Multidimensional tropical forest recovery

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FOREST ECOLOGY
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Tropical forests disappear rapidly because of deforestation, yet they have the potential to regrow naturally on abandoned lands. We analyze how 12 forest attributes recover during secondary succession and how their recovery is interrelated using 77 sites across the tropics. Tropical forests are highly resilient to low-intensity land use; after 20 years, forest attributes attain 78% (33 to 100%) of their old-growth values. Recovery to 90% of old-growth values is fastest for soil (<1 decade) and plant functioning (<2.5 decades), intermediate for structure and species diversity (2.5 to 6 decades), and slowest for biomass and species composition (>12 decades). Network analysis shows three independent clusters of attribute recovery, related to structure, species diversity, and species composition. Secondary forests should be embraced as a low-cost, natural solution for ecosystem restoration, climate change mitigation, and biodiversity conservation.

T ropical forests are converted at alarming rates to other land uses (*1*), yet they also have the potential to regrow naturally on abandoned agricultural fields and pastures. Widespread land abandonment because of fertility loss, migration, or alternative livelihood options has led to a rapid increase in the extent of regrowing forests. Currently, regrowth covers as much as 28% (2.4 million km²) of the neotropics alone (*2*). Regrowing secondary forests (SFs) form a large and important component of human-modified tropical landscapes and have the potential to play a key role in biodiversity conservation (*3*), climate change mitigation (*2*), and landscape restoration (*4*). A holistic, quantitative understanding of the recovery of multiple SF functions is needed to inform and design effective policies that benefit nature and people from local to global scales.

In this study, we assess the resilience of 12 forest attributes to recover from agriculture and pasture use. Resilience is the ability of a system to absorb disturbances and return to its previous state (*5*). Resilience is driven by two underlying components: the ability

to resist disturbance and the ability to recover after disturbance (*6*). We defined "resistance" as the difference between the value of the forest attribute at the start of succession and the average old-growth forest (OGF) values [compare (*7*)], which reflects the combined legacies of previous forest and previous land use, and "recovery" as the ability to return to OGF attribute values after succession. Succession is defined as a change in vegetation structure, species composition (SC), and ecosystem functioning over time after a disturbance (*8*). Secondary succession occurs on previously vegetated lands when a disturbance removes most of the aboveground vegetation and can proceed at fast rates due to legacy effects of previous forest or previous land use, such as a developed soil, seed bank, remnant trees, and resprouting stumps. Successional pathways are, to some extent, predictable but, because of local stochastic factors, are also, to some extent, uncertain (*9*).

Most successional theories have focused on specific ecosystem attributes, such as SC (*10*), species richness (SR) (*11*), forest structure (*12*),

or soils (*13*), but they have rarely been conceptually integrated and assessed together. Recovery of these different ecosystem attributes (i.e., dimensions) is likely to depend on one another. For example, rapid recovery of biomass may lead to high litter production and decomposition and, hence, rapid recovery of soil organic carbon.

Chronosequence studies allow us to infer long-term trends in forest recovery by comparing forests with similar land-use history that differ in age since agricultural or pasture abandonment. Single-site studies have assessed the recovery of multiple attributes [summarized in (*14*)], and several synthetic analyses have assessed the recovery of single attributes. They have found that ecosystem functioning, such as nitrogen fixation, recovers fast [in about three decades (*15*)], whereas aboveground biomass (AGB) and SR recover more slowly [three to seven decades (*16*, *17*)] and SC recovers slowest [i.e., centuries (*17*)]. To date, we lack a comprehensive understanding on how multiple attributes differ in recovery rates and how recovery of these attributes is interrelated.

In this study, we analyze how 12 forest attributes recover during secondary succession and how their recovery is interrelated. We focused on four complementary groups of attributes that capture successional changes in soils [bulk density (BD), carbon (C), and nitrogen (N)], ecosystem functioning [community nitrogen fixers, wood density (WD), and specific leaf area (SLA)], forest structure [AGB, maximum tree diameter, and structural heterogeneity (SH)], and diversity and composition (SR, species diversity, and similarity to OGF). These four groups are key components of ecosystem functioning (*18*), and knowledge of their recovery during succession is a prerequisite for the formulation of global policies on biodiversity conservation, climate change mitigation, and forest restoration. We ask (i) how multiple forest attributes recover during succession, (ii) how their relative recovery is interrelated, and (iii) whether one (or several) attribute(s) can be used as a simple proxy for multidimensional recovery. We advance previous analyses by (i) including a wider range of forest attributes for a larger number of sites (77) compared with those in previous studies, (ii) developing and applying an original conceptual framework to model forest recovery, (iii) examining how recovery among forest attributes is interrelated, and (iv) identifying simple indicators to monitor the progress of forest restoration.

