Applied Vegetation Science IAVS

Rules of thumb for predicting tropical forest recovery

Karen D. Holl[1] | John Leighton Reid[2] | Federico Oviedo-Brenes[3] | Andy J. Kulikowski[1] | Rakan A. Zahawi[1,3,4]

[1]Environmental Studies Department, University of California, Santa Cruz, California

[2]Center for Conservation and Sustainable Development, Missouri Botanical Garden, St. Louis, Missouri

[3]Las Cruces Biological Station, Organization for Tropical Studies, San Vito, Costa Rica

[4]Lyon Arboretum, University of Hawai'i at Mānoa, Honolulu, Hawaii

Correspondence
Karen D. Holl, Environmental Studies Department, University of California, Santa Cruz, CA 95064.
Email: kholl@ucsc.edu

Funding information
US National Science Foundation, Grant/Award Number: DEB 05-15577, DEB 09-18112 and DEB 14-56520

Co-ordinating Editor: John Morgan

Abstract

Questions: Natural regeneration is increasingly recognized as a potentially cost-effective strategy to reach ambitious forest landscape restoration targets, but rates of recovery are notoriously variable. We asked how well initial habitat conditions after cessation of agriculture predict forest recovery after nearly a decade. We aimed to provide land managers with general rules of thumb to assess when it is necessary to invest resources in active restoration, such as tree planting, to accelerate forest recovery.

Location: Coto Brus County, Puntarenas, Costa Rica.

Methods: We compiled data on initial vegetation structure, soil nutrients, prior land-use history and surrounding forest cover at 13 sites. After 8.5 years, we measured vegetation indicators commonly used to assess forest recovery, namely amount of canopy closure and number and diversity of woody recruits.

Results: Two variables, grass cover and canopy closure, measured 1.5 years after site abandonment, explained 47–87% of five of the six response variables after 8.5 years; recovery was faster in sites with lower grass cover and higher canopy closure initially. Waiting an additional year to measure initial vegetation variables did not improve model fit. Time since the original forest was cleared explained 62% of change in canopy cover, whereas percentage of surrounding forest cover, length of pasture use and soil variables explained minimal additional variation.

Conclusions: Our results suggest that two easily measurable vegetation variables can provide guidance to land managers and policy makers about where to invest scarce restoration resources to facilitate forest recovery.

KEYWORDS
canopy closure, forest recovery indicators, forest restoration, grass cover, natural regeneration, secondary succession, seedling recruitment

1 | INTRODUCTION

Ambitious targets have been set for tropical forest landscape restoration at the international, national and regional scales. For example, the New York Declaration on forests aims to restore 350 million ha of forest globally by 2030 (United Nations 2014) and the Initiative 20 × 20 has set a target of 20 million ha in Latin America by 2020 (Vergara, Gallardo Lomeli, Franco Chuaire, Weber, & Zamora Cristales, 2015). Natural regeneration is increasingly being recognized as an important, cost-effective approach to achieving these goals (Chazdon & Guariguata, 2016), and large areas of secondary forest already exist that have recovered passively after agriculture, grazing or logging ceased with no human intervention beyond removing the prior anthropogenic land use

(Chazdon, 2014). At the same time, rates of natural regeneration vary greatly, ranging from sites that show substantial recovery of forest structure within a decade or two to those that remain dominated by highly competitive forage grasses with little woody establishment over the same time period (Brancalion et al., 2016; Uhl, Buschbacher, & Serrao, 1988).

A critical question is how to predict the rates of recovery, so that land managers know whether natural regeneration is a viable approach at a given site, or whether it is necessary to invest additional resources in actively restoring sites (e.g. tree planting) to overcome barriers and accelerate the process (Holl & Aide, 2011; Török & Helm, 2017). Providing land managers with simple rules of thumb for predicting forest recovery is key to most effectively allocating the limited funding for forest landscape restoration (Shoo et al., 2017), yet guidance on which specific measurements are most important to collect and how well they predict longer term trajectories is lacking.

Most past studies of factors affecting rates of tropical forest recovery have necessarily relied on chronosequences (e.g. Norden et al., 2015; Suganuma & Durigan, 2015). By substituting space for time, this approach allows researchers to study forest change over decades or centuries; however, such studies often confound differences in site conditions and interventions with time and are vulnerable to biased case selection (Reid, Fagan, & Zahawi, 2018). For example, a deforested site that showed minimal regeneration likely would not be selected for a chronosequence study. These issues limit the potential for such studies to predict the probability of forest recovery on a given site. Hence, results of chronosequence assessments often differ from those of long-term studies (Chazdon et al., 2007; Feldpausch, Prates-Clark, Fernandes, & Riha, 2007).

Here, we draw on a multi-year, well-replicated study in southern Costa Rica to ask how well initial habitat variables measured within 3 years of cessation of agriculture (cattle grazing or coffee production) predicts forest recovery after 8.5 years. We compared the predictive value of key habitat variables that have been shown to affect the rate of tropical forest recovery. These variables include (a) *grass cover* – as forage grasses have been shown to inhibit the establishment of woody recruits (García-Orth & Martínez-Ramos, 2011; Hooper, Legendre, & Condit, 2005); (b) *canopy closure* – which attracts faunal seed dispersers and shades out light-demanding pasture grasses (Holl, 2012; Hooper et al., 2005); (c) *soil P, cation exchange capacity and organic matter* – which affect seedling growth (dos Santos, Goncalves, & Feldpausch, 2006); (d) *length of prior land use for pasture or agriculture* – which typically negatively affects recovery rates (Holl & Zahawi, 2014; Steininger, 2000); and (e) *nearby forest cover* – which typically increases seed availability (Griscom, Griscom, & Ashton, 2009; Kauano, Cardoso, Torezan, & Marques, 2014). We then measured several indicators commonly associated with forest recovery, namely high canopy closure and number and diversity of woody recruits. Since one goal was to provide guidance to land managers, we deliberately used field measurements and analytical approaches that could be easily adopted for a wide range of projects and monitoring protocols.

