






Comparing forest structure and biodiversity on private and public land: secondary tropical dry forests in Costa Rica

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ABSTRACT

Secondary forests constitute a substantial proportion of tropical forestlands. These forests occur on both public and private lands and different underlying environmental variables and management regimes may affect post-abandonment successional processes and resultant forest structure and biodiversity. We examined whether differences in ownership led to differences in forest structure, tree diversity, and tree species composition across a gradient of soil fertility and forest age. We collected soil samples and surveyed all trees in 82 public and 66 private 0.1-ha forest plots arrayed across forest age and soil gradients in Guanacaste, Costa Rica. We found that soil fertility appeared to drive the spatial structure of public vs. private ownership; public conservation lands appeared to be non-randomly located on areas of lower soil fertility. On private lands, areas of crops/pasture appeared to be non-randomly located on higher soil fertility areas while forests occupied areas of lower soil fertility. We found that forest structure and tree species diversity did not differ significantly between public and private ownership. However, public and private forests differed in tree species composition: 11 percent were more prevalent in public forest and 7 percent were more prevalent in private forest. *Swietenia macrophylla*, *Cedrela odorata*, and *Astronium graveolens* were more prevalent in public forests likely because public forests provide stronger protection for these highly prized timber species. *Guaazuma ulmifolia* was the most abundant tree in private forests likely because this species is widely consumed and dispersed by cattle. Furthermore, some compositional differences appear to result from soil fertility differences due to non-random placement of public and private land holdings with respect to soil fertility. Land ownership creates a distinctive species composition signature that is likely the result of differences in soil fertility and management between the ownership types. Both biophysical and social variables should be considered to advance understanding of tropical secondary forest structure and biodiversity.

Abstract in Spanish is available with online material.

Key words: ecosystem services; forest biomass; forest conservation; forest management; forest succession; Guanacaste; Costa Rica; land tenure; secondary forests; species composition.

SECONDARY FORESTS THAT HAVE NATURALLY REGENERATED AFTER HUMAN DISTURBANCES COMPOSE MORE THAN HALF OF TROPICAL FORESTS and are key areas for biodiversity protection and provision of ecosystem services (Wright 2005, Chazdon *et al.* 2009). Secondary forests are likely to compose an increasingly sizable component of tropical forestlands due to a global combination of continuing megatrends—doubling of global food demands by 2050 (Foley *et al.* 2011), tropical agricultural extensification (Laurance *et al.* 2014), and disproportionate clearing of intact tropical forests (Gibbs *et al.* 2010). Humans have a lengthy history of reshaping forest ecosystems (Williams 2003); thus, human land use gradients (*e.g.*, rural to urban) or typologies (*e.g.*, public vs. private lands) that affect differences in land management may influence secondary forest biodiversity, structure, and above-ground biomass (Mcalpine *et al.* 2007).

Land tenure has long been an active area of scholarship as a driver of forest dynamics (Ostrom 1990). The influence of ownership is particularly relevant for tropical secondary forests as they often develop on abandoned agricultural or pasture lands and such lands are frequently privately owned. Guanacaste province in Costa Rica is a pertinent example of this: 90 percent of the secondary forest that developed from 1986 to 2005 occurred on private lands (Calvo-Alvarado *et al.* 2009). Land ownership and the tenure rights linked with different ownership categories may affect forest management, leading to differences in forest structure, aboveground biomass, diversity, and species composition (Lovett-Doust & Kuntz 2001, Hudiburg *et al.* 2009, Mihorski *et al.* 2010, Bergès *et al.* 2013, Schaich & Plieninger 2013). Land under different ownership categories can also differ in environmental attributes (*e.g.*, topography and soil fertility). In Guanacaste, for example, private lands with complex topography were the first lands to be abandoned and regenerate after the collapse of the beef market, resulting in a sharp increase in the number of forest patches on private lands (Arroyo-Mora 2002,

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Arroyo-Mora *et al.* 2005). Thus, both management and ecological attributes can differ between ownership types and differences ascribed to public and private categories are likely the result of these underlying factors (Mihorski *et al.* 2010, Bergès *et al.* 2013).

Costa Rica is a particular germane place to assess differences between public and private forests because all forests that are ≥ 2 ha with a mix of species are protected by the national forest policy—regardless of whether they are publicly or privately owned (Forestry Law 1999). Thus, one would expect public and private forests to be more similar than not; yet, forestry laws are not always followed, and both land use history and land management surrounding forests can affect forest post-abandonment successional trajectories. Management between public and private lands in Guanacaste is distinct on a few important dimensions. Foremost, overarching objectives are different: Public lands are managed for conservation, whereas private lands that have forests are often working lands that can be subject to grazing, fire, and selective logging (Allen 2001). Differential management practices pertaining to fire (Kauffman *et al.* 2003), cattle (Stern *et al.* 2002, Griscom *et al.* 2009), selective logging (Ruiz *et al.* 2005), and remnant species selection (Esquivel-Mimenza *et al.* 2011) may lead to differences between public and private forests in biodiversity, forest structure, and biomass accumulation during post-abandonment successional processes.

