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TYPE:	Article CC:CCG
JOURNAL TITLE:	Nature Reviews Biodiversity
USER JOURNAL TITLE:	Nature Reviews Biodiversity
ARTICLE TITLE:	Drivers and benefits of natural regeneration in tropical forests
ARTICLE AUTHOR:	Robin L. Chazdon, Nico Blüthgen, Pedro H. S. Branc
VOLUME:	
ISSUE:	
MONTH:	
YEAR:	2025
PAGES:	
ISSN:	3005-0677
OCLC #:	

Processed by RapidX:	5/13/2025 11:36:32 AM

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nature reviews biodiversity

https://doi.org/10.1038/s44358-025-00043-y

Review article

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Drivers and benefits of natural regeneration in tropical forests

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Abstract

Natural regeneration of tropical forests following deforestation and land degradation offers scalable and cost-effective opportunities for recovery of forest structure, return of native species and delivery of ecosystem services, but requires suitable biophysical and socioeconomic conditions. In this Review, we assess the global extent and distribution of regenerating moist and dry tropical forests and review their contributions to nature and people. Local and landscape factors (such as the extent and type of agriculture and forests in surrounding areas) influence whether forest regeneration occurs and to what extent forest properties can recover. Advances in detection, monitoring and prediction of natural regeneration potential inform how to scale-up cost-effective restoration programmes and to create policies that promote forest recovery. We frame forest regeneration as a complex socioecological system and encourage transdisciplinary research agendas that focus on how to promote broad social, cultural, economic and environmental benefits offered by effective management and protection of regenerating tropical forests. Key steps to harness the local and regional potential for natural regeneration are to integrate forest regeneration with management, conservation and productive activities that benefit local communities, support livelihoods and provide attractive returns on investments.

Sections

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Key points

- Advances in detection, monitoring and prediction of natural regeneration inform how to scale-up cost-effective restoration programmes and to create policies that support forest recovery.

- Tropical forest regeneration is a key nature-based solution for climate change mitigation and biodiversity conservation. Regenerating forests offer substantial, but overlooked, potential for emerging markets of carbon and biodiversity credits and payments for environmental services programmes. Such initiatives could mobilize critically needed financial resources for restoration of native forests for local communities.

- A combination of ecological, social and policy drivers influences the quality and quantity of natural regeneration in a particular area. Recovery trajectories and attributes of natural regeneration vary considerably over time and across different contexts, reflecting land-use legacies, management of recovering forests, climate, soils, landscape composition and regional species pools.

- Recovering forests can be assessed in terms of structure, diversity and taxonomic and functional composition, with recovery times for different forest attributes varying from a few months to over a century. Recovery is fastest for soil and plant functioning, intermediate for structure and tree species diversity and slowest for biomass accumulation and tree species composition.

- Although many animal taxa are lost when forests are converted to agriculture, their diversity and abundance can recover during forest regeneration. Plant–animal mutualisms such as seed dispersal, pollination, herbivory and seed predation shape tropical forest recovery. Recovery of species interaction networks could improve the level and potentially the stability of ecosystem functions.

- The dynamics of regenerating forests are embedded within the dynamics of complex spatial units such as landscapes and watersheds, directly linking the fate of these forests to livelihoods, values and rights of people who live and work in these landscapes.

Introduction

Tropical forests make critical global contributions to climate change mitigation[1] and to human well-being[2]. Although they cover only 18% of global land area, tropical forests are habitats for 62% of the world's terrestrial vertebrate species[3], for more than 77% of the tree species[4] and for hundreds of thousands of insect species, most of which are currently undescribed[5]. Between 14% and 34% of the world's migratory bird species spend their winters in tropical forests[3]. Threatened tree species compose 30–41% of the tree flora in tropical moist and dry forests[6], with the value rising to 80% in some highly deforested regions[7]. Despite increased carbon emissions from tropical deforestation, the net carbon sink in Earth's forests from 1990 to 2019 remained positive, with regrowth of tropical forests and new plantations accounting for 58% of the tropical forest carbon sink[8]. Given their importance to biodiversity and carbon storage, the natural regeneration of tropical forests offers vital opportunities for recovery of forest functions, return of local native species, re-establishment of key species interactions and delivery of multiple ecosystem services including climate mitigation[9,10].

Natural regeneration of forests is an ecological process that leads to the re-establishment and recovery of a native forest ecosystem through natural seedling establishment or resprouting. Also known in the ecological literature as secondary succession, natural regeneration allows forest ecosystems to rebuild and reassemble over long timescales following natural and human-caused disturbances, such as selective logging, fire, windthrow and large-scale conversion to agricultural land uses. Regenerating forests can be classified into two different types, depending on the intensity and type of disturbance: (1) when the disturbance was below a certain threshold of intensity, such that the post-disturbance system can still be classified as a forest, the forest is called a 'recovering degraded forest' or (2) when the disturbance resulted in complete conversion of forest to another land-use type before regrowth occurred, the forest is called a 'secondary regrowth forest'. The recovery of degraded forests following logging or fire typically requires a baseline level of abundance and diversity of remnant forest species. However, regeneration capacity can be limited by intensive former land use and persistent forest degradation and loss[11].

Natural regeneration of tropical forests can contribute substantially to the Kunming–Montreal Biodiversity Framework[12], the UN Sustainable Development Goals[13], the Bonn Challenge[14] and the UN Decade on Ecosystem Restoration[15]. Regenerating forests provide habitats and connectivity for forest-dependent plant, animal and insect species[16] and buffer human impacts on old-growth forest fragments[17]. After avoiding deforestation, natural forest regeneration is the most cost-effective climate mitigation strategy in many tropical countries, especially in Brazil, Indonesia and Democratic Republic of Congo[18]. Tropical forest regeneration can be a key approach for emerging markets of carbon and biodiversity credits and payments for environmental services programmes, which could mobilize unprecedented financial resources for restoration and provide critical economic support for local communities[19]. Targeted human interventions aimed to assist natural regeneration (Box 1) can accelerate ecological recovery processes while enhancing economic benefits for communities within landscapes and watersheds[20,21]. Assisting the regeneration of tropical forests through practices that enhance native species diversity, useful species, productivity and persistence (Box 1) serves the needs of local communities and Indigenous Peoples who appreciate their cultural value, economic uses and management potential[22,23].

Ongoing high rates of tropical deforestation and the associated expansion of agricultural land uses have created an enormous opportunity for natural regeneration to restore native biodiversity[24], forest functions[25] and ecosystem services[26]. Although tropical forest regeneration is the theme of previous synthesis and reviews[27–29], the knowledge base on tropical forest regeneration is rapidly growing and has increasing relevance to contemporary decision-making processes, justifying an updated review of the state-of-the-art knowledge on the drivers and outcomes of tropical forest regeneration in a socioecological systems context.

This Review highlights key research and methodological advances that can propel the relevance and application of natural forest regeneration in the tropics as a nature-based solution for multiple global problems. After presenting the latest assessments of global cover and distribution of regenerating tropical moist and dry forests, we highlight findings regarding the ecology of natural regeneration, including predictors of the quality and quantity of regeneration; variation in recovery trajectories; recovery of species attributes, functional traits and interactions; and recovery of ecosystem functions and services.

We place natural regeneration in a socioecological systems context by summarizing how ecosystem goods, services and contributions to people recover during secondary forest regrowth. We conclude by identifying research and policy gaps that motivate interdisciplinary research agendas aimed to complement knowledge of ecological recovery processes and tools for assessment and monitoring of tropical forest regeneration across the global tropics.

Detection and monitoring of natural regeneration

In this section, we summarize how natural regeneration is detected, measured and mapped across the world's tropical regions. We discuss advances in technology that facilitate the detection and monitoring of naturally regenerating forests and their biodiversity and show the current known global extent of regenerating tropical forests.

Monitoring advances

The Landsat archive[30] in combination with new satellite-based sensors has advanced understanding of regenerating forests and land-use dynamics. Although Landsat's moderate spatial resolution (30 m) combined with its inability to penetrate through clouds offers challenges for monitoring tropical moist forest dynamics, the long temporal record of Landsat has resulted in the creation of numerous forest disturbance datasets. Such datasets disaggregate natural regeneration from plantations and other land uses[31–33], crucial for determining different types of regeneration. Combining this long-term record with static multisensor maps of biomass[34] improves the ability to quantify the rate of carbon recovery in young regenerating forests[35,36]. Using a combination of different wall-to-wall (complete spatial coverage) satellite-based products identifying forest age classes and their associated aboveground biomass demonstrates the ability of Earth observation data to produce biomass stock values that are comparable to current definitions used by the Intergovernmental Panel on Climate Change[37]. Large uncertainties and biases in global maps remain, especially in low biomass areas (for example, young secondary forest), requiring adjustments with high density field data[38].

