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RESEARCH ARTICLE

Divergent rates of change between tree cover types in a tropical pastoral region

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Abstract

Context Forest cover change analyses have revealed net forest gain in many tropical regions. While most analyses have focused solely on forest cover, trees outside forests are vital components of landscape integrity. Quantifying regional-scale patterns of tree cover change, including non-forest trees, could benefit forest and landscape restoration (FLR) efforts.

Objectives We analyzed tree cover change in Southwestern Panama to quantify: (1) patterns of change from 1998 to 2014, (2) differences in rates of change between forest and non-forest classes, and (3) the relative importance of social-ecological predictors of tree cover change between classes.

Methods We digitized tree cover classes, including dispersed trees, live fences, riparian forest, and forest, in very high resolution images from 1998 to 2014. We then applied hurdle models to relate social-ecological predictors to the probability and amount of tree cover gain.

Results All tree cover classes increased in extent, but gains were highly variable between classes. Non-forest tree cover accounted for 21% of tree cover gains, while riparian trees constituted 31% of forest cover gains. Drivers of tree cover change varied widely between classes, with opposite impacts of some social-ecological predictors on non-forest and forest cover.

Conclusions We demonstrate that key drivers of forest cover change, including topography, road distance and historical forest cover, do not explain rates of non-forest tree cover change. Consequently, predictions from medium-resolution forest cover change analyses may not apply to finer-scale patterns of tree cover. We highlight the opportunity for FLR projects to target tree cover classes adapted to local social and ecological conditions.

Keywords Forest and landscape restoration · Reforestation · Panama · Live fences · Silvopasture ·

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Cadastral data · Remote sensing · Land cover change · Trees outside forests

Introduction

Calls for forest and landscape restoration (FLR) to recover ecosystem function across hundreds of millions of hectares of degraded landscapes are gaining global traction (Chazdon 2008; WRI 2012; Aronson and Alexander 2013; Pinto et al. 2014; Chazdon et al. 2015; Suding et al. 2015). These FLR projects seek to conserve biodiversity, mitigate climate change, increase social-ecological resiliency in the face of climate change (i.e., adaptation), and enhance the provision of a variety of ecosystem services (Chazdon 2008; Zhou et al. 2008; Alexander et al. 2011; Pramova et al. 2012; Barral et al. 2015; Latawiec et al. 2016; Omeja et al. 2016). Ambitious goals of restoring forest cover at regional scales are partly inspired by evidence that widespread increases in forest cover are already occurring across many tropical countries (Meyfroidt and Lambin 2011; Aide et al. 2013). Analyses of forest cover change over large spatial extents could promote FLR by informing policies that enable favorable socioeconomic conditions for reforestation (Sloan 2015), identifying biophysical factors that increase forest recovery rates (Poorter et al. 2016), and locating sites where natural regeneration may be sufficient to restore forest cover (Chazdon and Uriarte 2016). However, while FLR emphasizes the importance of a diverse range of tree cover in agricultural landscapes, from native secondary forest, to agroforestry, to pasture trees (Harvey et al. 2008; Chazdon et al. 2015), regional scale analyses of non-forest tree cover change are rare (Plieninger et al. 2012; Schnell et al. 2015).

Our limited understanding of trends in non-forest tree cover at regional scales is problematic because the ecological integrity of agricultural landscapes depends on heterogeneous, often non-forest, tree cover (Harvey et al. 2008; Perfecto and Vandermeer 2008). Non-forest tree cover enhances the provisioning of ecosystem services such as carbon storage, seed dispersal, pollination, pest control, soil stabilization and hydrological function, while also facilitating biodiversity conservation (Guevara et al. 2004; Ricketts 2004; Bianchi et al. 2006; Harvey et al. 2006; Ilstedt et al. 2007; Van Bael et al. 2008; Tscharntke et al. 2011; Mendoza et al. 2014; Zomer et al. 2016). Dispersed (or 'scattered') trees in pastures and agricultural fields are a keystone ecological feature that provide ecological functions and services disproportionately greater than the space they occupy in the landscape (e.g., biodiversity maintenance, nutrient cycling; Manning et al. 2006; Fischer et al. 2010). Live fences increase connectivity between otherwise isolated forest fragments, reducing the likelihood of local extirpations (Harvey et al. 2005; Francesconi 2006; Pulido-Santacruz and Renjifo 2011). A variety of agroforestry systems (e.g., silvopastures, shade coffee, cocoa and cardamom) provide habitat for a greater diversity of species in the agricultural matrix than conventional agricultural and pastoral systems, with some agroforestry systems nearing the species richness and composition of forests (Saenz et al. 2007; Perfecto and Vandermeer 2010; Buechley et al. 2015). Non-forest tree cover also has the potential to balance food production and conservation (e.g., "land-sharing"; Perfecto and Vandermeer 2010; Tscharntke et al. 2012). Because non-forest tree cover is critical for both human livelihoods and ecosystem services, changes in agricultural tree cover could have large impacts on the success of FLR projects (Harvey et al. 2008).