Due to these differences, we expected private forests to have lower stem density (*e.g.*, cattle trampling), lower biomass (*e.g.*, increased fire frequency), lower biodiversity (*e.g.*, fragmented forests), and distinct composition (*e.g.*, selective timber harvesting, remnant species selection). Here, we use an extensive dataset of forest inventory plots arrayed across soil and successional gradients in both private and public lands in Guanacaste, Costa Rica. We were interested in understanding (1) whether forest stand structure, tree diversity, and tree species composition were related to ownership and (2) whether that relationship was significant after controlling for differences in forest age and soil.

METHODS

SITE DESCRIPTION AND LAND USE HISTORY.—Our study was conducted in tropical dry forests of Guanacaste, Costa Rica. Mean annual temperature is $\sim 25^{\circ}\text{C}$ and dry season length ranges from 5 to 6 months (Holdridge 1967, Gillespie *et al.* 2000). Public forest data were collected from 19 plots in 2007 and 2010 in Palo Verde National Park ($10^{\circ}36'90''\text{N}$, $85^{\circ}35'97''\text{W}$) and 63 plots in the Área de Conservación Guanacaste ($10^{\circ}85'00''\text{N}$, $85^{\circ}61'67''\text{W}$) (Powers *et al.* 2009, Becknell & Powers 2014). In 2011, we sampled 17 plots on private lands near Palo Verde National Park National Park (Palo Verde) and 49 plots near Área de Conservación Guanacaste (ACG). Sampling criteria followed Powers *et al.* (2009). Private forest plots were necessarily more spread out than public forest plots due to the nature of the agricultural matrix and pattern of large privately owned parcels (>300 -ha) in Guanacaste (Edelman 1985).

As described in previous studies, historical land use in Guanacaste was broadly similar for both public and private lands. Guanacaste was dominated by extensive ranches (Edelman 1985), and the wave of deforestation from ~ 1950 s to 1980s was closely tied to Costa Rica's integration into the international beef market; when prices decreased and the government withdrew subsidies, widespread forest recovery was evident (Calvo-Alvarado *et al.* 2009). Countervailing land use policies focused on conservation took hold in the early the 1970s, which is when the ACG and Palo Verde National Parks were created.

Although we recognize the importance of land use history in affecting successional trajectories (Uhl *et al.* 1988, Guariguata & Ostertag 2001), we did not assess plot-specific land use history for several reasons. First, public forest plot inventories conducted prior to private forest plot inventories did not assess land use history; because our goal was to compare public and private forests, it did not make sense to collect data in private forests for which we did not have comparable data in public forests. Second, in areas with landowner turnover and absentee landowners, it is difficult to find information on land use and management history. Finally, 17 of 31 of the private farms we sampled were >300 -ha (range 14-ha to 9000-ha, median 318-ha) and detailing plot-specific land use of a 0.1-ha plot on a 300-ha or larger farm would likely not have provided accurate results (for example, the number of cattle allowed to graze in that 0.1-ha area before forests regenerated). We did interview private landowners about their farm practices and present qualitative data from those interviews.

In and around ACG, there is a distinctive forest community characterized by a high abundance of *Quercus oleoides*; we sampled both forests with and without abundant *Q. oleoides* (Fig. S1). Previous work on public lands showed that *Quercus*-dominated forests had low soil fertility compared to diverse species forests (Powers *et al.* 2009). Therefore, we distinguished between *Quercus*-dominated and diverse species forest plots for the soil and species composition ordinations. Both *Quercus*-dominated and diverse species forest were evident at ACG, but Palo Verde did not have *Quercus*-dominated forests. Forest stand age was estimated by a local botanical expert (the same individual estimated every plot age) and satellite imagery. We used a time series of georectified Landsat images from 1986, 1996, 2000, and 2007 to corroborate local expert estimates. For older forests, we are less confident in the precision of age estimates as we relied exclusively on local expert knowledge. The older forest patches in our study were likely cleared and regenerated before the most recent wave of deforestation from ~ 1950 s to 1980s. Stand age between public and private forests was not statistically different (Table 1; Fig. S1).

LANDOWNER INTERVIEWS.—The first author conducted interviews with landowners from private farms from which forest data were collected. Results reported here focus on practices related to forest management. We also asked Likert scale questions concerning why landowners allowed forests to regenerate on their farms. We developed a list of rare species and remnant species (species that are often left standing when the rest of the forest is removed).

TABLE 1. Mean and standard deviation for forest metrics between public and private tropical dry forests in Guanacaste, Costa Rica. Forest metrics for individuals ≥ 10 cm DBH include forest stand age, community-weighted mean wood density (CWMWD), Shannon–Wiener diversity index, aboveground biomass, basal area, stem density, and sapling stem density (< 10 cm DBH and ≥ 1.3 m in height). The exponential of the Shannon–Wiener diversity index (the effective number of species) was 7.6 ± 2 for public forests and 6.1 ± 2 for private forests. The number of private forest plots was 66 while public forest plots were 82.

Response variable	Public Mean and SD	Private Mean and SD	<i>t</i>
Forest stand age (yr)	31 \pm 21	25 \pm 17	-1.482
CWMWD (g/cm ³)	0.65 \pm 0.07	0.62 \pm 0.08	-3.182*
Shannon–Wiener diversity index	2.03 \pm 0.73	1.8 \pm 0.71	-1.975
Aboveground biomass (Mg/ha)	173.23 \pm 83.24	148.63 \pm 83.95	-1.78
Basal area (m ² /ha)	24.2 \pm 9.17	23.91 \pm 12.35	-0.157
Stem density (stems/ha)	411.34 \pm 163.3	346.67 \pm 167.82	-2.366
Sapling stem density (stem/ha)	485.73 \pm 276.52	454.54 \pm 291.43	-0.666

The results of each *t*-test between public and private forests for each metric are shown (**P* < 0.05).

