

Species-level tree crown maps improve predictions of tree recruit abundance in a tropical landscape

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Open Research:

Data (Barber, et al. 2022) are available in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.dr7sqvb0d>.

Abstract

Predicting forest recovery at landscape scales will aid forest restoration efforts. The first step in successful forest recovery is tree recruitment. Forecasts of tree recruit abundance, derived from the landscape-scale distribution of seed sources (i.e. adult trees), could assist efforts to identify sites with high potential for natural regeneration. However, previous work has revealed wide variation in the effect of seed sources on seedling abundance, from positive to no effect. We quantified the relationship between adult tree seed sources and tree recruits, and predicted where natural recruitment would occur in a fragmented, tropical, agricultural landscape. We integrated species-specific tree crown maps generated from hyperspectral imagery and property ownership data with field data on the spatial distribution of tree recruits from five species. We then developed hierarchical Bayesian models to predict landscape-scale recruit abundance. Our models revealed that species-specific maps of tree crowns improved recruit abundance predictions. Conspecific crown area had a much stronger impact on recruitment abundance (8.00% increase in recruit abundance when conspecific tree density increases from zero to one tree; 95% CI: 0.80 to 11.57%) than heterospecific crown area (0.03% increase with the addition of a single heterospecific tree, 95% CI: -0.60 to 0.68%). Individual property ownership was also an important predictor of recruit abundance: the best performing model had varying effects of conspecific and heterospecific crown area on recruit abundance, depending on individual property ownership. We demonstrate how novel remote sensing approaches and cadastral data can be used to generate high-resolution and landscape-level maps of tree recruit abundance. Spatial models parameterized with field, cadastral, and remote sensing data are poised to assist decision support for forest landscape restoration.

KEYWORDS

Agricultural landscape, forest landscape restoration, hyperspectral imagery, lidar data, natural regeneration, operational species mapping, tree crown maps, tree recruitment, trees outside the forest.

Introduction

Natural regeneration in tropical landscapes is a low-cost climate solution that can sequester carbon while supporting other ecosystem services (Chazdon and Uriarte 2016, Lennox et al. 2018, Matos et al. 2020, Cook-Patton et al. 2020). Operationalizing natural regeneration as a strategy in forest landscape restoration (FLR) plans will require identifying locations where native tree cover will return without active restoration (Chazdon and Guariguata 2018). However, natural regeneration in tropical landscapes is unpredictable, with high variability in successional trajectories among sites (Norden et al. 2015). Understanding the demographic mechanisms that drive landscape-scale forest recovery could reduce uncertainty in forecasts of secondary forest succession (Menge and Chazdon 2016, Cauglin et al. 2019b).

Tree recruitment is a demographic rate required for forest recovery, but is poorly understood at landscape scales. A minimum number of seeds must arrive to initiate forest recovery (Cauglin et al. 2016a). Low recruitment, including seed dispersal, germination, and seedling survival, can be a critical impediment for reforestation (Holl et al. 2000). Nevertheless, attempts to relate seed sources (e.g., forest cover) to tree recruitment in reforesting landscapes have shown mixed results. For example, some studies have found that recruit abundance increases with closer proximity to forest fragments (Parrotta 1993, Griscom et al. 2009, Crk et al. 2009, Robiglio and Sinclair 2011, Elliott et al. 2013, Crouzeilles and Curran 2016, Breugel et al. 2019), while others have found weak or undetectable effects of surrounding forest cover on recruit abundance (Duncan and Duncan 2000, Lopes et al. 2012, Zahawi et al. 2013, Holl et al. 2017). Resolving the question of why seed sources have a variable effect on recruitment will advance our ability to forecast natural regeneration over large areas.

A challenge of quantifying the relationship between seed sources and recruitment rates is that seed dispersal occurs at large spatial scales (>km) but recruitment success varies spatially at fine scales (m). The spatial patterns of dispersal and recruitment are modified by differences in dispersal syndromes and functional traits among species and the relative abundance of reproductive trees in the landscape. Attempts to understand recruitment patterns by lumping multiple tree species into a single metric (e.g., distance-to-forest-edge or percent forest cover; Robiglio and Sinclair 2011, Crouzeilles and Curran 2016, Holl et al. 2017) do not take species-specific dispersal syndromes and abundances into account. Therefore, these attempts may

erroneously predict high recruitment potential for species that are absent as reproductive trees in the landscape. Alternately, a high abundance of conspecific trees (trees of the same species) could negatively affect recruitment due to conspecific negative density dependence (Comita et al. 2010, Johnson et al. 2012, Uriarte et al. 2018). We hypothesize that predictions of tree recruitment in tropical agricultural landscapes will improve when based on maps containing all reproductive trees identified to species (Harvey et al. 2004, Graves et al. 2016, Tarbox et al. 2018).

Another potential factor explaining the high uncertainty in forest recovery trajectories is human land use. Land management choices can result in different disturbance regimes (e.g. burning, clearing) that influence forest recovery (Mesquita et al. 2001). Landowner preferences also influence species abundance and ecological dynamics that shape recruitment (Griscom et al. 2009, Metzel and Montagnini 2014). For example, when deciding whether or not to enable natural regeneration on their properties, some farmers may favor rare species' natural regeneration rather than common species (Lengkeek 2003). Thus, land management is likely to alter tree recruitment patterns in ways that are species-specific and vary across the landscape.

High-resolution spatial information on position and species identity of trees on land management may help to improve predictions of tree recruitment. In particular, aerial lidar and hyperspectral imagery can be used to map individual adult tree crowns and species across multiple property ownership units (Fischer et al. 2019). Segmented tree crowns from lidar data can be paired with hyperspectral imagery to identify individual adult trees to species (Graves et al. 2016). Species-specific tree crown maps derived from airborne high spatial and spectral resolution imagery have demonstrated the potential to address ecological questions that require a landscape perspective (Schimel et al. 2015) for example, community assembly across elevation gradients (Durán et al. 2019).

Our objective is to predict the abundance of tree recruits at broad spatial scales in a diverse tropical agricultural landscape. We combined a) species-specific mapped tree crowns derived from fused hyperspectral and lidar imagery, b) field data on recruit abundance, and c) property boundary data to quantify how abundance and spatial distribution of tree recruits is related to seed sources and land management, and to predict landscape-level recruit abundance. Our work is directly relevant to landscape-scale reforestation activities because it improves our ability to identify areas where native tree recruitment will occur with minimal intervention. We answer the following questions:

1) Can species-specific tree crown maps from hyperspectral and lidar data improve the ability to predict the abundance of tree species recruits?

2) Does the effect of the total neighboring tree crown area on recruit abundance vary between tree species?

3) Does individual property ownership influence tree recruitment abundance?

Given answers to questions (1-3), we then demonstrate how spatial models for tree recruit abundance could provide decision-support for where natural regeneration is likely to occur.

Materials and methods

Study site

Our study area is located in the Azuero Peninsula of southwestern Panama (Figure 1). Average rainfall is 1,700 mm yr⁻¹, and the dry season is from December to March. The soils are Cambisols (Nachtergael et al. 2010) derived from volcanic, plutonic, and sedimentary rocks (Buchs et al. 2010, Batista-Rodríguez et al. 2017). Elevation ranges from near sea level to a maximum elevation of 156.91 m. Slope ranges from 0 degrees to 89.69 degrees. The Azuero Peninsula was historically dominated by dry tropical forest but was cleared for timber and ranching during the 20th century, resulting in less than 2% remnant forest cover (Griscom et al. 2011). Recently, as off-farm economic activities have led to declines in agricultural activity, tree cover has increased across the region (Sloan 2015) in the form of forest patches, isolated pasture trees, riparian forest

corridors, and live fences (Griscom et al. 2011). However, areas with tree cover increases are spatially-dispersed and counterbalanced by areas with tree cover loss (Tarbox et al. 2018). Stakeholders in the Azuero increasingly express concern over forest scarcity, leading to community-driven efforts to restore tree cover to degraded lands (Garen et al. 2009, Metzel and Montagnini 2014). Local interest in restoration parallels national-scale initiatives, such as Panama's "Alliance for one Million", which seeks to restore tree cover to one million hectares of degraded land. Identifying areas suitable for natural regeneration will aid these large-scale reforestation initiatives.

Tree species selection

To relate the abundance of tree recruits to adult trees in the surrounding landscape, we used a map of adult tree species derived from aerial lidar and hyperspectral data (Graves et al. 2016). These aerial data were collected by the Global Airborne Observatory (GAO; formerly the Carnegie Airborne Observatory) in January 2012 (Asner et al. 2012). The dual-laser waveform lidar scanned data were used to develop a canopy height model with a pixel size of ~1.13 m that enabled individual tree crown segmentation (Dalponte and Coomes 2016), resulting in 298,971 crowns across 23 000 ha. The hyperspectral imagery (380–2510 nm; 5 nm bandwidth) was then used in a support vector machine (SVM) model to classify segmented crowns to tree species, with a training data set of 1,112 field-identified tree crowns (see Graves et al. 2016 for additional details). For our study, we selected five focal species based on two criteria: (1) the SVM could classify the tree species with high predictive accuracy ($F\text{-score} > 70\%$) and (2) the presence of recruits in landscape-scale plots within our study area (Hall and Ashton 2016). The five species include *Byrsonima crassifolia*, *Calycophyllum candidissimum*, *Cedrela odorata*, *Guazuma ulmifolia*, and *Enterolobium cyclocarpum*. Together, these five species represent a range of phylogeny, functional traits, and human use (Table 1). Although the focal study species belong to different successional stages, all five species survive and grow well in full sunlight during their first years (Hall and Ashton 2016).