The space-based LiDAR (light detection and ranging) mission – Global Ecosystem Dynamics Investigation (GEDI) – gives higher levels of detail on vertical forest structural changes during recovery[39] compared with prior remote-sensing missions. However, studying very young forests with GEDI can be challenging because vegetation shorter than ~2.5 m interferes with the ground signal[40]. Datasets from GEDI, Sentinel-1's cloud-penetrating 10 m RADAR (radio detection and ranging) and Planet imagery are limited in their temporal coverage (since 2015, 2017 and 2018 for Sentinel-1, Planet and GEDI, respectively), but offer high spatial and subannual detail, crucial aspects for detecting disturbance and recovery across the tropics[41–43]. For example, GEDI and Sentinel-2 data or other multispectral data can be combined to estimate post-disturbance aboveground carbon fluxes[44].

High-resolution data collection using aeroplanes and unmanned aerial vehicles allows for deeper insights about the recovery of tropical forest structure and diversity in regenerating forests than can be obtained solely from satellite-based sensors (Fig. 1). These methods include passive sensors, such as those collecting hyperspectral and multispectral and thermal images, and active sensors, such as LiDAR and RADAR[45]. The main applications include the assessment of (1) forest aboveground biomass, which closely correlates with LiDAR and RADAR metrics of forest structure such as canopy height[46,47], (2) tree diversity, estimated on the basis of the association between tree diversity and canopy spectral diversity[48,49] and (3) tree composition, evaluated through combining high-resolution optical images with different artificial intelligence approaches[50,51]. Advances in these technologies enable monitoring of many other features of tropical forests, including canopy openness[52,53], vertical stratification[54] and liana abundance[55].

Parallel to the improved sensor-based techniques to identify trees and vegetation, technological advances including environmental DNA and metabarcoding sequencing, automated detection by image or sound sensors and artificial intelligence species identification have been used to assess the recovery of animal species. Sound recorders deployed along successional gradients confirmed the recovery of bird communities in secondary dry forests following ranching and farming[56] and wet tropical forest following pasture and cacao plantations[57]. The latter study used automated detection of a subset of bird sounds using deep learning in addition to established expert identification, highlighting the potential for autonomous monitoring programmes including other sound-producing taxa such as mammals, amphibians and insects[58].

Molecular methods such as barcoding and metabarcoding DNA or RNA sequences can greatly enhance the scope of biodiversity monitoring across regions by broadening the monitoring targets and including species interactions and poorly known taxonomic groups[59]. Metabarcoding is standard for monitoring microorganisms in recovering forest soils[60], but also improves surveys of all larger organisms by sampling environmental DNA or for large mixed samples collected by insect traps[57,61]. These methods are used to quantify resource use and interactions between species, such as gut content of predators, mammal dung used by dung beetles[62] or pollen carried by flower visitors[63].

Spatial extent

Efforts to detect regenerating and recovering forests following land conversion and forest degradation have increased since 2015. Much of this large-scale research has focused on the tropical moist forest domain, which includes all closed forests in the humid tropics[32,36]. Earth

Box 1 | Assisted natural regeneration

Where and when local and landscape conditions impede natural regeneration processes[28,268], management interventions are needed to overcome these obstacles to assist the recovery of vegetation, diversity of native species and enhance establishment of later successional species or functional groups[269–271]. Assisted natural regeneration (ANR) is a set of restoration practices and interventions designed to enhance and accelerate the recovery of ecosystems by overcoming specific barriers[272–274]. These strategies can include the rewilding of animal species; control of invasive grasses, ferns or shrubs, hyperabundant lianas; protection from wildfires and cattle grazing; and targeted enrichment planting of native species that fail to regenerate on their own[220,275–277]. The most appropriate ANR interventions are tailored to particular natural and managed ecosystems, socioeconomic conditions and landscape contexts. For example, in grazing landscapes, fencing is often needed to restrict grazing animals from consuming or trampling regenerating vegetation, and removal of invasive species is often required when they compete with native species. Under suitable conditions, ANR can facilitate the recovery of native biodiversity, contribute to climate change mitigation and adaptation and enhance ecosystem resilience. Native tree species regenerated through ANR can exhibit superior adaptation to local site conditions and climate change than planted trees, especially non-native tree species[278–280].

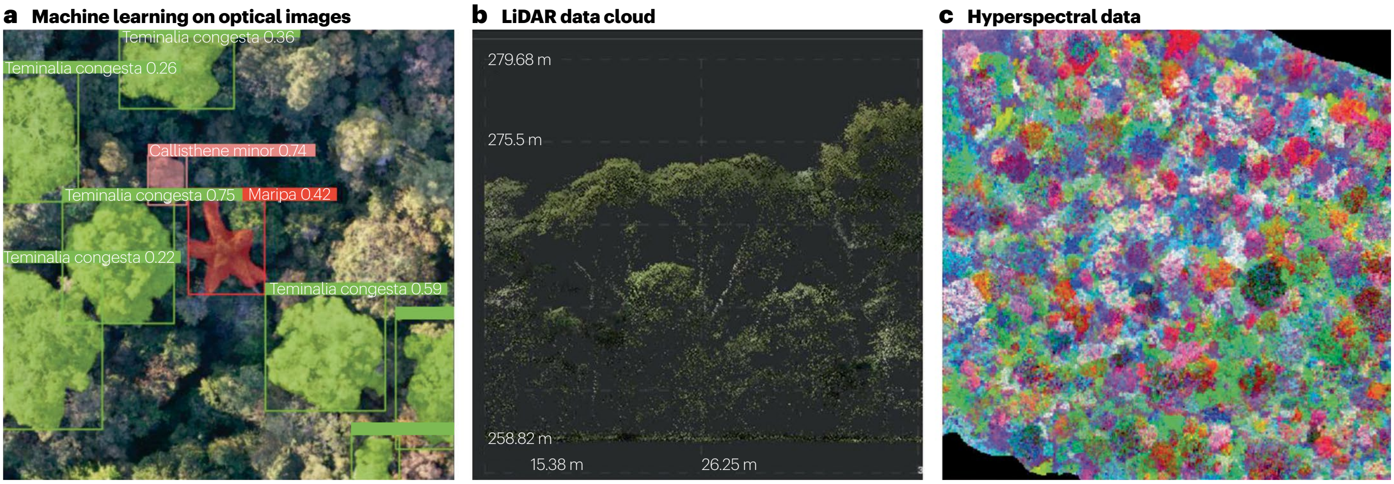


Fig. 1 | Examples of remote-sensing technologies to monitor tropical forest regeneration. a, High-resolution optical images analysed with machine-learning algorithms can identify individual tree and palm species. **b**, A light detection and ranging (LiDAR) data cloud can be used to generate different metrics of forest structure. **c**, Spectral reflectance using hyperspectral data can be used to assess tree species and functional diversity. Images courtesy of Paulo Guilherme Molin.

observation datasets, such as the Landsat archive beginning in the 1980s, enable detection of where forests are regenerating following degradation and conversion to non-forest land uses, with the 'years since the last disturbance' (YSLD) as a proxy for forest age (Fig. 2).

In Brazil alone, an estimated 14.9 million (M) ha of forests were regrowing on previously deforested land in 2018 (ref. 64). Since 2021, large-scale datasets reveal the spatial extent and temporal patterns of regenerating forests following both degradation (degraded forest baseline) and deforestation (non-forest land-use baseline)[32,65,66] based on two major disturbance categories for tropical forest lands (Fig. 2). Forests that have not been disturbed for at least 40 (wet regions) and 20 (dry regions) years ('Recently undisturbed forests') still predominate across tropical land (Supplementary Fig. 1 and Table 1). Outside these recently undisturbed forest areas, tree cover (including forest plantations) is composed of young, naturally regenerating forests with less than 40 (moist regions) or 20 (dry regions) years since disturbance.