We asked landowners open-ended but specific questions (e.g., ‘why do you tend to select those specific tree species as remnants?’). For open-ended questions, we coded landowner responses and classified them by key themes (Glaser 1992).

SAMPLING AND BIOMASS CALCULATIONS.—In total, we sampled 82 public plots from two national parks and 66 private plots from 31 private farms. We sampled multiple plots on large private farms that had forests of different ages. In each 50 \times 20 m (0.1-ha) plot, trees were sampled in nested subplots. Every tree ≥ 10 cm diameter at breast height (dbh) was measured and identified. We collected samples for species we could not identify in the field. In total, we sampled 5662 individuals from 166 species. There were two individuals of different species that we were unable to identify. In 50 2 \times 4 m subplots within each plot, we counted and recorded the dbh of saplings < 10 cm dbh and ≥ 1.3 m in height but did not determine the species. In private forest plots, we also noted the presence/absence of cattle in 50 1-m² subplots assessed by the presence/absence of feces, hoof prints, or well-defined cow paths.

We collected wood density samples with an increment borer from three different individuals per species if the species had not been previously sampled in public forests (Powers & Tiffin 2010). We used those species-specific wood density values in an allometric equation to calculate aboveground biomass for each tree (Chave *et al.* 2005). We also calculated the mean wood density for all individuals ≥ 10 cm dbh weighted by species abundance per plot; this is the community-weighted mean wood

density (CWMWD). The CWMWD was used to calculate aboveground biomass for trees < 10 cm dbh and ≥ 1.3 m in height as we did not identify those trees to species.

For soil samples, we collected and averaged three volumetric samples of 192 cm³ to 10 cm depth per plot to calculate soil bulk density. Samples were oven-dried at 110 degrees C for 48 h and then passed through a 2-mm sieve; stone content was defined as stones that did not pass through the 2-mm sieve. We also collected and homogenized 10 samples per plot to a depth of 10 cm; these were air-dried, sieved, and shipped to the University of Minnesota Research Analytical Laboratory (St. Paul, MN) for furthermore processing. Samples were analyzed for the following elements following a hot nitric acid digest and quantification via inductively coupled plasma spectroscopy: 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.

STATISTICAL METHODS.—We were interested in understanding (1) differences in forest stand structure, tree diversity, and tree species composition between ownership types and (2) differences between ownership types after controlling for soil and stand age differences. However, the statistical techniques for species richness and composition were not able to control for covariates; thus, we were not able to answer our second question for species richness or composition. Below, we explain the statistical methods we used in more depth.

For the soil elements, we used a correlation-based principle components analysis (PCA) to summarize linear patterns of covariation and reduce the number of variables for use in subsequent statistical analyses. To assess whether there were differences between public and private lands, we employed multiresponse permutation procedure (MRPP) on the soil PCA axes with a Euclidian distance measure. Results from a MRPP include a *P*-value and *A* value. A significant *P*-value suggests that groups differed more than expected by chance. The *A* value is a measure of effect size and values for *A* are commonly below 0.1 for community ecology. An *A* > 0.3 is fairly high. We also used a pairwise MRPP to compare public and private subgroups coded for *Quercus*-dominated and diverse species forest groups (e.g., public diverse species plots vs. private *Quercus*-dominated). For the pairwise MRPP, a pairwise average is calculated—this is the average *P*-value and *A* value, respectively, of all the subgroups combined. We did not use plot location as a predictor in subsequent statistical analyses to avoid multicollinearity in predictor variables as plot location was correlated with the PCA axes (McClellan 2014). These analyses were conducted using PC-ORD v. 6.22 (McCune & Mefford 2011). Reported *P*-values for all statistical analyses are Holm’s corrected (Gaetano 2013).

To assess differences in stand-level metrics between public and private forests, we used both *t*-tests and a hierarchical multiple linear regression (MLR). First, we used multiple *t*-tests to assess whether aboveground biomass, basal area, stem density (trees ≥ 10 cm dbh), sapling stem density (trees < 10 cm dbh and

>1.3 m in height), CWMWD, and Shannon–Wiener diversity index were different between public and private forests. As the Shannon–Wiener diversity index is an index and not an intuitive, true diversity metric, we also calculated the exponential of the Shannon–Wiener diversity index for the effective number of species (Jost 2006). Next, we used a hierarchical MLR to assess whether these stand-level metrics were different between ownerships after accounting for stand age and soil. It is well known that age is correlated with both biodiversity and forest structure (Guariguata & Ostertag 2001), so forest age (log transformed) was input in step 1 of the MLR followed by the soils PCA1, PCA2, and PCA3 in step 2 and ownership (coded as a dummy variable) in step 3 (SPSS Inc. Released 2011 IBM Corp).

We used the EstimateS software program v. 8.2 (Colwell *et al.* 2004) to calculate sample-based species rarefaction curves using species abundance data of 166 species. We used subplots of 10x10 m, so the sample size was 660 for private forests and 820 for public. This technique was unable to control for soil or age differences.