Environmental and social covariates

In addition to the mapped tree crowns, we developed two additional covariates as predictors of tree recruit abundance at landscape scales: elevation and individual property ownership. Because topography influences secondary succession (Barbosa and Asner 2017, Breugel et al. 2019),

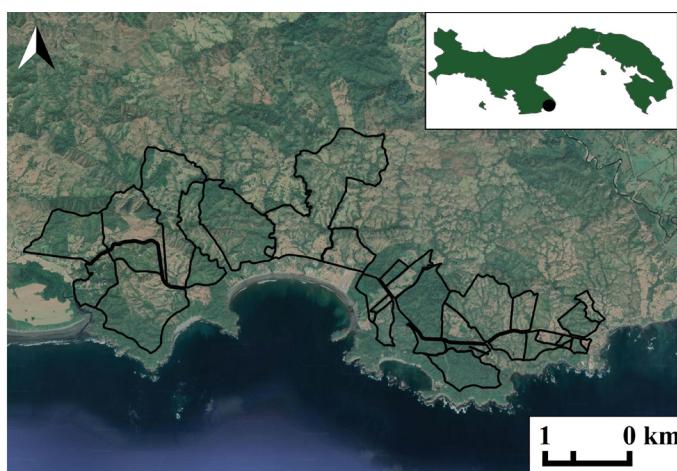


Figure 1

Study area in Southwestern Panama. The black lines represent the properties included in this study. Green colors indicate mostly forest vegetation cover, and tan colors indicate non-forested land covers. The black dot in the upper-right corner displays the location of the study site in Panama. Map data: Google, Airbus, Maxar Technologies.

Table 1

Main species characteristics included in this study. Family and successional stage was obtained from Kalacska et al. (2004). Human use of tree species by local framers was obtained from Metzel and Montagnini 2014. Uses: W =Wood, FR =Fruit/Food for humans, T =Traditional Use, FW =Firewood, PA =Physical Attributes, LF =Living Fence Posts, M =Medicinal, E =Environmental purpose, FL =Food for livestock. Dispersal syndromes were obtained from Griscom and Ashton (2011).

Species	Family	Dispersal syndrome	Successional stages	Human use
<i>Byrsonima crassifolia</i>	Malpighiaceae	Animal	Early to mid-succession	W, PA, FW, LF, FR, E
<i>Calycophyllum candissimum</i>	Rubiaceae	Wind	Mid to late- succession	W, PA, FW, LF
<i>Cedrela orodata</i>	Meliaceae	Wind	Early to mid-succession	W, LF, FW, FL
<i>Guazuma ulmifolia</i>	Sterculiaceae	Cattle	Early to mid-succession	PA, FW, LF, FR, FL, T
<i>Enterolobium cyclocarpum</i>	Fabaceae	Cattle & gravity	Early and late succession	W, PA, LF, FL, T

we incorporated it as a predictor variable in our models, using a digital elevation model with 1.13 m spatial resolution, developed from the aerial lidar over our study area (Asner et al. 2012). Preliminary model selection suggested that elevation outperformed slope, aspect, and topographic roughness indices for predicting tree recruit abundance, so we only included elevation in our final models.

The majority of land in the Azuero Peninsula is privately owned, and property boundaries in the region help explain spatial heterogeneity in land cover change (Caughlin et al. 2019b). In addition, private land parcels represent a unit commonly used in restoration interventions (Oliveira Fiorini et al. 2020). To account for individual property ownership in our models, we used a cadastral dataset developed by Panama's National Authority for the Administration of Lands and provided by the Fundación Pro Eco Azuero. As a predictor variable, we used the identity of the parcel in which recruit abundance was measured (Appendix S1: Figure S1). Properties are largely owned by smallholder farmers, with a mean (\pm SD) area of 49.15 ± 54.92 ha for properties in our dataset. Property boundaries do not correspond closely to biophysical features in the landscape, and differences in vegetation between properties most likely represent differences in land management (Valencia Mestre 2017).

Field data on tree recruit abundance

We measured tree recruit abundance in July 2018 by counting individuals of our focal species in transects stratified across the landscape. We defined tree recruits as individuals at least 0.5 m in height but < 1 cm in diameter at breast height (DBH). We measured tree recruit abundance in

transects of 100 m x 5 m, divided into 25 m² quadrats. The 100 m length of transects helped ensure that each transect could include a range of surrounding tree crown densities. To span a range of individual property ownerships, we stratified transect placement across 30 properties (Figure 2), placing between one and three transects within each property. When possible, we placed one transect per property into each of the three major habitats in the study area: riparian corridors, active pasture, and secondary forest. Some properties had less than three transects because they lacked one of the habitats within their boundaries. These habitats have different biotic and abiotic factors, with consequences for recruit abundance (Myster 2008). In total, our sampling scheme resulted in 1,100 quadrats representing 2.75 ha. Because ecological differences between transects were driven by habitat and property boundaries that vary over small distances, we used a stratified random sampling design to place transects without a minimum distance between them.

Linking mapped tree crowns to tree recruit abundance

We considered tree height and crown area as possible predictors to link the mapped adult trees with recruitment. Tree crown area and tree height metric were closely correlated (Pearson's R = 0.58; Appendix S1: Figure S2). Relative to tree height, tree crown area has the advantage that it can be derived from high-resolution imagery alone, without requiring lidar data, so we decided to use tree crown as a predictor. To develop models that account for the relationship between tree crowns and recruit abundance, we measured total tree crown area in neighboring landscapes

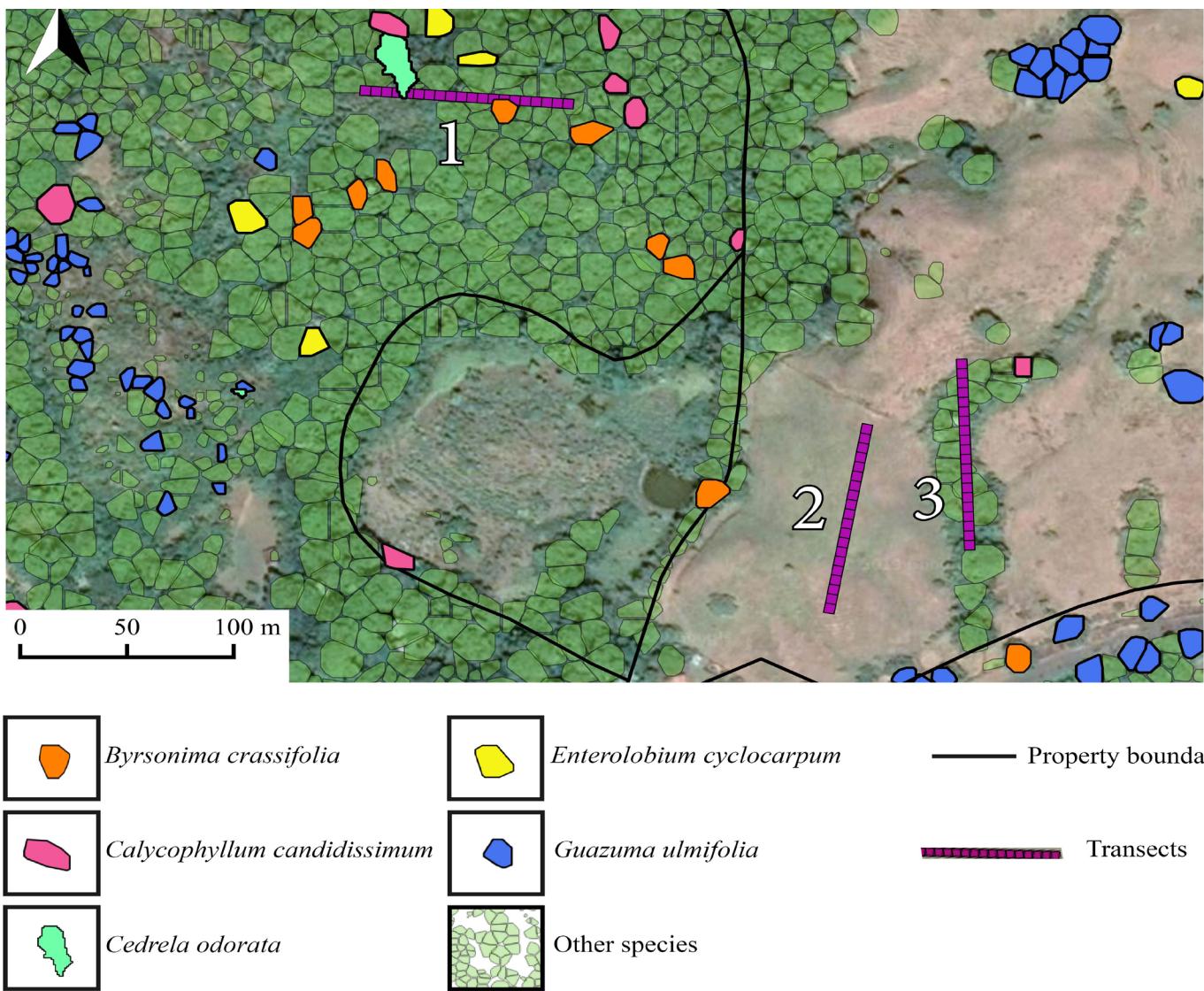


Figure 2

Placement of transects in the study area in a typical parcel. Transects on the field are allocated on (1) secondary forest, (2) active pasture, and (3) riparian forest. Colored polygons represent the five target species in the study and are a subset of mapped individual tree crowns from Graves et al. (2016). Map data: Google, Airbus, Maxar Technologies.

around quadrats. We separated the tree crown area into the conspecific crown area for each of our focal species, representing tree crowns of the same species as recruits, and heterospecific crown area, representing tree crowns of all other species. We then summed the tree crown area within 100 m of the center of each 25 m² quadrat. We chose a threshold of 100 m based on previous literature that suggests only a small percentage of tree seeds disperse >100 m (Nathan and Muller-Landau 2000). Conspecific and heterospecific tree crown areas were not correlated (Pearson's R = -0.023; 95% CI: -0.050 to 0.004). Preliminary analyses revealed improved model convergence and fit for summed tree crown area within 100 m, relative to spatially-explicit inverse models (i.e. Muller-Landau et al. 2008; Appendix S1: Section S1). Despite the increased biological realism of distance-based models, these models are

more complex including multiple parameters that interact in non-linear ways. Direct measurements of seed dispersal (e.g. de la Peña-Domene and Martínez-Garza 2018) would be one solution to increase the signal-to-noise and fit inverse models. Discrete habitat type was used to stratifying field sampling. However, habitat type was strongly correlated with heterospecific tree crown area (Appendix S1: Figure S3), limiting use of both variables in the same model. Because heterospecific tree crown area was more closely related to our overall objectives, we chose to use this variable, rather than habitat type, as a predictor variable in models. The remotely sensed data used to generate the tree crown map was acquired four years before our field data on recruits was collected. This temporal gap is unlikely to impact our results as tree cover changes slowly in our study region (Tarbox 2018). In addition, given our

size threshold for counting recruits (>0.5 m in height) we expect that dispersed seeds may require at least a year to grow large enough to be counted in our transects (Burns 1990).