Collectively, spatial datasets[32,65,66] show that regenerating tropical moist and dry forests across the Americas, Africa, Asia and Oceania span 202 Mha of land in 2023, almost equivalent to the area of forest loss that occurred across these areas (225.5 Mha) (Supplementary Fig. 2 and Table 1). The Americas have the largest area of regenerating tropical moist forest (74.2 Mha), whereas Africa contains the largest area of regenerating tropical dry forests (9.1 Mha) (Table 1). Because of frequent re-clearance for land use, forests regenerating following deforestation are generally young, with the median YSLD below 10 years across all regenerating tropical forests (Fig. 2). Determining the ages and extents of regenerating forests is currently limited by the 20–40-year period of satellite products, but can be extended using machine-learning approaches[67].

The ecology of natural regeneration

The regeneration process manifests as dynamics of individuals, populations, communities and ecosystem functions. At any particular place, forest regeneration is driven by the complex interaction of species traits and ecological requirements, regional species pools, disturbance regimes and land-use and landscape legacies[27,68,69]. At any particular time, a regenerating forest embodies elements of the past, present and future. Recovery trajectories generally follow deterministic themes, but vary widely, reflecting a high degree of stochasticity and land-use legacies[70–73]. In this section, we discuss emerging understanding of the process of natural regeneration, highlighting key studies about the predictors of the quantity and quality of natural regeneration following land-use conversion, and the patterns of recovery of forest attributes, species interactions and functional traits that affect ecosystem functions.

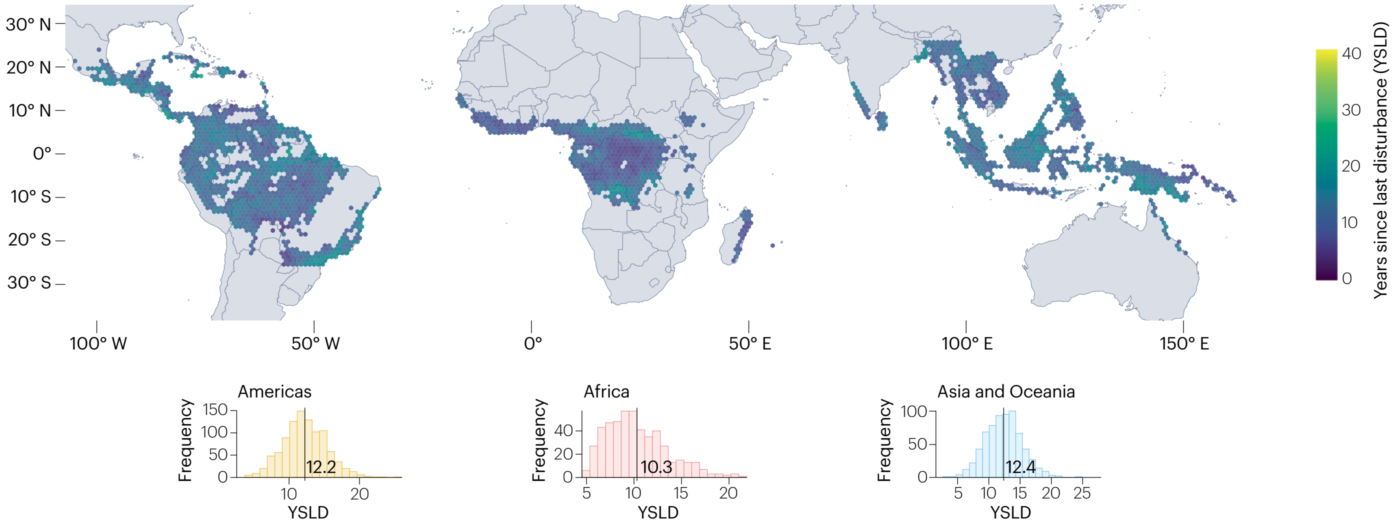
Predictors of the quantity and quality of natural regeneration

Conditions that vary widely within and across landscapes determine both the likelihood that regeneration occurs and the quality of regenerated forests (Fig. 3).

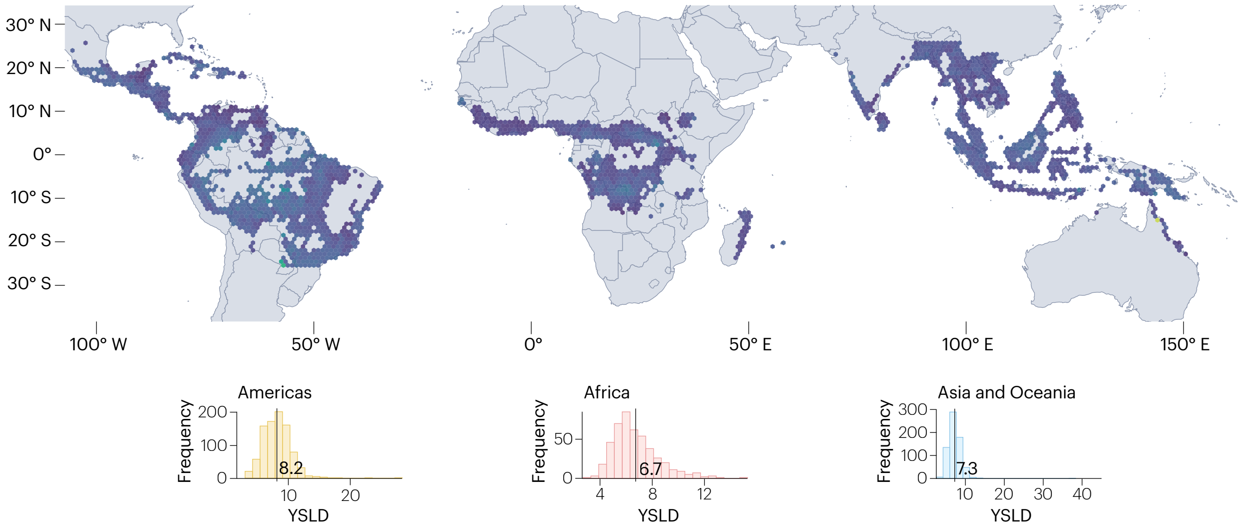
Quantity. Existing data on spontaneous forest regeneration confirm a strong spatial dependence on close proximity to mature forest

Fig. 2 | The average years since the last disturbance event and spatial distribution of regenerating tropical forests in 2023. a, The distribution of 'years since last disturbance' (YSLD) of recovering degraded tropical moist forest. Data from version 'TMFv2023' of the Joint Research Council Tropical Moist Forest dataset[32] are aggregated within each 1° hexagonal grid. Grid cells are only shown if the forest type occupies more than 1% of the gird space. Histograms below the map show the frequency distribution and average (vertical black line) of YSLD for each region. **b**, As in part **a**, but for secondary regrowth tropical moist forest. **c**, As in part **a**, but for regenerating tropical dry forest. Data are based on a compilation of datasets (Supplementary Fig. 2); unlike in tropical moist forests (parts **a** and **b**), it is not possible to determine whether a regenerating tropical dry forest was a recovering degraded or a secondary regrowth forest. For parts **a** and **b**, the time period is from 1984 to 2023 (40 years of disturbance history), and for part **c**, the time period is from 2001 to 2023 (23 years of disturbance history). Code to create the figure was based on published code from ref. 40.

a Recovering degraded tropical moist forest



b Secondary regrowth tropical moist forest



c Regenerating dry forest

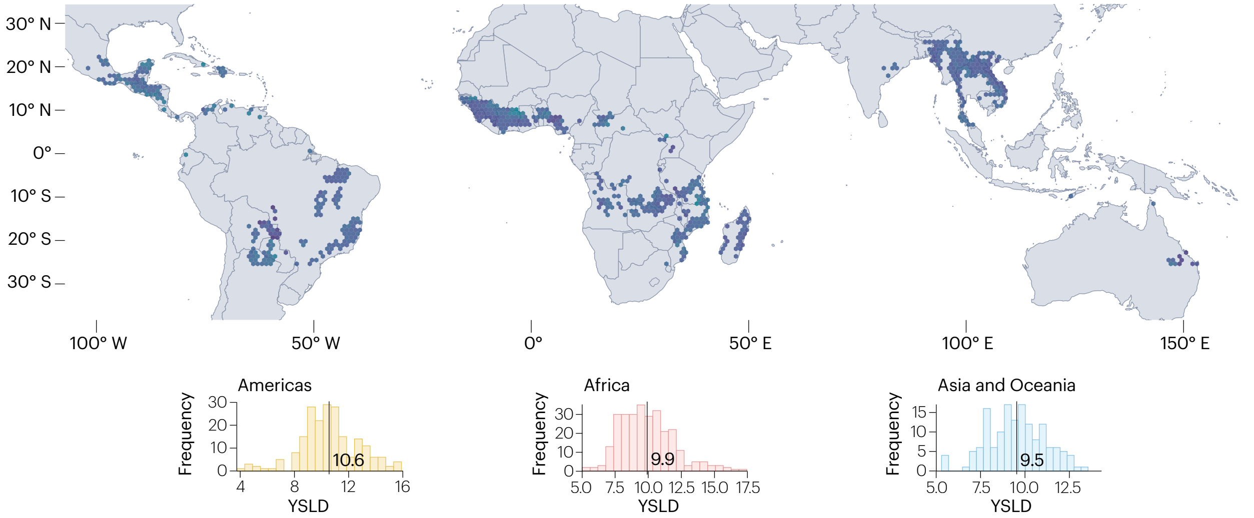


Table 1 | Area (in Mha) of different types of regenerating forests across the continents and different forest domains