We compiled original chronosequence data from three continents, 77 sites, 2275 plots, and 226,343 stems, spanning the major environmental and latitudinal gradients in the lowland neotropics and West Africa [[18]; Fig. 1D and table S1]. Chronosequences do not monitor plots

over time but rather substitute space for time to infer recovery. Plots were, on average, 0.1 ha, in which all woody plants were identified and measured for their stem diameter. Forest attributes were measured for 21 sites (for soils) up to 77 sites for the other variables. To quantify to what extent SF attributes recover toward OGF values, recovery was modeled for each chronosequence as a process in which SF values return exponentially to OGF values (Fig. 1A). When available, OGF plots were used to estimate OGF chronosequence reference values (supplementary text, section S1). For each study site, relative forest recovery was expressed as the similarity (ranging between 0 and 100%) between the predicted values for SF plots and OGF plots, thereby enabling direct comparisons of recovery across forests and attributes (Fig. 1, A and B). To assess how recovery of different forest attributes was connected during succession and which attributes can serve as proxies for multidimensional recovery, we carried out a network analysis (Fig. 1C).

Pace of recovery

Forest attributes differ in their starting values after land abandonment (i.e., resistance) and subsequent recovery (Fig. 2). Starting values varied from 1 to 90% (Fig. 3A), recovery after 20 years (R_{20y}) varied from 33 to 100% (Fig. 3B), and recovery time (RT) to 90% of OGF values varied from 0 to 120 years (Fig. 3D). The ranking in recovery of the four

different groups is maintained when recovery is evaluated in terms of intrinsic recovery rate (λ) instead of percentage of recovery (fig. S2). In the coming sections, we first briefly introduce each group of attributes. See (18) for a detailed explanation of their importance and how they recover during succession.

Soil functioning was evaluated in terms of organic C, N, and BD of the topsoil. Soil C concentration scales positively with soil organic matter content and, hence, with nutrients in organic material and water holding capacity. Abandoned agricultural fields and pastures may have low soil C because of combustion during slash and burn (19). Soil N concentration is an indicator of soil fertility and may be low in abandoned fields because of uptake by crops and cattle, volatilization, erosion, and leaching (19). Soil BD is soil dry mass over soil volume and may be high because of soil compaction by agricultural practices and livestock.

We expected soil recovery to occur more slowly than vegetation recovery because soil recovery depends on leaf and root litter inputs. Yet recovery of soil attributes was surprisingly fast [compare (7)], with an R_{20y} of 98 to 100% and an RT of 1 to 9 years (Fig. 3, B and D). Just after land abandonment of agriculture or pasture (t_0), the starting values of C, N, and BD were relatively high (62 to 90%; Fig. 3A), which indicates that they are less affected by

slashing or burning than aboveground vegetation, contain more legacies of previous land use, and have a high resistance to disturbance. Most of our data come from regrowth after light- to mid-intensity land uses during which soil degradation is not extreme. Soils may also recover quickly due to rapid recovery of the soil biotic community, because slash-and-burn management has transferred nutrients from the aboveground vegetation to the soil, or because productive grass roots and nitrogen-fixing herbs have increased soil C and N (19).

Soil C recovered in ~5 years to 90% of OGF values, probably because it is weakly affected by aboveground disturbances associated with land-use change, such as fire and clearing. A meta-analysis found that soil C of SF was similar to that of OGF and did not change during succession (20). Most soil nutrients may recover quickly because plants may acquire nutrients from deeper soil layers, because of high litter production early in succession due to ample light availability, and because of the high rates of leaf and root turnover of pioneer species (21). Litter quality may also be higher early in succession, because pioneers tend to have high concentrations of leaf nutrients (22) and nitrogen fixers are especially abundant (15) and active early in succession (23). Recovery of phosphorus may be slow because it can only be replenished through atmospheric deposition and mineral weathering (7). The observed fast soil recovery is important

