LETTER

WILEY **Conservation Letters**
A journal of the Society for Conservation Biology
Open Access

The ephemerality of secondary forests in southern Costa Rica

J. Leighton Reid[1] | Matthew E. Fagan[2] | James Lucas[3] | Joshua Slaughter[2] |
Rakan A. Zahawi[4]

[1]Center for Conservation and Sustainable Development, Missouri Botanical Garden, St Louis, Missouri, 63110, USA

[2]Department of Geography and Environmental Systems, University of Maryland Baltimore County, Baltimore, Maryland, 21250, USA

[3]Department of Biology, Washington University in St Louis, St Louis, Missouri, 63130, USA

[4]Lyon Arboretum, University of Hawai'i at Mānoa, Honolulu, Hawai'i, 96822, USA

Correspondence
J. Leighton Reid, Center for Conservation and Sustainable Development, Missouri Botanical Garden, 4344 Shaw Blvd, St Louis, Missouri 63110, USA.
Email: leighton.reid@mobot.org

Funding information
National Science Foundation, Grant/Award Number: DEB-1313788

Abstract

Secondary forests are increasingly recognized for conserving biodiversity and mitigating global climate change, but these and other desired outcomes can only be achieved after decades of regeneration, and secondary forests are frequently recleared before they recover to predisturbance conditions. We used a time series of aerial photographs (1947-2014) to evaluate multidecadal persistence of secondary forests across a 320 km^2 landscape in southern Costa Rica. Secondary forests had relatively short lifespans, with 50% recleared within 20 years and 85% recleared within 54 years of when they were first observed. Larger forest fragments and forests near rivers had a lower reclearance hazard, but forest persistence did not differ over time, indicating that regional forest regeneration may be generally ephemeral. Costa Rica has made an international commitment to restore 1 million ha of degraded land by 2020. Depending on how this is achieved, only half that target may remain forested by 2040.

KEYWORDS

biodiversity conservation, Bonn Challenge, carbon storage, deforestation, forest restoration, forest transitions, longevity, permanence, persistence, reforestation, survival analysis

1 | INTRODUCTION

Secondary tropical forests play a pivotal role in virtually all visions for a sustainable global future. These young forests now constitute more than half of extant tropical forests (Chazdon, 2014) and scientists and policy-makers alike anticipate that secondary forests will contribute significantly to preventing extinctions, mitigating climate change, and providing goods and services in the 21st century (Chazdon et al., 2016; Houghton, Byers, & Nassikas, 2015; Strassburg et al., 2016; Wright & Muller-Landau, 2006). Indeed, all three United Nations framework conventions on environmental policy now include the creation of secondary forests through restoration as a critical tool to address biodiversity loss, desertification, and climate change (UNCBD, 2012; UNCCD, 2015; UNFCCC, 2015), and these aspirations are buoyed by observations that the area of secondary tropical forests is increasing in several countries (Aide et al., 2013; Asner, Rudel, Aide, Defries, & Emerson, 2009; Rudel, 2005).

Implicit in all of these goals is the assumption that secondary forests will persist over an appreciable time period without being recleared for agriculture or other human land uses. While the pace of natural forest recovery is highly variable (Norden et al., 2015), several global meta-analyses find that species abundance, species diversity, and ecosystem functioning require several to many decades to recover to predisturbance conditions (Dent & Wright, 2009; Meli et al., 2017). For example, regenerating tropical forests typically take ~50 years to recover tree species richness to predisturbance levels, ~80 years to recover above-ground biomass, >80 years to recover below-ground biomass, and >100 years to recover predisturbance vascular epiphyte diversity (Martin, Newton,

& Bullock, 2013). As such, the degree to which secondary forests will conserve biodiversity and perform ecosystem functions like storing carbon will depend on how long secondary forests persist.
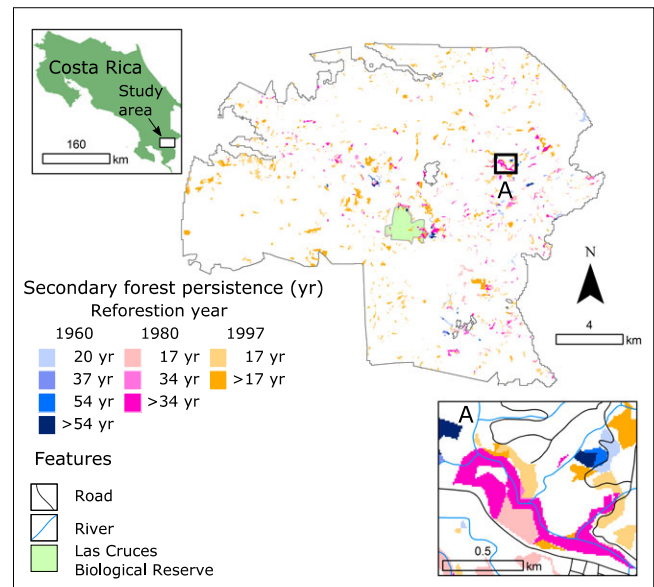
We conceptualize secondary forest persistence to be the maximum age that a secondary forest attains before being converted to a nonforest land cover (Reid et al., 2017). Several studies provide insights about how long and under what conditions secondary forests may persist, but prior research has been limited by short time windows (≤28 years), small sample sizes (≤54 patches), and/or coarsely resolved spatial data (≥30-m pixels; Fagan et al., 2013; Reid et al., 2017; Schwartz, Uriarte, DeFries, Gutierrez-Velez, & Pinedo-Vasquez, 2017). Existing works suggest that the factors that could influence secondary forest persistence may include stakeholder preferences and capabilities, environmental attributes, and the rules of governance that influence human-environment interactions (Reid et al., 2017). For example, forests may persist longer when landowners have secure land tenure (Le, Smith, Herbohn, & Harrison, 2012), when forests are relatively inaccessible or agriculturally marginal (Cropper, Puri, & Griffiths, 2001; Helmer, Brandeis, Lugo, & Kennaway, 2008; Schwartz et al., 2017, but see Sloan, Goosem, & Laurance, 2015), or when government regulation prohibits deforestation (Fagan et al., 2013). However, it is unclear how these dynamics may change over multidecadal time scales and across large, finely resolved landscapes.