Land type	Americas	Africa	Asia and Oceania
Tropical moist forest domain			
Undisturbed tropical moist forest[a]	532.9	193.5	161.8
Regenerating tropical moist forest (total)[a]	74.2	42.3	65.6
Recovering degraded forest	55.3	32.6	48.4
Secondary regrowth forest	18.9	9.7	17.3
Deforested tropical moist forest land (1982–2023)[b]	112.7	46.9	51.4
Plantation and afforestation[a,c]	30.7	15.2	57.5
Tropical dry forest			
Undisturbed dry forest[d]	135.7	351.8	83.0
Regenerating dry forest (since 2001)[d]	6.2	9.1	4.8
Deforested dry forest lands[d]	4.7	7.1	2.7
Total	**897.1**	**665.9**	**426.8**

See Supplementary Fig. 2 for summary of how non-tropical moist forests were identified. [a]Area estimates based on the Joint Research Council Tropical Moist Forest dataset (ref. 32). [b]Owing to how forest disturbance is defined by the Joint Research Council Tropical Moist Forest dataset, deforested tropical moist forest lands include both areas linked to direct deforestation and that first experienced degradation, if the disturbance persisted for longer than 2.5 years, it was considered deforested. If disturbance was no longer detected, it was considered as recovering. [c]Based on data from ref. 264. [d]Based on data from refs. 65,66.

fragments and surrounding forest cover[74,75]. For example, persistent spatial variability in the diversity of trees recruited into secondary forests in central Panama was shaped by both local site conditions and landscape context[76]. Spatial variables affect the availability and dispersal of propagules for regeneration as well as biophysical conditions that influence establishment, growth and survival of forest vegetation (Fig. 3). Overall, these biophysical variables include conditions that are favourable for tree colonization (such as proximity to remnant forests, waterways and protected areas, soils with high levels of organic carbon) and conditions that are associated with low economic potential of agricultural land uses (such as steep slopes, higher elevations, topographic positions with less intense solar radiation, and distance from population centres)[77–82] (Fig. 3).

Socioeconomic factors are increasingly being included alongside biophysical variables in models of natural regeneration potential[78,79,81]. Yet, when they are included as predictors, they do not tend to be as statistically significant as biophysical variables, potentially because the biophysical variables convey information regarding land-use variables that are proxies of socioeconomic drivers, such as farm size and intensity of land uses. The spatial pattern and temporal progression of deforestation generates a spatial footprint that can influence patterns of forest regeneration. For example, in the Brazilian Amazon, the fishbone pattern of deforestation (small, irregular polygons removed) led to more forest regeneration in landscapes over time compared with the geometric pattern (large blocks of forest removed), despite similar total extents of deforestation[83]. In Atlantic Forest of southern Bahia, Brazil, larger properties were associated with larger areas of naturally regenerating forest per property between 1985 and 2019, and the effect of forest cover on forest regeneration varied with property size[84].

The degree of agricultural suitability in the landscape is an important determinant of forest regeneration probability (Fig. 3). Across the global tropics, forest cover increase owing to natural regeneration was more frequent in areas with lower potential for agriculture compared with areas more suitable for mechanization[79]. Regeneration was also positively associated with native forest remnants that are more abundant in landscapes with lower levels of agricultural intensification[79]. For example, a parameterized landscape-scale modelling study found that landscapes dominated by sugarcane had lower forest regrowth potential than pasture-dominated landscapes owing to lower likelihood of land abandonment, limited rates of seed availability and low seedling growth[85]. In rural areas of southeastern Brazil, where native forest cover increased by 7.7% from 1995 to 2018, natural regeneration was generally favoured in areas with lower land suitability for agriculture, high proximity to forest remnants, higher diversity of land uses on farms and lower economic dependence of landowners on farm incomes[86]. Low agricultural yields or profits also favour natural regeneration in São Paulo State, Brazil[82].

Predictive models of natural regeneration potential can be built based on validated presence–absence maps of forest gain through natural regeneration. Such predictive models can help to identify target areas for using natural regeneration-based approaches for forest restoration. Models based on machine learning within the Atlantic Forest region of Brazil predicted that 2.8 Mha of new forest could regenerate by 2035 and an additional 18.8 Mha could regenerate with human assistance[80] (Box 1). A similar approach applied across the global tropics found that 215 Mha of deforested land have biophysical conditions suitable for natural regeneration, with five countries (Brazil, Indonesia, China, Mexico and Colombia) accounting for 52% of this potential[81].

Quality. The quality of naturally regenerating forests is also shaped by interacting local and landscape conditions[28] (Fig. 3). Assessments of the quality of natural regeneration are often based on indicators of forest structure, composition of both plant and animal species and ecosystem processes relative to more intact and mature forests in the surrounding landscape[87]. During early stages of forest regeneration, however, quality is best assessed in comparison with similarly aged forests regenerating under optimal conditions for re-establishment of diverse native assemblages[87].

The intensity and scale of surrounding land use directly affect regeneration trajectories. In some cases, surrounding landscape composition and prior land use are stronger predictors of bird and tree species richness and community structure than forest age[16,88]. In southern Mexico, species density, species diversity and basal area of trees in secondary regrowth in moist tropical forest declined as the fraction of area in cattle pasture increased across landscapes[75]. In Mexican dry forest, landscape context structures successional plant communities more strongly than land-use intensity at the site level[89]. A simple disturbance index based on information provided by landowners and farmers predicted several early regeneration indicators as well as or better than direct measurements of site conditions at the time of abandonment[90], highlighting the prolonged influence of land use and site-level disturbances on the quality of regenerating forests (Fig. 3). Across tropical forest regions of Mexico, higher land-use intensity and extent of landscape-scale forest fragmentation slowed the pace of forest recovery because of greater soil deterioration and lower availability of propagules[73].

Across the Neotropics, recovery trajectories of woody plant species richness, stem density and basal area were found to be less predictable in landscapes with intermediate (40–60%) forest cover than in landscapes with high (>60%) forest cover[72] owing to the patchy nature of suitable conditions for forest regeneration and the high variability in type and intensity of prior land use. In a global-scale analysis, defaunation caused by hunting and habitat fragmentation reduced seed dispersal of large-seeded tree species, with negative effects on forest regeneration[91]. In Brazil's Atlantic Forest region, tree cover of at least 40% is required to allow sufficient animal movement to enhance animal-mediated seed dispersal to permit the full recovery of tropical forest diversity and functionality[92]. In the lowland Chocó region of Ecuador where levels of forest cover (74% within a 1-km radius of each plot) and connectivity are high, wild mammalian species diversity in regenerating forests can recover to old-growth forest levels in 20–38 years[93,94].

Recovery of forest attributes and temporal trajectories

Recovering forests can be assessed in terms of structure, diversity, ecosystem properties and biotic composition (taxonomic, functional and phylogenetic), with different attributes varying in recovery times from a few months to over a century. Across 77 secondary forests in the Americas and West Africa, recovery is fastest for soil and plant functioning, intermediate for structure and species diversity and slowest for biomass and species composition[95] (Fig. 3b). In West African forests, tree diversity recovers within 35 years, whereas recovery of composition and biomass requires more than 60 years[96,97]. In Neotropical forests, recovery of tree species richness takes a median time of five decades, whereas full recovery of species composition can take centuries[98].

Long-term annual monitoring data confirm that recovery trajectories vary considerably over time and across different contexts[71,99,100]. Long-term studies also enable mechanistic understanding of impacts of climate variation[101], land-use legacies[73], priority effects[102] and alternative successional pathways[103]. In Central Amazonia, forest regenerating on frequently burned pastures was heavily dominated by three *Vismia* species that resprout vigorously after fires, whereas unburned clearcut areas were dominated by *Cecropia* species with numerous other tree species colonizing by seed[70]. Trajectories of species diversity and composition remain distinct for at least 30 years, demonstrating a long-term legacy of burning practices[70].