2 | METHODS

2.1 | Study region and sites

This study was conducted at 13 ~0.25-ha sites spread across a ~100 km^2 agriculture–forest landscape between the Las Cruces Biological Station (LCBS; 8°47′7″N, 82°57′32″W) and Agua Buena (8°44′42″N, 82°56′53″W) in southern Costa Rica (Supporting information Appendices S1 and S2). The forests in this region are at the boundary between Tropical Premontane Wet and Rain Forest zones (Holdridge, Grenke, Hatheway, Liang, & Tosi, 1971), range in elevation from 1,100 to 1,430 m and receive mean annual rainfall of 3,500–4,000 mm with a dry season from December to March. Mean annual temperature is ~21 °C. All sites are separated by ≥700 m and most are steeply sloped (15–35°). Soils are volcanic in origin, mildly acidic, low in P and high in organic matter (Holl & Zahawi, 2014).

All sites were farmed for ≥20 years, primarily for cattle grazing and coffee farming, prior to the start of this study. We compiled information about the types and lengths of past land uses from landowners. We ranked the sites according to time since clearing and length of pasture use, given that landowners could often only estimate dates to within a couple of years. Sites with values within 3 years of each other were given the same ranking.

At each site, we established a 50 m × 50 m plot in which anthropogenic uses were removed and we monitored natural recovery. These measurements were part of a larger study, set up over 3 years, comparing different restoration treatments (Zahawi, Holl, Cole, & Reid, 2013). Here, we focus on the natural regeneration plots, given our aim of predicting the rate of recovery without active restoration efforts, such as tree planting. All plots were cleared to ground level by machete or mechanical trimmer at ~3-months intervals for 2.5 years, after which management ceased and the areas were allowed to regenerate without human intervention (hereafter year of abandonment). Five sites were abandoned in Jan 2007, five in Jan 2008 and three in Jan 2009. We standardized the data to the number of years following abandonment (i.e. year of final measurement – year of abandonment = number of years since abandonment).

2.2 | Tree recruits and vegetation cover

We have recorded vegetation measurements (i.e. grass cover and woody recruitment) annually in June–July of each year since clearing ceased, and here test whether vegetation data from 0.5, 1.5 and 2.5 years following site abandonment predicts recovery after 8.5 years. We sampled tree recruits in all plots using a stratified sampling procedure with area sampled adjusted for recruit size (Supporting information Appendix S3). In four permanent, nested quadrats at each site, we recorded tree seedlings (≥0.2-m and <1.0-m tall) in eight adjacent 1 m × 1 m quadrats; saplings (≥1-m tall and <5 cm DBH) in four adjacent 2 m × 4 m quadrats; and small trees (≥5 cm and <10 cm DBH) in 8 m × 8 m quadrats. Trees ≥10 cm DBH were recorded throughout the entire 50 m × 50 m plot. We estimated total percentage grass cover, as well as cover of individual grass species

with >5% cover, in alternating 1 m × 1 m seedling quadrats (n = 16 per plot) using a modified Braun-Blanquet cover-abundance scale: 0, 1–5, 5–10, 10–25, 25–50, 50–75, 75–95 and 95–100% (Müller-Dombois & Ellenberg, 1974). We recorded canopy closure over the same quadrats by taking spherical densiometer measurements in four directions and averaging values. We categorized individual grass species into forage (mostly aggressive non-native species) and non-forage species (mostly native species) based on discussions with local farmers and species categorizations in a recent taxonomic review of the flora of Costa Rica (Hammel, Grayum, Herrera, & Zamora, 2003).

2.3 | Surface soil nutrients

In August 2007, we collected 25, 2.5 cm × 15.0 cm soil cores across each plot. Cores were mixed, air-dried and then passed through a 2-mm sieve. Samples were analysed for pH, organic matter and all macronutrients following standard procedures at Brookside Laboratories, New Bremen, OH, US (www.blinc.com/resources/testing-methods). As would be expected, many soil variables were correlated, so we included three uncorrelated variables as predictors: (a) *organic matter* – using the loss on ignition method (Schulte & Hopkins, 1996) as soil organic matter was highly correlated with both total C and N and affects soil fertility and water-holding capacity; (b) *cation exchange capacity* – by summation measured using Mehlich III extractions (Mehlich, 1984); (c) *phosphorus* – extracted using Mehlich III method, as P is often a limiting nutrient on variable-charged clay soils (Uehara & Gillman, 1981).

2.4 | Landscape forest cover

Like much of Central America, the surrounding landscape is a mosaic of agricultural fields and pasture interspersed with remnant forest patches (Zahawi, Duran, & Kormann, 2015). Forest cover within 100- and 500-m radius from the centre of each plot was hand-digitized from orthorectified 2005 aerial photographs (Cole, Holl, & Zahawi, 2010). Tree cover surrounding plots at the start of the study ranged from 0% to 61% at a 100-m buffer to 11% to 89% at a 500-m buffers (Supporting information Appendices S1 and S2).

2.5 | Data analysis

We used step-wise, linear regression with forward selection to test the relative effects of predictor variables on six measures of forest recovery after 8.5 years: the absolute value and net change in canopy closure, tree individuals/m^2 (recruit density) and species per plot (species richness). Potential predictor variables included vegetation variables collected at 0.5, 1.5 and 2.5 years following abandonment (grass cover, forage grass cover, canopy closure, initial numbers of recruits and initial species richness), soil variables (Mehlich III P, percentage organic matter and cation exchange capacity), percentage surrounding forest cover (at 100- and 500-m radii), site elevation and past land use (time since forest clearing and length of pasture use). We compared models by starting with a null model with no

predictors and then adding variables that entered the model at the $p < 0.05$ level; we focus on those significant after Bonferroni correction for multiple hypothesis tests. We report the partial R^2 of all variables that were included in the final model. We also calculated Pearson correlation coefficients between all predictor variables.

