Landscape-scale forest cover drives the predictability of forest regeneration across the Neotropics

Proceedings of the Royal Society B: Biological Sciences

Arroyo-Rodríguez, Víctor; Rito, Kátia F.; Farfán, Michelle; Navía, Iván C.; Mora, Francisco et al

https://doi.org/10.1098/rspb.2022.2203

This publication is made publicly available in the institutional repository of Wageningen University and Research, under the terms of article 25fa of the Dutch Copyright Act, also known as the Amendment Taverne.

Article 25fa states that the author of a short scientific work funded either wholly or partially by Dutch public funds is entitled to make that work publicly available for no consideration following a reasonable period of time after the work was first published, provided that clear reference is made to the source of the first publication of the work.

This publication is distributed using the principles as determined in the Association of Universities in the Netherlands (VSNU) 'Article 25fa implementation' project. According to these principles research outputs of researchers employed by Dutch Universities that comply with the legal requirements of Article 25fa of the Dutch Copyright Act are distributed online and free of cost or other barriers in institutional repositories. Research outputs are distributed six months after their first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and / or copyright owner(s) of this work. Any use of the publication or parts of it other than authorised under article 25fa of the Dutch Copyright act is prohibited. Wageningen University & Research and the author(s) of this publication shall not be held responsible or liable for any damages resulting from your (re)use of this publication.

For questions regarding the public availability of this publication please contact openaccess.library@wur.nl

PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Landscape-scale forest cover drives the predictability of forest regeneration across the Neotropics

Víctor Arroyo-Rodríguez[1,2], Kátia F. Rito[1], Michelle Farfán[3], Iván C. Navia[4], Francisco Mora[1], Felipe Arreola-Villa[1], Patricia Balvanera[1], Frans Bongers[5], Carolina Castellanos-Castro[6], Eduardo L. M. Catharino[7], Robin L. Chazdon[8,9], Juan M. Dupuy-Rada[10], Bruce G. Ferguson[11], Paul F. Foster[12,13], Noel González-Valdivia[14], Daniel M. Griffith[15], José L. Hernández-Stefanoni[10], Catarina C. Jakovac[16], André B. Junqueira[17], Bernardus H. J. Jong[18], Susan G. Letcher[19], Filogonio May-Pat[10], Jorge A. Meave[20], Susana Ochoa-Gaona[18], Gabriela S. Meirelles[21], Miguel A. Muñiz-Castro[22], Rodrigo Muñoz[5,20], Jennifer S. Powers[23], Gustavo P. E. Rocha[24], Ricardo P. G. Rosário[25], Bráulio A. Santos[26], Marcelo F. Simon[27], Marcelo Tabarelli[28], Fernando Tun-Dzul[10], Eduardo van den Berg[21], Daniel L. M. Vieira[26], Guadalupe Williams-Linera[29] and Miguel Martínez-Ramos[1]

[1]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, 58190 Morelia, Michoacán, Mexico
[2]Escuela Nacional de Estudios Superiores, Universidad Nacional Autónoma de México, 97357 Mérida, Yucatán, Mexico
[3]Departamento de Ingeniería Geomática e Hidráulica, División de Ingenierías, Universidad de Guanajuato, 36000 Guanajuato, Guanajuato, Mexico
[4]Instituto Nacional de los Pueblos Indígenas, 58219 Morelia, Michoacán, Mexico
[5]Forest Ecology and Forest Management Group, Wageningen University, 6700 AA Wageningen, Netherlands
[6]Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, 15-09 Bogotá, Bogotá, Colombia
[7]Instituto de Botânica de São Paulo, 04301-902 São Paulo, São Paulo, Brazil
[8]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA
[9]Tropical Forests and People Research Centre, University of the Sunshine Coast, 90 Sippy Downs Road, Sippy Downs, QLD 4556, Australia
[10]Centro de Investigación Científica de Yucatán, Unidad de Recursos Naturales, 97205 Mérida, Yucatán, Mexico
[11]El Colegio de la Frontera Sur, 29290 San Cristóbal de las Casas, Chiapas, Mexico
[12]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109, USA
[13]Bijagual Ecological Reserve, Apdo. 35-3069, Puerto Viejo de Sarapiquí, Heredia 41001, Costa Rica
[14]Tecnológico Nacional de México, Instituto Tecnológico de Chiná, Departamento de Ingenierías, 24520 Chiná, Campeche, Mexico
[15]Departamento de Ciencias Biológicas y Agropecuarias, EcoSs Lab, Universidad Técnica Particular de Loja, CP 1101608, Loja, Ecuador
[16]Departamento de Fitotecnia, Universidade Federal de Santa Catarina, 88040-900 Florianópolis, Santa Catarina, Brazil
[17]Institut de Ciencia i Tecnologia Ambientals, Universitat Autonoma de Barcelona, 08193 Bellatera, Barcelona, Spain
[18]Departmento de Ciencias de la Sustentabilidad, El Colegio de la Frontera Sur, 24500 Lerma, Campeche, Mexico
[19]College of the Atlantic, 04609 Bar Habor, Maine, USA
[20]Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de Mexico, Coyoacán 04510 Ciudad de México, Mexico
[21]Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, 37200-900 Lavras, Minas Gerais, Brazil
[22]Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, 45200 Zapopan, Jalisco, Mexico
[23]Departments of Ecology, Evolution, and Behavior and Plant and Microbial Biology, University of Minnesota, 55108 Saint Paul, Minnesota, USA

Cite this article: Arroyo-Rodríguez V *et al.* 2023 Landscape-scale forest cover drives the predictability of forest regeneration across the Neotropics. *Proc. R. Soc. B* **290**: 20222203. https://doi.org/10.1098/rspb.2022.2203

Received: 2 November 2022
Accepted: 5 December 2022

Subject Category:
Biological applications

Subject Areas:
biological applications

Keywords:
deforestation, landscape heterogeneity, recovery rate, secondary forests, successional trajectories, uncertainty

Author for correspondence:
Kátia F. Rito
e-mail: rito_pereira@yahoo.com.br

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.6350225.

THE ROYAL SOCIETY
PUBLISHING

[24]Departamento de Botânica, Universidade de Brasília, 70919-970 Brasília, Distrito Federal, Brazil
[25]Faculdade de Direito, Universidade Presbiteriana Mackenzie, 01302-907 São Paulo, São Paulo, Brazil
[26]Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, 58051-900 João Pessoa, Paraíba, Brazil
[27]Embrapa Recursos Genéticos e Biotecnologia, 70770-917 Brasília, Distrito Federal, Brazil
[28]Departamento de Botanica, Universidade Federal de Pernambuco, 50670-901 Recife, Pernambuco, Brazil
[29]Instituto de Ecología, A.C., 91073 Xalapa, Veracruz, Mexico

VA-R, 0000-0002-0858-0324; KFR, 0000-0001-6471-8722; MF, 0000-0002-4948-1453; FM, 0000-0003-0390-0189; PB, 0000-0001-6408-6876; FB, 0000-0002-8431-6189; CC-C, 0000-0002-5552-2506; RLC, 0000-0002-7349-5687; JMD-R, 0000-0001-7491-6837; NG-V, 0000-0003-0989-1789; DMG, 0000-0001-6870-9727; JLH-S, 0000-0002-9559-7131; CCJ, 0000-0002-8130-852X; ABJ, 0000-0003-3681-1705; BHJJ, 0000-0002-3264-2759; SGL, 0000-0002-9475-7674; FM-P, 0000-0003-1395-6936; JAM, 0000-0002-6241-8803; SO-G, 0000-0003-2145-5728; MAM-C, 0000-0002-9127-057X; RM, 0000-0001-9434-0126; JSP, 0000-0003-3451-4803; BAS, 0000-0001-6046-4024; MFS, 0000-0002-5732-1716; MT, 0000-0001-7573-7216; EvdB, 0000-0002-0843-6437; GW-L, 0000-0001-6341-6570; MM-R, 0000-0002-7785-1917