Challenges to measuring changes in tree cover in agricultural landscapes at regional scales are related to limitations of remotely sensed and field data. Medium-resolution satellite imagery used to analyze forest cover change is often classified as either "forest" or "non-forest" (e.g., Aide et al. 2013; Hansen et al. 2013), broad categories that overlook continuous variation in tree cover on agricultural land. A recent study in a Panamanian landscape dominated by cattle production found that discrete forest categories may substantially underestimate total tree cover increases, possibly because discrete categories overlook increases in agricultural tree cover (Caughlin et al. 2016b). Scaling up field sampling to the extent required to measure agricultural tree cover is a considerable challenge (Schnell et al. 2015). Field plots are often limited to a small spatial extent, thus while several field studies in pastoral systems have predicted declines in tree cover based on limited regeneration at the seedling or sapling stage (Lathrop et al. 1991; Plieninger et al. 2004; Fischer et al. 2009), whether these predicted declines are occurring at regional scales remains unknown. High-resolution imagery enables broader scale measurement of sparse and highly variable tree cover such as live fences and dispersed pasture trees (Platt and Schoennagel 2009; Aksoy et al. 2010), but historical imagery necessary for change analysis is often unavailable, particularly for tropical regions. A final challenge is accounting for differences in tree cover classes, (e.g. live fence vs. dispersed trees) over large areas. Different classes of tree cover provide different ecosystem services (Harvey et al. 2006; Ibrahim et al. 2007) and trends in tree cover change can vary dramatically between tree cover classes (Plieninger et al. 2012). To restore and reforest vast expanses of degraded agricultural land it will be necessary to accurately assess the state of tree cover in agricultural landscapes, including both forest and non-forest tree cover.

Understanding the causal pathways that lead to tree cover change in agricultural landscapes will also aid plans for FLR (Uriarte and Chazdon 2016). Analyses of forest cover change at landscape to regional scales have revealed several biophysical and socioeconomic drivers of reforestation, including topography, population density, distance to markets and historical forest cover (Yackulic et al. 2011; Bonilla-Moheno et al. 2012; Newman et al. 2014; Call et al. 2017). In Latin America, economic development, leading to abandonment of agriculturally marginal land and/or insufficient labor to clear encroaching trees off pasture, has emerged as a causal pathway that can explain national-scale forest transitions (i.e., a shift from net forest cover loss, to net forest cover gain; Rudel et al. 2002; Wright and Samaniego 2008; Redo et al. 2012; Sloan 2015). However, whether national-scale predictors of forest cover change are related to the dynamics of non-forest tree cover remains unclear. In part, this knowledge gap relates to the disparate scales at which forest versus non-forest tree cover is measured. Because most studies of non-forest tree cover take place at the farm or plot scale, explanations for why farmers allow trees in pastures often involve data on households, such as survey data (Barrance et al. 2003; Calle et al. 2009; Garen et al. 2011; Metzel and Montagnini 2014), rather than larger-scale, spatial variables, such as distance to market. Bridging the gap between forest cover change at regional scales and landholder decision-making at the household scale could enable better predictions for where and how to promote trees outside forests in working landscapes.

In Panama, the Azuero peninsula provides an ideal case study for quantifying the amount and drivers of agricultural tree cover change. Continental, national, and regional-scale studies have all found net increases of forest cover in the Azuero peninsula, suggesting that a forest transition is occurring (Wright and Samaniego 2008; Metzel 2010; Aide et al. 2013; Bauman 2015; Sloan 2015). Yet while estimates of forest cover change are similar across studies (approximately + 4% from 1990 to 2009), estimates of total forest cover vary dramatically (e.g., from 7 to 34%) due, in part, to differences in how forest cover is defined (Metzel 2010; Sloan 2015). One explanation for these divergent estimates of regional forest cover is that some studies include small scale (< 4 ha) patches of tree cover, while others do not (Caughlin et al. 2016b). To identify trends and drivers of tree cover, we used high-resolution imagery to digitize tree cover—often accounting for individual tree crowns—and classify tree cover into classes with varying ecological functions in the landscape. Our study is unique because we quantify patterns of fine-scale tree cover change at a broad spatial extent, encompassing 1589 km^2. Furthermore, by linking imagery to individual parcels, we are able to relate patterns of tree cover change to social-ecological predictors that reflect regional trends, landscape context, and landholder decision-making. We use this approach to answer three questions: (1) what are the patterns of agricultural tree cover change from 1998 to 2014, (2) how do changes in tree cover differ between forest and non-forest tree cover, and (3) how do social-ecological predictors of tree cover change vary between tree cover classes?

Methods

Study region

Our study takes place in Los Santos province, located in the southeast corner of the Azuero peninsula in southwestern Panama (< 2% of our plots are in the neighboring Herrera province; Fig. 1a). The region is classified as tropical dry forest, with an average annual precipitation of 1,700 mm, an average annual temperature of 25 °C, and a 5-month dry season. Regional