We ran separate models with vegetation predictor variables for time 0.5, 1.5 and 2.5 years, since values for a given variable (e.g. grass cover) were highly correlated across years; we use a subscript to indicate the time vegetation variables were collected (e.g. grass cover$_{1.5}$ refers to grass cover collected at 1.5 years). We ran preliminary models including initial numbers of recruits for recruit density$_{8.5}$ models and initial species richness for species richness$_{8.5}$ models, but both variables were strongly correlated with grass cover$_{1.5}$ (Supporting information Appendix S4), and grass cover$_{1.5}$ always explained more variation. So, we did not include recruit density$_{1.5}$ and species richness$_{1.5}$ in the models we present here. We ran models using either total grass cover or forage grass cover.

We inspected the distribution of the original data, as well as the residuals of our various models, and log-transformed absolute recruit density to meet assumptions of normality and homogeneity of variances. One site had extremely high recruit density compared to the rest of the sites (37% of all recruits in year 1.5 and 41% at year 8.5) and substantially higher canopy cover in year 1.5. We ran all analyses with and without the site, and the independent variables included in the model were identical in most cases. Therefore, we include this site in most models and note cases where the results were different. All analyses were done using R v. 3.2.4 (R Foundation for Statistical Computing, Vienna, Austria). Means ± 1 SE are reported. Data are available at https://merritt.cdlib.org/m/ucsc_lib_hollzahawi.

3 | RESULTS

3.1 | Overview

Two vegetation variables, grass cover and canopy closure, measured after 1.5 years, explained a significant amount of variation in the six vegetation response variables after 8.5 years (Figure 1, Table 1); in sum, recovery was faster in sites with lower initial grass cover and higher canopy closure. In all but one case, the best model including vegetation variables measured after 1.5 years explained more variance than did the model with vegetation measurements after 0.5 years (Table 2); for four out of six variables, the 1.5-year model explained more of the variation than did data from 2.5 years. Substituting forage grass cover for total grass cover yielded similar models, which is not surprising given that forage grass cover was highly correlated with total grass cover ($R = 0.97$, $p < 0.0001$; Supporting information Appendix S4); the forage grass cover models had lower or equal fit in all cases (Table 1). Time since original forest clearing explained the most variation in change in canopy cover, whereas the percentage of surrounding forest cover at 100 and 500 m, as well as the years of pasture use, elevation, Mehlich P and cation exchange capacity did not enter any of the models (Table 1). Surprisingly, the length of time sites
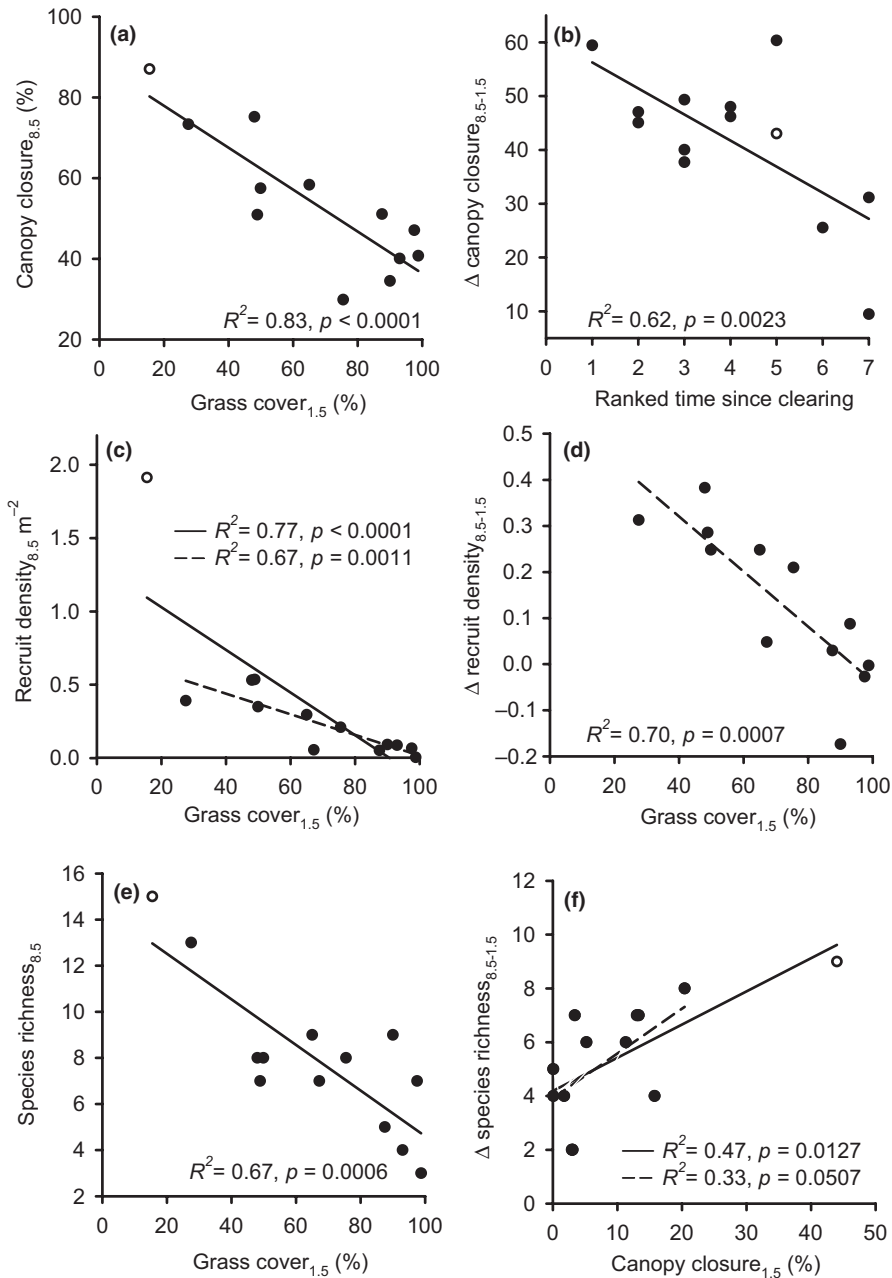
FIGURE 1 (a) Canopy closure$_{8.5}$, (b) Δ canopy closure$_{8.5-1.5}$, (c) recruit density$_{8.5}$, (d) Δ recruit density$_{8.5-1.5}$, (e) species richness$_{8.5}$, (f) Δ species richness$_{8.5-1.5}$ as a function of the predictor variable with the highest R^2. Solid regression lines include all sites. Dashed lines show regressions without the outlier site, indicated by an open circle. Partial R^2 and p-values are for the variable on the x-axis. Δ values are the difference between years 1.5 and 8.5. n = 12 or 13 sites

was used for pasture, or since clearing was not correlated with any soil or vegetation variables (Supporting information Appendix S4).