These long-term studies also provide insights into variation in tree demographic rates and community assembly during forest regeneration. Tree demographic strategies in four Neotropical sites shift from fast growth and low survival in young sites to slow growth and high survival in older sites, with long-lived pioneer species (fast growth, high survival and low recruitment) increasing in importance over time[104]. Ranges of demographic strategies largely overlapped across successional stages; however, early successional stages encompassed the full spectrum of demographic strategies found in old-growth forests[105]. The patterns and drivers of tree community assembly during forest regeneration are now becoming clearer, emphasizing species-specific functional traits and life history characteristics[95,106,107]. Although community assembly of trees during forest regeneration is influenced by both seed dispersal and species-specific establishment and growth requirements, seed dispersal limitation is often underestimated[108].

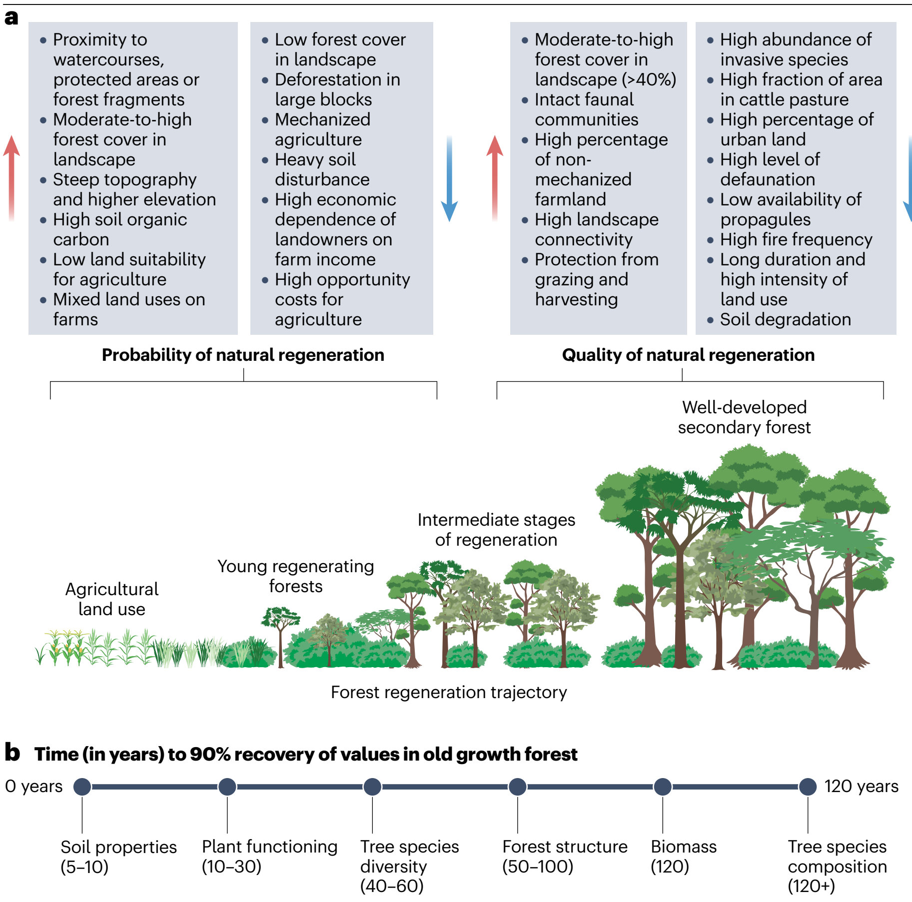


Fig. 3 | Forest regeneration quantity, quality and recovery timelines. a, Local and landscape biophysical and land-use factors that have been shown to positively (upward arrow) or negatively (downward arrow) affect the probability of natural regeneration (left) and the quality and trajectories of natural regeneration (right). Sources: refs. 28,70,72,77–83,92,265–267. **b**, Timelines of recovery vary for different forest attributions. Based on data from ref. 95.

Recovery of species attributes, fauna and species interactions

Beyond changes in species richness, other variables such as species abundance, phylogenetic diversity, endemic status, floristics, species interactions and ecological specializations change throughout the regeneration process[109,110] (Box 2). Studying these other characteristics provides understanding of the evolutionary and ecological filters that influence community assembly and habitat specialization during forest regeneration. Across a diverse range of Neotropical and Asian sites, tree species that specialize in successional moist forests tend to be from similar evolutionary lineages, suggesting that the adaptive radiation of particular species-rich genera and families is associated with occupation of early successional habitats[110–112]. Several studies in Brazil's Atlantic Forest show increasing abundance of endemic and threatened species of trees during forest regeneration[113,114]. As forests regenerate in the landscape matrix surrounding forest fragments in Central Amazonia, the occupancy and abundance of forest specialist bats[115] and birds[116] increase and the species composition of arthropods becomes similar to communities in continuous primary forests[117].

Animals are both drivers and beneficiaries of forest recovery[118], as tropical tree species have strong relationships with birds, mammals and insects. Tropical plants rely on animals for pollination[119], biotic defence[120] and seed dispersal[92,121–124]. Although many animal taxa are lost during forest disturbance or conversion to agriculture, their diversity and abundance recover during forest regeneration. A global study found that the relative proportion of forest-dependent bird species increased with age of secondary regrowth tropical forests across all sites, but overall species richness of birds did not differ between second-growth and old-growth forests[109]. Regenerating forests are important reservoirs of phylogenetic diversity of birds, particularly in landscapes with low levels of natural forest cover[125,126]. Species abundance and composition of birds in 31–36-year-old secondary forests in the Central Amazon varied across feeding guilds; frugivores, nectarivores and granivores showed high levels of recovery, whereas insectivores were far less represented than in old-growth forests[127]. In the Ecuadorian Chocó, ant communities showed a rapid recovery during forest regeneration, with former cacao sites reaching predicted primary forest conditions after just 20 years and pastures after 27 years[128]. Within the first 40 years of secondary forest regrowth in Pará, Brazil, species richness of dung beetles reached 76% of mean levels of species richness in undisturbed old-growth forest[129]. Reptile and amphibian faunas in regenerating forests in Chiapas, Mexico also show rapid recovery of species richness (within 30 years) but slow and incomplete recovery of species composition[130].

In addition to plant–animal mutualisms such as seed dispersal or pollination, other less-studied interaction types — such as herbivory and seed predation — shape tropical forest recovery. Experimental application of insecticide in early forest succession in Madang Province of Papua New Guinea led to reduced plant diversity and caused shifts in community composition, suggesting that insect herbivores favoured plant species with acquisitive leaf traits, enhancing plant diversity through conspecific negative density-dependent effects[131]. During forest succession in Morobe Province of Papua New Guinea, herbivores were more abundant and plant hosts had more species-rich herbivore assemblages during the earliest stages, reflecting higher palatability of early successional plant species owing to lower defensive investment[132].

Plant–animal interaction networks become more complex and generalized during later stages of forest restoration and regeneration[118,133]. Recovery of complex networks could improve the level and potentially the stability of ecosystem functions to which these interactions contribute. Studies on network recovery and functional consequences thus represent an important target for future research in ecosystem restoration[94], illustrated by improved plant-pollinator networks and fruit set in a restored island ecosystem[134] (Box 2).

Recovery of functional traits

Vegetative functional traits influence rates of tree growth, durability and palatability of leaf and stem tissues and rates of tissue decomposition. During succession in tropical moist forests, tree communities shift in average trait values (weighted by abundance or basal area) from traits associated with fast growth to traits associated with slow

Box 2 | Statistical approaches for assessing biodiversity and network metrics

Site-level species diversity of animals or plants (alpha-diversity) is often reported as an indicator of regeneration success. Although tree communities slowly recolonize disturbed habitats and often increase in alpha-diversity over time[95,98,106,107], patterns can be different for other taxa such as birds[57,61] or ants[128,281]. The actual composition of (forest) plant or animal species represents a more meaningful measure of regeneration success than alpha-diversity. For instance, ant species community composition gradually recovers and approaches the composition of old-growth forests[128,281], and communities of several taxa are more homogeneous in agricultural areas (low beta-diversity) than in secondary and old-growth forests[128,281].

