did not include saplings and I removed oak-dominated so the sample size was considerably smaller.

Conclusion

Forests provide multiple environmental services, protect biodiversity, and support people's livelihoods; in short, they are crucial building blocks in the global social-ecological system. Most forests, however, are not within the boundaries of public parks (FAO, 2010). Global environmental changes as a consequence of human actions are an endogenous component of our social-ecological system. We need to manage it as such and integrating the environmental services concept into decision-making processes has the potential to renovate political systems to encourage sustainable management of social-ecological systems (Carpenter 2002; Daily et al. 2009; Folke et al. 2004). To advance this endeavor, we need to understand how ecological functions vary along not only environmental and spatial gradients but also along human land use gradients and categories such as public and private lands (Mayfield et al. 2013). Natural forests in Costa Rica on both public and private lands are protected by law for conservation; however, the private forests are much more fragmented (Arroyo-Mora et al. 2005). Species more prevalent in public forests are indicative of high-grading in private forests (McClellan Ch. 2). Further, seed mass appears to be a determining factor in community reassembly between continuous and patchy forest landscapes. Our results for on farm use tree species use, although not significant, do show a trend towards increased tree species abundance within naturally regenerated forests of tree species people select for on farm uses and this results align with other studies that have found, for example, increased abundances of species used for living fences (Marin-Spiotta, Silver, and Ostertag 2007). Overall, these analyses show that public and private tropical dry forests in Guanacaste do not differ greatly.

Table 7 Hypothesized plant trait differences between public and private forests

Hypothesized differences in life-history, functional, and human use plant traits between public and private tropical dry secondary forests in Guanacaste, Costa Rica.

Public	Private
Life-History Traits	**Life-History Traits**
Animal dispersal	Wind dispersal
High seed mass	Low seed mass
Functional Traits	**Functional Traits**
Low SLA	High SLA
Evergreen	Deciduous
Simple leaves	Compound leaves
Higher wood density	Lower wood density
Lower leaf N	Higher leaf N
Higher leaf C	Lower leaf C
Higher C:N ratio	Lower C:N ratio
Human Use Traits	**Human Use Traits**
Higher value for 'Human Use Plant Trait Summary Destructive Harvest' (sawmill, construction, furniture, handicrafts, trees in pasture, and fence posts)	Lower value for 'Human Use Plant Trait Summary Destructive Harvest' (sawmill, construction, furniture, handicrafts, trees in pasture, and fence posts)
Lower value for 'Human Use Plant Trait Summary On Farm Use' (animal consumption, shade trees, live fence posts, and ornamentals)	Higher value for Human Use Plant Trait Summary On Farm Use (animal consumption, shade trees, live fence posts, and ornamentals)

Table 8 Plant trait comparisons for continuous data for species classified by CLAM as more prevalent in public or private forests. P-values reported here are not Holm's corrected

Moments	Seed Mass (mg)	Summary 'Distructive Harvest'	Summary 'On Farm Use'	Wood Density (mg/mm3)	SLA (mm2/mg)	Leaf N (mg/g)	Leaf C (mg/g)	Leaf C:N (g/g)
t-Statistic	-2.185	-0.5132	1.440	-1.954	1.339	-0.2031	0.0354	0.0871
df	1	1	1	1	1	1	1	1
p-value	0.035	0.61	0.15	0.054	0.19	0.98	0.97	0.93
Public Mean	245.7	2.451	0.951	0.683	10.22	24.01	463.6	21.16
Private Mean	141.7	2.084	1.584	0.573	11.56	23.54	464.0	21.36
Omega Squared	0.043	0.0009	0.005	0.033	0.0056129	0.025639	0.015006	0.02609

Table 9 Use categories and items defined by Cordero and Boshier (2003)

(www.arbolesdecentroamerica.info)

Use Category	Item	Variable Type
Use	Sawmill Wood	Binary
Use	Construction	Binary
Use	Fence Posts	Binary
Use	Fire Wood for Cooking	Binary
Use	Furniture	Binary
Use	Tools	Binary
Use	Animal Consumption	Binary
Use	Human Consumption	Binary
Use	Handicrafts	Binary
Use	Medicinal	Binary
On Farm Management	Shade Trees	Binary
On Farm Management	Trees in Pasture	Binary
On Farm Management	Intercropping Trees	Binary
On Farm Management	Live Fence Post Trees	Binary
On Farm Management	Plantations	Binary
On Farm Management	Erosion Control	Binary
On Farm Management	Gardens	Binary
On Farm Management	Windbreaks	Binary
On Farm Management	Ornamentals	Binary
On Farm Management	Natural Forest	Binary