To evaluate tree species composition, we used a nonmetric multidimensional scaling ordination (NMS) and MRPP (McCune & Mefford 2011). We excluded species singletons and doubletons (*i.e.*, species with only one or two individuals from within the full dataset); rare species do not provide information on patterns of species composition between groups and can complicate patterns (Peck 2010). We ran multiple NMS ordinations to insure consistent solutions and selected one for interpretation. The final stress score is reported to show how well the ordination fits the data; the stress score increases with both increasing sample units and number of species (McCune *et al.* 2002), so a stress score above 25 can still be interpretable (Peck 2016). A joint plot with age and soil variables was overlain to aid in interpretation of the NMS. We determined significance of the public and private

groups with a MRPP using the Bray–Curtis distance measure; we also compared public and private diverse species vs. *Quercus*-dominated groups with a pairwise MRPP. We considered using a canonical correspondence analysis (CCA) to enable us to compare species after accounting for forest age and soil differences (ter Braak 1986); however, the CCA chi-square distance measure is not robust to sparse data and our plot by species matrix had sparsity level of 90%, which is common for diverse tropical forest datasets. Thus, we could not account for differences in forest age or soil and instead restricted our comparisons to public and private forests.

We used a second approach, the Classification Method (CLAM), to evaluate species composition (Chazdon *et al.* 2011). With the CLAM, we assessed which species were too rare to classify between public and private, which were generalists, and which were more prevalent in either public or private forests. We calculated both a simple majority threshold of 0.5 and a super majority threshold of 0.677, each with a significance level of $\alpha = 0.005$. The CLAM method enables only two group comparisons and cannot account for covariates, so we restricted our comparisons to public and private forests.

RESULTS

SOILS.—We found three major axes in the principal components analysis (PCA) that represented different aspects of the soil fertility gradient. We interpreted PCA1 to be an axis of soil fertility because Ca, Mg, N, P, and K had correlations between 0.59 and 0.86 with PCA1 (Table S1). PCA1 explained 45 percent of the variation (Fig. 1). PCA2 likely represented an underlying geological gradient associated with thin, volcanic-derived soils near ACG to the fertile, alluvial soils near limestone cliffs in Palo Verde because Mn, Fe, B, Na and Ni had correlations above $r = 0.4$.

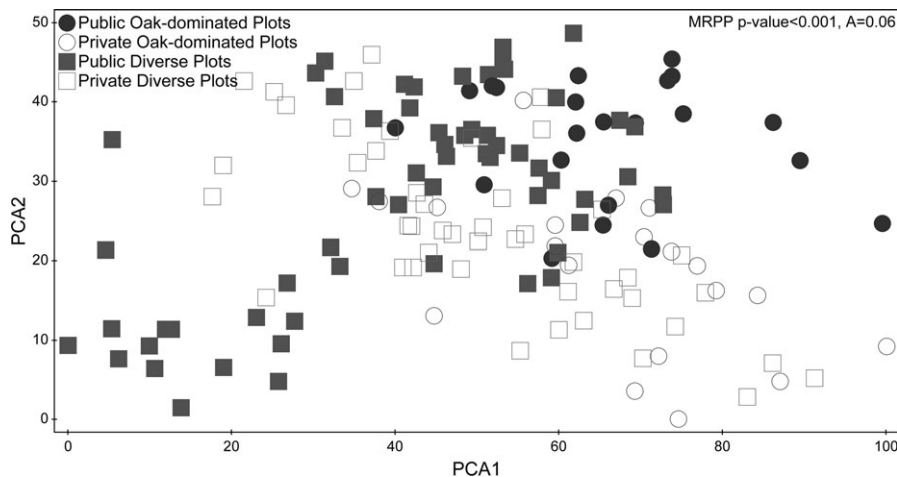


FIGURE 1. Soil principle components analysis (PCA) ordination of public and private forest inventory plots from tropical dry forests in Guanacaste, Costa Rica. PCA1 and PCA2 are shown and explained 45 percent and 14 percent of the variation, respectively. Public plots are labeled as solid colors while private are open; *Quercus*-dominated plots are labeled with circles while diverse forest plots are squares. MRPP *P*-value and *A* value results for public and private group comparisons are listed.

PCA2 explained 14 percent of the variation. PCA3 appeared to reflect differences in land use history such as grazing as soil bulk loaded strongest on this axis. PCA3 explained 13 percent of the variation. The MRPP test on the PCA ordination showed that soils differed significantly between public and private forests (Table 2).

We also compared the six subgroups using a pairwise MRPP (e.g., public *Quercus*-dominated vs. private *Quercus*-dominated) (Table 2). All subgroups that compared public and private forest soils were significantly different. The pairwise average (mean of all subgroupings) was also significant. The effect size (A value) was variable (0.04–0.09). Notably, the effect size for public *Quercus*-dominated vs. private *Quercus*-dominated group was the highest (0.09); thus, the soils between public vs. private *Quercus*-dominated were the most distinct. Private *Quercus*-dominated forest plots also had higher concentration of the soil macronutrients we measured (N, P, K, Ca, and Mg) (Fig. S2A-E).