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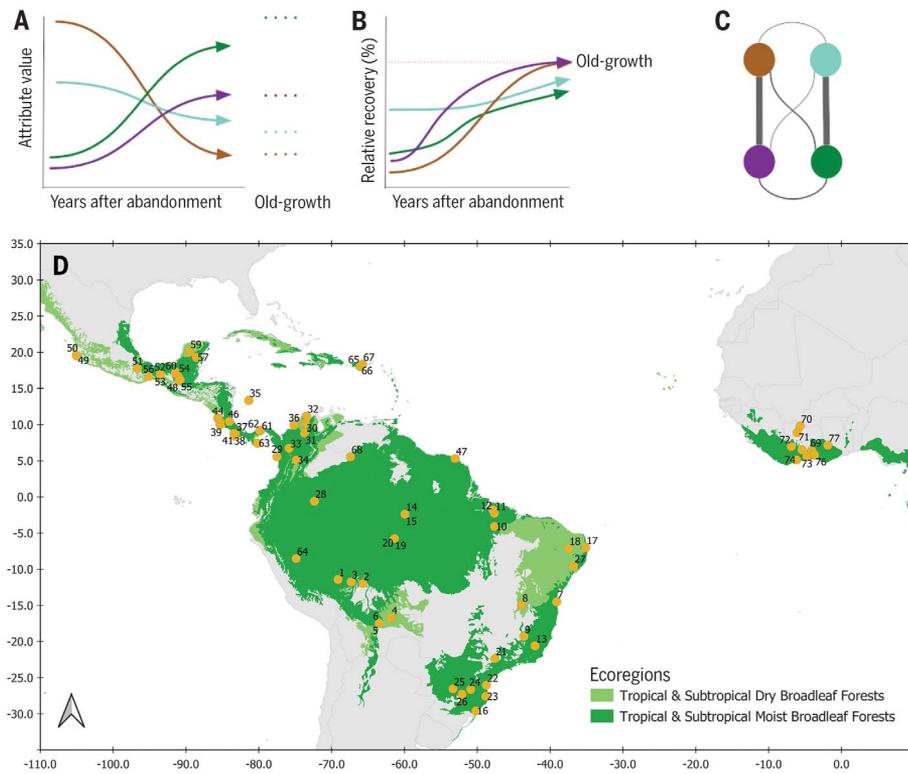*Corresponding author. Email: lourens.poorter@wur.nl

Fig. 1. Study approach to analyze recovery of different forest attributes. (**A** to **C**) Absolute recovery of SF attributes toward OGF values (A) can be standardized to relative recovery rates (B), which express how close each SF attribute is to OGF values, thereby allowing direct comparisons across attributes, such as in network analyses (C), which show how recovery is coordinated across forest attributes. The widths of paths among attributes indicate the strength of the coordination. The different colors indicate attribute category: soil (brown), plant functioning (purple), structure (green), and diversity (turquoise). (**D**) Map of the 77 study sites in the neotropics and West Africa (for site numbers, see table S1). Potential forest cover is shown in green.

for the sustainability of shifting cultivation agriculture, which coincides with agronomic studies that indicate that a fallow period of more than 8 to 10 years allows agricultural productivity to be maintained (*21*).

Plant functioning was evaluated in terms of basal area–weighted community WD and SLA and the percentage basal area of nitrogen-fixing trees. WD is the stem-wood dry mass divided by stem volume, and it increases tissue longevity and carbon residence time in trees and forests. SLA is the leaf area divided by the leaf mass. It reflects leaf display cost and scales positively with photosynthetic capacity and forest productivity and negatively with leaf longevity. WD and SLA change during secondary succession because pioneer species are typically replaced by later-successional species with opposite trait values (*24*). Nitrogen fixation indicates the potential for biological nitrogen input to trees and forests. Nitrogen fixation is generally high early in succession when irradiance is high and trees can support their nitrogen-fixing symbionts with carbohydrates (*23*) and declines over time as forests regrow

(*15*), light availability in the stand drops, and nitrogen fixation becomes too costly (*23*).

Recovery of ecosystem processes depends on the characteristics of species that make up the community. Although SC may recover slowly, we expected plant functioning to recover at an intermediate pace because many OGF species have similar (i.e., redundant) trait values. We found that plant functioning recovers surprisingly fast (R_{20y} of 82 to 100% and an average RT of 3 to 27 years; Fig. 3, B and D). During succession, short-lived pioneer species (with life spans of 10 to 30 years and extreme trait values) are rapidly replaced by later-successional species that are functionally similar to one another but different from pioneer species (*25*), which leads to a fast functional recovery. Additionally, resprouting is a common mode of regeneration on abandoned fields, which explains why the functional composition rapidly resembles that of the previous OGF [(*26*); Fig. 3A]. Finally, fast recovery also occurs because traits such as SLA and WD never have values of zero and, therefore, start closer to OGF values (85 and

76%, respectively) than, for example, the proportion of nitrogen-fixing trees (40%; Fig. 3A).

Forest structure was evaluated in terms of AGB, maximum tree size (Dmax), and SH. AGB is a strong driver of ecosystem processes (*27*) and important for carbon storage and climate change mitigation (*16*). Dmax reflects the presence of large trees that have a high conservation value, providing habitat and food for many organisms. SH refers to the tree size variation in a plot; it increases light capture and ecosystem productivity (*18*) and contributes to biodiversity conservation by providing a habitat for different species.

We expected forest structure to recover faster than soil and trait attributes because all trees and species contribute to forest structure, but we found that it occurs at an intermediate pace (R_{20y} of 33 to 83% and an average RT of 27 to 119 years; Fig. 3, B and D), probably because it often starts close to zero. SH recovered at an intermediate pace, probably because it increases with Dmax and because it reflects a gradual transition from even-aged forest that establishes just after land abandonment toward uneven-aged forest with continuous regeneration and multiple cohorts. Recovery of Dmax took more time because it depends on the identity and growth of individual trees. AGB had the slowest recovery because large trees drive AGB (*28*) and because of low productivity in later successional stages (*16*). The RT of 12 decades for AGB is substantially longer than the seven decades we previously estimated, owing to differences in the number of study sites (77 versus 43) and modeling approach (*18*).