Model development

Our primary modeling goal was to evaluate how neighboring tree crowns impact tree recruit abundance. To accomplish this goal, we developed models of increasing complexity to test spatial covariates' impact on model predictions.

Tree recruit abundance in heterogeneous landscapes exemplifies overdispersed count data, which are typically modeled with a negative binomial distribution (Caughlin et al. 2012). An alternate choice for count data with a large number of zeros is a zero-inflated model (Blasco-Moreno et al. 2019). Our fine-scale study design (25 m² quadrats) and the rarity of recruitment in agricultural landscapes resulted in data rich in zeros (Lachlan et al. 2019). Therefore, we developed a zero-inflated model that included a binomial distribution to represent whether recruitment occurred or not, and a negative binomial distribution representing the likelihood of recruit abundance, conditional on recruitment (Blasco-Moreno et al. 2019; Appendix S1: Section S3). Hereafter, recruit abundance refers to the recruit abundance predicted by the full zero-inflated model, the number of recruits refers to the negative binomial distribution of the model, and the probability of recruitment refers to the binomial distribution of the model.

We began by assessing intercept-only models representing different distributional assumptions for recruit abundance. The next step was to incorporate elevation as a covariate. We added elevation before any other covariates because relative to data on individual property ownership and mapped tree crowns, topographic data are widely available at global scales (Farr et al. 2007). We then added random effects representing individual property ownership and recruit species identity to the elevation-only model. We added individual property ownership and species identity as random effects, following best practices for modeling hierarchical data where sharing information improves group-level estimates, including repeated measurements within species (Turner et al. 2018, McElreath 2020).

These random effects enabled the baseline value for recruit abundance to vary by property membership or by recruit tree species (random intercept) and the relationship between elevation and recruit abundance to vary depending on property ownership or recruit tree species

(random slopes). In addition to models with either property membership or recruit tree species as a random effect, we tested models with both property membership and recruit tree species as random intercepts and slopes.

Building off models that incorporated elevation, property membership, and recruit species identity, we added heterospecific and conspecific tree crown area as additional covariates. Visual examination of the relationship between conspecific tree crown area and recruit abundance suggested a hump-shaped relationship (Appendix S1: Figure S4), and incorporating a quadratic term for the effect of conspecific tree crowns resulted in significant improvements in model fit. Thus, we included a quadratic term for conspecific tree crown area in negative binomial models for abundance. In contrast, including a quadratic term for heterospecific tree crowns in models for abundance did not improve model fit and resulted in convergence problems, so we modeled heterospecific tree crowns using only linear terms.

Next, we expanded models for tree crown area by including random effect terms that enabled the slope of the tree crown area to vary by recruit species identity and property membership. These random effects imply that recruit species identity and/or property membership mediate the relationship between tree crown area and recruit abundance. In sum, our most complex model included heterospecific and conspecific tree crown area and elevation as variables dependent on recruit species identity and property membership. After accounting for spatial covariates and property membership in our final model, we did not find evidence for spatial autocorrelation between neighboring quadrats (see Appendix S1: Section S2 for more details).

Model fitting

We used a Bayesian modeling framework with Hamiltonian Monte Carlo sampling to analyze our data. Our models were run in the Stan programming language using the brms package in R v. 3.6.3 (Bürkner 2017). To improve model convergence, we standardized covariates by centering around the mean and dividing by two standard deviations (Gelman 2008). We ran twelve chains for 8000 iterations with a warmup of 6000 iterations, resulting in 24000 posterior draws per model. We assessed the chain mixing and convergence of the parameters using the Gelman-Rubin statistic ($R\text{-hat} < 1.1$; Gelman and Rubin 1992, Gelman and Hennig 2017) and through visual examination of chains using trace plots.

Model selection

We assessed the predictive accuracy of our models for recruit abundance with out-of-sample data. Our out-of-sample assessment was based on a k-fold approach that iteratively split quadrat data into 90% training data and 10% test data withheld from model fitting. We repeated this procedure ten times, with no test data repetition between folds (Boyce et al. 2002). We then assessed model performance using mean absolute error (MAE) calculated for each of the ten folds test datasets. MAE can be interpreted on the original scale of the data as the difference between observed and predicted recruit counts in quadrats. MAE enabled us to evaluate how well recruit density in field data was predicted by our models.

Results

We located and identified 481 recruits, representing 53 recruits of *Byrsionima crassifolia*, 110 recruits of *Calycoiphyllum candidissimum*, 206 recruits of *Cedrela odorata*, 90 recruits of *Guazuma ulmifolia*, and 22 recruits of *Enterolobium cyclocarpum*. We observed high variability in recruit abundance between properties (Figure 3). We included a total of 23,875 adult tree crowns from the species-specific tree crown map with an average crown area of 93 m² (for more details about tree crowns see Appendix S1: Table S4).

Species-specific tree crown maps potential to predict tree species recruit abundance

The best model to predict recruits of all five species included the mapped tree crown area as a predictor variable with effects varying by individual property ownership (Appendix S1: Table S4). However, when looking at the model error by recruits' species, the best model for recruit abundance varied between species (Appendix S1: Table S4). For four out of five species (*Byrsionima crassifolia*, *Cedrela odorata*, *Calycoiphyllum candidissimum*, and *Enterolobium cyclocarpum*), including conspecific and heterospecific tree crown area as covariates provided better predictions than models without these covariates. Allowing variability between properties and recruit species also greatly improved the predictions of tree species recruit abundance (Appendix S1: Section S4 and Table S4).

Effect of total tree crown area by tree species

Recruit abundance was more strongly related to conspecific tree crown area than to heterospecific tree crown area (Figure 4). For an average focal tree species in an average property, adding one conspecific average-sized tree crown (93 m²) resulted in a predicted increase of 8.00% (95% CI: 0.80 to 11.56%) in the number of recruits. In contrast, adding one heterospecific average-sized tree crown (93 m²)

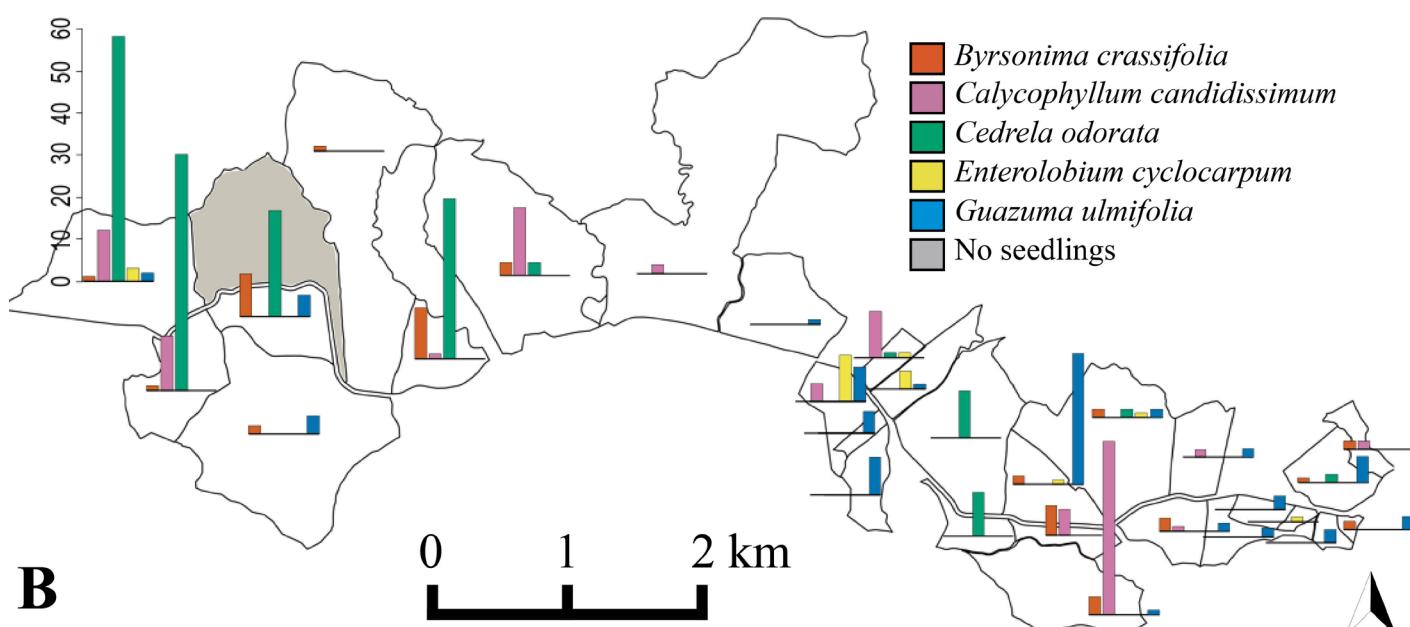


Figure 3

Landscape-scale abundance of tree species recruits in 2018, Panama. Black lines represent landowner property boundaries, and histograms display seedling abundance by species on each of the properties. A single property lacked recruits in all transects and is colored gray without a histogram in the map.

in an average property resulted in a predicted increase of only 0.03%, with high uncertainty over whether the heterospecific tree crown area had a positive or negative impact on the number of recruits (95% CI: -0.60 to 0.68%). Conspecific tree crown area also had a stronger impact on recruitment probability. For an average tree species in an average landowner property, adding one conspecific tree crown was predicted to increase the probability of recruitment by 0.05 (95% CI: -0.04 to 0.14), while adding one heterospecific tree crown had a near-zero impact on the probability of recruit abundance (95% CI: -2.26x10⁻³ to 3.57x10⁻³).