FOREST STRUCTURE, ABOVEGROUND BIOMASS, AND CWMWD.—Ownership was not a significant predictor of basal area, stem

density, sapling stem density, or aboveground biomass in *t*-tests (Table 1) or the hierarchal MLR (Table S2). CWMWD was significantly different between ownership types with slightly lower values for private forests (Table 1). In the hierarchal MLR, basal area and aboveground biomass were best explained by age alone, increasing with age (Table S2). The best model of stem density included both age and PCA2, with stem density increasing with age and PCA2. Sapling stem density (<10 cm dbh and ≥ 1.3 m in height) was not predicted by any of the independent variables we chose for the model. The best model of CWMWD included ownership, PCA1, and PCA3. Both PCA1 and PCA3 explained an independent fraction of the variation: Less fertile soils had higher CWMWD.

TREE SPECIES DIVERSITY.—Ownership was not predictive of tree species diversity. We found no strong differences in sample-based species rarefaction curves (Fig. S3). We also found no difference in the Shannon–Wiener diversity index using a *t*-test (Table 1). These results echo other studies that found no difference in biodiversity between public and private forests (Mihorski *et al.* 2010, Schaich & Plieninger 2013).

Although the Shannon–Wiener diversity index did not differ significantly between ownership types, previous research has shown that age and soil fertility affect tree species diversity, so we calculated the independent effects of ownership, age, and soil (Table S2). Even after controlling for soil and age, ownership was not a significant predictor. However, age was a significant predictor of Shannon–Wiener diversity index: As forest stand age increased, the Shannon–Wiener diversity index also increased (after accounting for the effects of ownership and soil). The Shannon–Wiener diversity index was positively correlated with PCA2, so it increased from the fertile, alluvial soils to the volcanic soils. It was also negatively correlated with PCA1, suggesting that it increased with increasing soil fertility, and negatively correlated with PCA3, suggesting that it decreased with higher soil compaction and lower N and P—possibly due to grazing and/or low soil fertility).

TREE COMPOSITION.—We found that species composition was related to ownership, soil, and age, according to the NMS and MRPP results (Table 2, Fig. 2). Tree species composition between public and private forests differed significantly, and the final stress score was 17, which is acceptable for large species datasets. Species composition was also significantly different for all subgroups (Table 2). Yet, the magnitude of the differences was variable. The magnitude between some subgroups was low, so there was overlap in species composition for some forests subgroups such as public diverse vs. private diverse forests (A = 0.01). Species composition was more distinctive between other subgroups such as public *Quercus*-dominated vs. private diverse forests (A = 0.07). A noticeable pattern in the magnitude of the effect was that all subgroup comparisons of diverse species vs. *Quercus*-dominated forests had comparatively higher A values: *Quercus*-dominated forests had a distinct suite of tree species compared to diverse species forests. Likely, this is because the cohort of

TABLE 2. Multiresponse permutation procedure (MRPP) and pairwise MRPP for principle components analysis (PCA) and nonmetric multidimensional scaling (NMS). MRPP was used to assess group differences with Euclidian distance measure for the PCA conducted on soil variables and Bray–Curtis distance measure for the NMS conducted on tree species composition. Both PCA and NMS groups are coded for (1) public and private tropical dry forest plots and (2) public *Quercus*-dominated, public diverse species, private *Quercus*-dominated, and private diverse species tropical dry forest plots. Values for chance-corrected within-group agreement (A) are provided to assess within-group homogeneity; when A = 0, all items in group are distinct and values of A in ecology are often below 0.1. Holm’s corrected P-values are provided to assess significance.

Ordination	Group 1	Group 2	A
PCA	Public	Private	0.06***
PCA	Pairwise Average	Pairwise Average	0.06**
PCA	Public Diverse	Private <i>Quercus</i>	0.08**
PCA	Public Diverse	Private Diverse	0.05**
PCA	Public <i>Quercus</i>	Private <i>Quercus</i>	0.09*
PCA	Public <i>Quercus</i>	Private Diverse	0.04*
PCA	Public <i>Quercus</i>	Public Diverse	0
PCA	Private <i>Quercus</i>	Private Diverse	0
NMS	Public	Private	0.02***
NMS	Pairwise Average	Pairwise Average	0.06***
NMS	Public Diverse	Private <i>Quercus</i>	0.05***
NMS	Public Diverse	Private Diverse	0.01***
NMS	Public <i>Quercus</i>	Private <i>Quercus</i>	0.04***
NMS	Public <i>Quercus</i>	Private Diverse	0.07***
NMS	Public <i>Quercus</i>	Public Diverse	0.04***
NMS	Private <i>Quercus</i>	Private Diverse	0.05***

The pairwise average is the average for the pairwise MRPP (*P < 0.05, **P < 0.01, ***P < 0.001).