Diversity was evaluated in terms of SR, Simpson diversity (SD), and SC. SR is directly relevant for conservation, because it indicates the number of locally co-occurring species. SD indicates the diversity of common species and reflects successional shifts in community structure from young forests dominated by few pioneer species to diverse forests with many rare species. SC indicates to what extent the SC in an area (i.e., the identity of species and their relative abundance) resembles that of an OGF and thus indicates the quality of diversity and the value of SFs for the conservation of old-growth species. SR, species diversity, and SC usually start close to zero (Fig. 3A) with few or no woody plants, owing to biomass and species removal for previous land use, and increase over time as seeds germinate from the seed bank and new species arrive and get established.

Recovery of species diversity and SC occurred at an intermediate to slow pace. SR recovered fastest (R_{20y} = 78%, RT = 37 years) because early in succession, biodiversity can be high because both light-demanding early-successional and shade-tolerant later-successional species coexist (*11, 29*). SD recovered more slowly (R_{20y} = 69%,

RT = 59 years) because it takes time before competition leads to more equal species abundances. SC recovered slowest (R$_{20y}$ = 33%, RT = 120 years) because it depends on overcoming dispersal and recruitment limitations, the accumulation of rare shade-tolerant species, and tree turnover (which takes decades to centuries). Recovery in SC varied substantially across sites (as indicated by wide credibility intervals; Fig. 3D), possibly because sites vary in the drivers of succession, such as land-use history, the number and identity of remnant trees, proximity to seed sources, resprouting ability, and the proportion of wind-dispersed tree species in the community (*17*).

We used a chronosequence approach to infer long-term recovery because few studies have monitored succession over time. Our approach assumes that all plots within a chronosequence had similar starting conditions and follow a similar recovery trajectory, which is not necessarily the case (*9, 30*). SF chronosequence studies that also monitored dynamics over time showed that dynamic pathways in species diversity, SC, and species structure generally matched chronosequence trends but also showed deviations for some plots (*31, 32*). Instantaneous trends could show a faster increase for diversity and similar trends for composition and basal area compared with chronosequence predictions (*31, 32*). Hence, the patterns we observed in this study should be corroborated by long-term studies that monitor SF dynamics over time.

Network properties and proxies for multidimensional recovery

We hypothesized that recovery of different forest attributes would be positively correlated, because recovery of certain attributes (e.g., biomass) can facilitate that of others (e.g., soil C) or can only occur when recovery of other attributes occurs simultaneously. We performed network analyses of relative recovery of multiple attributes after 20 years. The first network analysis was based on pairwise correlations among all 12 attributes and showed that recovery of attributes occurred in parallel (Fig. 4A), with the highest expected influence (i.e., many links with other attributes) for SC, followed by the three structural attributes and soil C (Fig. 4C). This was also confirmed by the results of a principal components analysis, which showed similar associations between recovery of different forest attributes (fig. S3).

The second network analysis was based on partial correlations—i.e., accounting for the variation explained by other attributes—thus showing independent, causal links between attributes. We focused on seven forest attributes that were measured at most study sites (*N* = 74). We found two clusters of attributes

whose recovery is likely to be causally linked (Fig. 4B). First, recovery of the three structural attributes was highly connected, because large trees (Dmax) lead to large SH and contribute disproportionally to forest biomass (AGB). Forests with more biomass also have a more complex structure. Second, recovery in SR and SD were positively linked, because both increase during succession when species arrive.

When the analysis was repeated for the 43 sites for which SC was also included, a third cluster emerged that showed that recovery in SC, WD, and nitrogen fixation were linked (fig. S4). This may be explained by the fact that succession in SC is underlain by concomitant changes in WD because in wet forests, pioneer species with low WD are replaced by OGF species with high WD, whereas in dry forests, pioneer species with high WD are replaced by OGF species with low WD (*24*).

The clustering of forest attributes into multiple groups suggests that recovery of different forest attributes is shaped by different drivers or processes. For example, recovery of biodi-

versity attributes may be driven by the landscape context (*17*), land-use history, and the availability of seed trees and dispersal vectors, whereas recovery of structural attributes may be driven by resource availability [i.e., water availability, soil fertility (*16*), and remnant trees].