Abandonment of agricultural lands promotes the global expansion of secondary forests, which are critical for preserving biodiversity and ecosystem functions and services. Such roles largely depend, however, on two essential successional attributes, trajectory and recovery rate, which are expected to depend on landscape-scale forest cover in nonlinear ways. Using a multi-scale approach and a large vegetation dataset (843 plots, 3511 tree species) from 22 secondary forest chronosequences distributed across the Neotropics, we show that successional trajectories of woody plant species richness, stem density and basal area are less predictable in landscapes (4 km radius) with intermediate (40–60%) forest cover than in landscapes with high (greater than 60%) forest cover. This supports theory suggesting that high spatial and environmental heterogeneity in intermediately deforested landscapes can increase the variation of key ecological factors for forest recovery (e.g. seed dispersal and seedling recruitment), increasing the uncertainty of successional trajectories. Regarding the recovery rate, only species richness is positively related to forest cover in relatively small (1 km radius) landscapes. These findings highlight the importance of using a spatially explicit landscape approach in restoration initiatives and suggest that these initiatives can be more effective in more forested landscapes, especially if implemented across spatial extents of 1–4 km radius.

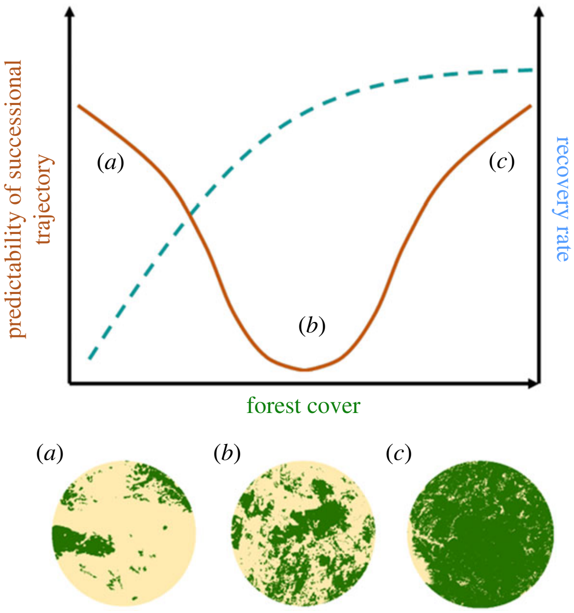

Figure 1. Hypothesized effect of percentage of remaining forest cover in the landscape on the predictability of successional trajectories (continuous line) and forest recovery rate (dashed line). We expected a relatively lower rate of forest recovery but higher predictability of successional trajectories at low forest cover (*a*), an intermediate to high rate of forest recovery and highly variable and consequently less predictable successional trajectories at intermediate forest cover (*b*) and a relatively high rate of recovery and more predictable successional trajectories at high forest cover (*c*). Circles represent 10 km radius landscapes, with the remaining forest shown in green. See [15] for further details. (Online version in colour.)

1. Introduction

Deforestation in the tropics is causing the loss of millions of hectares of old-growth forests every year [1]. Yet, regenerating (secondary) tropical forests are expanding across human-modified Neotropical landscapes [2,3]. As secondary forests can contribute to biodiversity persistence and provision of ecosystem services in human-modified landscapes [4–9], determining the factors affecting forest regeneration following land abandonment has gained increasing interest [10–14]. However, all potential contributions to ecosystem services and biodiversity conservation from secondary forests largely depend on two attributes of the successional process: the forest recovery rate and how plant community attributes change as forest regeneration proceeds (i.e. the forest successional trajectory) [9,15].

Forest regeneration in human-modified landscapes can proceed via alternative successional trajectories with varying recovery rates that are affected by drivers operating across multiple temporal and spatial scales [3,9,15]. Even regenerating forests exposed to similar local environmental conditions and disturbance histories can differ in recovery rate and trajectory [16–18]. For instance, forest regeneration can rapidly accumulate tree species and biomass; i.e. show a high recovery rate [8,9,19,20], but can also be erratic or even arrested, resulting in impoverished assemblages; i.e. show a low recovery rate [21,22]. While such variability in forest regeneration can be related to both local and landscape drivers, most forest succession research has focused on local variables [3,9,23], such as soil fertility, stand age and disturbance regime [24,25]. Therefore, considerable uncertainty remains about the influence of landscape drivers, such as the amount of forest cover surrounding regeneration stands, on successional trajectory and recovery rate [15]. Reducing this uncertainty is valuable to improve urgently needed conservation and restoration actions in human-modified landscapes [26].

To address the effect of landscape disturbance on forest regeneration, Arroyo-Rodríguez *et al.* [15] proposed a theoretical model for assessing the uncertainty (or predictability) of successional trajectories and forest recovery rate (figure 1). Yet, to our knowledge, this model has not yet been tested

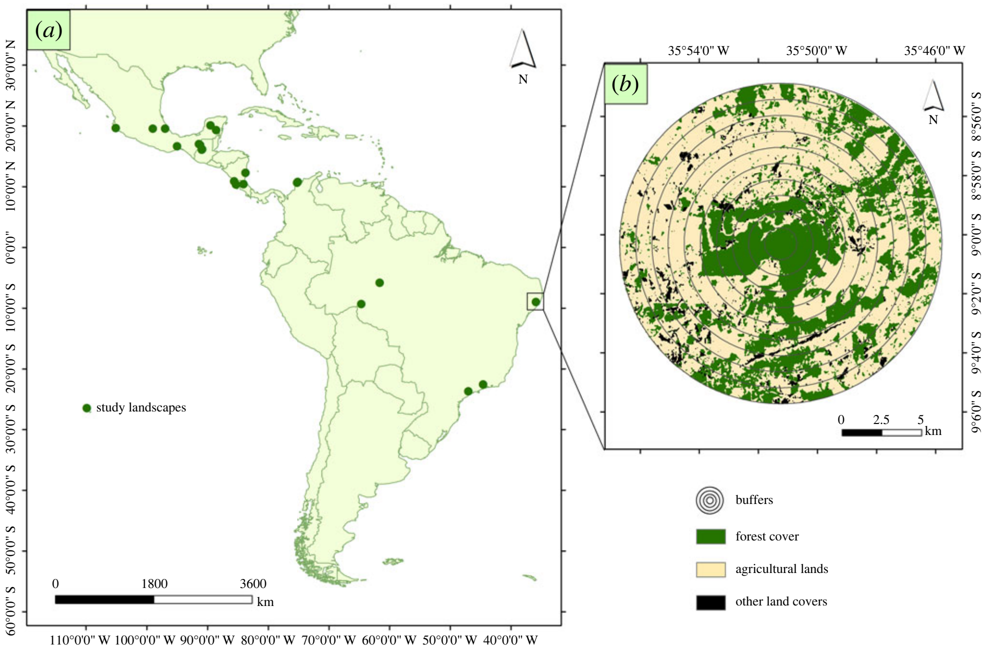

Figure 2. (*a*) Geographic distribution of the 22 study landscapes. Each point indicates the location of the centroid of each studied chronosequence. (*b*) The spatial extent (landscape size) that yields the strongest response of successional trajectory and recovery rate to changes in forest cover (i.e. scale of forest cover effect) was evaluated by testing such responses in 10 concentric landscapes of 1–10 km radius (at 1 km intervals). (Online version in colour.)