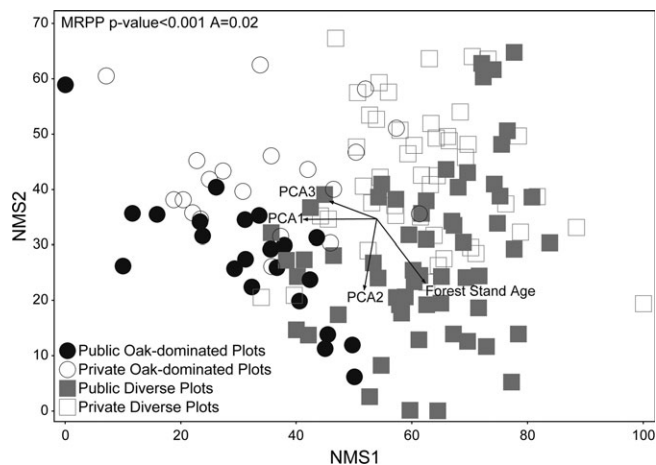


FIGURE 2. Nonmetric multidimensional scaling (NMS) ordination of tree species composition in public and private tropical dry forests in Guanacaste, Costa Rica. The ordination graph shows axis 1 (NMS1) and axis 2 (NMS2). Open circles are private forest plots; closed circles are public forest plots. Overlaid on the ordination is a joint plot of soil (PCA1, PCA2, and PCA3) and forest stand age; the correlations of each joint plot vector are indicated by the length and direction with the ordination axes.

species in *Quercus*-dominated forests can thrive in lower soil fertility. This compositional pattern related to low soil fertility is shown in the NMS Axis 1 (NMS1) correlations of $r = 0.5$ with PCA1 and $r = 0.4$ with PCA3—*Quercus*-dominated forest plots had lower soil fertility and higher bulk density compared to the diverse species forest plots. Plots separated along NMS2 by age and PCA2, which represents a gradient in soil from fertile, alluvial soils to thin, volcanic soils. NMS2 was also correlated with stand age ($r = 0.48$); as NMS2 scores increased, plots were younger.

The CLAM analysis revealed that 19 species were more prevalent in public forests (11%), 12 species were more abundant in private forests (7%), 53 showed no distributional bias (32%), and 82 species were too rare to classify (49%). Tree species categorized as more prevalent in public or private are listed in Table 3. For public forests, there were three notable timber species—*Swietenia macrophylla* (mahogany), *Cedrela odorata* (Spanish cedar), and *Astronium graveolens* (tigerwood). For private forests, species associated with the *Quercus*-dominate forest type were more prevalent, specifically *Quercus oleoides*, *Byrsonima crassifolia*, *Curatella americana*, *Apeiba tibourbon*, and *Bixa orellana*; furthermore, the most abundant species in private forests was a popular tree for cattle fodder, *Guazuma ulmifolia*.

LANDOWNER INTERVIEWS.—The most frequently mentioned rare species were *S. macrophylla* (21 of 28) (frequency mentioned/ $N = 28$, two refusals), *Dalbergia retusa* (20 of 28), *C. odorata* (19 of 28), and *A. graveolens* (19/28) (Fig. S4). From the coded landowner transcriptions, two key themes emerged as follows: Landowners noted declines in abundance of these species as a result of species-specific timber extraction and, more generally,

TABLE 3. Relative abundance of species more prevalent in public and private tropical dry forests. Individual species relative abundance per category was calculated as total species-level abundance divided by the total stems in each category multiplied by 1000 for ease of interpretation. A threshold of $P = 0.005$ was used in the multinomial CLAM algorithm to classify a species as more prevalent in either public or private forests at a simple majority of 0.5. Species in the 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 in secondary tropical dry forests in Guanacaste, Costa Rica

Species	Relative abundance ($\times 1000$)		More Prevalent in Private	
	Public	Private	Species	Public Private
<i>Rebdera trinervis</i> *	121	7	<i>Guazuma ulmifolia</i>	56 114
<i>Luebea speciosa</i>	59	26	<i>Quercus oleoides</i>	68 112
<i>Manilkara chicle</i> *	21	0	<i>Cochlospermum vitifolium</i>	39 57
<i>Ateleia herbert-smithii</i> *	19	0	<i>Byrsonima crassifolia</i> *	4 54
<i>Sebastiania pavoniana</i> *	16	2	<i>Cordia alliodora</i>	16 47
<i>Lysiloma divaricatum</i>	14	7	<i>Luebea candida</i>	6 40
<i>Exostema mexicanum</i> *	11	0	<i>Chomelia spinosa</i>	9 24
<i>Brosimum alicastrum</i>	11	4	<i>Curatella americana</i> *	1 17
<i>Astronium graveolens</i>	9	2	<i>Ocotea veraguensis</i>	6 13
<i>Lonchocarpus parviflorus</i> *	9	0	<i>Apeiba tibourbon</i> *	2 12
<i>Cedrela odorata</i> *	9	0	<i>Acrocomia vinifera</i>	1 6
<i>Sapranthus palanga</i> *	5	0	<i>Bixa orellana</i> *	0 5
<i>Swietenia macrophylla</i> *	5	0		
<i>Acosmium panamense</i>	5	1		
<i>Coccoloba guanacastensis</i> *	4	0		
<i>Cordia collococca</i>	4	0		
<i>Mabea occidentalis</i>	4	0		
<i>Karwinskia calderonii</i>	3	0		
<i>Pitbecellobium dulce</i>	3	0		

forest clearing during agropastoral development. The most frequently mentioned remnant species were *Enterolobium cyclocarpum* (27 of 29), *Samanea saman* (23 of 29), *Gliricidia sepium* (21 of 29), *C. odorata* (20 of 29), *Guazuma ulmifolia* (18 of 29), and *Manilkara chicle* (18 of 29) (Fig. S5). Landowners' commonly reported that they chose remnant species for timber. A second common theme was that they selected remnant tree species that provided fodder and shade for their cattle. Although evidence of cattle was not assessed in public forests, the private forest assessment showed that 68 percent of private forest plots had evidence of cattle. In Likert scale questions, 73 percent of landowners ($N = 26$) agreed that they 'allowed forest to regenerate to provide fodder for my cattle' while 81 percent ($N = 26$) agreed that they 'allowed forest to regenerate to provide shade for my cattle' (Table S3). To a lesser extent, landowners also mentioned that they kept remnant species on their farm for esthetics.