Biodiversity monitoring assessments in regenerating tropical forests rely heavily on site-level sampling, and the high species richness in tropical forests makes it virtually impossible to include all species in samples. Advances in statistical methods for assessing and monitoring biodiversity recovery account for the incomplete detection of species in samples, overcoming sampling limitations and facilitating broader assessments and comparisons across sites that vary in sample completeness. Statistical approaches and software help to overcome these limitations for assessing site differences in species diversity and evenness through coverage-based rarefaction and extrapolation[100,282–284]. Standardized methods can also be applied to assessments of among-site (beta) diversity[285] and to metrics of taxonomic, functional and phylogenetic diversity[286,287].

Similar to biodiversity metrics, interaction networks require appropriate standardization of sampling and species abundances for meaningful comparisons across species within a network, across networks or across sites. Important tools to interpret variation in network metrics against sampling biases include null models that maintain the number and abundance of species, rarefaction techniques or covariates[288]. Corrections for abundance or sampling biases are crucial for understanding the biological drivers of trends. For instance, species diversity and network patterns can change along recovery gradients because of shifts in environmental or resource heterogeneity that can enhance biodiversity or in resource densities that could increase species abundances[288].

growth and persistence[135]. The range of trait values also increases during succession[106]. In general, the trait range can be narrow early in succession because of strong environmental filtering, whereas later in succession, trait range can increase because of accumulation of new species with different trait values, the persistence of long-lived pioneers with early successional trait values and competitive interactions that favour trait divergence of co-occurring species[136]. Functional traits related to seed dispersal show strong successional trajectories, emphasizing the key role of plant–animal interactions in community assembly. In tropical moist forests of northeastern Costa Rica, for all life stages of canopy tree species, the relative abundance of wind-dispersed and small-seeded species decreased and the relative abundance of animal-dispersed and large-seeded species increased over time[137].

Tree functional diversity generally increases over time during forest succession[107,138], but dry and moist forests exhibit different patterns of change in tree functional composition[139]. This difference results from higher drought stress during early succession in dry forests compared with moist forests, but trait values converge over time as the vegetation increases in structural complexity and abiotic and biotic conditions of dry and moist forests become more similar[106]. In tropical moist forests, functional traits of trees shift from acquisitive traits that confer fast growth rates in early stages to conservative traits that favour high survival in later stages[135]. Tropical dry forests generally show an opposing trend, with conservative (stress-tolerant) traits in young stages shifting towards acquisitive traits in later stages[140]. For example, wood density (where high values are conservative) increases throughout succession in tropical moist forests but decreases throughout succession in tropical dry forests[141].

Functional traits of animal taxa also exhibit shifts during forest regeneration. During forest regeneration in Ecuador, ant communities showed shifts and convergence in functional traits during forest recovery consistent with environmental changes; in older, cooler and darker regenerating forests, ants were brighter, had a less sculptured cuticle and reduced relative eye size[142]. Life history traits also shift in mixed-species bird flocks during tropical forest regeneration; species with smaller body size and larger clutch size were gradually replaced over time by species with larger body mass and smaller clutch sizes[143].

Tipping points

Escalating environmental pressures can drive forest ecosystems towards a tipping point, or an abrupt transition (regime shift) towards an alternate steady state, making recovery to the original state improbable without major interventions[144–146]. In the context of forest regeneration, these alternate states can be brought on by wide-scale deforestation, extreme forest fragmentation, droughts, repeated or severe fires[147], persistent invasive species[148,149], defaunation[150] or disease outbreaks[151]. Although climate change impacts such as increased temperatures and reduced rainfall can negatively impact seedling and tree growth and survival in regenerating tropical forests[101,152,153], the effects of these impacts on trajectories of forest regeneration following deforestation and forest degradation remain poorly understood. In dry Caatinga forests on sandy soils in northeastern Brazil, forest recovery on abandoned crop fields occurs predominantly through resprouting from root suckers[154,155], and tree species composition remains similar across successional stages. Resprouting mechanisms can enable some dry forest ecosystems and forests adapted to frequent hurricanes[156] to achieve higher resilience than other forest ecosystems in the face of climate change and other disturbances. Moreover, disturbances can interact in their effects on forest dynamics. For example, forests regrowing after hurricane disturbances in Puerto Rico are more vulnerable to drought-induced tree mortality[157]. In Amazonia, repeated cycles of shifting cultivation with short fallow periods reduced rates of vegetation recovery and species diversity[158] can lead to alternate steady states that fail to regenerate back to forest[159].

Regime shifts have probably already occurred in many deforested regions across the tropics, requiring costly interventions to restore tropical forest ecosystems through replanting or to rehabilitate these areas for productive land uses[160]. By carefully observing regeneration trajectories following different types of disturbances, it is possible to characterize where regime shifts have occurred and where active interventions are needed to restore forest functions and biodiversity[161]. Systems thinking – a holistic approach that considers how a system's constituent parts interrelate and change within the context of larger systems[162] – helps to identify features of resilient restoration trajectories and to guide expectations regarding how quickly and how predictably tropical forest ecosystems can recover[163]. For example, understanding the complex feedbacks between local and landscape processes that affect forest regeneration can help to select areas where natural regeneration outcomes provide greater ecological and socioeconomic benefits than tree planting approaches.

The socioecological context

Ecological factors alone do not determine forest recovery. As the dynamics of regenerating forests are embedded within the dynamics of complex spatial units such as landscapes and watersheds, the fate of these forests is directly linked to activities and rights of people who live and work in these landscapes. We now discuss the contributions of regenerating tropical forests to people, the potential for harnessing them as nature-based solutions and the role of regenerating forests in socioecological systems. We adopt a broad concept that integrates the original ecosystem services framework[164] with the Nature's Contributions to People framework of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services[165].

Contributions of regenerating forests to people

Ecosystem services. Many of the ecosystem services lost following deforestation or degradation recover during forest regeneration, contributing to human well-being in multifaceted ways and at multiple spatial scales[166–168]. Inherent trade-offs in the quality and quantity of ecosystem services provided by regenerating forests underlie different socioeconomic outcomes of forest transitions[26,166,169,170]. Although naturally regenerating forests provide a higher diversity of regulating ecosystem services, monoculture tree plantations excel in wood production[10,26] and can foster native woody regeneration beneath planted canopy trees[171]. Fast-growing tree plantations use large quantities of groundwater and can reduce stream flow, depriving native vegetation of water supplies[172,173].

Carbon storage is an essential contribution to people. As they grow, regenerating forests accumulate carbon in plant tissues and in the soil, driving other recovery processes[174]. Regrowing forests accumulate carbon in aboveground biomass at a rate up to 11 times faster than old-growth forests[175] and offer a substantial contribution to mitigate climate change[1,36]. Recovery of aboveground carbon stocks is an asymptotic function of forest age, with median recovery of 90% of mature forest carbon stocks in 66 years under best-case scenarios[175]. Tropical moist forests accumulate carbon faster than seasonally dry forests during regeneration[176], and many other factors (including human disturbance before and after regrowth) influence rates of

Box 3 | Biodiversity credits to support tropical regeneration

Regional and global initiatives for generating biodiversity credits applied to tropical regenerating forests have steeply increased. Examples include Terrasos in Colombia, ValueNature, BioCarbon Registry, Plan Vivo Biodiversity Standards, LIFE and Verra Nature Framework. These initiatives have already established publicly available frameworks that have been applied in pilot or commercial projects, giving rise to the first batch of biodiversity credits traded in the market. Unlike carbon credits, which are based on a single traded outcome (verifiable carbon units), a plethora of biodiversity metrics and approaches to estimate additionality (for example, impacts on diversity, landscape connectivity and threatened species) have been used to determine the number of credits issued by a given project.

Tropical forest regeneration is expected to be more competitive for biodiversity credits than for carbon credits, because carbon credits are more effectively generated by plantations of fast-growing exotic species[10,171]. Alternatively, tropical forest regeneration is expected to be the most cost-effective solution for both carbon and biodiversity in less disturbed tropical forest landscapes. Therefore, combining carbon and biodiversity credits is a promising approach for unlocking investments[289], as it captures this dual and synergistic contribution of regenerating tropical forests. Use of biodiversity credits for regenerating forests is limited by the development of reliable, traceable and tradable credits that go beyond compensation mechanisms (in other words, that are 'nature-positive') and are based on scientifically robust monitoring frameworks[290–292].

carbon storage[177]. In regenerating forests of the Yucatan Peninsula of southeastern Mexico, biomass accumulation of soft-wooded tree species recovers more rapidly than that of dense-wooded species, which can take over a century[178].