We hypothesized that AGB would be the best predictor of multidimensional recovery because ecosystem processes and flux rates strongly depend upon the amount of vegetation. Instead, we found that recovery of Dmax had the highest influence (Fig. 4D), indicating that it is strongly linked with other forest structural attributes. The largest tree can be one that regenerated during succession or is a remnant from previous land use. Remnant trees may act as nuclei of forest regeneration (*33*) and kickstart succession (*34*) because they improve microclimate and soil conditions, attract frugivorous seed dispersers (*35*), and favor regeneration of old-growth species. This network structure of forest recovery may be affected by future climate change, but at this stage, we cannot predict how.
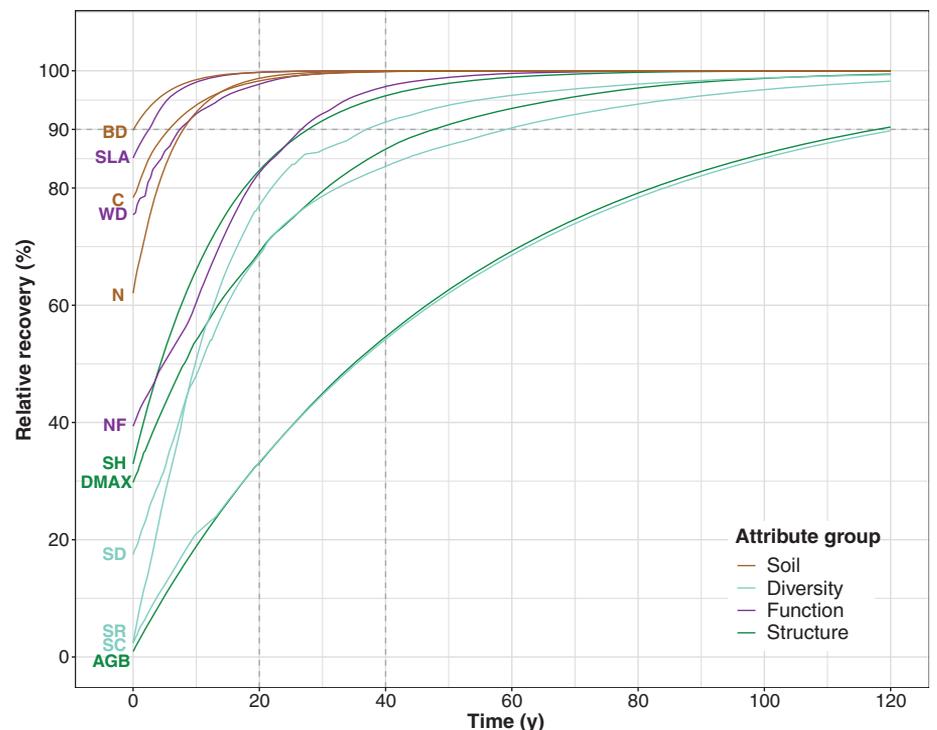

Fig. 2. Predicted relative recovery trajectories over time for 12 forest attributes. The attributes are related to soil (brown), plant functioning (purple), structure (green), and diversity (turquoise). Relative recovery is expressed for each attribute as the similarity (in percentage) between the predicted age-dependent SF value and the OGF value. For some attributes, absolute values increase over time (e.g., AGB), whereas for other attributes, the absolute values generally decrease over time (e.g., BD) (compare Fig. 1A). Here, we show similarity with OGF values, which, by definition, increases over time (compare Fig. 1B). Succession often starts with some remnant trees and soil legacies, and some attributes (SLA and WD) can never be zero, which explains why most attributes do not start at zero (see main text). Dashed lines indicate relative recovery at 20 years, recovery at 40 years, and RT until 90% recovery toward OGF values (see Fig. 3). Recovery trajectories are across-site median values were estimated by using Bayesian models for each attribute (see supplementary text S1). C, soil C; N, soil N; NF, proportional basal area of nitrogen-fixing species; SLA, community-weighted mean SLA; WD, community-weighted mean WD.

To assess and monitor ecosystem recovery, we aimed to identify indicators that change continuously during succession and that are closely correlated with recovery of other ecosystem properties and functions. To be operational, the indicators should be easy to measure, scalable, and cost-effective to implement and use (*36*). To serve simultaneously as resilience indicators, they should be slowly changing variables that underlie ecosystem capacity to recover (*5*). We identified three clusters of forest attributes, related to structure, species diversity, and SC (Fig. 4D and fig. S4B). Dmax and SH are robust indicators of structural recovery; they take, respectively, 5 and 2.5 decades to recover, have a central position in the multidimensional recovery network, and can easily be measured and monitored, either in the field or by remote sensing (*37*). Recovery of Dmax is strongly linked to recovery of AGB, which is more time consuming to measure, but Dmax is weakly linked to

recovery of biodiversity attributes (Fig. 4B). Hence, SR should be used as an additional indicator, because it is more closely linked to the recovery of other biodiversity attributes. A large number of species also ensures that there is a large diversity in species responses to environmental conditions, which increases the adaptive capacity of ecosystems to deal with environmental change (*38*). When these slower indicators have recovered, faster attributes, such as soil and plant functioning, will have recovered as well (Fig. 3D).