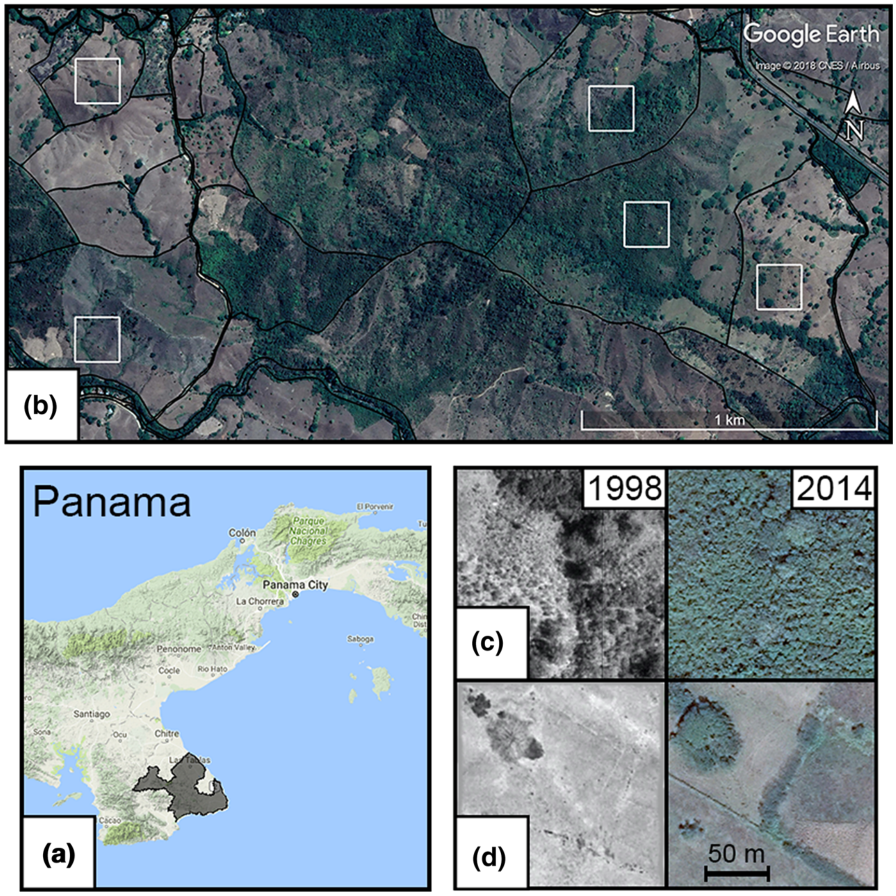

Fig. 1 Study region and sampling design. **a** Our study region is outlined in black in the southeast corner of the Azuero peninsula. **b** Stratified sampling design; white squares are 2.25 ha sampling plots and black lines represent parcel boundaries. **c** Transition from fallow and riparian forest in 1998 to forest in 2014. **d** Growth of dispersed trees and establishment of live fence by 2014

deforestation peaked during the first half of the 20th century, as forest was cleared for cattle production. Currently, the landscape is dominated by pasture, but also includes annual crops, riparian forest buffers, various stages of fallow, secondary forest fragments, and a small number of teak (*Tectona grandis*) plantations (Heckadon-Moreno 2009; Griscom et al. 2011). More recently, there has been a shift towards tourism and other industries, as well as environmental restoration projects (Bauman 2015). Altogether, rural economic development has likely caused an increase in regional forest cover (Sloan 2015).

Tree cover classification and change analysis

Our tree cover classification was derived from a combination of aerial photographs, taken in 1998 and obtained from the Tommy Guardia National Geographic Institute of the Republic of Panama, and Google Earth images, taken in 2014 (Google 2014). Both datasets offer very high resolutions ($\leq$ 0.5 m) that allow small patches of tree cover (often including individual tree crowns) to be mapped. Because results of land cover change studies vary depending on spatial scale (Evans et al. 2002; Call et al. 2017), choosing an appropriate unit of analysis is critical. In Los Santos Province, most land (> 95%) is privately-owned property used for cattle ranching (ANATI 2000). In the province, property boundaries create discrete units (parcels) that explain variability in tree cover in the landscape and reflect landholder decision-making (Caughlin et al. 2016b). Thus, we chose parcels as our unit of analysis. We began with a cadastral dataset of property boundaries in 2000 (ANATI 2000). From the 4343 parcels located within coverage of aerial photos, we randomly selected 438 parcels for our study. In each of these parcels, we randomly placed one 2.25 ha square plot (excluding parcels too small or narrow to accommodate a 150 m $\times$ 150 m plot;

Fig. 1b). Within these squares, tree cover was hand digitized in Google Earth Pro (Google 2014).

Digitization was conducted by research assistants at an altitude of 350 ± 50 m with terrain and tilting turned off. While automated methods for segmentation and object-oriented classification show great promise for assessing fine-scale patterns of woody vegetation cover (Fauvel et al. 2013; Meneguzzo et al. 2013; Adhikari et al. 2017), the capacity of machine learning techniques to distinguish between functionally-different tree cover types (e.g. live fence vs. riparian corridor) remains unknown. Because our main objective was to identify these tree cover types, we used hand digitization by research assistants with on-the-ground experience in Latin American cattle pastures. We envision that our extensive set of digitized polygons could serve as training data for an algorithm to classify tree cover type from high resolution imagery. To that end, we have deposited all digitized polygons in the Dryad Digital Repository where they are freely reusable (https://doi.org/10.5061/dryad.q5r472k).

We classified each polygon as dispersed tree(s), fallow, forest, live fence, riparian forest or teak plantation (Fig. 1). We chose these classes because they were the most dominant forms of tree cover on the landscape and are known to provide important ecological and economic services. Together, dispersed trees, live fences and teak plantations constituted non-forest tree cover. These non-forest tree cover classes are more directly linked to landholder decision-making, while forest and riparian forest classes represent more natural types of tree cover. Because fallow cover does not necessarily represent full-grown trees and is likely to be cleared, we did not include fallow under measures of total tree cover, or as a response variable in our models. Instead, we used percent fallow as a predictor of change in other cover classes. The remainder of undigitized area in our sample was predominately pasture, and is hereafter referred to as such. Dispersed trees included isolated trees in open fields and pastures, more densely occurring trees in silvopastures, and trees that were cultivated in near-home gardens. Dispersed trees with a canopy < 6 m in diameter were not digitized. A similar threshold was used to help distinguish between fallow and (riparian) forest, with the presence of many tree crowns > 6 m diameter and at least 80% canopy closure required for classification as (riparian) forest. Riparian forest was differentiated from forest by proximity to a waterway and a width < 50 m. Live fences consisted of rows of 5 or more trees, with at least 3 canopies exceeding a 6 m diameter. Teak plantations were identified by a combination of a streaked appearance (resulting from row plantings), small and uniform crown sizes and distinct borders. Most tree cover polygons represented groups of trees (i.e., tree cover patches), although dispersed tree and live fence polygons often consisted of individual trees. As such, we did not account for overlap between individual tree crowns, and could not calculate tree density. Deciduous trees were frequently visible on the landscape in both time periods, and were included in our analyses. We verified the accuracy of our tree cover classifications by visiting randomly-assigned points in July 2015 (n = 43) and assigning a class (e.g., live fence, riparian forest) to these points in the field. Three people then independently classified these ground-truthed points using the previously described image classification methodology with a mean accuracy of 86%. After the initial digitization, the lead author reviewed and revised the initial set of polygons, with input from the other authors on questionable polygons.