The ecosystems service of groundwater recharge also gradually recovers throughout the regeneration process. As trees establish and grow on compacted or eroded soils, deep penetration of tree roots into the ground increases infiltration and groundwater recharge, reducing overland flow that previously caused flooding and sedimentation[179]. During early succession stages, rapidly growing trees have high water demands, however, so groundwater recharge takes time[173,180]. The optimal level of tree cover in which the increased water infiltration into soils promoted by trees compensates for their increased evapotranspiration varies with levels of water availability[181]. Deep-rooted trees connect groundwater with the atmosphere[182] and affect precipitation over large distances[183,184], promoting atmospheric water recycling and 'flying rivers' that generate rainfall elsewhere, but at the expense of local stream flow[185].

Water quality impairment can occur after some disturbances, but the regeneration process can recover this ecosystem service. Natural regeneration of tropical forests can rapidly enhance water quality and stream microbial diversity after only a few years of forest regrowth by improving river bank stability, in-stream vegetation and stream margin vegetation[186]. Riparian buffers filter runoff and have been shown to improve stream water quality by reducing the velocity of runoff and promoting infiltration, sediment deposition and nutrient retention. In regenerating riparian forests of central Panama, soil bacteria communities recovered within a decade, along with improvements in water quality[187]. Retaining and increasing forest cover in upland areas of watersheds improves downstream water quality[188] and reduces diarrhoeal disease, a major cause of child mortality in the tropics[189].

Natural regeneration on former agricultural fields and pastures improved soil attributes such as bulk density (lower) and carbon and nitrogen (both higher), recovering to 90% of old-growth forest values[95]. But soil recovery is slow after severe soil compaction[73] and nutrient limitation and high intensity of prior land use can slow forest recovery[28,190–192]. Soil recovery is positively linked to biomass increase and total carbon storage[193,194] through increased production and decomposition of litter[174].

Across the world's tropics, 1.2 billion people – 30% of the total population – depend heavily on nature for at least three of four basic needs: housing materials, water, energy and livelihoods[195]. Regenerating forests provide a wide range of timber and non-timber forest products. Although many commercially valuable tree species regenerate in young secondary forests[196–198], limited data suggest that sustainable harvest in regenerating forests has low economic feasibility[199,200]. That said, many useful and underutilized tree and plant species offer the potential for sustainably produced foods, improving human nutrition[201,202]. For instance, regenerating forests in Nigeria improve people's dietary quality[2]. Traditionally, shifting cultivation fallows (former cropland left to regenerate) are co-managed for multiple ecosystem services including food, medicinal plants, fibre and firewood[203–205].

Income generation from naturally regenerating forests. Regenerating forests have potential to generate timber and non-timber products from native species that have commercial value, creating income streams for farmers and communities[198,206–209]. Upscaling and intensifying the practice of farmer-managed natural regeneration on farmlands could be a viable pathway for the development of the rural economy in four West African countries[210]. Value-chain analysis and cost–benefit analysis of products that can be sustainably sourced from assisted natural regeneration across different forest biomes remain an urgent area of research[199,211,212].

Economic models show that naturally regenerating forests are more cost-effective than tree plantations for producing carbon offsets across 46% of the 593 Mha classified as suitable for reforestation, whereas plantations have higher cost–effectiveness for producing carbon offsets across 54% of the areas considered suitable for restoration[213]. In particular, carbon offsets derived from natural regeneration are more cost-effective than from plantation forestry in much of Western Mexico, the Andean region, Southern Cone of South America, West and Central Africa, India, Southern China, Malaysia and Indonesia[213].

Naturally regenerating forests could be an even more competitive land use than business-as-usual commercial tree plantations or even agriculture if additional ecosystem services – such as watershed protection, soil recovery and local livelihoods – were effectively and equitably rewarded by the market and incorporated into reforestation finance. The paradox lies in the neoliberal, carbon-centred project finance, quantifying the technical carbon sink potential, whereas long-term project success depends on non-carbon benefits for people and nature[214]. Further challenges result from a mismatch between needs of global stakeholders and needs of local stakeholders[215,216] and inadequate frameworks to facilitate credit issuance and certification for small-scale projects. This constraint could be at least partially overcome by the consolidation of the market for high-quality carbon credits and emergence of biodiversity credits (Box 3). Such mechanisms could allow overcoming barriers of land opportunity costs, allowing long-lived regenerating forests to become economically viable lands with value to farmers and investors.

Enabling factors and barriers for natural regeneration. Compared with tree planting, natural regeneration best optimizes enabling factors, as it has progressed in areas less intensively used by agriculture, with lower leakage potential and competition for land. Furthermore, it does not rely on nursery-grown seedlings, specialized labour and equipment or facilitated access to land, which increases the scalability and reduces costs[217]. Consequently, natural regeneration represents a 'low hanging fruit' on the menu of tropical reforestation options[217]. However, the enabling factors for natural regeneration (Fig. 4) are not always in place, as evidenced by the high rates of reconversion of young regenerating forests in the tropics[177,218,219]. A next step is to identify the most critical local and regional barriers for natural regeneration establishment and longevity.

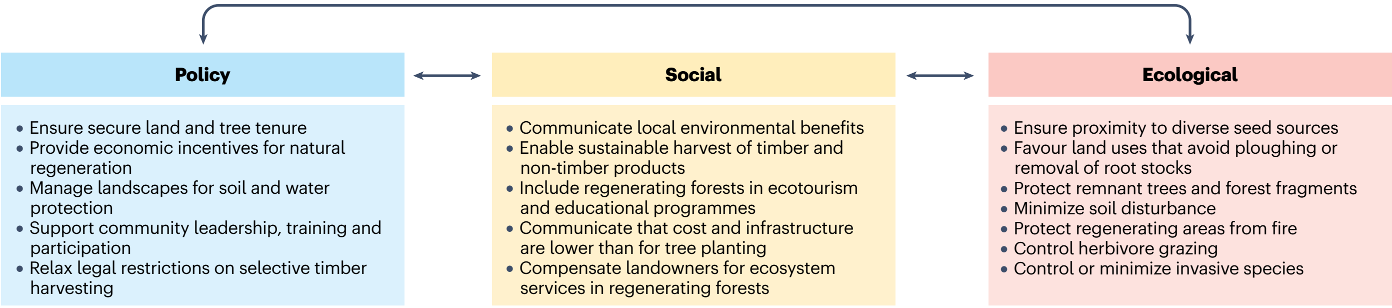
The generation of carbon and biodiversity credits (Box 3) from naturally regenerating forests could open new avenues for overcoming the opportunity costs of natural regeneration, but some important methodological and governance barriers must be overcome. For carbon, the first barrier includes the high uncertainty and, quite often, the low rate of carbon accumulation[220]. Predicting specific recovery trajectories is more challenging for natural regeneration than for tree plantings[29,71,72,111]. In addition, current carbon accumulation estimates from tropical forest regeneration are potentially overestimated owing to a positive bias in selecting study sites[221] and in accurately assessing forest age based on satellite imagery. Across 182 carbon offset projects in Australia, project-based activities were often not the major factor contributing to changes in woody vegetation cover, and credited areas showed limited evidence of forest regeneration[222].

A further obstacle is that carbon crediting mechanisms prefer that reforested lands remain treeless before project initiation to maximize additionality (evidence that emissions reductions or removals would not have occurred without revenue from the sale of carbon credits), whereas areas with high potential for natural regeneration usually exhibit some level of tree cover in previous years[19]. These limitations encourage carbon projects to favour tree planting rather than spontaneous or assisted regeneration; the majority (45%) of restoration commitments from countries are monoculture plantations[223]. Biodiversity recovery through natural regeneration might proceed best if both carbon and biodiversity credits are applied (Box 3). Most of these aforementioned limitations are addressable and should be the focus of further research and credits issuing mechanisms to unlock the potential of natural regeneration. Complementarily, as the pace of prevention and reconversion of natural regeneration has been much faster than the development of effective financial mechanisms, it is critical to strengthen the development of, and compliance with, legal frameworks protecting secondary forests[224].