Use Category	Item	Variable Type
Use	Sawmill Wood	Binary
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Use	Animal Consumption	Binary
Use	Human Consumption	Binary
Use	Handicrafts	Binary
Use	Medicinal	Binary
On Farm Management	Shade Trees	Binary
On Farm Management	Trees in Pasture	Binary
On Farm Management	Intercropping Trees	Binary
On Farm Management	Live Fence Post Trees	Binary
On Farm Management	Plantations	Binary
On Farm Management	Erosion Control	Binary
On Farm Management	Gardens	Binary
On Farm Management	Windbreaks	Binary
On Farm Management	Ornamentals	Binary
On Farm Management	Natural Forest	Binary

Table 10 List of plant traits used in analyses

Trait	Variable type
Seed Dispersal	Animal, Wind, Drop, Explosion, Unassisted
Leaf Habit	Deciduous or Evergreen
Seed Mass	Continuous
Leaf Type	Simple or Compound
Wood Density	Continuous
SLA	Continuous
Leaf N	Continuous
Leaf C:N	Continuous
Human Use Plant Trait Summary Destructive Harvest	Categorical Summary
Human Use Plant Trait Summary On Farm Use	Categorical Summary

Table 11 CLAM species categorized as more prevalent in public or private forests

Tree species categorized as more prevalent in public or private forests using the Classification Method (CLAM) (Robin L. Chazdon et al. 2011). Relative abundance in decreasing order is displayed for public and then private prevalent species for the simple majorly CLAM threshold of 0.5. Super majority CLAM species (0.667) are marked with an asterisk. Relative abundance is multiplied by 1000 for ease of interpretation.

More prevalent in public	Relative Abundance* 1000	Relative Abundance* 1000	More prevalent in private	Relative Abundance* 1000	Relative Abundance* 1000
Species	**Public**	**Private**	**Species**	**Public**	**Private**
*Rehdera trinervis**	89	7	*Guazuma ulmifolia*	56	105
Luehea speciosa	52	19	*Cochlospermum vitifolium*	22	40
*Manilkara chicle**	19	0	*Cordia alliodora**	15	40
*Ateleia herbert-smithii**	19	0	*Luehea candida**	5	37
*Sebastiania pavoniana**	14	1	*Lonchocarpus minimiflorus*	27	35
Brosimum alicastrum	11	3	*Gliricidia sepium*	20	29
*Exostema mexicanum**	11	0	*Byrsonima crassifolia**	2	18
*Lonchocarpus parviflorus**	9	0	*Ocotea veraguensis*	6	13
Machaerium biovulatum	9	3	*Curatella americana**	1	7
Astronium graveolens	9	2	*Enterolobium cyclocarpum*	1	6
*Cedrela odorata**	9	0	*Bixa orellana**	0	5
*Quercus oleoides**	8	0	*Acrocomia vinifera*	1	4
Genipa americana	7	2			
*Sapranthus palanga**	5	0			
*Acosmium panamense**	5	0			
*Swietenia macrophylla**	5	0			
Coccoloba guanacastensis	4	0			
Samanea saman	4	1			
Cordia collococca	4	0			
Karwinskia calderonii	3	0			

Table 12 Statistical moments for Community Weighted Mean (CWM) of discrete plant traits compared between public and private forests

Moments	CWM Leaf Habit	CWM Leaf Type	CWM Dispersal
Chi-sq Statistic	1.1694	0.0661	5.5439
df	1	1	4
p-value	0.2795	0.7971	0.2359
Phi/Cramer's V	0.105032	0.02497427	0.228695

Table 13 Community Weighted Mean (CWM) of continuous variables compared between public and private forests

Results from t-tests for continuous plant trait variables between public and private forests in Guanacaste, Costa Rica.

Moments	CWM Seed Mass (mg)	CWM 'Destructive Harvest'	CWM 'On Farm Use'	CWM Wood Density (mg/mm3)	CWM SLA (mm2 mg-1)	CWM Leaf N (mg/g)	CWM Leaf C (mg/g)	CWM Leaf C:N (g/g)
t-statistic	3.30	-1.29	-2.05	1.60	-2.54	-1.20	-0.95	1.27
df	104.00	104.00	104.00	104.00	104.00	104.00	104.00	104.00
p-value	0.00	0.20	0.04	0.11	0.01	0.23	0.34	0.21
Public mean	304.12	2.43	1.54	0.64	10.20	23.32	461.86	22.55
Private mean	171.45	2.68	1.80	0.61	10.86	24.07	463.38	21.92
Effect Size (Cohen's d)	0.65	0.25	0.40	0.31	0.50	0.23	0.19	0.25

CHAPTER 5

Conclusion

Here, I used an interdisciplinary approach to assess forest biodiversity and structure between public and private lands and evaluate factors that may influence private landowners' decisions to allow tropical dry forest regeneration in Guanacaste, Costa Rica. I conducted two simultaneous field campaigns in Guanacaste, an ecological forest inventory survey of private forests and in-person interviews with the landowners who managed those forests. The private forest plots were compared to an existing forest dataset of public forests in Guanacaste, Costa Rica and private and public plots were matched for age and soil fertility. The interviews were conducted with a questionnaire and assessed both quantitatively to provide, for example, data on farm size and production scale and qualitatively to develop a nuanced understanding of how these landowners considered their forests.