3.2 | Grass cover and canopy closure

The ground layer at most sites was dominated by grasses early in the study (Table 3), 86% of which was comprised of forage grasses, primarily *Axonopus scoparius* (Flüggé) Kuhlm., *Pennisetum purpureum* Schumach. and *Urochloa brizantha* (Hochst. Ex. A. Rich.) R.D. Webster. Mean grass cover after 8.5 years was lower, although grass cover was still >50% in eight sites. Not surprisingly, grass cover$_{1.5}$ was strongly correlated with grass cover$_{8.5}$ (R = 0.78, p = 0.0016).

Canopy closure$_{1.5}$ was quite low (<20%) in all sites, except for one site with a value of 44% that was an outlier in the models

(Table 3). Canopy closure$_{8.5}$ was higher in sites that had lower grass cover initially (Figure 1a) and to a lesser degree in sites with longer time periods since the original forest was cleared. The importance of the latter variables was reversed for Δ canopy closure$_{8.5-1.5}$; time since clearing explained 62% of the variation (Figure 1b, Table 1). Canopy closure was strongly negatively correlated with grass cover after 1.5 (R = −0.74, p = 0.0041) and 8.5 (R = −0.74, p = 0.0042) years.

3.3 | Recruit density, composition and species richness

Recruit density$_{8.5}$ varied by two orders of magnitude across sites (Table 3), with higher recruit density$_{8.5}$ best explained by low initial

TABLE 1 Models explaining recovery response variables after 8.5 years using vegetation variables from 1.5 years after abandonment

Response variable	Model	Variable 1	Partial R^2	p	Variable 2	Partial R^2	p
Canopy cover$_{8.5}$	Standard[a]	Grass cover$_{1.5}$	0.83	**<0.0001**	Time cleared	0.52	0.0118
Δ canopy cover$_{8.5-1.5}$	Standard	Time cleared	0.62	**0.0023**	Grass cover$_{1.5}$	0.40	0.0263
Recruit density$_{8.5}$	Standard	Grass cover$_{1.5}$	0.77	**<0.0001**			
Recruit density$_{8.5}$	Forage grass[b]	Forage cover$_{1.5}$	0.60	**0.0019**			
Δ recruit density$_{8.5-1.5}$	Standard	Canopy closure$_{1.5}$	0.87	**<0.0001**	Organic matter	0.34	0.0453
Δ recruit density$_{8.5-1.5}$	Forage grass	Canopy closure$_{1.5}$	0.87	**<0.0001**	Organic matter	0.34	0.0453
Δ recruit density$_{8.5-1.5}$	No outlier site[c]	Grass cover$_{1.5}$	0.70	**0.0007**			
Species richness$_{8.5}$	Standard	Grass cover$_{1.5}$	0.67	**0.0006**			
Species richness$_{8.5}$	Forage grass	Canopy closure$_{1.5}$	0.61	**0.0016**			
Δ recruit richness$_{8.5-1.5}$	Standard	Canopy closure$_{1.5}$	0.47	0.0127			
Δ recruit richness$_{8.5-1.5}$	Forage grass	Canopy closure$_{1.5}$	0.47	0.0103			
Δ recruit richness$_{8.5-1.5}$	No outlier site	Canopy closure$_{1.5}$	0.33	0.0507			

Notes. Δ values are year 8.5 – year 1.5. n = 12 or 13 sites. p-values that are bolded are significant after Bonferroni correction.
[a]Standard model included initial grass cover, canopy closure, percentage organic matter, cation exchange capacity, Mehlich III P, time in pasture use, time cleared, elevation and percentage forest cover at 100- and 500-m radii (see Methods for details). [b]Forage grass model was same as the standard model but forage grass cover replaced grass cover. [c]Same as the standard model but with the one outlier site excluded.

grass cover$_{1.5}$, regardless of whether the outlier site was included (Figure 1c). Mean recruit density increased nearly three-fold between 1.5 and 8.5 years, but in a couple of sites recruit density declined slightly (Table 3), as early establishing seedlings were outcompeted by grass. Recruit density$_{1.5}$ was strongly correlated with Δ recruit density between years 1.5 and 8.5 (R = 0.75, p = 0.0031), indicating that the sites that had high establishment early on continued to have high recruitment thereafter. Δ recruit density$_{8.5}$ was best explained by canopy closure$_{1.5}$ but that was largely driven by the outlier site (Supporting information Appendix S5), and grass cover$_{1.5}$ was a better predictor when that site was removed from the model (Figure 1d).

Forty-one species of recruits were recorded across all sites, and the vast majority of recruits were native, small-seeded (<5 mm) animal- (71.3%) or wind- (19.3%) dispersed species (Supporting information Appendix S6). Almost half (46.6%) were from the *Melastomataceae* family, primarily *Conostegia xalapensis* and *Miconia* spp. Only one individual was an invasive species (*Syzygium jambos*), and 5.1% were species that are planted and/or naturalized in the agricultural landscape (e.g. *Citrus* spp., *Erythrina* spp.).