empirically. In particular, the model predicts that uncertainty in successional trajectories is higher in landscapes with intermediate disturbance levels (e.g. with 40% to 60% of remaining forest cover) than in landscapes undergoing very high or very low disturbance levels (figure 1). This prediction is based on the fact that landscapes with intermediate disturbance typically show high spatial heterogeneity both in terms of landscape configuration (e.g. high variation in the number of patches and total length of forest edges [27]) and landscape composition (e.g. high variation in the number of land cover types and management regimes [28,29]). Such heterogeneity exposes regenerating stands to high spatial and temporal variation in key ecological factors affecting succession, including environmental conditions, distance to seed sources, seed dispersal and seedling recruitment processes, as well as human activities like hunting and extraction of firewood and non-timber forest products [15]. Variation in these factors can result in highly variable rates of change in plant abundance, species richness and biomass, resulting in successional trajectories that are less predictable than those in landscapes with high or low disturbance levels (figure 1).

In landscapes undergoing high disturbance levels (i.e. with low remaining forest cover; figure 1*a*), the model predicts consistently low rates of forest recovery [15]. Yet predictability of successional trajectories is expected to be relatively high (figure 1*a*) because these landscapes are spatially more homogeneous, characterized by a low number of relatively small and biologically impoverished forest patches embedded in a matrix of agricultural lands. In these landscapes, factors such as topsoil loss, scarcity of seed dispersers and dominance of grasses, lianas and/or invasive ferns reduce seed sources and dispersal, and limit seedling recruitment and establishment. Under such circumstances, secondary forests are predicted to be dominated by a few disturbance-adapted species with wide regional distributions [30]. By contrast, the presence of large contiguous forest patches in less disturbed landscapes (i.e. with higher remaining forest cover; figure 1*c*) enhances the regional species pool [31], facilitates pollination and seed dispersal services, and reduces negative edge effects [9,32–34]. In these relatively well-preserved landscapes, vegetation attributes such as species richness and biomass are expected to recover relatively quickly and more predictably as vegetation attributes converge towards those of nearby old-growth forests [5].

Here we test this model using a large vegetation dataset (843 plots, 51 033 stems, 3511 tree species) from 22 chronosequences distributed across five Neotropical countries (figure 2*a*; electronic supplementary material, table S1). We used extent of forest cover estimated during the same year that secondary vegetation was inventoried as a proxy of landscape-scale disturbance [31,35]. We selected this landscape variable because it is significantly related to other landscape spatial factors, like forest fragmentation and inter-patch isolation distance [36]. Within each chronosequence, we estimated the predictability of successional trajectories based on plant species richness, individual density and basal area. For each chronosequence, we first fitted generalized additive models (GAMs) to assess the association between each community attribute and forest stand age. We used the goodness-of-fit of each model (R^2_{adj}) as an indicator of the predictability of successional trajectory. The rate of forest recovery within each chronosequence was estimated as change rate in the predicted values of each vegetation attribute in a 5-year interval (i.e. between 15 and 20 years of succession). We then analysed how predictability and forest recovery rate varied as a function of the percentage of forest cover in the surrounding landscape. As we do not know *a priori* the spatial extent at which forest cover best-predict vegetation responses (i.e. the so-called ‘scale of effect’ [37]), we used a multi-scale approach (figure 2*b*). Such an approach is not only needed to obtain more accurate and confident conclusions [37]; identifying the landscape size that makes forest cover effects on predictability and rate of forest recovery the strongest is critical to identify the scale at which restoration initiatives may be more effective [38].

2. Material and methods

(a) Data compilation

We compiled 22 independent databases from studies of woody plant species recovery across five Neotropical countries (figure 2*a*; electronic supplementary material, table S1). Each study included plots established in secondary forest stands of different ages forming a chronosequence. Plots within each chronosequence have similar disturbance histories (i.e. agricultural and farming disturbance) and climatic conditions. Plot size and the inclusion criteria of plant diameter varied among studies (electronic supplementary material, table S1), but such differences were controlled statistically (see below). Because the effect of precipitation on all response variables was very weak and non-significant (electronic supplementary material, appendix S1, tables S2 and S3), we did not include this covariate in our models. We used taxonomic species richness, species dominance, density of individuals and total basal area per plot to evaluate the successional trajectories and recovery rate of vegetation structure.

(b) Imagery selection and pre-processing

Following Crouzeilles & Curran [38], for each site we defined a landscape of 10 km radius from the centroid of the set of plots from each study (figure 2*b*). We choose this radius to standardize landscape size and enable an adequate analysis of landscape-level forest cover for the chronosequence stands in all databases. We obtained Landsat ETM+ and Landsat 8 satellite imagery with 30 m spatial resolution in the multispectral bands from the United States Geological Survey database (USGS, https://glovis.usgs.gov/app). Images were selected based on the location of the landscape of interest, the year of vegetation inventories of each study and cloudiness. For databases containing data collected in different years, we selected imagery corresponding to the median year of the study and containing less than 10% cloudiness. During pre-processing of images, we corrected for cloud cover by creating both a cloud and a cloud shadow mask using the Cloud Masking tool and *fmask* function in QGIS 2.18.14 software, as recommended for Landsat TM/ETM+/OLI/TIRS images [39]. For each image in a landscape, we conducted panchromatic and spectral image fusion (i.e. *pansharpend* compound) to improve spatial resolution in the Landsat image using the *Intensity Hue Saturation* method [40]. Due to a failure in the Scan Line Corrector of the Landsat ETM satellite sensor since May 2003, some images have wedge-shaped gaps on each side, resulting in the loss of *ca* 22% of information. To correct this, we applied the Gapfill tool with the ENVI 4.7 program [41] according to the filling technique developed by Scaramuzza *et al.* [42]. This technique fills gaps in a Landsat image with data from another image and applies a linear transformation to adjust the corrected image based on the standard deviation and mean values of each band of each scene [42].

(c) Image classification and estimation of percentage forest cover

We carried out a supervised classification of images based on training data and validation. We considered three categories of land cover in the classification: native forest cover, agricultural lands and other land covers (e.g. water and human settlements). Following previous studies [43,44], forest cover included both old-growth and late successional second-growth forests because vegetation structure in the later forest type is quite similar to old-growth forests [5,8]. First, we selected regions of interest based on expert knowledge (i.e. polygons with land cover information) of the raster layer as a reference to classify unknown pixels by comparing the digital value of pixels with training data [45]. To this end, we used the support vector machine non-parametric method for nonlinear data. This method uses the Kernel class of algorithm [46,47]. Overall satellite image classification accuracy was relatively high (greater than 85%). To reduce the salt and pepper effect, we applied post-classification Majority/Minority analysis. Next, we used the classified vectors to estimate the percentage forest cover within each study landscape, using 10 differently sized buffers, ranging from 1 to 10 km, at 1 km intervals (corresponding to landscapes of 314.1 to 31 415.6 ha; figure 2*b*). We next calculated forest cover for each buffer using the Dinamica EGO 4 program (http://csr.ufmg.br/dinamica). All classified vectors were sent to the authors of each database for revision and approval before estimation of the percentage forest cover.