In Ch. 2, I found that integrative metrics of forest structure and biodiversity between public and private forests, including basal area, stem density, aboveground biomass, and Shannon-Wiener diversity index, did not differ significantly. In light of the billions of conservation dollars being spent through REDD+ towards mitigating climate change, it is encouraging to know that in this small corner of tropical dry forests in Guanacaste, Costa Rica, the carbon storage is equivalent between public and private forests. Although biomass and integrative metrics of biodiversity were similar between public and private forests, I found evidence that public and private forests differed in tree species composition. Species that were significantly more prevalent in public forests included internationally traded timber species *Swietenia macrophylla* (mahogany) and *Cedrela odorata* (cedar). Whereas the most abundant species in private forests was *Guazuma ulmifolia,* a species widely consumed and dispersed by cattle. I suggest that differences in tree composition result in part from non-random selection of public and private land holdings with respect to soil fertility; additionally, at the farm scale, forest regeneration occurs on areas of the farm with lower soil fertility. There appears to be an ownership signature that is not attributable to soil fertility and I suggest that management differences between public and private forests could drive these compositional differences.

In Ch. 3, I explored how forest tenure, farm size, livelihoods, and landowner motivations may affect secondary forest regeneration on private lands in Guanacaste, Costa Rica. Although Guanacaste has large public parks, the majority of forestlands are privately owned (Calvo-Alvarado et al. 2009). Thus private landowners in Guanacaste are the *de facto* stewards of forest-based ecosystem goods and services, so, to the extent possible, I assessed the context from a landowner's perspective. Forest tenure policies in Costa Rica have strongly influenced forest cover dynamics through time (B&G2002). In the most recent major national forest policy change, Forestry Law 7575, landowners effectively lost management rights to any of their land that Forestry Law 7575 defined as forest and any land that they allow to regenerate into an 'official forest'. Allowing forest regeneration limits other land use options in current or future market conditions. Given that economic markets shift, it may not be in landowners' long-term economic interests to allow forest regeneration on their farms. Thus, the fact that there was very low forest additionality, or forest conservation funds that resulted in landowners conserving forest that they would not have conserved without those funds, in my sample is not surprising. The only variable that correlated with forest allowed to regenerate was farm size; larger farms had significantly more forest regeneration. Landowner's livelihoods can differentially affect forest cover dynamics; agrotourism may be a positive option for both landowners' livelihoods and forest regeneration but agrotourism does not appear to be widely prevalent. Landowners recognize and appreciate the benefits their forests provide to them and society at large; however, when making land use decisions that may affect forest cover, market prices are the dominant driver. I was also interested in evaluating how landowners' decisions might affect forest ecological attributes. As I found in Ch. 2, public forests had significantly higher abundances of prized timber species. In Ch. 3, I assessed which species landowners tended to leave as remnant trees, encourage on their properties, or have noted as being less common; the most mentioned species for these use categories was timber species.

In Ch. 4, I assessed plant functional traits to further understanding of how ecosystem functions may differ between public and private tropical dry forests in

Guanacaste. I also developed a summary of human use attributes that separately considered human use attributes expected to be less evident in private forests (e.g. timber) and those expected to be more evident in private forests (e.g. ornamentals, living fences). In the species abundance weighted means, I found that destructive human use attributes were not significantly more evident in private forests. However, human use attributes for 'on farm use' did show a trend towards being higher in private forests and a higher abundance of species used for living fences in naturally regenerated forests has been noted in other studies. Seed mass was significantly larger in public compared to private forests; animal vector dispersal behavior between continuous and patch forest landscapes may be the cause.

Driving through any urban area, it is easy to see how people affect plant community structure, diversity, and abundance. Tall, leafy trees are planted in neat rows along neighborhood streets, flowers in the front yard, grass clipped and manicured. The scale of urban compared to forest land use is vastly different: urban land area across the globe accounts for 3% of terrestrial lands (Shlomo et al. 2005) while forest covers 31% (FAO 2010). Thus, how people shape forest structure, plant diversity, and community abundances in rural areas may be less conspicuous but more consequential. Our management decisions affect the ecosystem functions and environmental services on which global society depends. Quantifying how our decisions affect ecosystem functions and environmental services along environmental and human land use gradients and, further, bringing that knowledge into political spheres will shift us towards a resilient social-ecological system.

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