To determine where gains and losses of different tree cover classes occurred, we analyzed tree cover transitions from one class (in 1998) to another (in 2014). We used the union function in QGIS (QGIS Development Team 2016) to combine tree cover class of polygons created from 2014 imagery to polygons created from 1998 imagery. We used the resulting attribute table to calculate what percent of each tree cover class remained the same, or transitioned into other classes, by 2014. Mean patch area was determined by calculating the area of each polygon in QGIS (QGIS Development Team 2016) and deriving a mean for each tree cover class. Number of patches is synonymous with number of polygons. Including the number of patches enabled us to quantify both the total area within a sample unit that had undergone a change in tree cover as well as change in the number of discrete patch units.

Predictor variables

To determine whether drivers of tree cover change vary between tree cover classes we selected a set of eight predictor variables that previous studies had identified as important for regional forest cover change (Online Appendix 1). Slope was calculated in R using the package 'raster' (Hijmans et al. 2015) and 30 m x 30 m resolution data from the Shuttle Radar Topography Mission (SRTM). Mean annual precipitation from 2000 to 2014 was obtained from Climate Hazards Group Infrared Precipitation with Stations (Funk et al. 2014). Distance to highway was the Euclidean distance to the nearest highway. Percent off-site residences in 2000 and change in population density from 2000 to 2010 were acquired from the 2000 Panama National Population Census and interpolated to each square (Online Appendix 2). Surrounding forest refers to the percent of forest cover within a 500 m radius of each plot, based off of a 2008 national forest cover classification (ANAM 2009). Parcel size was obtained from the ANATI cadastral dataset. Percent fallow was calculated as the percent cover of fallow within each plot in 1998.

Statistical analysis

We employed a hurdle model approach to analyze the predictors of tree cover change in our study (Mullahy 1986; Neelon et al. 2013). Hurdle models partition a response variable into two types of data, first, a binary variable (in our case, whether tree cover increased or not), and second, a continuous non-zero variable (in our case, how much tree cover increased). We chose this analytical method because it accounts for the fact that two separate decision-making processes—possibly driven by dissimilar factors—are occurring. First, landholders are either allowing tree cover to regenerate or not, and second, they are deciding how much area to allow to revegetate. Whether or not tree cover gain occurred was analyzed with generalized linear models (GLM) using a binomial distribution and a logit-link function, while the magnitude of tree cover gain, if it did occur, was analyzed with GLMs using a gamma distribution and a log-link function (Gelman and Hill 2006). The hurdle model required grouping tree cover loss and no change in tree cover into the same category (i.e., no gain in tree cover). We believe this is acceptable because in our study system trees are constantly recruiting naturally, meaning that a lack of change in tree cover in a plot can only result if newly recruited saplings are cleared from the field; thus, no change in tree cover represents a variety of tree cover loss (Metzel 2010). To assess spatial autocorrelation in model residuals, we used the pgirmess package in R (Giraudoux 2017) to generate correlograms for Moran's I statistic. We found minimal evidence for spatial autocorrelation in model residuals (Online Appendix 3). We excluded teak plantations from our models because they were so rare that drivers of change in this class could not be analyzed. To interpret coefficients relative to one another, we standardized all predictor variables by centering around the mean and dividing by two standard deviations (Gelman 2008). To assess model fit, we calculated R^2 values as R^2 sum of squares (Hardin and Hilbe 2007).

Results

Tree cover change

Total tree cover increased from 15.1 ± 20.0% (mean ± SD) in 1998 to 19.3 ± 22.3% in 2014. All tree cover classes increased in cover, with the largest gains from forest and smallest gains from dispersed trees (Fig. 2). Mean percent change was positive for all tree cover classes, but was highly variable, with SDs ranging from 2.1 to 18.7% (Fig. 2). Riparian forest and forest were the most prevalent tree cover classes throughout the study period, from 1998 to 2014 (7.2 ± 11.5%, and 6.3 ± 20.1%, respectively), while dispersed trees, live fences and teak plantations covered the least area (3.0 ± 3.7%, 0.5 ± 1.7% and 0.3 ± 3.5%, respectively). Fallow covered more area than any tree cover class throughout the study period (11.5 ± 22.7% cover). Mean patch area increased for riparian forest (+ 15%), dispersed trees (+ 27%) and teak plantation (+ 314%), decreased for fallow (− 11%) and live fence (− 10%), and did not change for forest. The total number of patches increased for forest (+ 40%), riparian forest (+3%), live fence (+ 46%) and teak plantation (+ 60%), and decreased for fallow (− 2%) and dispersed trees (− 17%; Online Appendix 4). By far the most dominant net transitions in tree cover were from fallow to forest, and from pasture to riparian forest. These two changes accounted for 2.7% of the entire study area (Fig. 3). Net transitions from riparian forest to forest, pasture to fallow, and fallow to riparian forest were the next most common, accounting for another 1.2% of the study area. The geographic distribution of tree cover change varied widely from class to class (Fig. 4). Change in