Resilience

We assessed the resilience of forest attributes on the basis of the relative starting value at agricultural abandonment (t_0; resistance) and subsequent recovery rates (λ) during secondary succession. Aboveground attributes such as structure and diversity had low starting values because of the nearly complete removal of woody vegetation for agricultural use, whereas

soil attributes had high starting values because of belowground legacies (Fig. 3A). We found that resistance and recovery were positively correlated [correlation coefficient (r) = 0.78, P = 0.0026; fig. S5), which partially explains why some attributes recover quickly and others slowly. All 12 attributes recovered close to their predisturbance values within ~120 years (Figs. 2 and 3D), which is notably fast given that tropical forests are complex in terms of structure, SR, evenness, and plant interactions (*6*). Fast forest recovery during secondary succession can be explained by the many legacies and the relatively productive, warm, and wet conditions of most study sites. We show that tropical forests are resilient to agricultural use, provided that agricultural use has not been too long, intense (*39*), or extensive and that there is sufficient forest in the surrounding area to provide seeds (*40*). Average RTs of the 12 attributes varied from <1 to 12 decades. To assess ecological resilience, the attributes
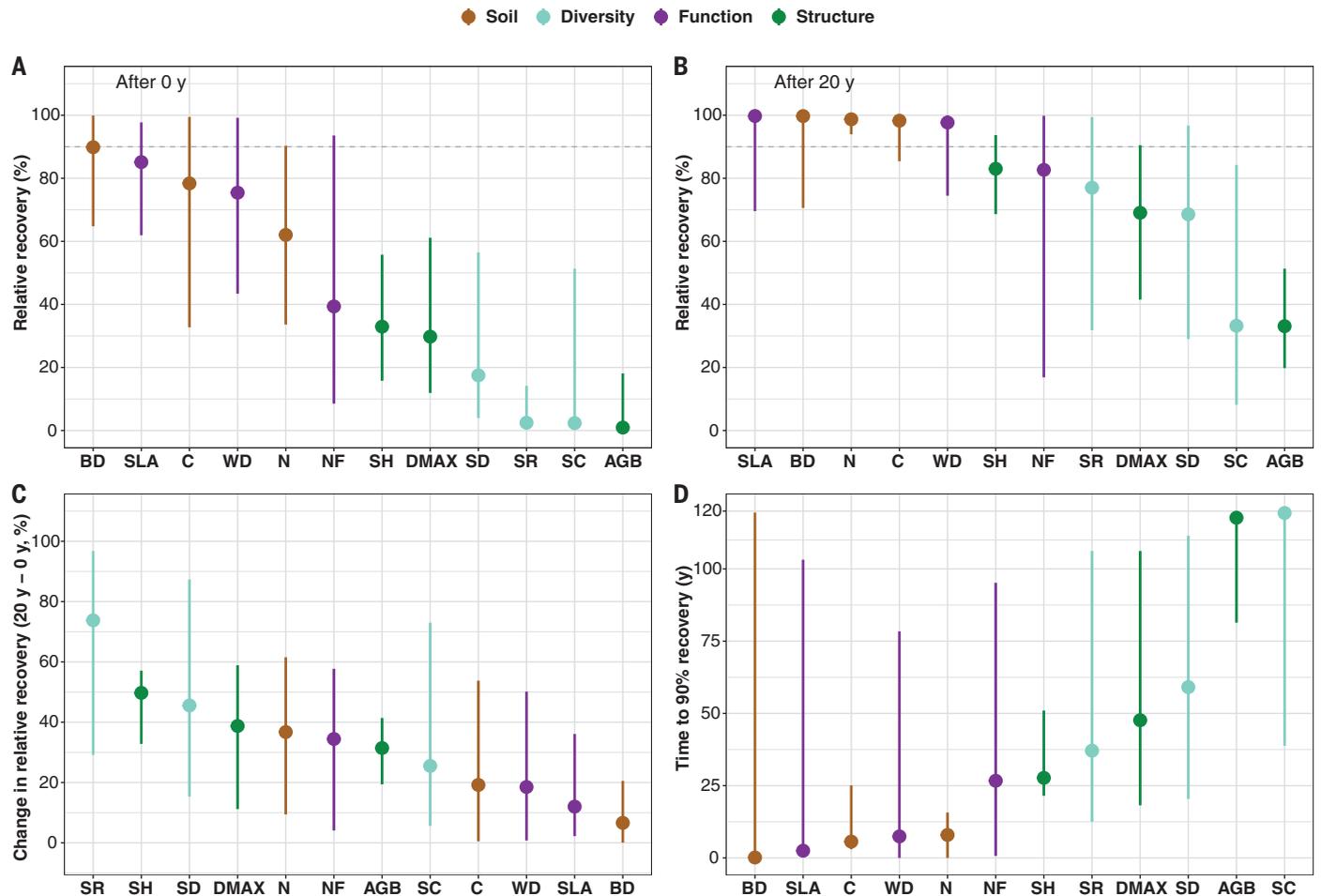
Fig. 3. Relative recovery of SF attributes. (**A**) Recovery at land abandonment (0 year). (**B**) Recovery at 20 years. (**C**) Difference in recovery between 0 and 20 years ($R_{20y} − R_{0y}$). (**D**) RT until 90% recovery toward OGF values. Relative recovery is expressed as the similarity (in percentage) between the SF value and the OGF value. Medians and 95% credible intervals are based on site predictions;