Here, we extend our knowledge of secondary forest persistence spatially, temporally, and conceptually using a 67-year time series of forest coverage across 320 km^2 in southern Costa Rica (1947-2014). This high resolution (10 m) data set allows us to analyze the fates of both large and small forest patches in relation to fine-scaled topographic features, such as locally steep slopes and riparian zones.

2 | METHODS

2.1 | Study area

We evaluated secondary forest persistence in Coto Brus County, Puntarenas, Costa Rica (Figure 1). The study area was defined by a 13-km radius around the Las Cruces Biological Station (LCBS; 8°47′7″N; 82°57′32″W), excluding land in Panama (8 km away) and low-lying areas below 700 m.a.s.l. The remaining area ranged from 701 to 1,583 m.a.s.l. This region receives 3.5-4.0 m of annual rainfall (LCBS), with a pronounced dry season from December to March. Mean annual temperature at LCBS is ~21°C. The native forest type is at the boundary between tropical premontane wet forest and rain forest zones (Holdridge, Grenke, Hatheway, Liang, & Tosi, 1971), and two-thirds of this forest was cleared for coffee cultivation between 1947 and 1980 (Zahawi, Duran, & Kormann, 2015).

FIGURE 1 Secondary forest persistence across a 320 km^2 landscape in southern Costa Rica (1947-2014)

Note: Polygon colors denote the year of observed reforestation, and darker shades denote longer secondary forest persistence. Inset A illustrates the positive relationship between distance to a river and the proportional hazard of secondary forest reclearance.

2.2 | Data processing

We used forest cover layers from five time slices (1947, 1960, 1980, 1997, and 2014) to designate patches with unique reforestation/deforestation histories. Forest cover layers were based on orthorectified, high-resolution aerial and satellite images that were hand-classified as forest or nonforest in a prior study (Zahawi et al., 2015). To ensure data quality, each candidate reforestation patch was manually reinspected. Coffee plantations and early successional vegetation were classified as nonforest. Reforested patches were identified as areas that were deforested in one set of aerial images but were forested in a subsequent set of aerial images. After excluding patches that were never deforested, were never reforested, or were reforested only in the final time slice (precluding temporal analysis), our sample was composed of 1,750 secondary forest patches ranging from 0.1 to 29.2 ha and representing a total area of 17.3 km^2.

For each reforested patch, we measured forest persistence as the maximum age attained before the patch was recleared, or the time from reforestation to the final time slice (2014) in the case of patches that were not recleared. Thus, a patch that was nonforest in 1947, was reforested by 1960, and retained forest until it was recleared in 2014 had an observed persistence of 54 years, with a potential age range of 37-67 years given that reforestation could have occurred at any time between 1947 and 1960, and deforestation could have occurred at any time between 1997 and 2014

TABLE 1 Observed persistence and potential ages (years) of secondary forests by reforestation cohort and year of reclearance

	Year recleared			
Year reforested	**1960-1980**	**1980-1997**	**1997-2014**	**>2014**
1947-1960	20 (0-33)	37 (20-50)	54 (37-67)	>54 (>54-67)
1960-1980		17 (0-37)	34 (17-54)	>34 (>34-54)
1980-1997			17 (0-34)	>17 (>17-34)

(Table 1, Figure S1). For patches that were reforested and deforested multiple times (<1% of patches), only the first instance was analyzed due to sample size limitations. This indicates that contemporary, regional forests are not characterized by repeated clearing cycles typical of some tropical forest regions.

We calculated the following potential predictors of secondary forest persistence for each reforested patch: (1) minimum distance to the nearest road, (2) mean distance to the nearest river, (3) mean elevation, (4) maximum terrain ruggedness (Riley, DeGloria, & Elliot, 1999), (5) patch area, and (6) mean distance to the nearest protected area. Distance to the nearest road represents potential access to a forest patch and is an important predictor of tropical deforestation (Cropper et al., 2001; Laurance et al., 2002). Distance to the nearest river may also represent logging access in some landscapes (Wyman & Stein, 2010), though in this premontane landscape river corridors are often too steep for agriculture and frequently remain forested (Mendenhall, Sekercioglu, Brenes, Ehrlich, & Daily, 2011). Elevation and terrain ruggedness were both calculated from a digital elevation model with 5-m resolution (LCBS), and these two variables represent independent components of suitability for agriculture, the most important competing land use in this region (Zahawi et al., 2015). Slope was strongly correlated with terrain ruggedness (Pearson's coefficient = 0.82), and we used the latter because it had a stronger relationship with forest persistence. We expected that forest persistence would be greater in protected areas, however, we had an insufficient sample size (five patches) to address this prediction. Instead, we used mean distance to the nearest protected area as a predictor.