We found evidence for conspecific negative density dependence (CNDD) with a decrease in the predicted number of recruits in plots with high conspecific tree crown area (Figure 4). Our models produced a negative estimate for conspecific tree crown area's quadratic effect on the count of tree recruits (-0.99; 95% CI: -1.63 to -0.37). For a low total area of conspecific tree crowns, the linear term dominated, resulting in an increased number of recruits. For a high total area of conspecific tree crowns, the quadratic term dominated, resulting in fewer recruits. For example, at a high density of 60 average-sized conspecific

trees within 100 m, predicted abundance had a median value of 0.01 recruits (95% CI: 0.00 to 2.8), while at a low density of 23 conspecific trees, recruitment abundance had a median value of 0.38 recruits (95% CI: 0.01 to 1.93).

Models predicted a robust positive relationship between conspecific total tree crown area and the number of recruits for all individual species. Effects of increasing conspecific tree crowns from zero to one led to a range of increases in recruit abundance from 7.00% (95% CI: -2.00 % to 15.00 %) for *Enterolobium cyclocarpum* recruit abundance to 8.80% (95% CI: 1.40 % to 16.00 %) increase for *Cedrela odorata*. Across species, the effects of the heterospecific crown area on the number of recruits were generally smaller and more uncertain than the effects of conspecific total tree crown area and varied across species from positive to negative (Figure 5). The effects of heterospecific total tree crown area on recruitment also varied across species from positive to negative. The binomial distribution indicated a weakly positive relationship between conspecific total tree crown area and the probability of recruitment for all species ranging from increases in 0.19 (95% CI: -0.06 to 0.31) to 5.04x10⁻⁴(95% CI: -0.01 to 0.041) when conspecific tree crowns in the surrounding

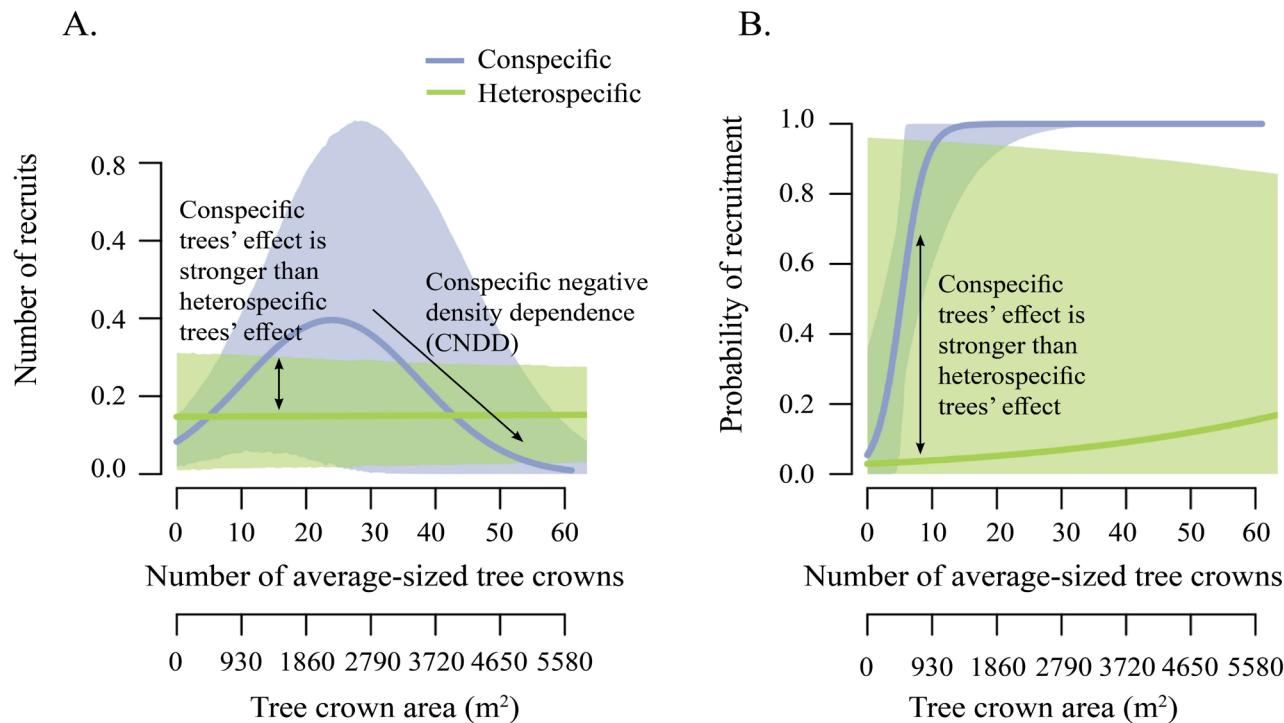
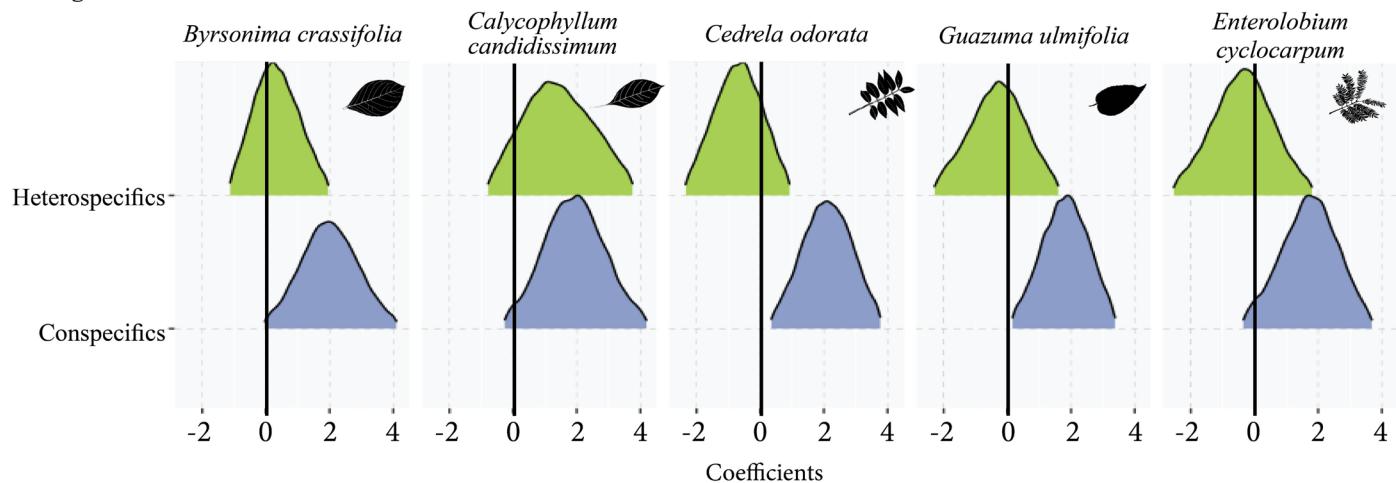


Figure 4

Conspecific tree crown area has a stronger positive effect on recruit abundance than the heterospecific tree crown area. These curves were created using the model structure of "Individual tree crowns, Species & Property" (Appendix S1: Table S4). Panel A shows the effect of increasing the number of conspecific and heterospecific tree crowns on the number of recruits of an average species in an average property, corresponding to the negative binomial model. Panel B shows the effect of increasing the number of conspecific and heterospecific tree crowns on the probability of recruiting an average species in an average property, corresponding to the binomial model. The shaded area in both panels represents 80% credible intervals.

A. Negative binomial- Number of recruits



B. Binomial- Probability of recruitment

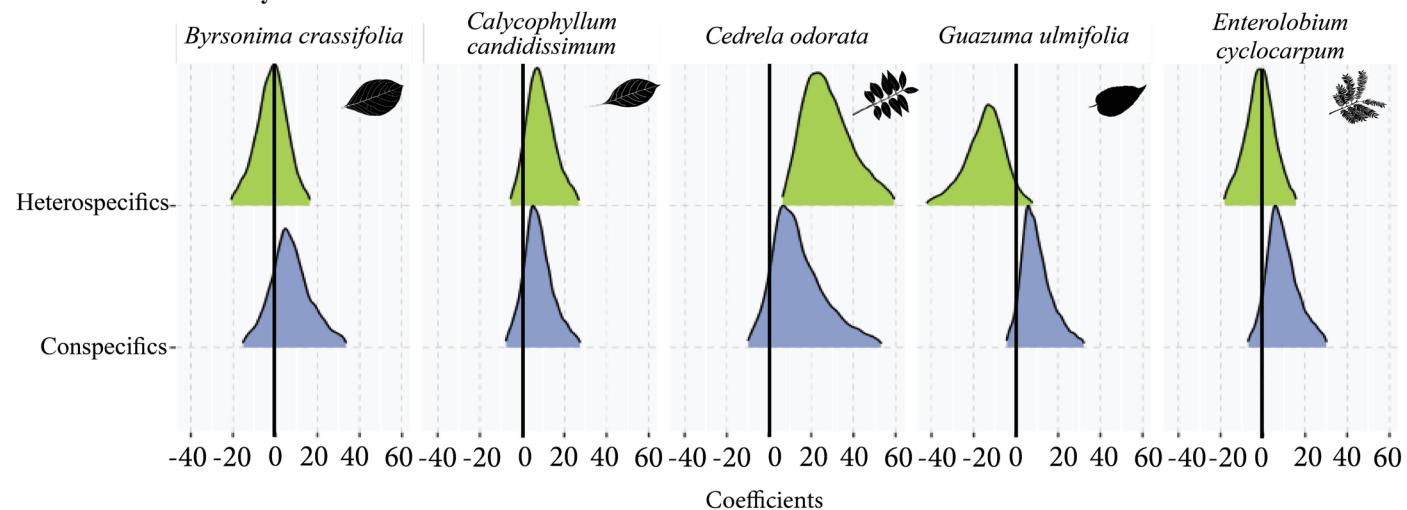


Figure 5

Conspecific total tree crown area and heterospecific tree crown area have different effects on the number of recruits and the probability of recruitment across all species. Panel A shows the posterior distribution for the model coefficients of conspecific and heterospecific crown area on the number of recruits on the log-linear scale, corresponding to the negative binomial model. Panel B shows the posterior distribution for the model coefficients of conspecific and heterospecific trees on the probability of recruitment on the logit scale, corresponding to the binomial model. The effects shown represent the total effects of total tree crown area on recruit abundance with 95% CI, including the community-level (fixed) effects and the species-level (random) effects.

landscape increased from zero to one. Across species, the effects of heterospecific crown area on recruitment probability varied from positive to negative (Figure 5).

