nature ecology & evolution

Article

https://doi.org/10.1038/s41559-026-03154-7

Variation in the costs and ecological benefits of tropical natural forest regeneration

Received: 19 April 2025

Accepted: 17 July 2026

Published online: 20 August 2026

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Natural regeneration is a cost-effective alternative to tree planting for restoring degraded and converted tropical forests, contributing to climate mitigation and biodiversity recovery. However, global variation in its costs and benefits remains poorly quantified, limiting the ability of restoration programmes to strategically leverage its full potential. Here we assess this variation by integrating data on costs and ecological benefits across the tropics, spanning 7.49 million km^2 of land with biophysical potential for natural forest regeneration. If completely regenerated, this additional forested area could accumulate approximately 9.57 Gt C over 30 years and reduce the overall extinction risk of forest-dependent species by about 31% relative to a baseline. We show that Indonesia, Madagascar, Philippines, México and Malaysia have the largest areas with high carbon and biodiversity benefits at low costs, which we refer to as 'holistic hotspots' for natural regeneration. We find that cost-effective areas with high carbon or high biodiversity benefits alone show different spatial patterns from holistic hotspots. These tradeoffs in achieving both benefits reduce the area of holistic hotspots to 9.67% of the entire study region. The cost–benefit maps we provide can enable decision-makers to improve their spatial planning and investment to achieve their forest restoration goals.

Tropical forests are the most biodiverse terrestrial ecosystems on Earth[1], play a critical role in mitigating climate change[2] and provide a plethora of ecosystem services to people[3]. However, their area declined by 2.3 million km^2 between 2000 and 2012, accounting for 32% of total global forest loss[4]. Deforestation increased extinction risk for 28–34% of species endemic to tropical forests across all taxonomic groups since the Anthropocene[1] and exacerbated climate change through increasing emissions of 0.86 ± 0.08 Gt C per year[2,5,6]. The loss of ecosystem services associated with tropical forests also threatens the well-being of 1.5 billion people who directly depend on tropical forests for food, timber, fibre and medicines[7–9]. In response, global climate change mitigation and biodiversity conservation policy platforms have set ambitious forest restoration targets, such as the Bonn Challenge, which aims to restore 3.5 million km^2 of degraded and deforested landscapes by 2030[10,11] and Target 2 of the recently adopted Global Biodiversity Framework, which calls for 30% of the degraded ecosystem areas to be brought under restoration by 2030[12]. However, for many nations, achieving these goals simultaneously is constrained by the high costs of active restoration[13–16]. Achieving restoration goals at scale therefore requires cost-effective methods that deliver both climate and biodiversity benefits, especially for low- and middle-income countries (LMICs).

The ambitious forest restoration targets of many countries will require a combination of active planting and natural regeneration approaches. However, achieving these targets at scale and within

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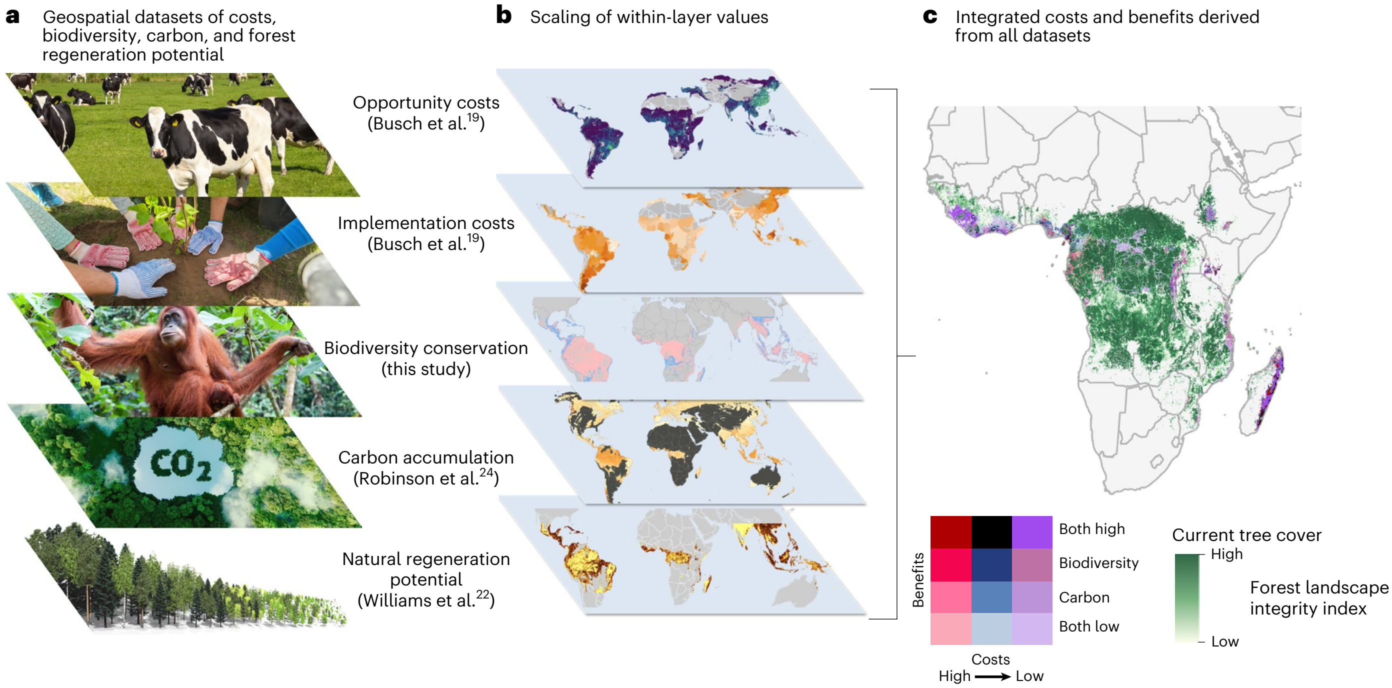