We also addressed the potential impact of the Costa Rican Payment for Ecosystem Services (PES) program on forest persistence by calculating the minimum distance from each patch to the nearest PES project. This was done using point (1996-2001) and polygon (2003-2014) data on PES project locations obtained directly from the Costa Rican government. Our expectation was that being in or near a PES project would increase a forest's persistence. We considered patches with a distance <10 m from the nearest PES project to be inside of the PES program ($N = 128$). We included both forest protection and forest restoration PES projects, recognizing that either could contribute to encouraging and maintaining secondary forest regeneration.

2.3 | Data analysis

We evaluated the associations between secondary forest patch persistence and geographic predictors using Cox proportional hazards models (Therneau & Grambsch, 2000), with number of years until deforestation as the dependent variable. Patches that were not deforested by the final time slice, 2015, were censored. Starting with a full model including all six predictors, we used backward, stepwise elimination to remove predictors with an insignificant contribution ($P > 0.05$). We used AIC model selection to determine the most parsimonious combination of the remaining predictors. An assumption of Cox models is that predictors are proportional, that is, their effect on survival does not vary over time. We tested this assumption using Shoenfeld residuals with the *cox.zph* function. To test for spatial autocorrelation in the residuals of the best-fit model, we calculated Moran's *I*. Proportional hazards models were implemented in the *survival* package and Moran's *I* in the *ape* package in R version 3.4.3 (R Development Core Team, Vienna, Austria). Geographic analyses were performed in ArcGIS version 10.5 (ESRI, Redlands, CA, USA).

To test whether inclusion in or distance from PES projects influenced secondary forest persistence, we used logistic regression. Only patches with observed reforestation in 1997 were included, reflecting the initiation of the national PES program in the same year. We used logistic regression rather than a Cox model because with only one subsequent observation in 2014, the only possible outcomes were deforestation or none, so right censoring was unnecessary.

3 | RESULTS

Of 1,750 secondary forest patches that regenerated between 1947 and 1997, 50% were recleared within 20 years, 78% within 37 years, and 85% within 54 years of when they were first observed (Figure 2, Table S1). Given the decadal spacing of observations, the most conservative interpretation is that 50% of forest patches were cleared within 0-37 years, 78% within 17-54 years, and 85% within 37-67 years of when they were first reforested (Table 1). The rate of secondary forest loss by area ranged from 2.2% to 3.5% per year (Table S2).

Secondary forest patches persisted for longer periods of time when they were larger and close to rivers (Tables S3
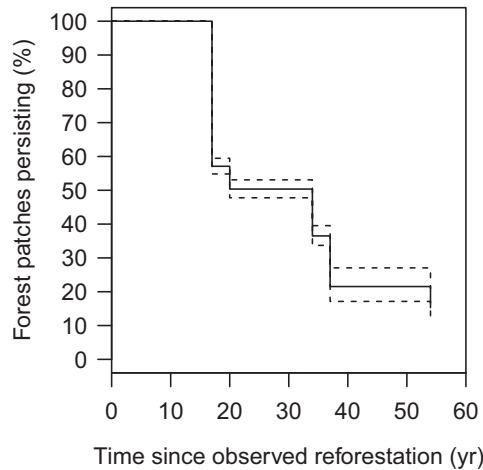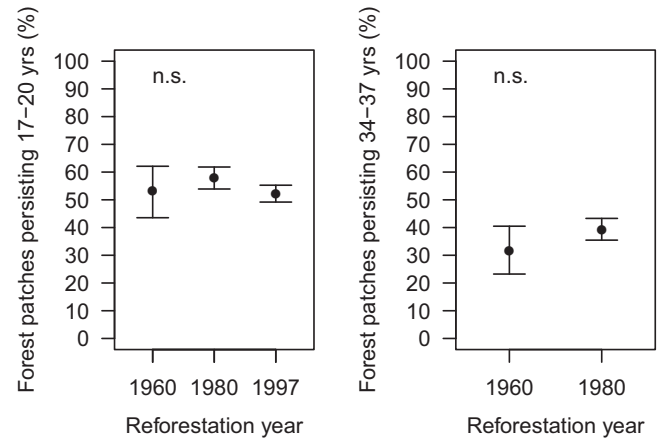
FIGURE 2 Secondary forest persistence in southern Costa Rica (1947-2014)
Note: Error bars denote 95% confidence intervals.
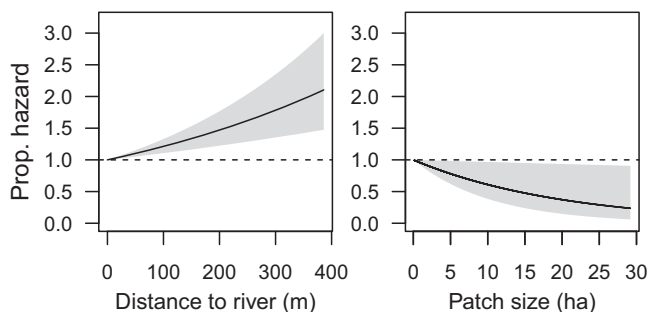
FIGURE 3 Estimated proportional hazard of secondary forest reclearance as a function of distance to the nearest river and patch size
Note: Shaded area denotes 95% confidence intervals. Hazard values >1 indicate an increased risk of deforestation at a proportion that is consistent over time. For example, a secondary forest >200 m from the nearest river has approximately 150% the risk of reclearance compared to a secondary forest immediately adjacent to a river.