Enterolobium cyclocarpum was mentioned most frequently as a remnant, and it is often a prominent feature of the landscape in Guanacaste; this species is used for timber and can provide fodder and shade for cattle, but landowners may have also selected it because of the cultural value ascribed to *E. cyclocarpum* as the namesake of Guanacaste, Costa Rica.

DISCUSSION

In many tropical areas, secondary forest regeneration occurs on agricultural fields followed as a result of soil degradation or shifts in market demands (Wright 2005); many of these lands are privately owned. Even after controlling for differences in stand age and soil, we found no difference in aboveground biomass, forest structure, or diversity measures between public and private forests; this suggests that, for these metrics, public and private tropical dry forests in Guanacaste provide similar value. We found statistically significant differences in ownership for community-weighted mean wood density, but the mean difference was small and did not result in significant differences in aboveground biomass. We found strong evidence of species compositional differences between public and private forests. These differences are likely due to a combination of different factors such as landowner management, forest fragmentation, and soil fertility. However, the statistical techniques used were unable to isolate the differential effects of stand age and soil. The differences in species composition suggest that public and private forests offer different conservation value for this area. Specifically, public forests protect high-value timber species such as *S. macrophylla*, *C. odorata*, and *A. graveolens*.

PUBLIC AND PRIVATE EDAPHIC CONDITIONS.—Spatial heterogeneity of soil quality affects land use (Evans & Moran 2002). In our study, soil appeared to be a strong driver of the spatial structure of ownership. The southern region of our study area in and around Palo Verde had the highest 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 to public forests; this may suggest that landowners non-randomly cultivate the portions of their land that have higher soil fertility with the effect that private forests are restricted to less fertile soils. In other words, private landowners non-randomly cultivate crops/pasture in high soil fertility areas; thus, we likely sampled a lower soil fertility subset of the full range on private lands as we sampled only forest soils and not crop/pasture soils. Given that public lands were largely forested, we were able to sample the full soil fertility range on public lands; therefore, some of the public plots in the southern region had high soil fertility. This bias toward forests occupying land that have 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). Moreover, as deforestation and reforestation in Guanacaste closely tracked the rise and fall of international beef prices (Calvo-Alvarado *et al.* 2009), even marginal pasture lands

(*e.g.*, steep slopes/shallow soils) were put into production during the peak of the cattle market. When market pressure abated and forest regeneration began, these marginal lands were among the first to recover (Arroyo-Mora *et al.* 2005).

Both public and private *Quercus*-dominated forests in the northern region of our study area in and around ACG had low soil fertility. The northern region is dominated by pasture lands and lacks the fertile, alluvial soils evident in the southern crop land region. Public *Quercus*-dominated forests had significantly different soil compared to private *Quercus*-dominated forests and lower levels of soil macronutrients. The lower levels of macronutrients in public forests may be due to a combination of factors. Early public land purchasing campaigns for ACG purposefully sought land with the largest mature forest remnants (Allen 2001). Some of the *Quercus*-dominated plots were not in the first round of land purchases but were located close to those initial purchases; ACG expansion campaigns likely focused on land that was close to the park so as to consolidate land holdings. Additionally, given that the public *Quercus*-dominated plots had lower levels of macronutrients compared to private, the public land likely did not support rich pasture grass and so was not highly valuable for pasture land: The pasture land value may have been less than the conservation land value. Conservation areas are often disproportionately situated in areas with poor soil quality, complex topography, low accessibility, and/or high elevations (Pressey 1995). Indeed, existing tropical dry forests in Central America at large are usually found in inaccessible areas and areas with poor soil fertility (Griscom & Ashton 2011).

FOREST STRUCTURE, ABOVEGROUND BIOMASS, AND CWMWD.—We expected that differences in management, the presence/abundance of cattle, and selective harvesting of high wood density species between public and private forests would result in differences in structural measurements and biomass. However, this was not the case; likely, this is because secondary forests recover structural complexity and biomass swiftly (Letcher and Chazdon 2009). Forest structure and biomass were best predicted by stand age as found in other studies (Guariguata & Ostertag 2001).

CWMWD did not differ significantly along the forest age gradient but differed with the PCA soil gradients (Chave *et al.* 2006). CWMWD was also higher for public forests: Public forests were 0.04 g/cm³ or 3 percent higher than private forests. Yet, the slight CWMWD difference did not translate into a significant difference in aboveground biomass between ownership types. This result is analogous to results across multiple tropical forest sites that showed no correlation 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.

FOREST TREE SPECIES BIOLOGICAL DIVERSITY AND COMPOSITION.—We predicted that public vs. private forests would differ in species diversity, richness, and composition as a result of underlying

factors such as soil fertility, forest fragmentation, differential fire management, the presence/abundance of cattle, and timber harvesting. We found no differences in diversity or richness, but species composition differed significantly between public and private forests.