The mean number of species per site tripled between 1.5 and 8.5 years (Table 3). Species richness$_{1.5}$ was not significantly correlated with Δ species richness$_{8.5-1.5}$ (R = 0.17, p = 0.5850). Species richness$_{8.5}$ showed similar but weaker trends than recruit density$_{8.5}$, as the two variables were correlated (R = 0.75, p = 0.0030). Total species richness was higher in sites with lower grass cover$_{1.5}$ (Figure 1e), and species richness increased more over time in sites

TABLE 2 Comparative R^2 of best models of restoration response variables after 8.5 years using vegetation predictor variables from 0.5, 1.5 and 2.5 years after site abandonment. n = 13 sites

Variable	Best model R^2		
	0.5 years	1.5 years	2.5 years
Canopy closure	0.74	0.86	0.81
Δ canopy closure	0.73	0.68	0.75
Recruit density	0.73	0.77	0.59
Δ recruit density	0.70	0.90	0.87
Species richness	0.53	0.67	0.71
Δ species richness	—[a]	0.47	—[a]

Note. [a]No model explained a significant amount ($p < 0.05$) of the variance.

with greater initial canopy closure, a trend that was only marginally significant if the outlier site was removed (Figure 1f).

4 | DISCUSSION

Our results show that two easily measured variables, grass cover and canopy closure, assessed 1.5 years after land abandonment, predicted between 60% and 87% of the variation in recovery of four vegetation variables, and smaller but significant amounts in the other two response variables 7 years later. In general, vegetation variables

Variable	Year 1.5 Mean ± *SE*	(Min-Max)	Year 8.5 Mean ± *SE*	(Min-Max)
Grass cover (%)	66.5 ± 7.5	(15–99)	49.2 ± 7.0	(5–90)
Forage grass cover (%)	56.8 ± 8.7	(8–98)	—	
Canopy closure (%)	10.3 ± 3.4	(0–44)	51.7 ± 5.0	(26–87)
Δ canopy closure	—		41.7 ± 3.8	(9.5–60.3)
Recruit density/m^2	0.13 ± 0.05	(0.00–0.61)	0.35 ± 0.14	(0.01–1.91)
Δ recruit density/m^2	—		0.23 ± 0.10	(−0.17 to 1.30)
Species richness	2.5 ± 0.6	(0–6)	7.9 ± 0.9	(3–15)
Δ species richness	—		5.5 ± 0.6	(2–9)

measured after 0.5 years explained less variance, and rarely did waiting an additional year improve predictions. A considerable body of literature supports our results that grass cover (primarily dense, 1.5- to 3.0-m tall forage grasses) inhibits establishment of woody seedlings (Griscom et al., 2009; Hooper et al., 2005; Meli, Rey Benayas, Martínez Ramos, & Carabias, 2015) and that tree cover increases seedling establishment both by shading out light-demanding grasses and by enhancing dispersal of zoochorous seeds (Viani et al., 2015; Zahawi et al., 2013). Nonetheless, we know of no other studies demonstrating that measurements within a couple years following abandonment can provide such a strong predictive value of recovery several years later. Canopy closure and grass cover were strongly negatively correlated in years 1.5, 2.5 and 8.5 (*R* ≥ 0.74, *p* ≤ 0.0040 in all cases), so it is impossible to conclude with our data which of these variables have a stronger effect on woody recruitment; it is almost certainly a combination of the two. It is also noteworthy that identifying individual grass species to distinguish forage vs. non-forage grasses, which requires strong botanical identification skills and increases field measurement time, did not improve predictions.

Some past studies have shown that the amount of surrounding forest cover can be a good predictor of the rate of forest recovery (Crouzeilles & Curran, 2016; Letcher & Chazdon, 2009; Rocha, Vieira, & Simon, 2016). However, our result that surrounding forest cover was not a strong predictor is consistent with some other studies (Howe, Urincho-Pantaleon, de la Peña-Domene, & Martínez-Garza, 2010; Letcher & Chazdon, 2009; Rocha et al., 2016) and with earlier analyses of seed rain and seedling recruitment in our system, in which we analysed a range of forest buffer distances (Holl, Reid, Chaves-Fallas, Oviedo-Brenes, & Zahawi, 2017; Reid, Holl, & Zahawi, 2015). We attribute the lack of a forest cover effect to a few factors. First, our study landscape includes numerous isolated trees, live fences and riparian corridors that facilitate movement of dispersers between forest remnants, and are themselves sources of tree seeds, particularly of the most common small-seeded species recorded in our study (Sekercioglu et al., 2015; Zahawi, Duran, et al., 2015). Second, many of the small-seeded, early successional species we commonly recorded (e.g. various *Melastomataceae*, *Heliocarpus appendiculatus* and *Myrsine coriacea*) are often abundant in tropical seed banks (Cubiña & Aide, 2001; Silveira, Fernandes, & Lemos-Filho, 2013; Williams-Linera, Bonilla-Moheno, & López-Barrera, 2016). Third, like many field and remote sensing studies, we evaluated the effect of overall forest cover, rather than the influence of a specific individual species around each plot. We anticipate that surrounding forest cover will have a stronger effect in the coming decades as more later successional, large-seeded species recruit in our plots.

For the most part, surface soil variables were not good predictors of recovery, although an earlier study showed that they do explain a significant amount of variation in the above-ground biomass accumulation rate (Holl & Zahawi, 2014). Indeed, soil parameters are more likely to strongly affect woody seedling growth than recruitment and generally have weaker effects on forest recovery than competition with grasses and proximity to forest (Hooper et al., 2005; Lawrence, Suma, & Mogea, 2005).