Individual property ownership and elevation influence tree recruit abundance

Property membership can alter relationships between total tree crown area and recruit abundance (Appendix S1: Figure S5). Depending on the property, adding one conspecific tree crown of average size can lead anywhere from a decrease in recruit abundance of 1.75% (95% CI: -16.25% to 14.16%) to an increase of 13.43% (95% CI: 2.43% to 25.75%). Dependence of relationships between total tree crown area and recruit abundance on property membership was also evident in probability of recruitment, albeit with less variation than in the number of recruits. Relative

to other covariates, elevation had a weak effect on recruit abundance (Appendix S1: Figure S6).

Recruit abundance predictions have potential to provide decision support

We applied our best-fitting model (Model “Individual tree crowns & Property” in Appendix S1: Table S4) to forecast recruit abundance as a continuous surface across two properties in our study area. Considering a threshold for natural regeneration as >1 recruit per 25 m², differences within and between properties are apparent (Figure 6). In property one, the presence of conspecific tree crowns of *Byrsinoma crassifolia* results in predicted natural regeneration of this species in 10.05% of the property area (95% CI: 0.00 to 13.59%). On the other hand, *Calycophyllum candidissimum* is predicted to have low natural regenera-

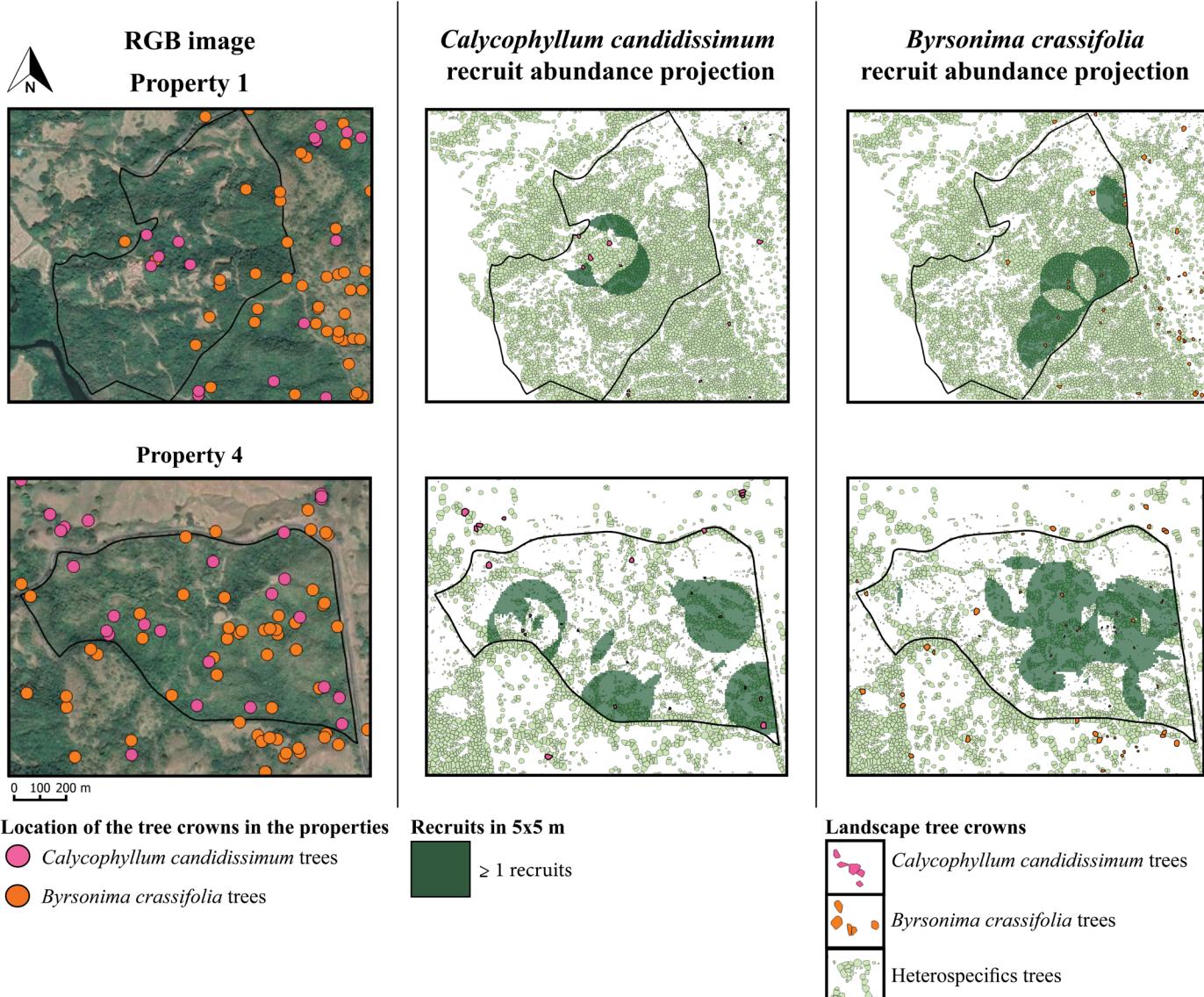


Figure 6

Potential application of models for reforestation decision support. We applied the best-fitting model (Model "Individual tree crowns & Property" in Appendix S1: Table S4) to predict tree recruit abundance in property one and property four. Parcel identity in Appendix S1: Figure S1. The dark green color in the recruit abundance projections represents at least one recruit in a 25m² area, not colored areas represent less than one recruits in 25 m² area. The pink and orange points in the RGB images are the locations of *Calycophyllum candidissimum* and *Byrsonima crassifolia* trees respectively.

tion in this property (3.51% of the property area; 95% CI: 0.00 to 6.38%), primarily due to negative density dependence and adverse effects of individual property ownership on the baseline recruit abundance for this species. In property four, these species-specific predictions show high natural regeneration for both species, where 21.83% (95% CI: 0.00 to 36.44%) of property area meets our threshold for natural regeneration of *Byrsonima crassifolia*, and 20.70% (95% CI: 0.00 to 28.50%) of the area of this property meets our threshold for natural regeneration for *Calycophyllum candidissimum*.

Discussion

Large-scale restoration projects could benefit from ecosystem services provided by low-cost natural regeneration if we can predict where native species will recruit (Holl et al. 2000). We applied a species-specific map of tree crown area, to predict tree recruit abundance in an agricultural landscape. Accounting for the species identity of neighboring tree crowns improved predictions of tree recruit abundance. However, the effect of the conspecific and heterospecific tree crown area was conditional on individual property ownership. Predicting tree recruit abundance in tropical landscapes will require accounting for the identity of trees by separating conspecific trees from heterospecific-

ic trees. Altogether, our results enable predictions of tree species recruit abundance at the resolution of individual trees and the extent of land management units. High spatial resolution predictions of tree recruitment potential will enable species and property-specific decision-making and facilitate the integration of natural regeneration into forest landscape restoration plans.

Predicting tree recruitment from species-specific tree crown maps

We have demonstrated the potential of species-specific tree crown maps from hyperspectral and lidar data to improve our ability to predict the abundance of tree species recruits. Our best model for all species included species variability by differentiating conspecific from heterospecific neighboring tree crowns. This approach also allowed including conspecific negative density dependence (CNDD), which provides another example of a species-specific process key to predictive capacity in our models. An additional benefit of high spatial resolution data on tree crown abundance in heterogeneous landscapes is the ability to account for trees outside forests, including dispersed pasture trees and live fence trees, that may not be included in coarse forest cover metrics (Caughlin et al. 2016, Tarbox et al. 2018). Our models reveal a correlation between tree crown area and recruit abundance but do not shed light on the numerous processes that underlie tree recruitment, from seed production to seedling survival. Disentangling these processes will be key for effective restoration practice (Holl et al. 2000).

While airborne imagery was crucial to our capacity to predict tree recruit abundance, high-resolution remote sensing products are still limited in availability, particularly for the tropics (Tay et al. 2018). Unmanned Aerial Vehicles (UAVs) could provide a relatively low-cost solution with customizable spatial and temporal extents (Zhang et al. 2016, Dalponte et al. 2019). Hyperspectral sensors with hundreds of spectral bands can now be mounted on UAVs, potentially enabling similar species classification ability as the imagery used in our study (Liu et al. 2020). Ecological observatory network such as National Ecological Observatory Network (NEON) and Forest Global Earth Observatory (ForestGEO) will also increase the availability of tree crown maps that could be applied to answer landscape-scale questions on tree species distributions and demography (Marconi et al. 2019).

Improving species classification algorithms' accuracy will aid our capacity to predict ecological processes, including tree species recruitment. As more accurate methods for tree crown segmentation and species classifica-

tion are developed (e.g., Dalponte et al. 2019, Sothe et al. 2019), we anticipate that the predictive capacity of ecological patterns from tree crown maps will improve. A current limitation is the trade-off between the training sample size and the number of species that can be accurately classified (Baldeck and Asner 2014), which leads studies classifying between 4 to 6 species to reach accuracies over 90% (Zhang et al. 2020). In contrast, studies classifying higher number of species, including rare species, reach lower classification accuracies due to lower available samples of rare species (Graves et al. 2016). Nevertheless, work is ongoing to improve classification accuracy, including the development of workflows that can pool data from multiple sites to increase training data size (Marrs and Ni-Meister 2019). Future efforts to include functional traits as the basis for tree species classification from remotely sensed data may further improve accuracy (Shi et al. 2018). Statistical models that account for misclassification in species identity present an alternate approach with potential to improve ecological models that rely on remote sensing classification (Conn et al. 2013). A related challenge will be propagating uncertainty from tree crown segmentation and species classification based on remotely sensed data through to ecological predictions (Maddox et al. 2019, Wen et al. 2019). A benefit of propagating uncertainty from tree species classification to recruit abundance models will be to identify the relative importance of species misclassification and biological variability for model uncertainty.