Species may be categorized as more common in public or private forests for a variety of reasons; for example, selective harvesting may occur less frequently in public forests, so they have a higher relative abundance of valuable timber species. Indeed, illegal timber harvesting in Costa Rica occurs primarily on private lands (Miller 2011). In the CLAM analysis, we found that species more prevalent in public forests included those well known in international hardwood markets, specifically *S. macrophylla* (mahogany), *C. odorata* (Spanish cedar), and *A. graveolens* (tigerwood). In interviews, landowners ranked those species among the top four rare species due to selective timber harvesting and, more generally, widespread agricultural development. Private forest species also included a commercial timber species, *Cordia alliodora*. This species may be more abundant on private lands because it is a pioneer species with a fast growth rate (Lang & Knight 1983), while highly prized and overharvested timber species such as *S. macrophylla*, *C. odorata*, and *A. graveolens* have slow growth rates (Madrigal 1993). *Rebdera trinervis*—the most abundant public forest species—has strong wood and is used locally as ornamental structural support in buildings, so overharvesting in 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). Other studies in tropical dry forests have attributed a notable lack in valuable timber species abundance due to selective harvesting (Ruiz *et al.* 2005 and references therein).

Landowners may also retain particular species on their farms to provide cattle fodder/shade. Cattle–forest interactions have been noted as potential drivers of particular species abundance within tropical dry forests (Janzen 1985, Griscom *et al.* 2009) and may drive differences between public and private forests under different cattle management regimes. The most abundant species in private forest was *Guaazuma ulmifolia*. Fruits of this species are favored, consumed, and dispersed by domesticated ungulates (Janzen 1985); both landowners' remnant selection of tree species for cattle fodder and cattle dispersal of seeds may have led to this species high abundance within private forests. The majority of private landowners in this study noted that they kept *G. ulmifolia* as a remnant species, and landowners chose remnant species primarily for timber and/or cattle shade/fodder. Furthermore, the majority of landowners agreed that they allowed forest regeneration to provide shade/fodder. In private forests, we found that 68 percent of plots had evidence of the cattle presence. Palo Verde uses cattle in park management to reduce the fire fuel load (Stern *et al.* 2002, Powers *et al.* 2009), so including public and private forest plots in the Palo Verde National Park region could confound results. 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 (data not shown).

Additionally, species may be categorized as more common in public or private forests due to their plant life history strategies that influence success in different types of forest fragments (Lavorel *et al.* 2007). Arroyo-Mora *et al.* (2005) found that public lands had fewer forest patches with a higher mean patch size and lower edge density than private lands in Guanacaste between 1960 and 2000. The higher forest fragmentation on private lands can affect species dispersal, recruitment, and survival (Harper *et al.* 2005). Highly fragmented forests can also cause habitats to remain in early successional phases populated with early seral species (Tabarelli *et al.* 2008). For example, *Cochlospermum vitifolium* is an early seral species with light, wind-dispersed seeds and was significantly more prevalent in private forests, likely due to the highly fragmented private forest landscape.

Soil differences between public and private forests also appeared to be a strong driver of species compositional differences between public and private forests. *Quercus oleoides*, *Byrsonima crassifolia*, *Curatella americana*, *Apeiba tibourbou*, and *Bixa orellana* were all more prevalent in private forests; these species tend to co-occur in areas of low soil fertility—the *Quercus*-dominated forests. Both public and private lands had *Quercus*-dominated forests, yet this suite of species was significantly more abundant in private forests. The higher abundance was likely because *Quercus*-dominated forests on private lands had higher concentrations of macronutrients compared to *Quercus*-dominated forests on public lands.

CONCLUSION

Secondary forests compose an increasingly important component of tropical forests and often regenerate on private lands. Compared to other countries, Costa Rica has strict forest conservation policies that protect both public and private forests equally under the law. Therefore, one would expect forests to be very similar; yet, people do not always follow regulations and land use surrounding forests can affect post-abandonment successional processes. We found that public and private forests were similar in species diversity and aboveground biomass. However, we also found that species composition between the two types of ownership was distinct. These composition differences are likely due to differences in management: Management on private lands may include burning pasture close to forests, allowing cattle grazing in or near forests, choosing particular remnant tree species, and selectively harvesting timber species. Moreover, public and private lands may have been established non-randomly with respect to soil fertility, and these differences in soil fertility may also drive differences in species composition. Future work should examine how forest fragmentation differences between ownership types affect species compositional and functional assemblages (Fahrig 2017).

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.57s62> (McClellan *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Public and private plot age stratifications.

TABLE S1. *Principle Components Analysis of soil variables from public and private forests.*

FIGURE S2 A-E. Principle Components Analysis (PCA) axes one and two for soil macronutrients (N, P, K, Ca, and Mg).

FIGURE S3. Public and private forest sample-based species rarefaction curves.

TABLE S2. *Hierarchical Multiple Linear Regression comparing biodiversity and forest structure.*

FIGURE S4. This figure lists all rare species mentioned by five or more landowners.

FIGURE S5. This figure lists remnant species mentioned by three or more landowners.

TABLE S3. Likert statements to evaluate how landowners' value their forests.

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