N = 21 sites for soil attributes, 31 for SLA, 46 for SC, and 77 for all the other attributes. The credible intervals nearly correspond to the range of observations, and in (D), it has been truncated to 120 years to increase resolution. The attributes are related to soil, plant functioning, structure, and diversity and are ranked from fast (left) to slow (right).

and time frames that are considered [compare (5)] are therefore crucial, because soil scientists would consider forests to be highly resilient on the basis of soil legacies, whereas conservationists would consider forests to have low resilience on the basis of the slow recovery of SC.

Applied implications

SFs cover large areas and provide multiple services to local and global stakeholders (3). Their fast multidimensional recovery has important implications for ecosystem restoration, climate change mitigation, and biodiversity conservation. Rapid recovery of plant functioning suggests that restoration of ecosystem functioning (such as productivity) should be similarly rapid, because it is underpinned by the traits used in this study (41). Rapid soil N and C recovery indicate that natural regrowth provides an inexpensive, nature-based solution to restore the fertility of agricultural lands. Rapid recovery of soil C is crucial for climate

change mitigation. The soil C pool exceeds that of biomass and is more persistent because it is less affected by aboveground disturbances, such as fire and clearing. Rapid recovery in SR means that SFs form an important biodiversity reservoir in human-modified landscapes and should be conserved (17). This will also lead to greater connectivity for plants and animals in fragmented, human-modified landscapes.

Although SFs show, on average, a rapid recovery, there is also substantial variation across the study region (see credibility intervals in Fig. 3), which indicates that some areas may show arrested succession because of a lack of seed sources or dominance of invasive grass, ferns, or woody species. Under such conditions, management practices for assisted natural regeneration—such as weeding, controlling invasive species, enrichment planting, and the establishment of ecological corridors—are needed to safeguard multidimensional recovery.

Given the local and global importance of SFs and their substantial R_{20y} (on average, 78%;

range, 33 to 100%; Fig. 3B), we urge the embrace of SFs as a low-cost, nature-based solution to meet the United Nations' Sustainable Development goals and the United Nations' Decade on Ecosystem Restoration goals (42). Enabling policies combined with careful landscape planning should identify areas where SFs are best conserved and provide the most co-benefits while minimizing socioecological conflicts [e.g., (3, 4)]. SFs should feature prominently in restoration portfolios, where older SFs and OGFs are conserved, severely degraded areas are actively restored, and young regrowth is protected from deforestation. For example, SFs can only deliver their full conservation potential if they are conserved for a sufficient amount of time, such that tree species can attain reproductive maturity and maintain viable populations (43). In addition, substantial gains are made when young, 20-year-old SFs are conserved for 20 years more, because AGB, SR, and similarity with OGFs increase by 15 to 22% (fig. S1C). All OGFs

Fig. 4. Network analysis for relative recovery of attributes after 20 years. (**A** to **D**) The networks are based on Pearson's correlations for 12 attributes (left panels) and partial correlations for seven attributes (right panels). (A) and (B) show connectivity among SF attributes. (C) and (D) show expected influence of individual attributes on the network. The correlation network to the left indicates how attributes are associated with one another and uses, for each pairwise correlation, the maximum number of sites possible (N = 17 to 77; table S2). The partial correlation network indicates the direct links between two attributes, independent from others, and is based on a subset of attributes available for most sites (N = 74 sites). In (A) and (B), the line thickness indicates the strength of the (partial) correlation, and lines indicate significant pairwise correlations (i.e., with a 95% confidence interval that does not overlap with zero). The expected influence is the sum of the partial correlations between the target attribute and other attributes. Edge weights and expected influence were estimated from 10,000 bootstraps of the empirical network, and the bootstraps were used to calculate the 95% confidence intervals displayed in (C) and (D). Soil attributes were based on a smaller sample size (N = 21)