The relevance of species identity for recruitment

We found that the effect of conspecific tree crowns on recruit abundance is stronger than that of heterospecific trees. This is consistent with patterns observed in other tropical landscapes (Comita et al. 2010) and indicates that differentiating conspecific from heterospecific trees is essential to understand patterns in natural regeneration (Zahawi et al. 2021). Previous tree recruitment studies in tropical landscapes have aggregated conspecific and heterospecific tree crown area into non species specific forest cover (Zahawi et al. 2013, Holl et al. 2017, Duncan and Duncan 2000, Lopes et al. 2012). Our results suggest that the varying impacts (from weak to strong effects) of forest cover on seedling recruitment from previous studies may have partially resulted from the lack of species identity data on reproductive trees in existing forests.

Landscape-scale CNDD provides an example of an ecological process where differentiating between same and different species is essential for accurate prediction. We also found evidence for CNDD in our study, with

decreased recruit abundance when conspecific total tree crown area was high (Figure 4). In natural landscapes, CNDD is prevalent across many tropical tree species and is likely driven by host-specific natural enemies (Comita and Stump 2020). We suggest that CNDD may also play a role in agricultural landscapes, including our study area, an agropastoral region subject to hundreds of years of cattle ranching and continued management. Multiple ecological processes, from seed arrival to growth and survival of established plants, could drive the hump-shaped relationship between conspecific tree crown area and recruit abundance observed in our study. Seed dispersal kernels can have a non-monotonic shape, due to wind dynamics (Maurer et al. 2013) or animal movement (Rehm et al. 2019), resulting in highest seed arrival at some distance from the parent plant. Mature trees can also limit seedling establishment in a variety of ways, from increasing density of competing seedlings (Schwinning and Kelly 2013), to hosting species-specific pests and pathogens (Liu and He 2019), to limiting water and light availability (Derroire et al. 2016). In working landscapes, where farmers manage tree species abundance, human decision-making could also influence CNDD if rare species are preferentially allowed to recruit (Lengkeek 2003). Understanding the processes that generate spatial patterns of tree recruit abundance during secondary succession will require additional research that goes beyond counting recruit abundance at a single time period. Seed traps provide a way to directly quantify seed dispersal kernels (Reid et al. 2015), and seed addition experiments can quantify establishment limitation across environmental gradients (Clark et al. 2007). However, deploying seed traps or experimental plots at spatial extents that match heterogeneity in natural regeneration across agropastoral landscapes presents logistical challenges. Remotely sensed data, including tree crown maps, could help by generating hypotheses and informing stratified sampling schemes.

In contrast to the effects of conspecific total tree crown area, which were fairly consistent across all species, effects of heterospecific total tree crown area varied widely between species. Differences in heterospecific tree crown area effects between species are suggestive of intraspecific differences in life history. For example, *Calycophyllum canndissimum* had a strong positive relationship with heterospecific total tree crown area, potentially resulting from this species' relatively high abundance during mid-late succession. Alternately, recruit abundance of *Guazuma ulmifolia*, a light-demanding early successional species (Kalacska et al. 2004, Hall and Ashton 2016), exhibited a more negative relationship with heterospecific total tree

crown area. While a higher sample size of tree species with variable functional traits will be necessary to test these relationships rigorously, landscape-level, species-specific tree crown maps provide a rich dataset to improve our understanding of how species functional traits and dispersal syndromes impact forest succession (Asner and Martin 2016, Durán et al. 2019).

Individual property ownership influence on tree recruitment

Cadastral data on individual property ownership was an important data source for models' predictive capacity. In our study area, where the vast majority of the land is privately owned, cadastral data represents differences in land management history with far-reaching consequences for ecological processes (Caughlin et al. 2016, Valencia Mestre 2017). This spatial variability could result from differences in landowners' decision-making (Metzel and Montagnini 2014) or underlying biophysical differences between properties (e.g. soil fertility; Hall et al. 2011). Property boundaries alone do not provide insight into the socioeconomic drivers of spatial heterogeneity. In the Azuero Peninsula, we expect that factors including dependence on wage labor (Valencia Mestre et al. 2018), income from off-farm employment (Sloan 2015), and tree planting and protecting practices (Garen et al. 2011) could underlie variable tree recruit abundance between properties. Understanding how these and other socioeconomic processes will require data that go beyond property boundaries, such as interviews with cattle ranchers (Lerner et al. 2015, Valencia Mestre 2017). High-resolution remotely sensed data, including tree crown maps, could assist participatory research to collect these data in collaboration with local stakeholders (Caughlin et al. 2019a). A limitation in this study is that we cannot extrapolate recruitment predictions beyond the sampled properties. Identifying drivers of tree recruitment variability that can be measured using remote sensing could enable predictions across larger areas. For example, hyperspectral imagery can detect invasive grass species (Schmidt and Skidmoore 2001) that inhibit forest succession in cattle pastures (Griscom et al. 2009). In the context of an ongoing forest transition in the Azuero Peninsula driven by regional socioeconomic changes (Sloan 2015), understanding the human drivers of spatial heterogeneity at farm scales remains a critical research need.

We modeled property identity as a random effect, including separate estimates for each property in our data. This approach has advantages and disadvantages for forecasting tree recruitment across large areas. An increasing number of national governments mandate public access to

cadastral data (Femenia-Ribera and Mora-Navarro 2018, Chekole et al. 2021). Following the public release of cadastral data, policy interventions to promote reforestation and reduce deforestation are being applied at the level of properties, including payments for ecosystem services (Oliveira Fiorini et al. 2020). The wide availability and policy relevance of cadastral data means that frameworks to include cadastral data in ecological models have broad applicability (Requena-Mullor et al. 2019). A disadvantage of modeling property identity as a categorical variable is that estimating effects for properties not included in the data used to fit the model is not possible. Nevertheless, we expect that incorporating property identity as a random effect in ecological models will generally improve model predictions, as accounting for spatial variation improves estimation of other effects in the model (McElreath 2020). For example, we expect that our estimated effects of tree crown area are more reliable after accounting for property identity in our models.

Recruitment abundance predictions potential to provide decision support

Overall, predicting tree species recruitment at the scale of individual trees and properties will improve decision support for reforestation projects (Brancalion et al. 2019, Crouzeilles et al. 2020). Using models similar to the one we have developed here, restoration managers could identify target areas with high natural regeneration as low cost opportunities for forest recovery (Chazdon and Guariguata 2018), at the scale of landowner properties where restoration interventions take place (Oliveira Fiorini et al. 2020). Given that different tree species provide different ecosystem services, and farmer preference for particular species can vary (Garen et al. 2009), forecasts of individual species recruitment will boost the value of natural regeneration maps. Altogether, these examples demonstrate how our models enable species-and property-specific predictions of tree species recruit abundance in a heterogeneous landscape. Our work is the first step towards a decision support tool that could improve species and site selection by providing information on which tree species are likely to recruit naturally in a given farm (Chazdon and Guariguata 2018).

Acknowledgements

Funding for this research was provided by the National Science Foundation under grant #1415297 in the SBE program and the Smithsonian Tropical Research Institute (STRI) short term fellowship. The Global Airborne Ob-

servatory is made possible by grants and gifts from private foundations, visionary individuals, and Arizona State University. The GAO Panama flights were supported by the Grantham Foundation for the Protection of the Environment. We thank the Fundación Pro Eco Azuero for support during fieldwork. Ruth Metzel, Juan Requena, Andrii Zaiats, Anand Roopsind, Anna Roser, and Cara Applestein provided valuable feedback on the manuscript.

References

- Asner, G. P., D. E. Knapp, J. Boardman, R. O. Green, T. Kennedy-Bowdoin, M. Eastwood, R. E. Martin, C. Anderson, and C. B. Field. 2012. Carnegie Airborne Observatory-2: Increasing science data dimensionality via high-fidelity multi-sensor fusion. *Remote Sensing of Environment* 124:454–465.
- Asner, G. P., and R. E. Martin. 2016. Spectranomics: Emerging science and conservation opportunities at the interface of biodiversity and remote sensing. *Global Ecology and Conservation* 8:212–219.
- Baldeck, C. A., and G. P. Asner. 2014. Improving Remote Species Identification through Efficient Training Data Collection. *Remote Sensing* 6:2682–2698.
- Barbosa, J. M., and G. P. Asner. 2017. Prioritizing landscapes for restoration based on spatial patterns of ecosystem controls and plant-plant interactions. *Journal of Applied Ecology* 54:1459–1468.
- Batista-Rodríguez, J. A., A. Caballero, M. A. Pérez-Flores, and Y. Almaguer-Carmenates. 2017. 3D inversion of aeromagnetic Data on Las Tablas District, Panama. *Journal of Applied Geophysics* 138:9–16.
- Blasco-Moreno, A., M. Pérez-Casany, P. Puig, M. Morante, and E. Castells. 2019. What does a zero mean? Understanding false, random and structural zeros in ecology. *Methods in Ecology and Evolution*.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Brancalion, P. H. S., A. Niamir, E. Broadbent, R. Crouzeilles, F. S. M. Barros, A. M. Almeyda Zambrano, A. Baccini, J. Aronson, S. Goetz, J. L. Reid, B. B. N. Strassburg, S. Wilson, and R. L. Chazdon. 2019. Global restoration opportunities in tropical rainforest landscapes. *Science Advances* 5:eaav3223.