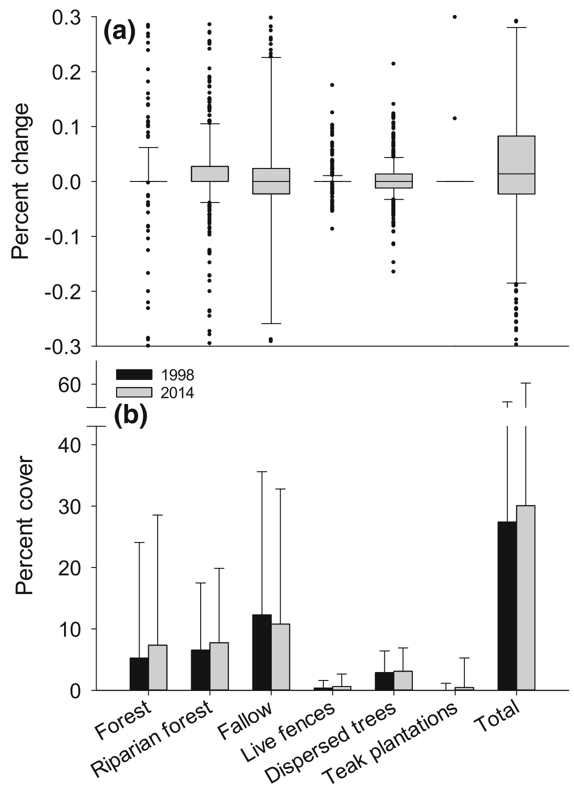

Fig. 2 **a** Change in percent cover and **b** mean cover (± SD) in 1998 and 2014 for each non-pasture cover class and total tree cover

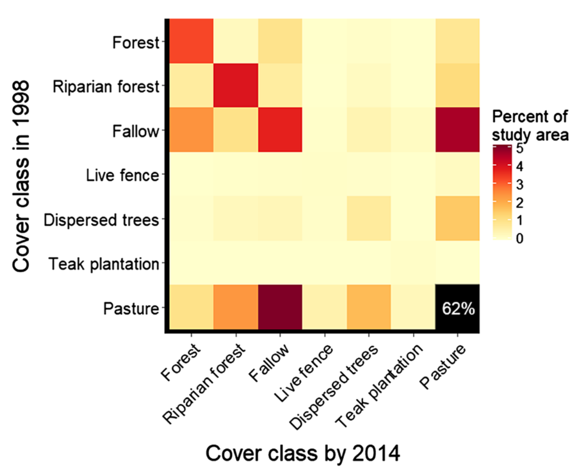

Fig. 3 Heat map of transitions from each tree cover class in 1998 to 2014

forest cover mostly occurred within hilly regions along the Rio Oria. While riparian forest cover change was also most prevalent in this region, compared to forest cover, riparian cover was more evenly distributed across the study area. Live fences mostly occurred in the area surrounding Las Tablas, and dispersed tree cover change was the most evenly and widely distributed type of tree cover change.

Social-ecological predictors of tree cover change

The results of the binomial and gamma models varied substantially both within and between tree cover classes (Fig. 5). The probability of gains in forest cover occurring was positively influenced by percent fallow, slope, and surrounding forest cover ($p < 0.001$ for each), and negatively influenced by distance to highway ($p = 0.03$; Online Appendix 5). The magnitude of gains in forest cover was positively influenced by percent fallow and surrounding forest cover ($p < 0.001$ and $p = 0.03$, respectively). Surrounding forest cover and slope had a negative, though marginally significant, influence on probability of gains in riparian forest ($p = 0.06$ for both; Online Appendix 5), while the magnitude of riparian forest gain was positively influenced by percent fallow ($p < 0.001$), and negatively influenced by percent off-site residences and parcel size ($p = 0.004$ and 0.008, respectively). The probability of increase in live fence cover was positively associated with population density, but the relationship was not statistically significant ($p = 0.08$). The gamma model for live fences did not converge due to limited instances of increases in live fence cover. The probability of gains in dispersed tree cover occurring was positively influenced by parcel size and distance to highway ($p = 0.002$ and 0.02, respectively; Online Appendix 5) and negatively influenced by surrounding forest cover ($p = 0.02$). The magnitude of gain in dispersed tree cover was positively influenced by percent fallow ($p = 0.001$). The probability of gain in total tree cover was negatively influenced by percent fallow ($p < 0.001$). The magnitude of gain in total tree cover was positively influenced by percent fallow ($p < 0.001$) and slope ($p = 0.02$; Online Appendix 5). R^2 was highly variable between tree cover classes and models, ranging from nearly zero variance explained (total tree cover gamma model) to 36% (forest cover binomial model; Fig. 5).