and therefore had wider credibility intervals. The spinglass algorithm identified three clusters in (A) (AGB-Dmax-SH-C-N, BD-NF, and SC-SR-SD-SLA-WD) and two clusters in (B) (AGB-Dmax-SH and SR-SD). For the partial network, the correlation stability coefficient was 0.43 for edge weights and 0.51 for expected influence. Attributes are colored according to their category: soil (brown), plant functioning (purple), structure (green), and diversity (turquoise).
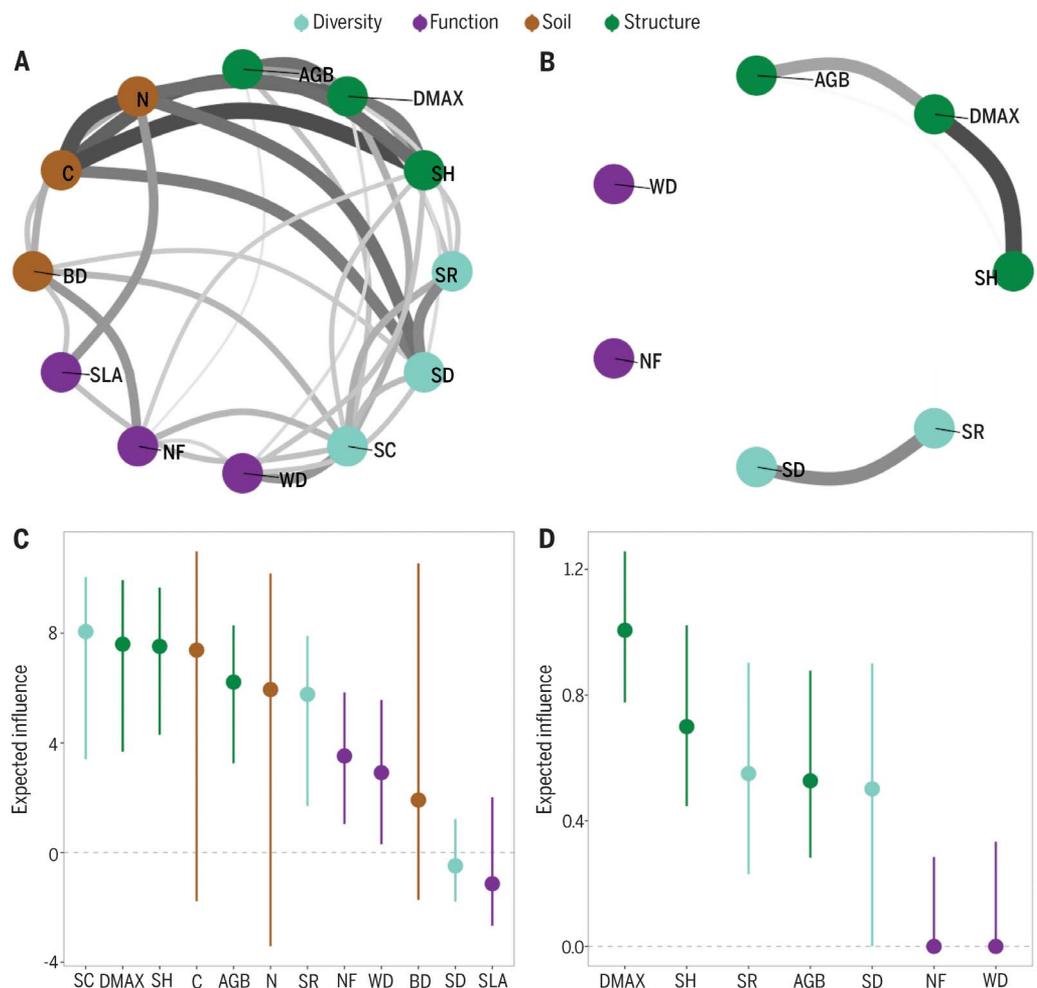
should be conserved because little remains; they harbor many distinctive OGF species and provide seed sources and dispersers to assure landscape resilience (*17, 40*). To monitor passive and active restoration success, we recommend using simple indicators in different phases of succession, in which SH can be used for the first 25 years (Fig. 3D) and Dmax and SR in the following 25 years.

Conclusions

Our analysis shows that tropical forests and their soils are highly resilient because all attributes recover within 12 decades after low- to moderate-intensity land use. Recovery of soil attributes (<1 decade) and plant functional attributes (<2.5 decades) is very fast, followed by recovery of structure and diversity (2.5 to 6 decades), and recovery of AGB and SC is slowest (12 decades). Network analysis shows that recovery is multidimensional, with three clusters of attributes related to structure, SR, and SC. Monitoring of forest restoration could use Dmax, SH, and SR as complementary indicators of multidimensional recovery.

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Multidimensional tropical forest recovery

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Resilient secondary tropical forests?

Although deforestation is rampant across the tropics, forest has a strong capacity to regrow on abandoned lands. These "secondary" forests may increasingly play important roles in biodiversity conservation, climate change mitigation, and landscape restoration. Poorter *et al.* analyzed the patterns of recovery in forest attributes (related to soil, plant functioning, structure, and diversity) in 77 secondary forest sites in the Americas and West Africa. They found that different attributes recovered at different rates, with soil recovering in less than a decade and species diversity and biomass recovering in little more than a century. The authors discuss how these findings can be applied in efforts to promote forest restoration. —AMS

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