FIGURE 4 Secondary forest persistence by reforestation cohort over 17-20 years (*left*) and 34-37 years (*right*)
Note: Error bars denote 95% confidence intervals.

and S4, Figure 3). For example, secondary forest patches 200 m from the nearest river were approximately 1.5× more likely to be recleared than forests immediately adjacent to rivers, and patches that were 14 ha were approximately 0.5× as likely to be recleared as patches that were only 0.1 ha. Two other hypothesized predictors, elevation and distance to protected area, had weak relationships with secondary forest persistence (Table S3, Figure S2), but others, including year of observed reforestation, were not significantly correlated with forest persistence (Figure 4). Also, neither inclusion nor proximity to PES projects affected secondary forest persistence ($P \geq 0.08$). We found no evidence of spatial autocorrelation in the residuals of the most parsimonious Cox model (Moran's I; $P = 0.13$). Schoenfeld residuals indicated that the proportionality assumption was met for all predictors (cox.zph; $P \geq 0.17$).

4 | DISCUSSION

Our results indicate that secondary forests in southern Costa Rica generally persisted for far less time than is needed to recover old growth levels of biomass or biodiversity. With the vast majority of new forests persisting <54 years, regenerating forests in this region could appropriately be termed *ephemeral*. We also determined that secondary forest persistence was not stochastic. Rather, which forests persisted for longer periods of time was predictable based on their size and their location relative to rivers. We expect that these historical trends are representative of contemporary forests beyond southern Costa Rica. To the extent that our observations can be generalized, there are several implications for biodiversity conservation, climate change mitigation, and large-scale forest restoration initiatives.

Our analysis indicates that approximately 2.2%-3.5% of secondary forest was cleared each year in southern Costa Rica from 1960 to 2014. This rate is congruent with the attrition of tropical forest restoration plots in the same area (2.8%-3.3% per year in 2004-2016; Reid et al., 2017), and it is lower than the ranges of secondary forest clearing rates observed in northeastern Costa Rica (3%-10% per year in 1985-2011; Fagan et al., 2013) and central Peru (3%-23% per year in 1985-2013; Schwartz et al., 2017). More cases are needed, but from these few studies it appears that secondary forests elsewhere in Latin America may persist for even shorter intervals than we observed in southern Costa Rica.

If an average secondary tropical forest persists for only 20 years, meta-analytical models predict that it typically would recover ~40% of predisturbance carbon stocks and <80% of predisturbance bird, reptile, amphibian, tree, and epiphyte species before being cleared again (Dent & Wright, 2009; Martin et al., 2013). Specific levels of recovery can be much lower and will vary widely depending in part on

landscape context, prior land use history, and other factors (Meli et al., 2017; Norden et al., 2015). If forest persistence in southern Costa Rica is typical of secondary forests in Latin America, regional carbon sequestration estimates for 2008-2048 could be constrained to ∼0-1 Pg out of a possible 8.5-10.5 Pg, with a high potential for net carbon loss due to secondary forest clearing (Chazdon et al., 2016).

Whereas secondary forests in southern Costa Rica were generally short-lived, under some conditions the hazard of reclearance was much lower. Longer-lived secondary forests were concentrated near rivers, possibly because of the 10-50 m riparian buffer stipulated by the first Costa Rican forest law (1969) and landowners seeking to protect water sources, but also potentially due to once-arable lands eroding, subsiding, and becoming agriculturally marginal following initial deforestation (Cole-Christensen, 1997). Larger secondary forests also persisted longer than smaller ones, suggesting that large, riparian forests should be prioritized in future conservation and landscape restoration efforts.

Several other geographic factors were expected to correspond to secondary forest persistence and did not. For example, secondary forests that were associated with Costa Rica's national PES program were not more likely to persist than forests not affiliated with the program, consistent with the findings of Sierra and Russman (2006). Also, prior studies have found that the risk of deforestation is lower and the emergence of secondary forests is greater in relatively inaccessible or agriculturally marginal areas, such as those far from roads and at high elevation (Aide et al., 2013; Asner et al., 2009; Cropper et al., 2001; Laurance et al., 2002; Rudel, 2005; but see Sloan et al., 2015). We did not find this, but we expect that these factors may be predictive of secondary forest persistence over a larger spatial scale than was available for our study. Similarly, social studies may be needed to learn about the specific motivations for landowners conserving or converting secondary forests.

The stability of secondary forest reclearance rates over time suggests that we should not expect contemporary forests to persist longer than the historical ones described here. Secondary forests that appeared in the period from 1980 to 1997 had equivalent chances of persisting for over two decades as compared to secondary forests that appeared in 1947-1960 or 1960-1980. This consistency occurred despite major changes in government policy and dominant land use practices during the interceding years, including the removal of tax penalties on uncultivated land in 1977, the conversion of many coffee plantations to cattle pasture in the wake of the 1989 coffee crisis, and the criminalization of deforestation in 1997 (Evans, 2010; Rickert, 2005).