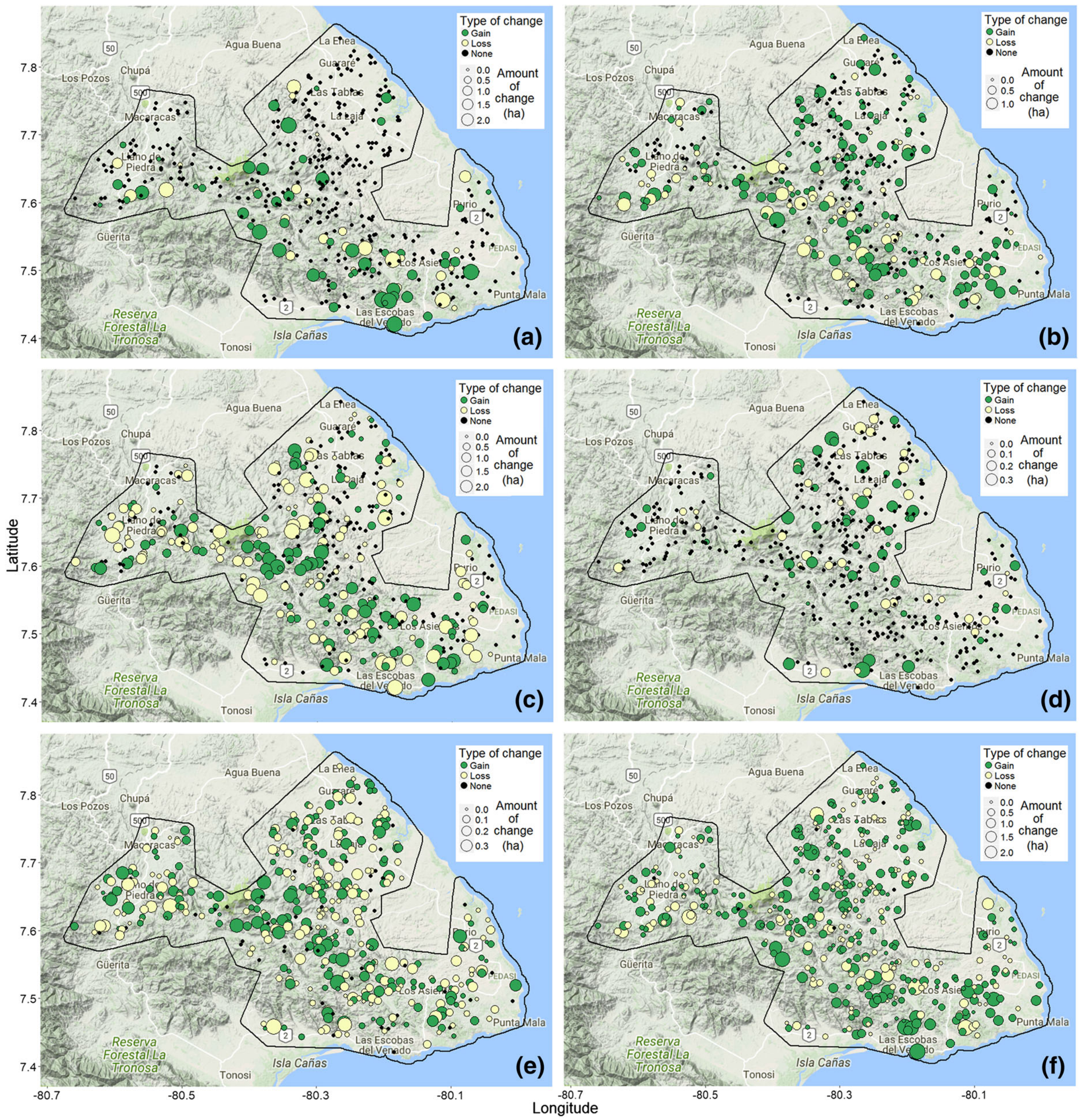

Fig. 4 Maps of gain and loss by cover class (Kahle and Wickham 2013). **a** Forest, **b** riparian forest, **c** fallow, **d** live fences, **e** dispersed trees, and **f** total tree cover (does not include fallow)

Discussion

Forest and landscape restoration (FLR) will require promoting a variety of tree cover types in agricultural landscapes, including trees outside forests that provide critical ecosystem services. However, studies that quantify reforestation at landscape to regional scales have almost all focused on change within a single forest cover class and have not investigated change in non-forest tree cover. We demonstrate that this land cover simplification overlooks major differences in rates and drivers of change between tree cover types. We found an increase in total tree cover from 1998 to 2014, similar to previous studies in southwestern Panama that have revealed net forest gain over the past decade (Wright and Samaniego 2008; Metzel 2010;