(d) Data analyses

To test the model described in figure 1, we evaluated three community attributes: species richness, density of individuals and basal area. As species richness is highly dependent on the accuracy of plant inventories, we used the coverage estimator ($\hat{C}_n$) recommended by Chao & Jost [48] to assess the completeness of each tree inventory using the *entropart* package [49] in R v. 3.5.1 (R Core Team, 2018). This estimator calculates the proportion of the total number of individuals in an assemblage that belong to the species represented in the sample. When a given plot presented a relatively low coverage (less than 0.6), we excluded this sample from the analyses to avoid any bias associated with differences in completeness among samples [48]. For the remaining samples, we calculated the extrapolated values of species richness considering the maximum sample coverage ($\hat{C}_n = 1.0$), following the protocols proposed by Chao & Jost [48] available in the *entropart* package for R [49].

To assess the predictability of successional trajectories, we related each community attribute (species richness, density of individuals and basal area) to stand age for each chronosequence ($n = 22$). Applying the *gam* function in the *mgvc* package for R [50], we derived the adjusted R^2 values from GAMs [51] to use as a proxy for predictability of the successional trajectories. Because R^2_{adj} represents the fraction of the variance in the dependent variable that is explained by the independent variable [51], this parameter can be used as a proxy of the predictability of the relationship between each vegetation attribute and stand age. We then used GAMs to model the effect of landscape forest cover on the predictability of successional trajectories of each vegetation attribute. To control for differences in plot number among studies, we included the sample size of each chronosequence as an offset, using the *offset* function in the *mgvc* package for R [50,51]. For all GAMs, we included predictor variables as *smooth* terms to specify that linear predictors depend on smooth functions of predictors [50,51].

To assess the recovery rate of successional trajectories, we extracted the predicted value of the GAM relating each vegetation attribute and stand age for the fixed age of 15 and 20 years of succession. Then, we calculated the recovery rate values through the equation: [(15 years predicted value − 20 years predicted value) / 5], where 5 corresponds to the age interval in years. This measure was established under the assumption that 5 years is a short interval of recovery and therefore presents a lineal behaviour. We used the age interval from 15 to 20 years as reference because this was included in the age range of most chronosequences and is an ecologically relevant and representative age for secondary forests [5,8,52]. We calculated the predicted values using the *predict* function in the *car* package for R [53]. We then applied GAMs to evaluate the effect of forest cover on the recovery rate of each community attribute. To control the effects associated with differences in plot size and minimum tree diameter among studies, we included these predictors as covariables in the models. GAMs were fitted including predictor variables forest cover and plot size (log) as *smooth* terms [50,51]. Minimum diameter was included as a categorical variable of three levels: less than or equal to 2.5 cm; 5 cm and greater than or equal to10 cm.

Given that the spatial extent (landscape size) that best fits the response of predictability and recovery rate to landscape forest cover (i.e. so-called ‘scale of effect’ [37]) is unknown, we ran the models for each buffer size (1–10 km, at 1 km intervals). We fitted a total of 30 models (3 community attributes × 10 buffers) for each response variable (predictability or successional recovery rate). We used the percentage of deviance explained by the models to identify the buffer size at which landscape forest cover best-predicted plant community responses. As recovery rate analysis included covariables, we additionally compared model adjustment using the Akaike’s information criterion corrected for small samples (AICc) to confirm the best model scale.

3. Results

The predictability of all three community attributes was strongly and significantly related to remaining landscape forest cover (figure 3), with more than 70% of the explained deviance by the models (electronic supplementary material, table S4). In particular, the predictability of successional trajectories for species richness, stem density and basal area was lower in landscapes with intermediate (40–60%) forest cover than in landscapes with low (less than 40%) and high (greater than 80%) forest cover (figure 3). Although this finding supports our theoretical model (figure 1), the poor representation of landscapes with less than 40% of forest cover suggests caution with interpretations, as the confidence intervals of the predicted trends were notably high, revealing a significant lack of statistical power within this range of forest cover. Yet, the pattern was clear and accurate for all studied successional trajectories in intermediate-to-high (i.e. 40–100%) forest cover landscapes (figure 3). Importantly, the spatial scale at which forest cover best predicted uncertainty in forest recovery was the same for all community attributes (4 km landscape radius; electronic supplementary material, table S4).

Landscape forest cover was a significant predictor of species richness recovery rate ($F = 7.41$, $p = 0.02$; whole model: $R^2_{adj} = 0.41$, deviance explained = 0.57; figure 4), but a poor predictor of stem density and basal area recovery rate (electronic supplementary material, tables S5 and S6). In particular, we observed a proportional (linear) increase of species recovery in landscapes with higher forest cover (figure 4), with such an increase being stronger when measuring forest cover across landscapes of 1 km radius (electronic supplementary material, table S6).

4. Discussion

This study provides the strongest evidence to date on the critical role played by landscape-scale forest cover in regulating successional trajectories of secondary tropical forests. Supporting our theoretical model (figure 1), the predictability of successional trajectories was significantly lower in landscapes with intermediate forest cover (40–60%) than in landscapes with low (less than 40%) or high (greater than 60%) forest cover, especially when considering the remaining forest cover within a 4 km radius. Yet, the predicted negative trends for the lower range (i.e. 0–40%) of forest cover should be interpreted with care, as we only found two chronosequences in landscapes within this range, which decreased the explanatory power of our model in landscapes with less than 40% of forest cover. Regarding the effect of forest cover on recovery rate, only the species richness was