- Breugel, M. van, D. Craven, H. R. Lai, M. Baillon, B. L. Turner, and J. S. Hall. 2019. Soil nutrients and dispersal limitation shape compositional variation in secondary tropical forests across multiple scales. *Journal of Ecology* 107:566–581.
- Buchs, D. M., R. J. Arculus, P. O. Baumgartner, C. Baumgartner-Mora, and A. Ulianov. 2010. Late Cretaceous arc development on the SW margin of the Caribbean Plate: Insights from the Golfito, Costa Rica, and Azuero, Panama, complexes. *Geochemistry, Geophysics, Geosystems* 11.
- Bürkner, P.-C. 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* 80:1–28.
- Burns, R. M. 1990. *Silvics of North America: Hardwoods*. U.S. Department of Agriculture, Forest Service.
- Caughlin, T. T., T. Ganesh, and M. D. Lowman. 2012. Sacred fig trees promote frugivore visitation and tree seedling abundance in South India. *CURRENT SCIENCE* 102:5.
- Caughlin, T. T., S. J. Graves, G. P. Asner, B. C. Tarbox, and S. A. Bohlman. 2019a. High-Resolution Remote Sensing Data as a Boundary Object to Facilitate Interdisciplinary Collaboration. Pages 295–326 in S. G. Perz, editor. *Collaboration Across Boundaries for Social-Ecological Systems Science*. Springer International Publishing.
- Caughlin, T. T., M. de la Peña-Domene, and C. Martínez-Garza. 2019b. Demographic costs and benefits of natural regeneration during tropical forest restoration. *Ecology Letters* 22:34–44.
- Caughlin, T. T., S. W. Rifai, S. J. Graves, G. P. Asner, and S. A. Bohlman. 2016. Integrating LiDAR-derived tree height and Landsat satellite reflectance to estimate forest regrowth in a tropical agricultural landscape. *Remote Sensing in Ecology and Conservation* 2:190–203.
- Chazdon, R. L., and M. R. Guariguata. 2018. Decision support tools for forest landscape restoration: Current status and future outlook. *Ocasional paper* 183, Bogor, Indonesia: CIFOR.
- Chazdon, R. L., and M. Uriarte. 2016. Natural regeneration in the context of large-scale forest and landscape restoration in the tropics. *Biotropica* 48:709–715.
- Chekole, S. D., W. T. de Vries, P. Durán-Díaz, and G. B. Shibeshi. 2021. Analyzing the Effects of Institutional Merger: Case of Cadastral Information Registration and Landholding Right Providing Institutions in Ethiopia. *Land* 10:404.
- Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are Plant Populations Seed Limited? A Critique and Meta-Analysis of Seed Addition Experiments. *The American Naturalist* 170:128–142.
- Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. *Science* 329:330–332.
- Comita, L. S., and S. M. Stump. 2020. Natural Enemies and the Maintenance of Tropical Tree Diversity: Recent Insights and Implications for the Future of Biodiversity in a Changing World1. *Annals of the Missouri Botanical Garden* 105:377–392.
- Conn, P. B., B. T. McClintock, M. F. Cameron, D. S. Johnson, E. E. Moreland, and P. L. Boveng. 2013. Accommodating species identification errors in transect surveys. *Ecology* 94:2607–2618.
- Cook-Patton, S. C., S. M. Leavitt, D. Gibbs, N. L. Harris, K. Lister, K. J. Anderson-Teixeira, R. D. Briggs, R. L. Chazdon, T. W. Crowther, P. W. Ellis, H. P. Griscom, V. Herrmann, K. D. Holl, R. A. Houghton, C. Larrosa, G. Lomax, R. Lucas, P. Madsen, Y. Malhi, A. Paquette, J. D. Parker, K. Paul, D. Routh, S. Roxburgh, S. Saatchi, J. van den Hoogen, W. S. Walker, C. E. Wheeler, S. A. Wood, L. Xu, and B. W. Griscom. 2020. Mapping carbon accumulation potential from global natural forest regrowth. *Nature* 585:545–550.
- Crk, T., M. Uriarte, F. Corsi, and D. Flynn. 2009. Forest recovery in a tropical landscape: what is the relative importance of biophysical, socioeconomic, and landscape variables? *Landscape Ecology* 24:629–642.
- Crouzeilles, R., H. L. Beyer, L. M. Monteiro, R. Feltran-Barbieri, A. C. M. Pessôa, F. S. M. Barros, D. B. Lindenmayer, E. D. S. M. Lino, C. E. V. Grelle, R. L. Chazdon, M. Matsumoto, M. Rosa, A. E. Latawiec, and B. B. N. Strassburg. 2020. Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. *Conservation Letters*

- 13:e12709.
- Crouzeilles, R., and M. Curran. 2016. Which landscape size best predicts the influence of forest cover on restoration success? A global meta-analysis on the scale of effect. *Journal of Applied Ecology* 53:440–448.
- Dalponte, M., and D. A. Coomes. 2016. Tree-centric mapping of forest carbon density from airborne laser scanning and hyperspectral data. *Methods in Ecology and Evolution* 7:1236–1245.
- Dalponte, M., L. Frizzera, and D. Ganelle. 2019. Individual tree crown delineation and tree species classification with hyperspectral and LiDAR data. *PeerJ* 6.
- Derroire, G., M. Tigabu, P. C. Odén, and J. R. Healey. 2016. The Effects of Established Trees on Woody Regeneration during Secondary Succession in Tropical Dry Forests. *Biotropica* 48:290–300.
- Duncan, R. S., and V. E. Duncan. 2000. Forest Succession and Distance from Forest Edge in an Afro-Tropical Grassland. *Biotropica* 32:33–41.
- Durán, S. M., R. E. Martin, S. Díaz, B. S. Maitner, Y. Malhi, N. Salinas, A. Shenkin, M. R. Silman, D. J. Wieczynski, G. P. Asner, L. P. Bentley, V. M. Savage, and B. J. Enquist. 2019. Informing trait-based ecology by assessing remotely sensed functional diversity across a broad tropical temperature gradient. *Science Advances* 5:eaaw8114.
- Elliott, S., D. Blakesley, and K. Hardwick. 2013. Restoring tropical forests: a practical guide. Royal Botanic Gardens.
- Farr, T. G., P. A. Rosen, E. Caro, R. Crippen, R. Duren, S. Hensley, M. Kobrick, M. Paller, E. Rodriguez, L. Roth, D. Seal, S. Shaffer, J. Shimada, J. Umland, M. Werner, M. Oskin, D. Burbank, and D. Alsdorf. 2007. The Shuttle Radar Topography Mission. *Reviews of Geophysics* 45.
- Femenia-Ribera, C., and G. Mora-Navarro. 2018. Cadastre-Land Registry Coordination in Spain: Application of Law 13/2015 and Its Effects.
- Fischer, F. J., I. Maréchaux, and J. Chave. 2019. Improving plant allometry by fusing forest models and remote sensing. *New Phytologist* 223:1159–1165.
- Garen, E. J., K. Saltonstall, M. S. Ashton, J. L. Slusser, S. Mathias, and J. S. Hall. 2011. The tree planting and protecting culture of cattle ranchers and small-scale agriculturalists in rural Panama: Opportunities for reforestation and land restoration. *Forest Ecology and Management* 261:1684–1695.
- Garen, E. J., K. Saltonstall, J. L. Slusser, S. Mathias, M. S. Ashton, and J. S. Hall. 2009. An evaluation of farmers' experiences planting native trees in rural Panama: implications for reforestation with native species in agricultural landscapes. *Agroforestry Systems* 76:219–236.
- Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in medicine* 27:2865–2873.
- Gelman, A., and C. Hennig. 2017. Beyond subjective and objective in statistics. *Journal of the Royal Statistical Society: Series A (Statistics in Society)* 180:967–1033.
- Gelman, A., and D. B. Rubin. 1992. Inference from Iterative Simulation Using Multiple Sequences. *Statistical Science* 7:457–472.
- Graves, S. J., G. P. Asner, R. E. Martin, C. B. Anderson, M. S. Colgan, L. Kalantari, and S. A. Bohlman. 2016. Tree Species Abundance Predictions in a Tropical Agricultural Landscape with a Supervised Classification Model and Imbalanced Data. *Remote Sensing* 8:161.
- Griscom, H. P., and M. S. Ashton. 2011. Restoration of dry tropical forests in Central America: A review of pattern and process. *Forest Ecology and Management* 261:1564–1579.
- Griscom, H. P., A. M. Connelly, M. S. Ashton, M. Wishnie, and J. Deago. 2011. The Structure and Composition of a Tropical Dry Forest Landscape After Land Clearance; Azuero Peninsula, Panama. *Journal of Sustainable Forestry* 30:756–774.
- Griscom, H. P., B. W. Griscom, and M. S. Ashton. 2009. Forest Regeneration from Pasture in the Dry Tropics of Panama: Effects of Cattle, Exotic Grass, and Forested Riparia. *Restoration Ecology* 17:117–126.
- Hall, J. S., and M. S. Ashton. 2016. Guide to early growth and survival in plantations of 64 tree species native to Panama and the neotropics. Smithsonian Tropical Research Institute.
- Hall, J. S., B. E. Love, E. J. Garen, J. L. Slusser, K. Saltonstall, S. Mathias, M. van Breugel, D. Ibarra, E. W.