Canopy cover increased more slowly in sites that had been cleared earlier and hence used longer for agriculture, which is consistent with some past studies (Marín-Spiotta, Cusack, Ostertag, & Silver, 2008), but time since clearing did not explain variation in other variables. It was surprising that length of pasture usage was not correlated with grass cover or any of the soil variables, since pasture usage typically increases erosion and reduces soil fertility (Buschbacher, Uhl, & Serrao, 1988; Huth, Porder, Chaves, & Whiteside, 2012), and many past studies suggest that land-use intensity strongly affects recovery (Hughes, Kauffman, & Jaramillo, 1999; Lawrence et al., 2005; Rocha et al., 2016). The relatively weak land-use history effects we observed likely result from the facts that (a) most of our sites were used for a mix of pasture and other agricultural crops (primarily coffee) over time but there was a great deal of variation in the management practices within those uses, and (b) the proximal effect of grass cover was stronger than our best estimates of time that the land was under cultivation, which was necessarily approximated given the 40–50-year time span.

Nonetheless, past land use may be one reason for the high tree recruitment in the outlier site (BB). It was one of the few sites used for coffee immediately prior to the study, so initial grass cover was low. The initial recruits in this site were dominated by a single small-seeded, early successional species, *Conostegia xalapensis* (*Melastomataceae*), which comprised 95% of recruits at 1.5 years but had declined to 50% of recruits after 8.5 years as other species

colonized. This result suggests the possible presence of a *C. xalapensis* seed bank at the site that germinated readily in response to high light and temperature conditions when coffee cultivation ceased (Sánchez, Montejo, Gamboa, Albert-Puentes, & Hernández, 2015). The BB site has low surrounding tree cover (Supporting information Appendix S2), but *C. xalapensis* is widely distributed throughout the agricultural landscape, particularly along fence rows.

In sites that have higher recruit establishment, the species composition is dominated by a variety of native, small-seeded, early successional species, which is expected 8.5 years after site abandonment. Studies in other tropical regions suggest that dominance by a single early successional species can arrest succession (Mesquita, Massoca, Jakovac, Bentos, & Williamson, 2015; Yeo & Fensham, 2014; Zahawi & Augspurger, 1999), but we do not observe this pattern in our sites. In the sites studied here, only one was initially dominated by a single species, and in all sites, the number of species is increasing over time. We also have observed mortality of *C. xalapensis*, particularly as it is shaded out by taller trees (Holl & Zahawi, unpub. data). Moreover, in adjacent sites where trees were planted initially resulting in much faster canopy closure (Holl et al., 2017), early successional species colonized in the first few years and larger-seeded species continue to increase in number.

5 | CONCLUSIONS

Our results suggest that monitoring two variables, grass cover and canopy closure, within 1–2 years following removal of agricultural land uses may provide a simple rule of thumb for predicting the rates of tropical forest recovery, which is often highly variable even within the same landscape (Chazdon & Guariguata, 2016; Kauano et al., 2014; Steininger, 2000). Both of these variables are quick to measure qualitatively or quantitatively by somebody with minimal expertise, funding and equipment. Moreover, quantifying canopy cover is becoming easier with readily available remotely sensed data such as Google Earth and imagery from unmanned aerial vehicles (Singh, Evans, Friess, Tan, & Nin, 2015; Zahawi, Dandois, et al., 2015). In contrast, analysing soil samples can be expensive and requires access to laboratory facilities.

More testing is needed in other systems to determine whether the rule is generalizable, a challenge given the few long-term data sets of forest recovery at multiple sites in the same region. If this rule holds true across other studies, it has important implications for forest landscape restoration. First, identifying sites early on that are more likely to benefit from active interventions, such as tree planting, can help to allocate scarce restoration resources. Second, land managers should wait a couple years after land abandonment to determine the likelihood of rapid natural regeneration. For example, the new Forest Code for four states in Brazil recommends waiting for 2–4 years to allow farmers to decide whether natural regeneration is proceeding at a pace that active restoration is not necessary (Brancalion et al., 2016). Finally, secondary

tropical forests are included in a variety of payments for environmental services programmes to improve water quality and sequester carbon, and such rules of thumb could help to predict where the likelihood is highest that natural regeneration will successfully provide these benefits.

ORCID

Karen D. Holl http://orcid.org/0000-0003-2893-6161

REFERENCES

Brancalion, P. H. S., Schweizer, D., Gaudare, U., Mangueira, J. R., Lamonato, F., Farah, F. T., … Rodrigues, R. R. (2016). Balancing economic costs and ecological outcomes of passive and active restoration in agricultural landscapes: The case of Brazil. *Biotropica*, *48*, 856–867. https://doi.org/10.1111/btp.12383

Buschbacher, R., Uhl, C., & Serrao, E. A. S. (1988). Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. *Journal of Ecology*, *76*, 682–699. https://doi.org/10.2307/2260567

Chazdon, R. L. (2014). Second growth: The promise of tropical forest regeneration in an age of deforestation. *University of Chicago Press*, *Chicago, IL, US.*, https://doi.org/10.7208/chicago/9780226118109.001.0001

Chazdon, R. L., & Guariguata, M. R. (2016). Natural regeneration as a tool for large-scale forest restoration in the tropics: Prospects and challenges. *Biotropica*, *48*, 716–730. https://doi.org/10.1111/btp.12381

Chazdon, R. L., Letcher, S. G., van Breugel, M., Martínez-Ramos, M., Bongers, F., & Finegan, B. (2007). Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical Transactions of the Royal Society of London, series B, Biological Sciences*, *362*, 273–289. https://doi.org/10.1098/rstb.2006.1990

Cole, R. J., Holl, K. D., & Zahawi, R. A. (2010). Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. *Ecological Applications*, *20*, 1255–1269. https://doi.org/10.1890/09-0714.1

Crouzeilles, R., & Curran, M. (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. https://doi.org/10.1111/1365-2664.12590

Cubiña, A., & Aide, T. M. (2001). The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica*, *33*, 260–267. https://doi.org/10.1111/j.1744-7429.2001.tb00177.x

dos Santos, U. M., Goncalves, J. F. D., & Feldpausch, T. R. (2006). Growth, leaf nutrient concentration and photosynthetic nutrient use efficiency in tropical tree species planted in degraded areas in central Amazonia. *Forest Ecology and Management*, *226*, 299–309. https://doi.org/10.1016/j.foreco.2006.01.042