If secondary forests in southern Costa Rica are generally ephemeral, with only a small proportion filtering through to maturity, this raises an important dilemma for large-scale forest restoration. Should governments count natural forest regeneration detected by remote sensing toward their national restoration commitments? Costa Rica has committed to restore 1 million ha of degraded land by 2020 (IUCN, 2017), and natural regeneration has been proposed as an inexpensive and often effective strategy to meet this target (Chazdon, 2017; Holl 2017). Between 2001 and 2010, approximately 162,800 ha of new woody vegetation were detected in Costa Rica via remote sensing (Aide et al., 2013), potentially representing >16% of Costa Rica's commitment. However, if new forests generally behave as those in southern Costa Rica, only 50% (81,400 ha) of this forest cover will persist until 2040, and only 15% (24,420 ha) will persist until 2074. At the scale of the Bonn Challenge and New York Declaration on Forests, which aim to restore 350 million ha by 2030 (IUCN, 2017), an 85% attrition over 54 years would affect 297.5 million ha, an area more than one-third the size of Brazil.

A related question is whether governments could commit to more ambitious restoration targets, such as restoring a million hectares of 100-year-old forest by 2120 instead of a million hectares of young and likely ephemeral forest by 2020. Secondary forest persistence may be determined by stakeholder preferences, environmental constraints, and governance of human-environment interactions. As such, planning for forest persistence may entail prioritizing restoration of lands with minimal opportunity costs (Latawiec, Strassburg, Brancalion, Rodrigues, & Gardner, 2015), engaging and organizing local stakeholders (Lazos-Chavero et al., 2016), creating long-term economic incentives (Galatowitsch, 2009), and promoting stable land tenure systems (Le et al., 2012). Without a plan to ensure persistence, we cannot assume that secondary forests will persist long enough to accrue the environmental benefits that we require.

ACKNOWLEDGMENTS

REFERENCES

Aide, T. M., Clark, M. L., Grau, H. R., López-Carr, D., Levy, M. A., Redo, D., … Muñiz, M. (2013). Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica*, *45*, 262–271. Retrieved from https://doi.org/10.1111/j.1744-7429.2012.00908.x

Asner, G. P., Rudel, T. K., Aide, T. M., Defries, R., & Emerson, R. (2009). A contemporary assessment of change in humid tropical forests. *Conservation Biology*, *23*, 1386–1395. Retrieved from https://doi.org/10.1111/j.1523-1739.2009.01333.x

Chazdon, R. L. (2014). *Second growth: The promise of tropical forest regeneration in an age of deforestation*. Chicago, IL: University of Chicago Press.

Chazdon, R. L. (2017). Landscape restoration, natural regeneration, and the forests of the future. *Annals of the Missouri Botanical Garden*, *102*, 251–257. Retrieved from https://doi.org/10.3417/2016035

Chazdon, R. L., Broadbent, E. N., Rozendaal, D. M. A., Bongers, F., Zambrano, A. M. A., Aide, T. M., … Poorter, L. (2016). Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Science Advances*, *2*, 1–10. Retrieved from https://doi.org/10.1126/sciadv.1501639

Cole-Christensen, D. (1997). *A place in the rainforest: Settling the Costa Rican frontier*. Austin, TX: University of Texas Press.

Costa Rica. (1969). (La Asamblea Legislativa de la República de Costa Rica). Ley Forestal. *No, 4465*, 68.

Cropper, M., Puri, J., & Griffiths, C. (2001). Predicting the location of deforestation: The role of roads and protected areas in north Thailand. *Land Economics*, *77*, 172–186. Retrieved from https://doi.org/10.2307/3147088

Dent, D. H., & Wright, S. J. (2009). The future of tropical species in secondary forests: A quantitative review. *Biological Conservation*, *142*, 2833–2843. Retrieved from https://doi.org/10.1016/j.biocon.2009.05.035

Evans, S. (2010). *The green republic: A conservation history of Costa Rica*. Austin, TX: University of Texas Press.

Fagan, M. E., DeFries, R. S., Sesnie, S. E., Arroyo, J. P., Walker, W., Soto, C., … Sanchun, A. (2013). Land cover dynamics following a deforestation ban in northern Costa Rica. *Environmental Research Letters*, *8*, 1–9. Retrieved from https://doi.org/10.1088/1748-9326/8/3/034017

Galatowitsch, S. M. (2009). Carbon offsets as ecological restorations. *Restoration Ecology*, *17*, 563–570. Retrieved from https://doi.org/10.1111/j.1526-100X.2009.00587.x

Helmer, E. H., Brandeis, T. J., Lugo, A. E., & Kennaway, T. (2008). Factors influencing spatial pattern in tropical forest clearance and stand age: Implications for carbon storage and species diversity. *Journal of Geophysical Research: Biogeosciences*, *113*, 1–14. Retrieved from https://doi.org/10.1029/2007JG000568

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. (2017). Restoring tropical forests from the bottom up. *Science*, *355*, 455–456. Retrieved from https://doi.org/10.1126/science.aam5432

Houghton, R. A., Byers, B., & Nassikas, A. A. (2015). A role for tropical forests in stabilizing atmospheric CO_2. *Nature Climate Change*, *5*, 1022–1023. Retrieved from https://doi.org/10.1038/nclimate2869

IUCN (International Union for Conservation of Nature). (2017). The Bonn Challenge: Catalysing leadership in Latin America. *IUCN Forest Brief*, *14*, 1–8.