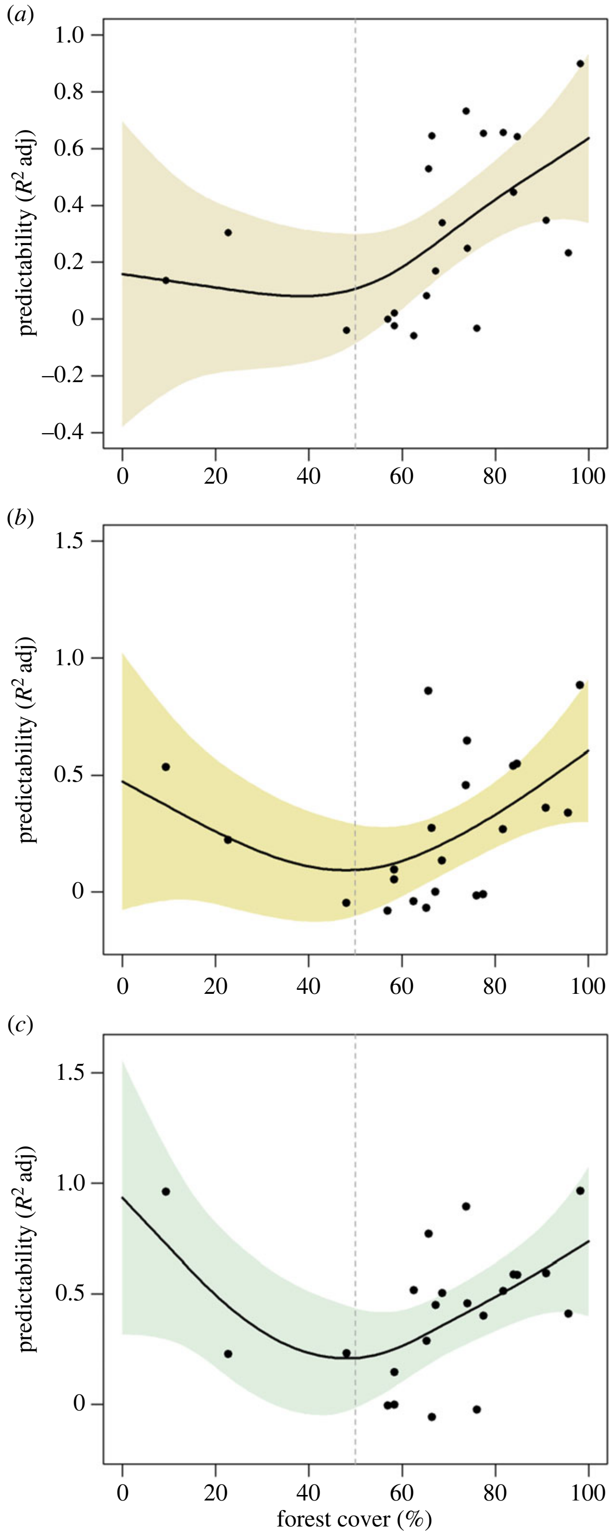

Figure 3. Effect of landscape forest cover on the predictability of successional trajectories in 22 Neotropical landscapes. We assessed three community attributes: (*a*) species richness, (*b*) density of individuals and (*c*) basal area. Each point represents the predictability of a community attribute in a particular chronosequence, estimated as the coefficient of determination (R^2_{adj}). Percentage forest cover was measured in 4 km radius landscapes. Smoothed curves and 95% confidence intervals (filled area) are indicated. Dashed lines indicate the 50% threshold of forest cover. (Online version in colour.)

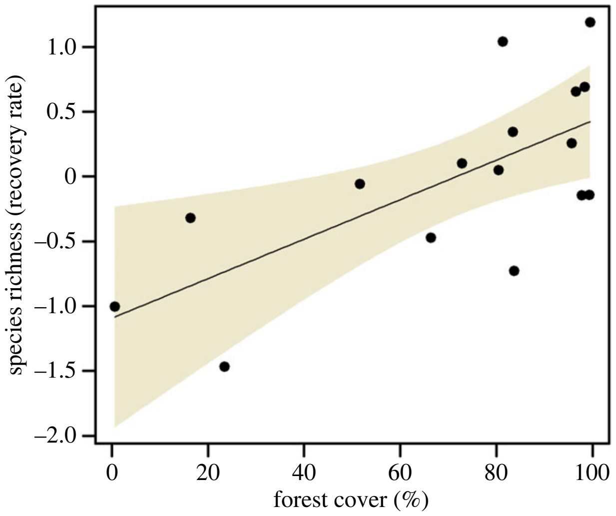

Figure 4. Effect of landscape forest cover on the species richness recovery rate in 22 Neotropical landscapes. We estimated recovery rate through the equation: [(15 years predicted value − 20 years predicted value) / 5], where 5 corresponds to the age interval in years. Points correspond to the partial residuals of the complete GAM model (see Material and methods), i.e. they specify the prediction of all predictors for each particular chronosequence. Percentage forest cover was measured in 1 km radius landscapes. 95% confidence intervals (filled area) are indicated. (Online version in colour.)

positively related to forest cover in relatively small (1 km radius) landscapes. These novel findings have key ecological and applied implications, especially in the context of tropical forest restoration planning.

The high uncertainty (i.e. low predictability) of successional trajectories in landscapes with intermediate forest cover can be related to the high spatial and environmental heterogeneity in these landscapes. For example, at intermediate forest covers, landscapes usually show higher variability in forest fragmentation indices, such as patch density and total forest edge [27,36]. This heterogeneity in forest spatial configuration is usually accompanied by higher compositional heterogeneity, such as a high number of land cover types and management regimes that occupy a relatively small extent of the landscape [29]. Regenerating stands in more heterogeneous landscapes are thus likely exposed to a relatively high spatial and temporal variation in fruit availability, seed dispersal, seed germination and seedling recruitment and growth, which in turn can lead to highly variable pathways in the recovery of species richness, stem density and biomass [15]. This is particularly true for species richness, which strongly depends on rare species whose distributions are difficult to predict because they are affected by dispersal limitation, competition and stochastic factors [54,55]. Therefore, the low predictability of tree species richness, stem density and basal area in tropical landscapes with intermediate forest cover is probably related to the high spatial heterogeneity and associated environmental heterogeneity characterizing these landscapes.

Interestingly, forest cover shows stronger effects on successional trajectories when assessed at the 4 km radius extent. This suggests that ecological mechanisms (e.g. seed source limitation and seed dispersal limitation) driving secondary succession through changes in forest cover act mainly at this spatial scale [56,57]. This is reasonable considering that up to 90% of tropical trees depend on vertebrate animals (e.g. bats, birds and terrestrial mammals) to disperse their seeds [58] and that most bats, birds and terrestrial mammals' responses to landscape structure are stronger when assessed in 1–4 km radius landscapes [37,59]. Thus, movements of seed dispersers and hence seed dispersal may depend on forest cover at this scale. Supporting this possibility, San-José *et al.* [34,57] demonstrate that the effect of forest cover on seed dispersal in two rainforest regions from southeastern Mexico is stronger when measuring forest cover in landscapes of 1–1.3 km radius. As discussed below, this suggests that restoration initiatives may be more effective if implemented across spatial extents of 1–4 km radius.

In agreement with this idea, we also found that forest cover in 1 km radius landscapes drives the recovery rate of species richness. Rozendaal *et al.* [8] and Pérez-Cárdenas *et al.* [14] also found that secondary forests across the Neotropics recover particularly fast in species richness, especially in more forested landscapes. As proposed by the 'habitat amount hypothesis' (*sensu* [31]), this could be at least partially explained by the sample area effect; i.e. more forested landscapes can hold a higher number of individuals and species than more deforested ones, which can, in turn, increase the colonization rate of new species to the regenerating stands [60,61]. In fact, the species richness of animal- and wind-dispersed seeds in the seed rain is known to be positively associated with the remaining forest cover at this scale (1 km radius) [34]. Therefore, there is evidence to suggest that most of the seeds (and species) colonizing regenerating stands might come from the available forest cover at this scale—an interesting avenue for future research.

The recovery rate of stem density and basal area was weakly related to forest cover. This is not totally unexpected; other studies have demonstrated that plant establishment and growth rates in secondary forests do not depend on forest cover but on other landscape and local factors. For example, Pérez-Cárdenas *et al.* [14] found that the recovery rate of aboveground biomass decreased principally with increasing pasture cover in the surrounding landscape, likely because this land cover is associated with disturbance risks (e.g. fire incidence and plant damage by cattle [62]). The recovery of stem density and biomass also depends on species' resprouting ability and other local factors such as land-use intensity, soil fertility, seed bank, invasive species, weeds, pathogens and herbivores [16,63–65], among others [3,66]. Thus, forest cover appears to play a major role in determining propagule availability and thus the recovery rate of species richness, but disturbance regimes at the stand level are likely more important for stem density and plant biomass, independently of forest cover [67].