Feldpausch, T. R., Prates-Clark, C. D., Fernandes, E. C. M., & Riha, S. J. (2007). Secondary forest growth deviation from chronosequence predictions in central Amazonia. *Global Change Biology*, *13*, 967–979. https://doi.org/10.1111/j.1365-2486.2007.01344.x

García-Orth, X., & Martínez-Ramos, M. (2011). Isolated trees and grass removal improve performance of transplanted *Trema micrantha* (L.) Blume (Ulmaceae) saplings in tropical pastures. *Restoration Ecology*, *19*, 24–34. https://doi.org/10.1111/j.1526-100X.2009.00536.x

Griscom, H. P., Griscom, B. W., & Ashton, M. S. (2009). Forest regeneration from pasture in the dry tropics of Panama: Effects of cattle, exotic grass, and forested riparia. *Restoration Ecology*, *17*, 117–126. https://doi.org/10.1111/j.1526-100X.2007.00342.x

Hammel, B. E., Grayum, M. H., Herrera, C., & Zamora, N. (2003). *Manual de Plantas de Costa Rica. Volumen III*. St. Louis, MO: Missouri Botanical Garden.

Holdridge, L. R., Grenke, W. C., Hatheway, W. H., Liang, T., & Tosi, J. A. Jr (1971). *Forest environments in tropical life zones*. Oxford, UK: Pergamon Press.

Holl, K. D. (2012). Tropical forest restoration. In J. Van Andel & J. Aronson (Eds.), *Restoration ecology* (pp. 103–114). Malden, MA: Blackwell. https://doi.org/10.1002/9781118223130

Holl, K. D., & Aide, T. M. (2011). When and where to actively restore ecosystems? *Forest Ecology and Management*, *261*, 1558–1563. https://doi.org/10.1016/j.foreco.2010.07.004

Holl, K. D., Reid, J. L., Chaves-Fallas, J. M., Oviedo-Brenes, F., & Zahawi, R. A. (2017). Local tropical forest restoration strategies affect tree recruitment more strongly than does landscape forest cover. *Journal of Applied Ecology*, *54*, 1091–1099. https://doi.org/10.1111/1365-2664.12814

Holl, K. D., & Zahawi, R. A. (2014). Factors explaining variability in woody above-ground biomass accumulation in restored tropical forest. *Forest Ecology and Management*, *319*, 36–43. https://doi.org/10.1016/j.foreco.2014.01.024

Hooper, E., Legendre, P., & Condit, R. (2005). Barriers to forest regeneration of deforested and abandoned land in Panama. *Journal of Applied Ecology*, *42*, 1165–1174. https://doi.org/10.1111/j.1365-2664.2005.01106.x

Howe, H. F., Urincho-Pantaleon, Y., de la Peña-Domene, M., & Martínez-Garza, C. (2010). Early seed fall and seedling emergence: Precursors to tropical restoration. *Oecologia*, *164*, 731–740. https://doi.org/10.1007/s00442-010-1669-2

Hughes, R. F., Kauffman, J. B., & Jaramillo, V. J. (1999). Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology*, *80*, 1892–1907.

Huth, T., Porder, S., Chaves, J., & Whiteside, J. H. (2012). Soil carbon and nutrient changes associated with deforestation for pasture in Southern Costa Rica. *Biotropica*, *44*, 661–667. https://doi.org/10.1111/j.1744-7429.2012.00863.x

Kauano, E. E., Cardoso, F. C. G., Torezan, J. M. D., & Marques, M. C. M. (2014). Micro- and meso-scale factors affect the restoration of Atlantic forest. *Natureza & Conservação*, *11*, 145–151.

Lawrence, D., Suma, V., & Mogea, J. P. (2005). Change in species composition with repeated shifting cultivation: limited role of soil nutrients. *Ecological Applications*, *15*, 1952–1967. https://doi.org/10.1890/04-0841

Letcher, S. G., & Chazdon, R. L. (2009). Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica*, *41*, 608–617. https://doi.org/10.1111/j.1744-7429.2009.00517.x

Marín-Spiotta, E., Cusack, D. F., Ostertag, R., & Silver, W. L. (2008). Trends in above- and belowground carbon with forest regrowth after agricultural abandonment in the neotropics. In R. Myster (Ed.), *Post-agricultural succession in the neotropics* (pp. 22–72). New York, NY: Springer. https://doi.org/10.1007/978-0-387-33642-8

Mehlich, A. (1984). Mehlich-3 soil test extractant: A modification of Mehlich-2 extractant. *Communications in Soil Science and Plant Analysis*, *15*, 1409–1416. https://doi.org/10.1080/00103628409367568

Meli, P., Rey Benayas, J. M., Martínez Ramos, M., & Carabias, J. (2015). Effects of grass clearing and soil tilling on establishment of planted tree seedlings in tropical riparian pastures. *New Forests*, *46*, 507–525. https://doi.org/10.1007/s11056-015-9479-3

Mesquita, R. D. G., Massoca, P. E. D., Jakovac, C. C., Bentos, T. V., & Williamson, G. B. (2015). Amazon rain forest succession: Stochasticity or land-use legacy? *BioScience*, *65*, 849–861. https://doi.org/10.1093/biosci/biv108

Müller-Dombois, D., & Ellenberg, H. (1974). *Aims and methods of vegetation ecology*. New York, NY: Wiley.