Latawiec, A. E., Strassburg, B. B. N., Brancalion, P. H. S., Rodrigues, R. R., & Gardner, T. (2015). Creating space for large-scale restoration in tropical agricultural landscapes. *Frontiers in Ecology and the Environment.*, *13*, 211–218. Retrieved from https://doi.org/10.1890/140052

Laurance, W. F., Albernaz, A. K. M., Schroth, G., Fearnside, P. M., Bergen, S., Venticinque, E. M., & Da Costa, C. (2002). Predictors of deforestation in the Brazilian Amazon. *Journal of Biogeography*, *29*, 737–748. Retrieved from https://doi.org/10.1046/j.1365-2699.2002.00721.x

Lazos-Chavero, E., Zinda, J., Bennett-Curry, A., Balvanera, P., Bloomfield, G., Lindell, C., & Negra, C. (2016). Stakeholders and tropical reforestation: Challenges, trade-offs, and strategies in dynamic environments. *Biotropica*, *48*, 900–914. Retrieved from https://doi.org/10.1111/btp.12391

Le, H. D., Smith, C., Herbohn, J., & Harrison, S. (2012). More than just trees: Assessing reforestation success in tropical developing countries. *Journal of Rural Studies*, *28*, 5–19. Retrieved from https://doi.org/10.1016/j.jrurstud.2011.07.006

Martin, P. A., Newton, A. C., & Bullock, J. M. (2013). Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 1–8. Retrieved from https://doi.org/10.1098/rspb.2013.2236

Meli, P., Holl, K. D., Rey Benayas, J. M., Jones, H. P., Jones, P. C., Montoya, D., & Moreno Mateos, D. (2017). A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. *PLoS One*, *12*, 1–17. Retrieved from https://doi.org/10.1371/journal.pone.0171368

Mendenhall, C. D., Sekercioglu, C. H., Brenes, F. O., Ehrlich, P. R., & Daily, G. C. (2011). Predictive model for sustaining biodiversity in tropical countryside. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 16313–16316. Retrieved from https://doi.org/10.1073/pnas.1111687108

Norden, N., Angarita, H. A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., van 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. Retrieved from https://doi.org/10.1073/pnas.1500403112

Reid, J. L., Wilson, S. J., Bloomfield, G. S., Cattau, M. E., Fagan, M. E., Holl, K. D., & Zahawi, R. A. (2017). How long do restored ecosystems persist? *Annals of the Missouri Botanical Garden*, *102*, 258–265. Retrieved from https://doi.org/10.3417/2017002

Rickert, E. (2005). *Environmental effects of the coffee crisis: A case study of land use and avian communities in Agua Buena, Costa Rica* (master's thesis). Evergreen State College, Olympia, WA.

Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, *5*, 23–27.

Rudel, T. (2005). *Tropical forests: Paths of destruction and regeneration*. New York: Columbia University Press.

Schwartz, N. B., Uriarte, M., DeFries, R., Gutierrez-Velez, V. H., & Pinedo-Vasquez, M. A. (2017). Land-use dynamics influence estimates of carbon sequestration potential in tropical second-growth forest. *Environmental Research Letters*, *12*, 1–10. Retrieved from https://doi.org/10.1088/1748-9326/aa708b

Sierra, R., & Russman, E. (2006). On the efficiency of environmental service payments: A forest conservation assessment in the Osa Peninsula, Costa Rica. *Ecological Economics*, *59*, 131–141. Retrieved from https://doi.org/10.1016/j.ecolecon.2005.10.010

Sloan, S., Goosem, M., & Laurance, S. (2015). Tropical forest regeneration following land abandonment is driven by primary rainforest distribution in an old pastoral region. *Landscape Ecology*, *31*, 601–618. Retrieved from https://doi.org/10.1007/s10980-015-0267-4

Strassburg, B. B. N., Barros, F. S. M., Crouzeilles, R., Iribarrem, A., dos Santos, J. S., Silva, D., … Latawiec, A. E. (2016). The role of natural regeneration to ecosystem services provision and habitat availability: A case study in the Brazilian Atlantic Forest. *Biotropica*, *48*, 890–899. Retrieved from https://doi.org/10.1111/btp.12393

Therneau, T., & Grambsch, P. M. (2000). *Modeling survival data: Extending the Cox model*. New York: Springer.

UNCBD (United Nations Convention on Biological Diversity). (2012). COP 11 decision XI/16: Ecosystem restoration. Retrieved from https://www.cbd.int/decision/cop/default.shtml?id=13177.

UNCCD (United Nations Convention to Combat Desertification). (2015). Land matters for climate: Reducing the gap and approaching the target. Retrieved from https://www.unccd.int/Lists/SiteDocumentLibrary/Publications/2015Nov_Land_matters_For_Climate_ENG.pdf.

UNFCCC (United Nations Framework Convention on Climate Change). (2015). Paris Agreement. Retrieved from https://unfccc.int/files/essential_background/convention/application/pdf/english_paris_agreement.pdf.