- Bork, D. Spaner, M. H. Wishnie, and M. S. Ashton. 2011. Tree plantations on farms: Evaluating growth and potential for success. *Forest Ecology and Management* 261:1675–1683.
- Harvey, C. A., N. I. J. Tucker, and A. Estrada. 2004. Live fences, isolated trees, and windbreaks: tools for conserving biodiversity in fragmented tropical landscapes. *Agroforestry and biodiversity conservation in tropical landscapes*. Island Press, Washington, DC:261–289.
- Holl, K. D., M. E. Loik, E. H. Lin, and I. A. Samuels. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration ecology* 8:339–349.
- Holl, K. D., J. L. Reid, J. M. Chaves-Fallas, F. Oviedo-Brenes, and R. A. Zahawi. 2017. Local tropical forest restoration strategies affect tree recruitment more strongly than does landscape forest cover. *Journal of Applied Ecology* 54:1091–1099.
- Johnson, D. J., W. T. Beaulieu, J. D. Bever, and K. Clay. 2012. Conspecific Negative Density Dependence and Forest Diversity. *Science* 336:904–907.
- Kalacska, M., G. A. Sanchez-Azofeifa, J. C. Calvo-Alvarado, M. Quesada, B. Rivard, and D. H. Janzen. 2004. Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. *Forest Ecology and Management* 200:227–247.
- Lachlan, C. S., J. M. Dwyer, H. M. Chapman, B. G. Yadok, and M. M. Mayfield. 2019. Landscape structure mediates zoothochorous-dispersed seed rain under isolated pasture trees across distinct tropical regions. *Landscape Ecology* 34:1347–1362.
- Lengkeek, A. G. 2003. 'Diversity makes a difference': farmers managing inter- and intra-specific tree species diversity in Meru Kenya:181.
- Lennox, G. D., T. A. Gardner, J. R. Thomson, J. Ferreira, E. Berenguer, A. C. Lees, R. M. Nally, L. E. O. C. Aragão, S. F. B. Ferraz, J. Louzada, N. G. Moura, V. H. F. Oliveira, R. Pardini, R. R. C. Solar, F. Z. V. Mello, I. C. G. Vieira, and J. Barlow. 2018. Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests. *Global Change Biology* 24:5680–5694.
- Lerner, A. M., T. K. Rudel, L. C. Schneider, M. McGroddy, D. V. Burbano, and C. F. Mena. 2015. The spontaneous emergence of silvo-pastoral landscapes in the Ecuadorian Amazon: patterns and processes. *Regional Environmental Change* 15:1421–1431.
- Liu, M., T. Yu, X. Gu, Z. Sun, J. Yang, Z. Zhang, X. Mi, W. Cao, and J. Li. 2020. The Impact of Spatial Resolution on the Classification of Vegetation Types in Highly Fragmented Planting Areas Based on Unmanned Aerial Vehicle Hyperspectral Images. *Remote Sensing* 12:146.
- Liu, Y., and F. He. 2019. Incorporating the disease triangle framework for testing the effect of soil-borne pathogens on tree species diversity. *Functional Ecology* 33:1211–1222.
- Lopes, C. G. R., E. M. N. Ferraz, C. C. de Castro, E. N. de Lima, J. M. F. F. dos Santos, D. M. dos Santos, and E. de L. Araújo. 2012. Forest succession and distance from preserved patches in the Brazilian semiarid region. *Forest Ecology and Management* 271:115–123.
- Maddox, W. J., P. Izmailov, T. Garipov, D. P. Vetrov, and A. G. Wilson. 2019. A Simple Baseline for Bayesian Uncertainty in Deep Learning. Pages 13153–13164 in H. Wallach, H. Larochelle, A. Beygelzimer, F. d'Alché-Buc, E. Fox, and R. Garnett, editors. *Advances in Neural Information Processing Systems* 32. Curran Associates, Inc.
- Marconi, S., S. J. Graves, D. Gong, M. S. Nia, M. L. Bras, B. J. Dorr, P. Fontana, J. Gearhart, C. Greenberg, D. J. Harris, S. A. Kumar, A. Nishant, J. Prarabdh, S. U. Rege, S. A. Bohlman, E. P. White, and D. Z. Wang. 2019. A data science challenge for converting airborne remote sensing data into ecological information. *PeerJ* 6:e5843.
- Marrs, J., and W. Ni-Meister. 2019. Machine Learning Techniques for Tree Species Classification Using Co-Registered LiDAR and Hyperspectral Data. *Remote Sensing* 11:819.
- Matos, F. A. R., L. F. S. Magnago, C. A. C. Miranda, L. F. T. de Menezes, M. Gastauer, N. V. H. Safar, C. E. G. R. Schaefer, M. P. da Silva, M. Simonelli, F. A. Edwards, S. V. Martins, J. A. A. Meira-Neto, and D. P. Edwards. 2020. Secondary forest fragments offer

- important carbon and biodiversity cobenefits. *Global Change Biology* 26:509–522.
- Maurer, K. D., G. Bohrer, D. Medvigy, and S. J. Wright. 2013. The timing of abscission affects dispersal distance in a wind-dispersed tropical tree. *Functional Ecology* 27:208–218.
- McElreath, R. 2020. Statistical rethinking: A Bayesian course with examples in R and Stan. CRC press.
- Menge, D. N. L., and R. L. Chazdon. 2016. Higher survival drives the success of nitrogen-fixing trees through succession in Costa Rican rainforests. *The New Phytologist* 209:965–977.
- Mesquita, R. C. G., K. Ickes, G. Ganade, and G. B. Williamson. 2001. Alternative successional pathways in the Amazon Basin. *Journal of Ecology* 89:528–537.
- Metzel, R., and F. Montagnini. 2014. From Farm to Forest: Factors Associated with Protecting and Planting Trees in a Panamanian Agricultural Landscape. *BOIS & FORETS DES TROPIQUES* 322:3.
- Muller-Landau, H. C., S. J. Wright, O. Calderón, R. Condit, and S. P. Hubbell. 2008. Interspecific Variation in Primary Seed Dispersal in a Tropical Forest. *Journal of Ecology* 96:653–667.
- Myster, R. W., editor. 2008. Post-agricultural succession in the neotropics. Springer, New York.
- Nachtergael, F., H. van Velthuizen, L. Verelst, N. H. Batjes, K. Dijkshoorn, V. W. P. van Engelen, G. Fischer, A. Jones, and L. Montanarella. 2010. The harmonized world soil database. Pages 34–37 Proceedings of the 19th World Congress of Soil Science, Soil Solutions for a Changing World, Brisbane, Australia, 1-6 August 2010.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15:278–285.
- Norden, N., H. A. Angarita, F. Bongers, M. Martínez-Ramos, I. G. la de la Cerda, M. van Breugel, E. Lebrija-Trejos, J. A. Meave, J. Vandermeer, G. B. Williamson, B. Finegan, R. Mesquita, and R. L. Chazdon. 2015. Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proceedings of the National Academy of Sciences* 112:8013–8018.
- Oliveira Fiorini, A. C., C. Mullally, M. Swisher, and F. E. Putz. 2020. Forest cover effects of payments for ecosystem services: Evidence from an impact evaluation in Brazil. *Ecological Economics* 169:106522.
- Parrotta, J. A. 1993. Secondary forest regeneration on degraded tropical lands. Pages 63–73 in H. Lieth and M. Lohmann, editors. *Restoration of Tropical Forest Ecosystems: Proceedings of the Symposium held on October 7–10, 1991*. Springer Netherlands, Dordrecht.
- de la Peña-Domene, M., and C. Martínez-Garza. 2018. Integrating Density into Dispersal and Establishment Limitation Equations in Tropical Forests. *Forests* 9:570.
- Rehm, E., E. Fricke, J. Bender, J. Savidge, and H. Rogers. 2019. Animal movement drives variation in seed dispersal distance in a plant–animal network. *Proceedings of the Royal Society B: Biological Sciences* 286:20182007.
- Reid, J. L., K. D. Holl, and R. A. Zahawi. 2015. Seed dispersal limitations shift over time in tropical forest restoration. *Ecological Applications* 25:1072–1082.
- Requena-Mullor, J. M., K. C. Maguire, D. J. Shinneman, and T. T. Caughlin. 2019. Integrating anthropogenic factors into regional-scale species distribution models—A novel application in the imperiled sagebrush biome. *Global Change Biology* 25:3844–3858.
- Robiglio, V., and F. Sinclair. 2011. Maintaining the Conservation Value of Shifting Cultivation Landscapes Requires Spatially Explicit Interventions. *Environmental Management* 48:289–306.
- Schimel, D., R. Pavlick, J. B. Fisher, G. P. Asner, S. Saatchi, P. Townsend, C. Miller, C. Frankenberg, K. Hibbard, and P. Cox. 2015. Observing terrestrial ecosystems and the carbon cycle from space. *Global Change Biology* 21:1762–1776.
- Schwinning, S., and C. K. Kelly. 2013. Plant competition, temporal niches and implications for productivity and adaptability to climate change in water-limited environments. *Functional Ecology* 27:886–897.
- Shi, Y., A. K. Skidmore, T. Wang, S. Holzwarth, U. Heiden, N. Pinnel, X. Zhu, and M. Heurich. 2018. Tree species classification using plant functional traits from LiDAR and hyperspectral data. *International Journal*

- of Applied Earth Observation and Geoinformation 73:207–219.
- Sloan, S. 2015. The development-driven forest transition and its utility for REDD+. *Ecological Economics* 116:1–11.
- Sothe, C., M. Dalponte, C. M. de Almeida, M. B. Schimski, C. L. Lima, V. Liesenberg, G. T. Miyoshi, and A. M. G. Tommaselli. 2019. Tree Species Classification in a Highly Diverse Subtropical Forest Integrating UAV-Based Photogrammetric Point Cloud and Hyperspectral Data. *Remote Sensing* 11:1338.
- Tarbox, B. C., C. Fiestas, and T. T. Caughlin. 2018. Divergent rates of change between tree cover types in a tropical pastoral region. *Landscape Ecology* 33:2153–2167.
- Tay, J. Y. L., A. Erfmeier, and J. M. Kalwij. 2018. Reaching new heights: can drones replace current methods to study plant population dynamics? *Plant Ecology* 219:1139–1150.
- Turner, B. L., T. Brenes-Arguedas, and R. Condit. 2018. Pervasive phosphorus limitation of tree species but not communities in tropical forests. *Nature* 555:367–370.
- Uriarte, M., R. Muscarella, and J. K. Zimmerman. 2018. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Global Change Biology* 24:e692–e704.
- Valencia Mestre, M. 2017. From Treeless Pastures to Silvo-pastoral Systems: The Extent and Drivers of Tree Management Styles. University of Michigan, Horace H. Rackham School of Graduate Studies.
- Valencia Mestre, M. C., B. G. Ferguson, and J. Vandermeer. 2018. Syndromes of production and tree-cover dynamics of Neotropical grazing land. *Agroecology and Sustainable Food Systems* 0:1–24.
- Wen, J., N. Zheng, J. Yuan, Z. Gong, and C. Chen. 2019. Bayesian Uncertainty Matching for Unsupervised Domain Adaptation. arXiv:1906.09693 [cs, stat].
- Zahawi, R. A., K. D. Holl, R. J. Cole, and J. L. Reid. 2013. Testing applied nucleation as a strategy to facilitate tropical forest recovery. *Journal of Applied Ecology* 50:88–96.
- Zahawi, R. A., L. K. Werden, M. San-José, J. A. Rosales, J. Flores, and K. D. Holl. 2021. Proximity and abundance of mother trees affects recruitment patterns in a long-term tropical forest restoration study. *Ecography*:ecog.05907.
- Zhang, B., L. Zhao, and X. Zhang. 2020. Three-dimensional convolutional neural network model for tree species classification using airborne hyperspectral images. *Remote Sensing of Environment* 247:111938.
- Zhang, J., J. Hu, J. Lian, Z. Fan, X. Ouyang, and W. Ye. 2016. Seeing the forest from drones: Testing the potential of lightweight drones as a tool for long-term forest monitoring. *Biological Conservation* 198:60–69.