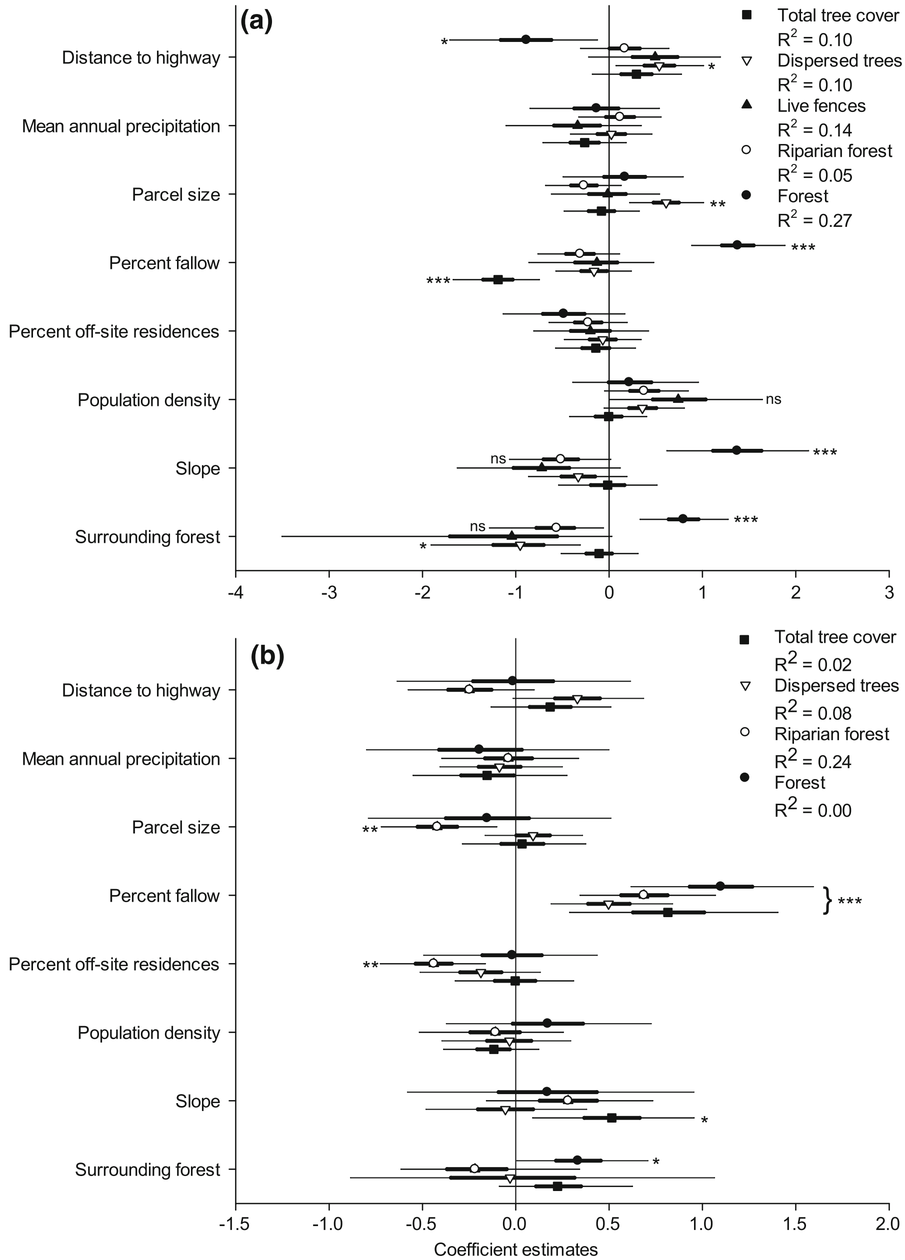

Fig. 5 Coefficient estimates for the influence of each predictor variable across model types and tree cover classes. Mean estimates are plotted with 50% (thick) and 95% (thin) confidence intervals for **a** binomial models and **b** gamma models. Estimates of gamma model coefficients are displayed on the log-link scale, while binomial model coefficients are displayed on the logit-link scale. Positive values indicate a positive influence on cover change, while negative values indicate a negative influence. Because predictor variables were standardized, the magnitude of regression coefficients within the gamma and binomial models is directly comparable

Aide et al. 2013; Bauman 2015; Sloan 2015; Caughlin et al. 2016b). Unlike these previous studies, we disentangled the contributions of forest and non-forest tree cover classes to this ongoing forest transition. While largest overall gains in forest cover occurred for forest fragments, the biggest proportionate gains in forest cover came from thin riparian corridors (i.e., riparian forest), ecologically-critical landscape features that may be excluded from land cover change studies at coarser spatial resolutions. In contrast, live fences remained stable over time, while gains in dispersed tree cover in some areas were counterbalanced by losses in other areas. The social-ecological predictors of tree cover change varied widely between tree cover classes, including opposite effects on forest versus non-forest tree cover for some predictors. While additional study will be required to understand the causal pathways behind the patterns we observed, our results suggest that there will be no “one size fits all” explanation for change in different classes of tree cover.

Tree cover change

Forest and riparian forest together constituted 78% of all tree cover throughout our study, and delivered 79% of net gains in tree cover during our study period. Increases in forest cover outpaced increases in riparian forest by a factor of 2:1, yet riparian forest remained slightly more prevalent than forest across our study in 2014. While thin riparian forests may provide fewer benefits in terms of biodiversity conservation than larger blocks of forest (Greenler and Ebersole 2015), in agricultural landscapes the richness and abundance of forest species is sometimes nearly indistinguishable between riparian forests and larger tracts of secondary forest (Harvey et al. 2006; Fajardo et al. 2009; Mendoza et al. 2014). In Los Santos province, where water scarcity limits agricultural productivity, restoring riparian forest cover may protect water resources and prevent soil erosion (Metzel and Montagnini 2014). With half of all forest cover and a third of all gains in forest cover deriving from riparian forest, we suggest that riparian corridors should be a focus of both land cover change research and ongoing reforestation efforts in southwestern Panama.

Non-forest tree cover classes composed a significant portion of total regional tree cover, and contributed 21% of net gains in tree cover from 1998 to 2014. Despite the inherently isolated nature and small individual spatial extent of dispersed trees, this tree cover class comprised 16% of all tree cover in 2014. While 9.9 ha of dispersed tree cover was lost from 1998 to 2014, 11.8 hectares were gained, resulting in a net (though dynamic) stability that appears to counter field-based studies that predict a lack of regeneration potential for dispersed agricultural trees (Lathrop et al. 1991; Plieninger et al. 2004; Fischer et al. 2009). However, the time span of our study may not have been long enough to detect declines in tree cover driven by limited regeneration. Moreover, we did not distinguish between different tree species, meaning that losses of tree diversity could be occurring without detection (Esquivel et al. 2008; Harvey et al. 2011). Nonetheless, the apparent stability of this keystone class of tree cover is promising for efforts aimed at FLR and biodiversity conservation (Manning et al. 2006; Gibbons et al. 2008; Fischer et al. 2010; Harvey et al. 2011). Relative to total area of other tree cover classes, live fences played an inconsequential role in tree cover dynamics in our study; however, live fence cover nearly doubled from 1998 to 2014. This large relative increase points to the potential for live fences to contribute to regional tree cover and landscape connectivity, if efforts to promote their establishment are intensified (Harvey et al. 2005; Metzel 2010).

Social-ecological predictors of tree cover change

The effect of social-ecological predictors of tree cover change depended both on tree cover class and on how tree cover change was quantified. Many studies of land cover change have quantified reforestation as a discrete transition between non-forest and forest pixels (Meyfroidt and Lambin 2008; Aide et al. 2013; Hansen et al. 2013; Sloan 2015). The closest analogue to these previous analyses in our study was a binomial model that predicted whether the forest cover class increased within a sampling unit. We found that three of the strongest predictors of forest cover gain were steeper slopes, proximity to the highway, and landscape-scale forest cover. The explanatory power of these variables closely matches previous studies on binary forest cover change in the region, which have shown increased reforestation on steep slopes (Yackulic et al. 2011; Bauman 2015), with proximity to forest fragments (Crk et al. 2009; Newman et al. 2014), and near major roads (Rudel et al. 2002). Rural economic development, including infrastructure development, has been proposed as a causal pathway to explain why these predictors are correlated with reforestation: as non-agricultural jobs become available, there is less labor to clear trees off pastures (Sloan 2015). However, our results also complicate this narrative: for different metrics of tree cover, we found divergent, and even opposite, effects of the same socio-ecological variables.

The effects of surrounding forest cover offer a prime example of how social-ecological predictors vary between tree cover classes. We predicted that surrounding forest cover would have a positive impact on tree cover gain across classes, due to the increased seed rain provided by adjacent forests (Holl 1999; Hooper et al. 2005; Martinez-Garza et al. 2009). For our forest cover class, gain in forest cover was strongly and positively influenced by surrounding forest cover.