Norden, N., Angarita, H. A., Bongers, F., Martinez-Ramos, M., deGranzow- la Cerda, I., Breugel, M., … Chazdon, R. L. (2015). Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 8013–8018. https://doi.org/10.1073/pnas.1500403112

Reid, J. L., Fagan, M. E., & Zahawi, R. A. (2018). Positive site selection bias in meta-analyses comparing natural regeneration to active forest restoration. *Science Advances*, *4*, eaas9143. https://doi.org/10.1126/sciadv.aas9143

Reid, J. L., Holl, K. D., & Zahawi, R. A. (2015). Seed dispersal limitations shift over time in tropical forest restoration. *Ecological Applications*, *25*, 1072–1082. https://doi.org/10.1890/14-1399.1

Rocha, G. P. E., Vieira, D. L. M., & Simon, M. F. (2016). Fast natural regeneration in abandoned pastures in southern Amazonia. *Forest Ecology and Management*, *370*, 93–101. https://doi.org/10.1016/j.foreco.2016.03.057

Sánchez, J., Montejo, L., Gamboa, A., Albert-Puentes, D., & Hernández, F. (2015). Germination and dormancy of shrubs and climbing plants of the evergreen forest of Sierra del Rosario, Cuba. *Pastos y Forrajes*, *38*, 11–28.

Schulte, E. E., & Hopkins, B. G. (1996). Estimation of Soil Organic Matter by Weight Loss-On-Ignition. In F. R. Magdoff, M. A. Tabatabai & E. A. HanlonJr (Eds.), *Soil organic matter: Analysis and interpretation Special publication No. 46*. (pp. 21–32). Madison, WI: Soil Science Society of America.

Sekercioglu, C. H., Loarie, S. R., Oviedo-Brenes, F., Mendenhall, C. D., Daily, G. C., & Ehrlich, P. R. (2015). Tropical countryside riparian corridors provide critical habitat and connectivity for seed-dispersing forest birds in a fragmented landscape. *Journal of Ornithology*, *156*, S343–S353. https://doi.org/10.1007/s10336-015-1299-x

Shoo, L. P., Catterall, C. P., Nicol, S., Christian, R., Rhodes, J., Atkinson, P., … Wilson, K. A. (2017). Navigating complex decisions in restoration investment. *Conservation Letters*, *10*, 748–756. https://doi.org/10.1111/conl.12327

Silveira, F. A. O., Fernandes, G. W., & Lemos-Filho, J. P. (2013). Seed and seedling ecophysiology of neotropical Melastomataceae: Implications for conservation and restoration of savannas and rainforests. *Annals of the Missouri Botanical Garden*, *99*, 82–99. https://doi.org/10.3417/2011054

Singh, M., Evans, D., Friess, D., Tan, B., & Nin, C. (2015). Mapping aboveground biomass in a tropical forest in Cambodia using canopy textures derived from Google Earth. *Remote Sensing*, *7*, 5057. https://doi.org/10.3390/rs70505057

Steininger, M. K. (2000). Secondary forest structure and biomass following short and extended land-use in central and southern Amazonia. *Journal of Tropical Ecology*, *16*, 689–708. https://doi.org/10.1017/S0266467400001656

Suganuma, M. S., & Durigan, G. (2015). Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. *Restoration Ecology*, *23*, 238–251. https://doi.org/10.1111/rec.12168

Török, P., & Helm, A. (2017). Ecological theory provides strong support for habitat restoration. *Biological Conservation*, *206*, 85–91. https://doi.org/10.1016/j.biocon.2016.12.024

Uehara, G., & Gillman, G. (1981). *The mineralogy, chemistry, and physics of tropical soils with variable charge clays*. Boulder, CO, US: Westview Press.

Uhl, C., Buschbacher, R., & Serrao, E. A. S. (1988). Abandoned pastures in eastern Amazonia. I. patterns of plant succession. *Journal of Ecology*, *76*, 663–681. https://doi.org/10.2307/2260566

United Nations (2014). *New York declaration on forests*. New York, NY: United Nations.

Vergara, W., Gallardo Lomeli, L., Franco Chuaire, M., Weber, S., & Zamora Cristales, R. (2015). *Initiative 20x20: A landscape restoration movement rises in Latin America and the Caribbean*. Washington, DC: World Resources Institute.

Viani, R. A. G., Vidas, N. B., Pardi, M. M., Castro, D. C. V., Gusson, E., & Brancalion, P. H. S. (2015). Animal-dispersed pioneer trees enhance the early regeneration in Atlantic Forest restoration plantations. *Natureza & Conservação*, *13*, 41–46. https://doi.org/10.1016/j.ncon.2015.03.005

Williams-Linera, G., Bonilla-Moheno, M., & López-Barrera, F. (2016). Tropical cloud forest recovery: The role of seed banks in pastures dominated by an exotic grass. *New Forests*, *47*, 481–496. https://doi.org/10.1007/s11056-016-9526-8

Yeo, W. L. J., & Fensham, R. J. (2014). Will Acacia secondary forest become rainforest in the Australian Wet Tropics? *Forest Ecology and Management*, *331*, 208–217. https://doi.org/10.1016/j.foreco.2014.08.015

Zahawi, R. A., & Augspurger, C. K. (1999). Early plant succession in abandoned pastures in Ecuador. *Biotropica*, *31*, 540–552. https://doi.org/10.1111/j.1744-7429.1999.tb00401.x

Zahawi, R. A., Dandois, J. P., Holl, K. D., Nadwodny, D., Reid, J. L., & Ellis, E. C. (2015). Using lightweight unmanned aerial vehicles to monitor tropical forest recovery. *Biological Conservation*, *186*, 287–295. https://doi.org/10.1016/j.biocon.2015.03.031

Zahawi, R. A., Duran, G., & Kormann, U. (2015). Sixty-seven years of land-use change in southern Costa Rica. *PLoS One*, *10*, e0143554. https://doi.org/10.1371/journal.pone.0143554

Zahawi, R. A., Holl, K. D., Cole, R. J., & Reid, J. L. (2013). Testing applied nucleation as a strategy to facilitate tropical forest recovery. *Journal of Applied Ecology*, *50*, 88–96. https://doi.org/10.1111/1365-2664.12014

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Study and site locations

Appendix S2. Site characteristics

Appendix S3. Vegetation sampling design

Appendix S4. Correlations between initial site variables

Appendix S5. Δ recruit density$_{8.5\text{-}1.5}$ as a function of canopy closure including outlier site

Appendix S6. Recruit species list