Importantly, albeit our models fitted the data reasonably well, the limited number of chronosequences in landscapes with less than 40% forest cover suggests caution with interpretations for the lower range of forest cover. The lack of research on secondary succession in highly degraded tropical landscapes has been noted in previous studies [5,68] and highlights the urgent need to fill this gap to attain a better understanding of the effect of landscape-scale disturbance on successional trajectories [69]. Yet the fact that most patterns encompassing intermediate to high forest cover were almost identical (figure 3) gives strong support to the hypothesis that vegetation attributes such as species richness, stem density and biomass recover in a more predictable manner (i.e. all these attributes increased with stand age; electronic supplementary material, figures S1–S3) in more forested landscapes.

5. Applied implications

Overall, our findings support previous theoretical [15] and empirical studies [8,14] on the critical role played by landscape forest cover in regulating successional trajectories. The applied implications of these findings are highly valuable, especially in the context of forest restoration. The simplest and most pragmatic implication is that restoration initiatives should use a spatially explicit landscape approach and consider the remaining forest cover in the surrounding landscape. Our findings also suggest that the 'surrounding landscape' specifically refers to spatial extents of 1–4 km radius. This is consistent with previous studies demonstrating the importance of forest cover in driving the success and uncertainty of restoration initiatives [70–72]. In fact, Crouzeilles & Curran [38] also found an increasing uncertainty in restoration success when forest cover falls below about 50%. This does not imply that intermediately deforested and environmentally more complex landscapes have a lower conservation value. There is strong evidence worldwide that these are optimal landscape scenarios for biodiversity conservation and the delivery of goods and services to humans [35,73,74]. Our findings rather suggest that restoration initiatives aimed at achieving faster recovery of richness and higher predictability of successional trajectories are likely more effective in more forested landscapes. Therefore, to increase the effectiveness of restoration initiatives in landscapes with an intermediate degree of disturbance, we encourage further empirical studies in these landscapes of the effects of local- and landscape-scale factors on secondary succession.

Data accessibility. The data supporting the results of this manuscript are available from the Dryad Data Repository: https://doi.org/10.5061/dryad.4mw6m90dr [75].

Supplementary data are provided in the electronic supplementary material [76].

Authors' contributions. V.A.-R.: conceptualization, funding acquisition, investigation, methodology, supervision, validation, writing—original draft and writing—review and editing; K.F.R.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, writing—original draft and writing—review and editing; M.F.: formal analysis, investigation, methodology, resources, visualization and writing—review and editing; I.C.N.: data curation, investigation, resources and writing—review and editing; F.M.: formal analysis, investigation, methodology, resources, supervision, visualization and writing—review and editing; F.A.-V.: data curation, investigation, resources and writing—review and editing; P.B.: data curation, investigation, resources and writing—review and editing; F.B.: data curation, investigation, resources and writing—review and editing; C.C.-C.: data curation, investigation, resources and writing—review and editing; E.L.M.C.: data curation, investigation, resources and writing—review and editing; R.L.C.: data curation, investigation, resources and writing—review and editing; J.M.D.-R.: data curation, investigation, resources and writing—review and editing; B.G.F.: data curation, investigation, resources and writing—review and editing; P.F.F.: data curation, investigation, resources and writing—review and editing; N.G.-V.: data curation, investigation, resources and writing—review and editing; D.M.G.: data curation, investigation, resources and writing—review and editing; J.L.H.-S.: data curation, investigation, resources and writing—review and editing; C.C.J.: data curation, investigation, resources and writing—review and editing; A.B.J.: data curation, investigation, resources and writing—review and editing; B.H.J.J.: data curation, investigation, resources and writing—review and editing; S.G.L.: data curation, investigation, resources and writing—review and editing; F.M.-P.: data curation, investigation, resources and writing—review and editing; J.A.M.: data curation, investigation, resources and writing—review and editing; S.O.-G.: data curation, investigation, resources and writing—review and editing; G.S.M.: data curation, investigation, resources and writing—review and editing; M.A.M.-C.: data curation, investigation, resources and writing—review and editing; R.M.: data curation, investigation, resources and writing—review and editing; J.S.P.: data curation, investigation, resources and writing—review and editing; G.P.E.R.: data curation, investigation, resources and writing—review and editing; R.P.G.R.: data curation, investigation, resources and writing—review and editing; B.A.S.: data curation, investigation, resources and writing—review and editing; M.F.S.: data curation, investigation, resources and writing—review and editing; M.T.: data curation, investigation, resources and writing—review and editing; F.T.-D.: data curation, investigation, resources and writing—review and editing; E.v.d.B.: data curation, investigation, resources and writing—review and editing; D.L.M.V.: data curation, investigation, resources and writing—review and editing; G.W.-L.: data curation, investigation, resources and writing—review and editing; M.M.-R.: data curation, investigation, resources and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. K.F.R. thanks DGAPA-UNAM for her postdoctoral scholarship. R.L.C. thanks the Andrew Mellon Foundation, US NSF awards 0424767, 0639393, 1147429 and 1110722, UConn Research Foundation, and NASA ROSES Grant NNH08ZDA001N-TE. P.B. thanks the funding provided by SEP-CONACYT (CB-2009-128136 and CB 2015- 255544) and PAPIIT-UNAM (projects 218416, 211114 and IN212617). J.L.H.-S., J.M.D.-R., F.M.-P. and F.T.-D. thank the funding provided by FOMIX-Yucatán (grant no. YUC-2008-C06-108863). D.M.G., B.G.F and P.F.F. thank the funding provided by NSF grant 9815369. K. Eastwood made valuable recommendations on the first draft.

References

1. World Resources Institute. 2022 World global forest watch. See http://www.globalforestwatch.org.
2. Aide TM *et al.* 2013 Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica* **45**, 262–271. (doi:10.1111/j.1744-7429.2012.00908.x)
3. Chazdon RL. 2014 *Second growth: the promise of tropical forest regeneration in an age of deforestation*. Chicago, IL: University of Chicago Press.
4. Chazdon RL, Peres CA, Dent D, Sheil D, Lugo AE, Lamb D, Stork N, Miller S. 2009 The potential for species conservation in tropical secondary forests. *Conserv. Biol.* **23**, 1406–1417. (doi:10.1111/j.1523-1739.2009.01338.x)
5. Poorter L *et al.* 2016 Biomass resilience of Neotropical secondary forests. *Nature* **530**, 211–214. (doi:10.1038/nature16512)
6. Strassburg BB *et al.* 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. (doi:10.1111/btp.12393)
7. Lennox GD *et al.* 2018 Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests. *Glob. Change Biol.* **24**, 5680–5694. (doi:10.1111/gcb.14443)
8. Rozendaal DMA *et al.* 2019 Biodiversity recovery of Neotropical secondary forests. *Sci. Adv.* **5**, eaau3114. (doi:10.1126/sciadv.aau3114)
9. Jakovac CC, Junqueira AB, Crouzeilles R, Peña-Claros M, Mesquita RCG, Bongers F. 2021 The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests. *Biol. Rev.* **96**, 1114–1134. (doi:10.1111/brv.12694)
10. Powers JS, Becknell JM, Irving J, Perez-Aviles D. 2009 Diversity and structure of regenerating tropical

dry forests in Costa Rica: geographic patterns and environmental drivers. *Forest Ecol. Manag.* **258**, 959–970. (doi:10.1016/j.foreco.2008.10.036)