In contrast, riparian forest and dispersed tree cover gain was negatively related to surrounding forest cover. The negative relationship between surrounding forest cover and increases in riparian and dispersed tree cover may indicate the importance of forest scarcity for dictating trends in some classes of deliberately maintained tree cover. The lack of available tree products (e.g., firewood, lumber, fence posts, fruits, etc.) near parcels far from forests may compel landholders to allow natural recruitment of trees in pastures, while landholders located near forests may be less motivated to allow new trees to grow (Eilu et al. 2007; Garen et al. 2009, 2011; Ordonez et al. 2014). The unexpected negative relationship between surrounding forest cover and some types of tree cover is a reminder that the ecological processes that normally dictate forest regeneration can be overridden by landholder decision-making in agricultural landscapes.

One variable with a consistently strong effect on magnitude of tree cover gain across tree cover classes was the area of fallow land at a site in 1998. Fallow land indicates "rough pasture," including tall grasses, weeds, and shrubs. In our landscape, fallow land can indicate rotational grazing, pasture abandonment, or inadequate labor to clear regenerating woody vegetation (Griscom et al. 2009). Fallow land is another casualty of the "forest" vs. "non-forest" dichotomy in many remote sensing studies of forest cover change, and is often classed as "non-forest" (Sloan 2015). Our results indicate that, at least for tree cover dynamics, fallow land is not equivalent to active pasture. Instead, fallow land may either represent the first step in a successional trajectory towards increased forest cover (Caughlin et al. 2016a) or a land management regime that promotes non-forest tree cover (Garen et al. 2011). For example, we found that fallow land was often converted to dispersed tree cover, suggesting that farmers may utilize fallow land to enable natural-recruitment of selected tree species that become isolated pasture trees (Lerner et al. 2015). An exception to the relationship between tree cover gain and fallow land was live fence cover, which did not show a strong relationship with percent fallow land. A possible explanation is that live fences require active maintenance to maintain the fence as a linear boundary and prevent trees from shading grass (Harvey et al. 2005). Field-based studies have demonstrated the importance of pasture management in determining reforestation rates, including spatial patterns of tree recruitment (Seifan and Kadmon 2006) and tree community composition (Uhl et al. 1988; Esquivel et al. 2008). As a step towards more ecologically-meaningful remote sensing of tropical reforestation, we recommend including a fallow class in land cover classifications.

Overall, our results point to the importance of landholder decision-making for tree cover gain. Differences in rates of change and social-ecological predictors of change between tree cover classes indicate that farmers are choosing to manage some types of tree cover differently than others. In addition, the differences between our gamma and binomial models suggest that whether tree cover gain occurs, and the amount of tree cover gain, are two separate processes, influenced by different social-ecological predictors. This result suggests that landholders make two separate decisions: (1) whether to allow any tree recruitment in pastures and (2) how much tree cover gain to allow. Parcel size is one predictor variable that is closely related to individual landholder characteristics (Manson et al. 2009) and that had a negative effect on magnitude of gain for riparian trees. One potential explanation for this result is that farmers with more land may tend to favor tree cover types with more immediate benefits for agricultural production. Future research that links individual decision-making with land cover change will play a critical role in understanding these fine-scale tree cover dynamics.

Scope and limitations

Our research demonstrates how very high resolution imagery can be applied to understand fine-scale patterns of tree cover change in an agricultural landscape. While our primary focus in this paper was to determine patterns of change between tree cover types, we anticipate that new developments in remote sensing and machine learning will increase our ability to quantify fine-scale patterns of woody vegetation change. In our landscape, the fusion of hyperspectral and LiDAR data has enabled species-level classification of dispersed pasture trees (Graves et al. 2016). While applying species classification algorithms to trees with overlapping canopies remains a challenge, analyzing tree species composition in agricultural land at regional scales is a clear next step. In addition, segmentation algorithms have demonstrated the ability to measure woody vegetation change with a high level of resolution that can be related to biomass and individual tree canopies with implications for restoration and other conservation issues (Laliberte et al. 2004; Platt and Schoennagel 2009; Adhikari et al. 2017). Object-oriented classification has demonstrated potential to map hedgerows in agricultural landscapes (Vannier and Hubert-Moy 2008; Aksoy et al. 2010). Applying these algorithms to distinguish between functional tree cover types could enable far greater spatial coverage than manual digitization.

Implications for management and conservation

Forest and landscape restoration in pastoral landscapes will depend on understanding tree cover dynamics, including trees outside forests that provide important ecosystem services (Harvey et al. 2008; Chazdon et al. 2015). Our study highlights the diversity of tree cover in a Panamanian landscape undergoing a forest transition and suggests multiple explanatory pathways for tree cover gain. Although the social-ecological variables that correlate with probability of forest cover gain are typical of a labor scarcity pathway, as loss of farm labor leads to pasture abandonment in marginal land (Rudel et al. 2005; Wright and Samaniego 2008), gain in non-forest tree cover may be more closely linked to deliberate maintenance of these trees by farmers, reflecting "forest scarcity" or "smallholder stewardship" (Rudel et al. 2005; Meyfroidt and Lambin 2008; Lambin and Meyfroidt 2010; Plieninger et al. 2012; Lerner et al. 2015; Sloan 2015). Our results demonstrate the value of including non-forest tree cover types in land cover change analyses of agricultural landscapes (Plieninger et al. 2012). Furthermore, our results provide insights into the effectiveness of targeting different classes of tree cover depending on the social-ecological context and scale of influence. FLR projects will be most successful if they tailor restoration objectives to the given social-ecological conditions of particular landscapes by taking advantage of the disparate factors that drive increases in different classes of tree cover.

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