Wright, S. J., & Muller-Landau, H. C. (2006). The future of tropical forest species. *Biotropica*, *38*, 287–301. Retrieved from https://doi.org/10.1111/j.1744-7429.2006.00154.x

Wyman, M. S., & Stein, T. V. (2010). Modeling social and land-use/land-cover change data to assess drivers of smallholder deforestation in Belize. *Applied Geography*, *30*, 329–342. Retrieved from https://doi.org/dOi:10.1016/j.apgeog.2009.10.001

Zahawi, R. A., Duran, G., & Kormann, U. (2015). Sixty-seven years of land-use change in southern Costa Rica. *PLoS One*, *10*, 1–17. Retrieved from https://doi.org/10.1371/journal.pone.0143554

SUPPORTING INFORMATION

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

Supplementary information for Reid, J.L., Fagan, M.E., Lucas, J., Slaughter, J., & Zahawi, R.A. The ephemerality of secondary forests in southern Costa Rica

Contents

Table S1. Secondary forest persistence and cumulative hazard in southern Costa Rica (1947-2014).

Time since first observed (yr)	No. patches at risk	No. patches re-cleared	No. patches censored	Patches persisting (%)	Lower 95% CI	Upper 95% CI	Cumulative hazard	SE
17	1750	751	542	57.10	54.83	59.46	0.56	0.01
20	457	54	0	50.36	47.78	53.08	0.69	0.01
34	403	111	234	36.51	33.70	39.54	1.01	0.01
37	58	24	0	21.53	17.14	27.05	1.54	0.03
54	34	10	24	15.29	11.19	20.89	1.88	0.02

Table S2. Estimated area and rate of secondary forest clearance in southern Costa Rica (1960-2014).

Period	Secondary forest at start of period (ha)	Area deforested (ha)	Area deforested (%)	Rate of loss (% y^{-1})
1960-1980	125.99	54.41	43.19	2.16
1980-1997	574.89	338.78	58.93	3.47
1997-2014	1338.57	796.17	59.48	3.50

Table S3. Model comparison for the effects of geographic predictors on the persistence of secondary forest patches in southern Costa Rica (1947-2014). Models with equal support (ΔAIC ≤ 4) are italicized, and the best, most parsimonious model is highlighted in bold.

Model	K	AIC	ΔAIC
River (m) + Elevation (m) + Patch size (m^2) + Distance to protected area (m)	*4*	*13021.60*	*0.00*
River (m) + Patch size (m^2) + Distance to protected area (m)	*3*	*13023.42*	*1.82*
Distance to river (m) + Patch size (m^2)	**2**	**13023.88**	**2.28**
Distance to river (m) + Patch size (m^2) + Elevation (m)	*3*	*13023.93*	*2.33*
Distance to river (m) + Elevation (m) + Distance to protected area (m)	*3*	*13025.03*	*3.43*
Distance to river (m) + Distance to protected area (m)	2	13026.48	4.88
Distance to river (m)	1	13026.98	5.38
Distance to river (m) + Elevation (m)	2	13027.27	5.67
Elevation (m) + Patch size (m^2) + Distance to protected area (m)	3	13036.10	14.50
Elevation (m) + Patch size (m^2)	2	13037.53	15.93
Patch size (m^2)	1	13037.62	16.02
Patch size (m^2) + Distance to protected area (m)	2	13037.78	16.18
Elevation (m) + Distance to protected area (m)	2	13037.89	16.29
Distance to protected area (m)	1	13039.26	17.66
Elevation (m)	1	13039.33	17.73

Table S4. Modeled hazard ratios for two geographic predictors of secondary forest persistence in southern Costa Rica (1947-2014).

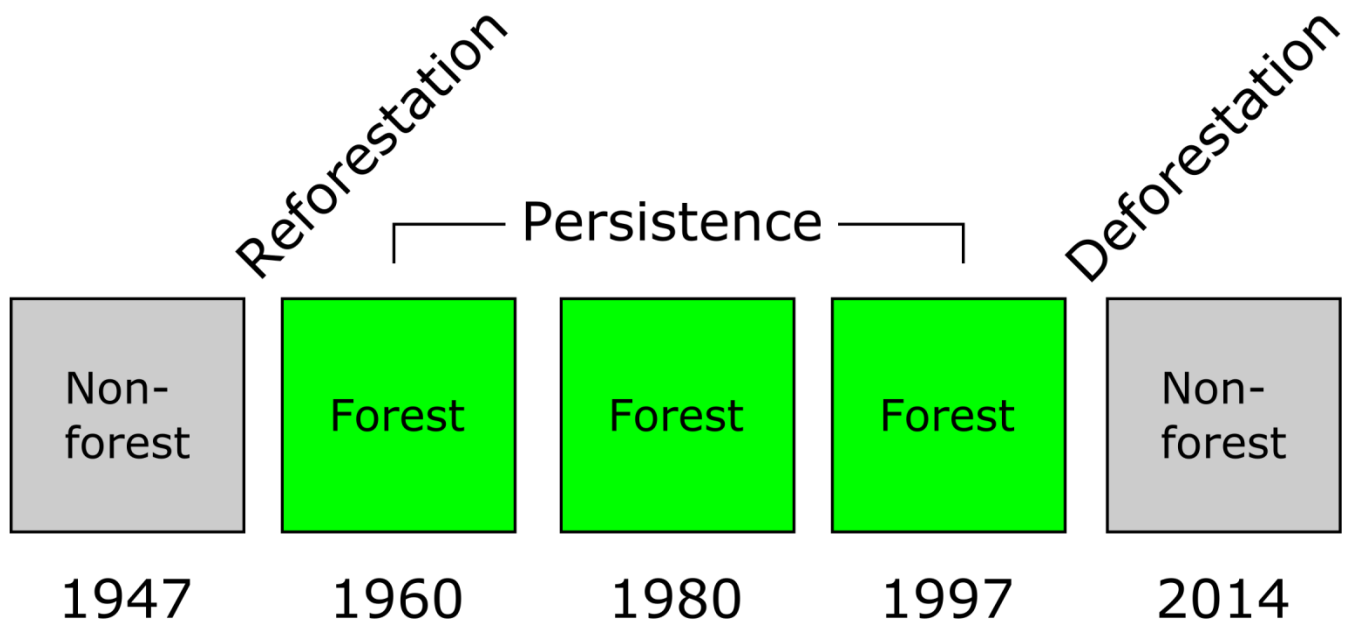| Predictor	Hazard ratio	Standard error	Z	P
Distance to river (m)	$\exp(1.93 \times 10^{-3})$	$\exp(4.69 \times 10^{-4})$	4.19	<0.001
Patch size (m^2)	$\exp(-4.95 \times 10^{-6})$	$\exp(2.35 \times 10^{-6})$	-2.10	0.035