11. Lohbeck M, Poorter L, Martínez-Ramos M, Bongers F. 2015 Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology* **96**, 1242–1252. (doi:10.1890/14-0472.1)
12. Lohbeck M, Poorter L, Martínez-Ramos M, Rodriguez-Velázquez J, Breugel M, Bongers F. 2014 Changing drivers of species dominance during tropical forest succession. *Funct. Ecol.* **28**, 1052–1058. (doi:10.1111/1365-2435.12240)
13. Rozendaal DMA *et al.* 2017 Demographic drivers of aboveground biomass dynamics during secondary succession in neotropical dry and wet forests. *Ecosystems* **20**, 340–353. (doi:10.1007/s10021-016-0029-4)
14. Pérez-Cárdenas N, Mora F, Arreola F, Arroyo-Rodríguez V, Balvanera P, Flores-Casas R, Navarrete A, Ortega-Huerta MA. 2021 Effects of landscape composition and site land-use intensity on secondary succession in a tropical dry forest. *For. Ecol. Manage.* **482**, 118818. (doi:10.1016/j.foreco.2020.118818)
15. Arroyo-Rodríguez V *et al.* 2017 Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biol. Rev.* **92**, 326–340. (doi:10.1111/brv.12231)
16. Vandermeer J, Granzow De La Cerda I, Perfecto I, Boucher D, Ruiz J, Kaufmann A. 2004 Multiple basins of attraction in a tropical forest: evidence for nonequilibrium community structure. *Ecology* **85**, 575–579. (doi:10.1890/02-3140)
17. Chazdon RL, Letcher SG, van Breugel M, Martínez-Ramos M, Bongers F, Finegan B. 2007 Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Phil. Trans. R. Soc. B***362**, 273–289. (doi:10.1098/rstb.2006.1990)
18. Norden N *et al.* 2015 Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proc. Natl Acad. Sci. USA* **112**, 8013–8018. (doi:10.1073/pnas.1500403112)
19. Letcher SG, Chazdon RL. 2009 Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica* **41**, 608–617. (doi:10.1111/j.1744-7429.2009.00517.x)
20. Norden N, Chazdon RL, Chao A, Jiang YH, Vilchez-Alvarado B. 2009 Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecol. Lett.* **12**, 385–394. (doi:10.1111/j.1461-0248.2009.01292.x)
21. Schnitzer SA, Dalling JW, Carson WP. 2000 The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *J. Ecol.* **88**, 655–666. (doi:10.1046/j.1365-2745.2000.00489.x)
22. Mesquita RCG, Ickes K, Ganade G, Williamson GB. 2001 Alternative successional pathways in the Amazon Basin. *J. Ecol.* **89**, 528–537. (doi:10.1046/j.1365-2745.2001.00583.x)
23. Bonner MTL, Schmidt S, Shoo LP. 2013 A meta-analytical global comparison of aboveground biomass accumulation between tropical secondary forests and monoculture plantations. *Forest Ecol. Manag.* **291**, 73–86. (doi:10.1016/j.foreco.2012.11.024)
24. Pickett STA, Collins SL, Armesto JJ. 1987 Models, mechanisms and pathways of succession. *Bot. Rev.* **53**, 335–371. (doi:10.1007/BF02858321)
25. Rocha GP, Vieira DL, Simon MF. 2016 Fast natural regeneration in abandoned pastures in southern Amazonia. *Forest Ecol. Manag.* **370**, 93–101. (doi:10.1016/j.foreco.2016.03.057)
26. Brancalion PHS *et al.* 2019 Global restoration opportunities in tropical rainforest landscapes. *Sci. Adv.* **5**, eaav3223. (doi:10.1126/sciadv.aav3223)
27. Villard MA, Metzger JP. 2014 Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. *J. Appl. Ecol.* **51**, 309–318. (doi:10.1111/1365-2664.12190)
28. Álvarez-Yépiz JC, Martínez-Yrízar A, Búrquez A, Lindquist C. 2008 Variation in vegetation structure and soil properties related to land use history of old-growth and secondary tropical dry forests in northwestern Mexico. *Forest Ecol. Manag.* **256**, 355–366. (doi:10.1016/j.foreco.2008.04.049)
29. Jakovac CC, Dutrieux LP, Siti L, Peña-Claros M, Bongers F. 2017 Spatial and temporal dynamics of shifting cultivation in the middle-Amazonas river: expansion and intensification. *PLoS ONE* **12**, e0181092. (doi:10.1371/journal.pone.0181092)
30. Poorter L *et al.* 2021 Functional recovery of secondary tropical forests. *Proc. Natl Acad. Sci. USA* **118**, e2003405118. (doi:10.1073/pnas.2003405118)
31. Fahrig L. 2013 Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.* **40**, 1649–1663. (doi:10.1111/jbi.12130)
32. Steffan-Dewenter I, Tscharntke T. 1999 Effects of habitat isolation on pollinator communities and seed set. *Oecologia* **121**, 432–440. (doi:10.1007/s004420050949)
33. Meiners SJ, Cadotte MW, Fridley JD, Pickett ST, Walker LR. 2015 Is successional research nearing its climax? New approaches for understanding dynamic communities. *Funct. Ecol.* **29**, 154–164. (doi:10.1111/1365-2435.12391)
34. San-José M, Arroyo-Rodríguez V, Meave JA. 2020 Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. *Ecol. Appl.* **30**, e02033. (doi:10.1002/eap.2033)
35. Arroyo-Rodríguez V *et al.* 2020 Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecol. Lett.* **23**, 1404–1420. (doi:10.1111/ele.13535)
36. Fahrig L. 2003 Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487–515. (doi:10.1146/annurev.ecolsys.34.011802.132419)
37. Jackson HB, Fahrig L. 2015 Are ecologists conducting research at the optimal scale? *Glob. Ecol. Biogeogr.* **24**, 52–63. (doi:10.1111/geb.12233)
38. Crouzeilles R, Curran M. 2015 Which landscape size best predicts the influence of forest cover on restoration success? A global meta-analysis on the scale of effect. *J. Appl. Ecol.* **53**, 440–448. (doi:10.1111/1365-2664.12590)
39. Zhu Z, Woodcock CE. 2012 Object-based cloud and cloud shadow detection in Landsat imagery. *Remote Sens. Environ.* **118**, 83–94. (doi:10.1016/j.rse.2011.10.028)
40. Zhang Y. 2002 Problems in the fusion of commercial high-resolution satelitte as well as Landsat 7 images and initial solutions. *ISPRS Arch.* **34**, 587–592.
41. ENVI. 2008 *ENVI on-line software user's manual*. Boulder, CO: ITT Visual Information Solutions.
42. Scaramuzza P, Micijevic E, Chander G. 2004 SLC gap-filled products phase one methodology. Landsat Technical Notes **5**. See https://landsat.usgs.gov/documents/SLC_Gap_Fill_Methodology.pdf.
43. Rocha-Santos L, Pessoa MS, Cassano CR, Talora DC, Orihuela RL, Mariano-Neto E, Morante-Filho JC, Faria D, Cazetta E. 2016 The shrinkage of a forest: landscape-scale deforestation leading to overall changes in local forest structure. *Biol. Conserv.* **196**, 1–9. (doi:10.1016/j.biocon.2016.01.028)
44. Morante-Filho JC, Arroyo-Rodríguez V, de Souza Pessoa M, Cazetta E, Faria D. 2018 Direct and cascading effects of landscape structure on tropical forest and non-forest frugivorous birds. *Ecol. Appl.* **28**, 2024–2032. (doi:10.1002/eap.1791)
45. Canty MJ. 2007 *Image analysis, classification and change detection in remote sensing: with algorithms for ENVI/IDL*, 3rd edn. Boca Raton, FL: CRC Press.
46. Foody GM, Mathur A. 2004 Toward intelligent training of supervised image classifications: directing training data acquisition for SVM classification. *Remote Sens. Environ.* **93**, 107–117. (doi:10.1016/j.rse.2004.06.017)
47. Tamma R, Rao TCM, Jaisankar G. 2013 An efficient hybrid classification system for high resolution remote sensor data. *Am. J. Remote Sens.* **1**, 21–32. (doi:10.11648/j.ajrs.20130102.12)
48. Chao A, Jost L. 2012 Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**, 2533–2547. (doi:10.1890/11-1952.1)
49. Marcon E, Hérault B. 2015 entropart: an R package to measure and partition diversity. *J. Stat. Softw.* **67**, 1–26.
50. Wood S. 2015 mgcv: mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation. See https://stat.ethz.ch/R-manual/R-devel/library/mgcv/html/mgcv-package.html.
51. Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009 *Mixed effects models and extensions in ecology with R*. Berlin, Germany: Springer.
52. Reid JL, Fagan ME, Lucas J, Slaughter J, Zahawi RA. 2018 The ephemerality of secondary forests in southern Costa Rica. *Conserv. Lett.* **12**, e12607.