Regenerating forests as socioecological systems

The dynamics of regenerating forests are driven by interacting social and ecological processes[225,226]: heterogeneous assemblages of species (including trees, animals, microorganisms and humans) closely interact through movements across landscapes, through ecological interactions, through past and present land use, through human-modified landscape composition and through markets for goods and other ecosystem services[28,226,227]. These spatial and temporal processes influence the capacity of regenerating forests to recover structure and composition under changing social and ecological conditions while maintaining essential forest functions (such as wood production or supporting habitats for native species)[228]. The ability of a forest to rebound and recover following environmental stresses and disturbances is a better indicator of adaptive capacity than rapid convergence to old-growth forest properties. Managing regenerating forests as socioecological systems should consider how forest functions can be maintained in the context of sustainable use and where local sites are embedded in a matrix of different land-use types.

Traditional fallow-based cultivation systems illustrate a reciprocal relationship between human societies and nature, based on a deep knowledge of regeneration cycles of tropical forests across all continental regions[203]. Current agriculture and forestry production systems and global trade have altered this reciprocal relationship, creating socioeconomic and policy drivers that influence the loss and gain of tropical forests in particular locations[229]. Local and regional processes of deforestation and forest regeneration are mediated by complex spatial and temporal effects of land ownership, markets for land and commodities, power relations and governance mechanisms[230]. For example, entrusting management of forests to local villages led to greater permanence and cover of regenerating forests in Village Land Forest Reserves of the Greater Gombe Ecosystem, Tanzania, compared with unprotected village land[231]. Conceptual frameworks of forest succession are evolving to incorporate farmers' decisions[86], demands for ecosystem services[232] and coupled socioecological dynamics[233]. Ref. 68 developed a comprehensive successional framework that views ecosystem succession as an integral part of a socioecological system, in which the well-being of rural communities is affected by the quality and quantity of forest cover[234] as well as by access to forests for commercial or subsistence use and property and resource rights[235,236].



Policy

- Ensure secure land and tree tenure
- Provide economic incentives for natural regeneration
- Manage landscapes for soil and water protection
- Support community leadership, training and participation
- Relax legal restrictions on selective timber harvesting

Social

- Communicate local environmental benefits
- Enable sustainable harvest of timber and non-timber products
- Include regenerating forests in ecotourism and educational programmes
- Communicate that cost and infrastructure are lower than for tree planting
- Compensate landowners for ecosystem services in regenerating forests

Ecological

- Ensure proximity to diverse seed sources
- Favour land uses that avoid ploughing or removal of root stocks
- Protect remnant trees and forest fragments
- Minimize soil disturbance
- Protect regenerating areas from fire
- Control herbivore grazing
- Control or minimize invasive species

Fig. 4 | Political, social and ecological enabling factors for natural regeneration of tropical forests. These enabling factors are based on ref. 248.

In human-modified landscapes, whether forests regenerate on deforested or degraded land ultimately relies on human decisions[237]. Ecological recovery processes can take place only when people decide to stop or transform agricultural use of the land, assist natural regeneration (Box 1) and protect regenerating forests over time[238]. Framing tropical forest regeneration as a socioecological system is important because most deforested lands have been permanently maintained as alternative land uses, even in marginal areas for production and with high regeneration potential, and a large proportion of naturally regenerating forests has been re-cleared within a few years after their establishment[218,219,239,240]. Following deforestation in the Brazilian Amazon, collective property rights in the form of Indigenous Territories favoured forest regeneration[241], probably because Indigenous Peoples in general strongly value protecting their native forests, which they depend on for their well-being, biocultural identities and livelihoods[242,243]. Nearly 300 million people live on lands with tropical forest restoration opportunity, and 1 billion live within 8 km of these lands, stressing the need for local communities to have rights to manage and restore these forests[244].

It is essential to understand what motivates people to regenerate forests and how resource rights, cultural practices and economic incentives – such as legal frameworks, payments for ecosystem services, marketing timber and non-timber forest products and ecotourism – can support effective, long-lasting regeneration[237,245]. The success of such incentives relies on socioeconomic factors such as governance[246], equitable benefit sharing[247], monitoring systems and the experience, beliefs and value systems of stakeholders[237,248,249]. Effective incentives need to address the main motivations of decision makers, from local farmers to investors, to promote or prevent natural regeneration[201,211,237,250]. Consequently, incentives need to be structured based on the particular socioecological context of restoration initiatives[248,251,252]. Such alignment will not only increase the likelihood of success but also prevent unintended negative consequences, such as those related to food security decline, losses of traditional and cultural practices, excessive restrictions on harvesting trees for livelihood use and displacement of deforestation to old-growth remnants[206,253].

Summary and future directions

Up to the past decade, most research on forest regeneration focused on patterns and trajectories of forest recovery and land-use change at local, landscape and global scales. Now that some clear patterns are emerging, it is time to focus on the underlying processes that created these patterns and adopt proactive approaches to enhance both the quantity and the quality of naturally regenerating tropical forests. Increasing awareness of the contributions of regenerating forests to people will help to protect them from reclearance. As forest regeneration is part of a broader socioecological system involving many actors, components and feedbacks[69,254], understanding of the nuances that link ecological processes and behavioural responses of stakeholders[255] with socioeconomic and policy drivers[68] is urgently needed (Fig. 4). Ultimately, the fate of tropical forests rests on choices and decisions of landowners, communities, companies, civil society organizations, financial institutions and government ministries. How these decisions affect forest regeneration processes and how these impacts can be favourably guided through policy arrangements are crucial topics for further study.

Major research and policy gaps include identifying effective economic incentives for natural forest regeneration on private and community-held land; addressing challenges for integrating regenerating forests in carbon markets; quantifying drivers of persistence and recovery dynamics of wet and dry forests; and recognizing and applying Indigenous knowledge for managing regenerating forests. Economic models of forest regeneration (including timber and non-timber products, ecosystem service markets and biodiversity credits) are essential to engage farmers and communities in beneficial and rewarding restoration activities based on natural regeneration that are biodiversity-positive. Advances in characterizing landscapes and their dynamics will allow better prediction of the quality and likely trajectories of natural regeneration[28,87], improving restoration planning and incentive mechanisms. Wider application and integration of state-of-the-art monitoring approaches such as unmanned aerial vehicle-based remote-sensing and environmental DNA can improve the detection of subtle biodiversity disturbances and responses in regenerating tropical forests[256].

Ecological studies of habitat associations and spillover of plant and animal species into and out of regenerating forests are needed[16,257] to understand how natural regeneration can contribute to landscape connectivity through biological corridors for species conservation and climate change adaptation[258,259]. Genetic structure of populations during forest regeneration and gene flow through pollination and seed dispersal are also poorly understood[260,261], as well as how non-tree plant communities recover overtime[262]. How climate change and other stressors influence forest restoration and biodiversity recovery, including climatic tipping points and alternate steady states[263], remains unknown. Moreover, compared with the Neotropical regions and in tropical moist forest systems, less research has been conducted in regenerating tropical Asian and African systems and on regenerating tropical dry forests. There is an urgent need to expand regional land-use–land-cover datasets, such as MapBiomas[31], across continents, creating verified, high-resolution datasets that can support evidence-based decision-making.

The key to tipping the balance towards natural regeneration and away from massive tree planting programmes is to integrate forest regeneration with management and conservation activities that benefit local communities and support livelihoods, as well as investors and businesses (Fig. 4). The knowledge and tools are available to take the initial steps towards this broad integration, but political will and targeted public policies are needed to unleash the full potential of regenerating forests at local, landscape and global scales.

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Acknowledgements

P.H.S.B. acknowledges the São Paulo Research Foundation (FAPESP, grant nos 2018/18416-2, 2021/10573-4, 2014/50279-4 and 2020/15230-5), the Dutch Research Council (grant no. 5160957745) and Shell Brazil (grant no. 22047-5) for financial support. V.H. was in part supported by the CGIAR MITIGATE+ project, the WRI Land & Carbon Lab and the Open Earth Monitor Project funded by the European Union (grant agreement no. 101059548). F.B. is supported by grants from the Dutch Research Council (SBEF-ALWOP.457 and NEWFOR-5160957745) and the European Research Council (PANTROP-834775). The authors thank L. Poorter for reviewing an earlier version of this manuscript and C. Jakovac for comments on Fig. 3.

Author contributions

All authors contributed to researching and writing the article. All authors contributed substantially to discussion and presentation of the content. R.L.C. led the organization and writing of the article. All authors reviewed and edited the manuscript before submission.

Competing interests

P.H.S.B. is partner at re.green, a restoration company. R.L.C. is global director of the Assisted Natural Regeneration Alliance, led by World Resources Institute.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s44358-025-00043-y.

Peer review information *Nature Reviews Biodiversity* thanks the anonymous reviewers for their contribution to the peer review of this work.