Figure S1. Conceptual method for determining the reforestation, persistence, and deforestation of secondary forest patches. Boxes represent a hypothetical area that has been classified as non-forest in 1947 and 2014 imagery based on the absence of trees and as forest in 1960, 1980, and 1997 based on the presence of trees. Based on this knowledge, we surmise that the area was reforested between 1947 and 1960, that the forest persisted until at least 1997, and that the area was deforested between 1997 and 2014. Given the temporal spacing between the observations, we calculate the observed persistence of this forest to be 54 years (1960 – 2014), but the potential persistence of this patch may have actually ranged between 37 years (if it was reforested in 1960 before the aerial image was taken and deforested in 1997 after the aerial image was taken) to 67 years (if it was reforested in 1947 and deforested in 2014). A complete key to observed and potential persistence values is in Table 1.
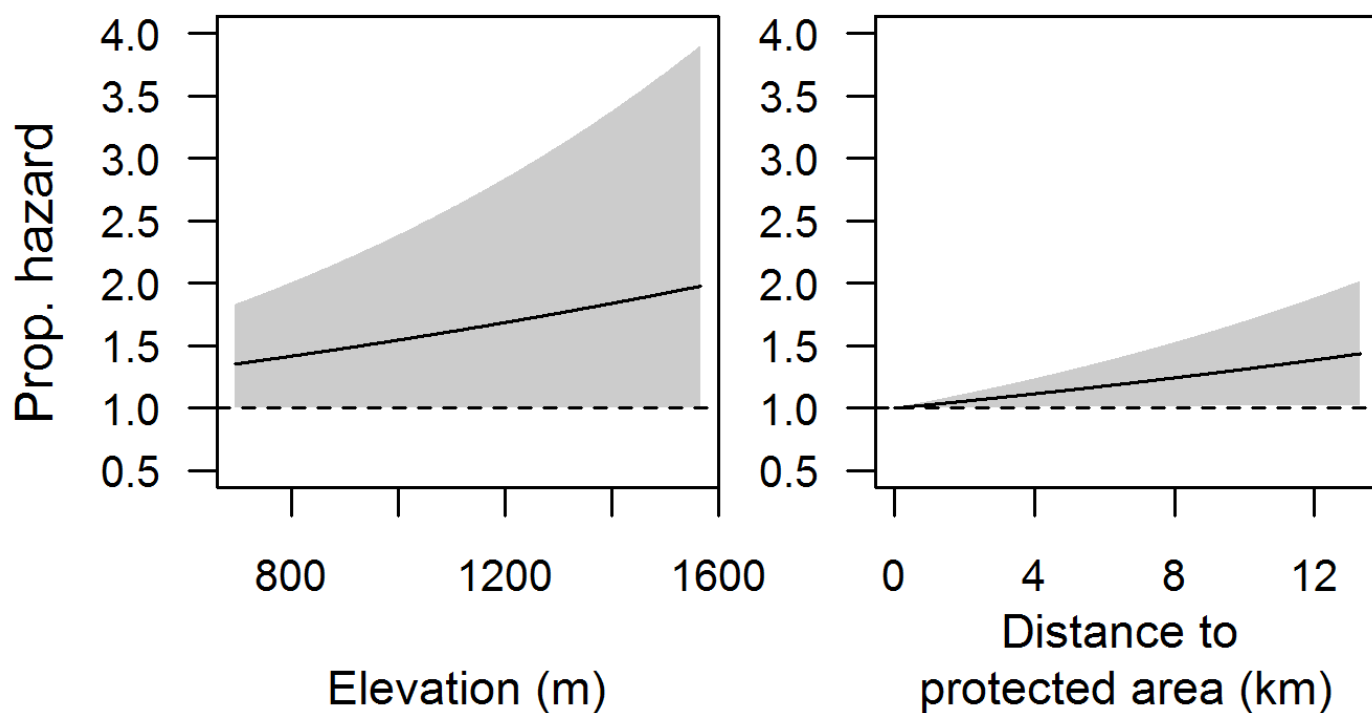
Figure S2. Estimated proportional hazard of secondary forest re-clearance as a function of elevation and distance to the nearest protected area. Shaded area denotes 95% confidence intervals. Hazard values >1 indicate an increased risk of deforestation at a proportion that is consistent over time.