53. Fox J *et al.* 2012 Package 'car'. See https://CRAN.R-project.org/package=car.
54. Gogol-Prokurat M. 2011 Predicting habitat suitability for rare plants at local spatial scales using a species distribution model. *Ecol. Appl.* **21**, 33–47. (doi:10.1890/09-1190.1)
55. McCune JL. 2016 Species distribution models predict rare species occurrences despite significant effects of landscape context. *J. Appl. Ecol.* **53**, 1871–1879. (doi:10.1111/1365-2664.12702)
56. Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L. 2016 What determines the spatial extent of landscape effects on species? *Landscape Ecol.* **31**, 1177–1194. (doi:10.1007/s10980-015-0314-1)
57. San-José M, Arroyo-Rodríguez V, Jordano P, Meave JA, Martínez-Ramos M. 2019 Regional context drives the spatial scale that best predicts seed rain responses to landscape structure. *Landsc. Ecol.* **34**, 1069–1080. (doi:10.1007/s10980-019-00821-y)
58. Howe HF, Smallwood J. 1982 Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* **13**, 201–228. (doi:10.1146/annurev.es.13.110182.001221)
59. Arroyo-Rodríguez V, Martínez-Ruiz M, Bezerra JS, Galán-Acedo C, San-José M, Fahrig L. In press. Does a species' mobility determine the scale at which it is influenced by the surrounding landscape pattern? *Curr. Landsc. Ecol. Rep.*
60. Jesus FM, Pivello VR, Meirelles AT, Franco GADC, Metzger JP. 2012 The importance of landscape structure for seed dispersal in rain forest fragments. *J. Veg. Sci.* **23**, 1126–1136. (doi:10.1111/j.1654-1103.2012.01418.x)
61. Cadavid-Florez L, Laborde J, Zahawi RA. 2019 Using landscape composition and configuration metrics as indicators of woody vegetation attributes in tropical pastures. *Ecol. Indic.* **101**, 679–691. (doi:10.1016/j.ecolind.2019.01.072)
62. Quisehuatl-Medina A, Averett JP, Endress BA, Lopez-Toledo L. 2020 Removal of cattle accelerates tropical dry forest succession in Northwestern Mexico. *Biotropica* **52**, 457–469. (doi:10.1111/btp.12748)
63. Mora F, Martínez-Ramos M, Ibarra-Manríquez G, Pérez-Jiménez A, Trilleras J, Balvanera P. 2015 Testing chronosequences through dynamic approaches: time and site effects on tropical dry forest succession. *Biotropica* **47**, 38–48. (doi:10.1111/btp.12187)
64. Pinho BX, Melo FPL, Arroyo-Rodríguez V, Pierce S, Lohbeck M, Tabarelli M. 2018 Soil-mediated filtering organizes plant assemblages in regenerating tropical forests. *J. Ecol.* **106**, 137–147. (doi:10.1111/1365-2745.12843)
65. Bezerra JS, Arroyo-Rodríguez V, Tavares JM, Leal A, Leal IR, Tabarelli M. 2022 Drastic impoverishment of the soil seed bank in a tropical dry forest exposed to slash-and-burn agriculture. *For. Ecol. Manage.* **513**, 120185. (doi:10.1016/j.foreco.2022.120185)
66. Martínez-Ramos M, Pingarroni A, Rodríguez-Velázquez J, Toledo-Chelala L, Zermeño-Hernández I, Bongers F. 2016 Natural forest regeneration and ecological restoration in human-modified tropical landscapes. *Biotropica* **48**, 745–757. (doi:10.1111/btp.12382)
67. Jakovac CC, Bongers F, Kuyper TW, Mesquita RC, Peña-Claros M. 2016 Land use as a filter for species composition in Amazonian secondary forests. *J. Veg. Sci.* **27**, 1104–1116. (doi:10.1111/jvs.12457)
68. Reid JL, Fagan ME, Zahawi RA. 2018 Positive site selection bias in meta-analyses comparing natural regeneration to active forest restoration. *Sci. Adv.* **4**, eaas9143. (doi:10.1126/sciadv.aas9143)
69. Ghazoul J, Chazdon R. 2017 Degradation and recovery in changing forest landscapes: a multiscale conceptual framework. *Annu. Rev. Environ. Resour.* **42**, 161–188. (doi:10.1146/annurev-environ-102016-060736)
70. Crouzeilles R, Beyer HL, Mills M, Grelle CE, Possingham HP. 2015 Incorporating habitat availability into systematic planning for restoration: a species-specific approach for Atlantic Forest mammals. *Divers. Distrib.* **21**, 1027–1037. (doi:10.1111/ddi.12349)
71. Crouzeilles R, Curran M, Ferreira MS, Lindenmayer DB, Grelle CE, Rey Benayas JM. 2016 A global meta-analysis on the ecological drivers of forest restoration success. *Nat. Commun.* **7**, 11666. (doi:10.1038/ncomms11666)
72. Brancalion PHS, Schweizer D, Gaudare U, Mangueira JR, Lamonato F, Farah FT, Nave AG, Rodrigues RR. 2016 Balancing economic costs and ecological outcomes of passive and active restoration in agricultural landscapes: the case of Brazil. *Biotropica* **48**, 856–867. (doi:10.1111/btp.12383)
73. Melo FPL, Arroyo-Rodríguez V, Fahrig L, Martínez-Ramos M, Tabarelli M. 2013 On the hope for biodiversity-friendly tropical landscapes. *Trends Ecol. Evol.* **28**, 462–468. (doi:10.1016/j.tree.2013.01.001)
74. Estrada-Carmona N, Sánchez AC, Remans R, Jones SK. 2022 Complex agricultural landscapes host more biodiversity than simple ones: a global meta-analysis. *Proc. Natl Acad. Sci. USA* **119**, e2203385119. (doi:10.1073/pnas.2203385119)
75. Rito KF *et al.* 2022 Landscape structure, predictability of forest regeneration trajectories, and recovery rate on secondary forests. Dryad Digital Repository. (doi:10.5061/dryad.4mw6m90dr)
76. Arroyo-Rodríguez V *et al.* 2023 Landscape-scale forest cover drives the predictability of forest regeneration across the Neotropics. Figshare. (doi:10.6084/m9.figshare.c.6350225)