Fig. 1 | How existing global natural-regeneration datasets are categorized. **a**, Key studies on natural regeneration. **b**, Scaling these five datasets to assess the costs and benefits of natural regeneration. **c**, How the outputs of the analysis could be used to inform where natural regeneration could be implemented, categorized by varying levels of costs and ecological benefits. Costs are represented on a gradient from high (red) to low (purple), and benefit levels increase with darker shades within each colour scheme. Currently forested areas are shown in the light to dark green gradient reflecting the forest landscape integrity index[91], with darker green indicating greater forest landscape integrity.

realistic budget constraints is unlikely without substantial contributions from unassisted and assisted natural regeneration. Natural regeneration is the process of tropical forests reestablishing on their own following ecological processes of species colonization and community assembly[15,17]. Natural regeneration often requires assistance, such as site evaluation and protection measures that aim to overcome obstacles to regeneration through fencing, fire protection and site protection from herbivory[14,18]. Natural regeneration approaches, unassisted and assisted, can be more cost-effective across roughly half (46%) of restorable land[15,19] where adequate seed sources are available and site conditions are suitable[15,19,20], being up to 96% cheaper than active forest restoration[20]. Recent evidence demonstrates the substantial biodiversity gains from natural regeneration following cropland abandonment, with globally 74.2% of birds and 86.3% of mammal species benefiting from habitat recovery following the cessation of grazing or cultivation[21]. Further, natural regeneration can enhance carbon accumulation and biodiversity more effectively than active restoration in many locations, due to the colonization of locally adapted species, leading to a greater diversity of native species[22].

A number of foundational studies have mapped spatial variation in potential for natural regeneration (PNR)[23], restoration costs[20] and carbon sequestration rates[24,25]. For example, Williams and colleagues[23] identified 2.15 million km^2 of tropical forest area with PNR, and Busch and colleagues[20] have mapped opportunity costs for restoration (at 1-km spatial resolution) and implementation costs at the state/province level. However, the biodiversity benefits of natural regeneration have been understudied relative to carbon sequestration, and additional nuance in spatial variation of restoration costs is needed. Doing so would facilitate analyses of geographic variation in restoration opportunities, which can be used to guide global decision-making processes and economic flows to the most effective and desirable areas.

Emerging carbon and biodiversity markets present a substantial opportunity for tropical forest restoration. Carbon markets incentivize atmospheric carbon removal through trading credits, and countries are now mobilizing similar frameworks for biodiversity credits[26]. This is an opportunity for LMICs, which contain the majority of Earth's degraded tropical forests[27,28] and have relatively higher biodiversity and carbon accumulation rates compared to other ecosystem types[29,30]. For example, allowing managed native timber forests (selectively logged) to regenerate through assisted enrichment planting and climber cutting in the Malaysian state of Sabah could generate US$0.725 billion to US$3.625 billion in carbon credit revenues over the recovery period (approximately 40 years), equivalent to US$19,000 to US$95,000 per km^2 across 36,000–38,000 km^2 of total forested area[31,32]. However, information about where cost-effective forest restoration opportunities could be leveraged jointly to meet climate-change mitigation and biodiversity conservation objectives is currently lacking.

Here, we build on the foundational studies by (1) modelling finer spatial variation in implementation costs and (2) estimating how restoring areas with PNR can reduce extinction risk for forest-dependent species. We then integrate these datasets with existing opportunity-cost data, carbon accumulation potential and PNR to comprehensively assess the economic costs and ecological benefits of natural regeneration across the tropics (see Fig. 1 for an overview of the workflow). We ask the following questions: (1) how do the costs and benefits of natural forest regeneration vary across the tropics? and (2) where can maximum cost-effective carbon and biodiversity co-benefits be jointly achieved in natural forest regeneration 'holistic hotspots'? We acknowledge that holistic restoration involves broader considerations, but we focus on carbon and biodiversity benefits in this study. Strategically considering restoration costs and benefits ensures that investments are directed to locations where they will have the most impactful outcomes according to stakeholder goals[33], thereby helping to guide international investments and inform restoration decision-making and cost-effective implementation.

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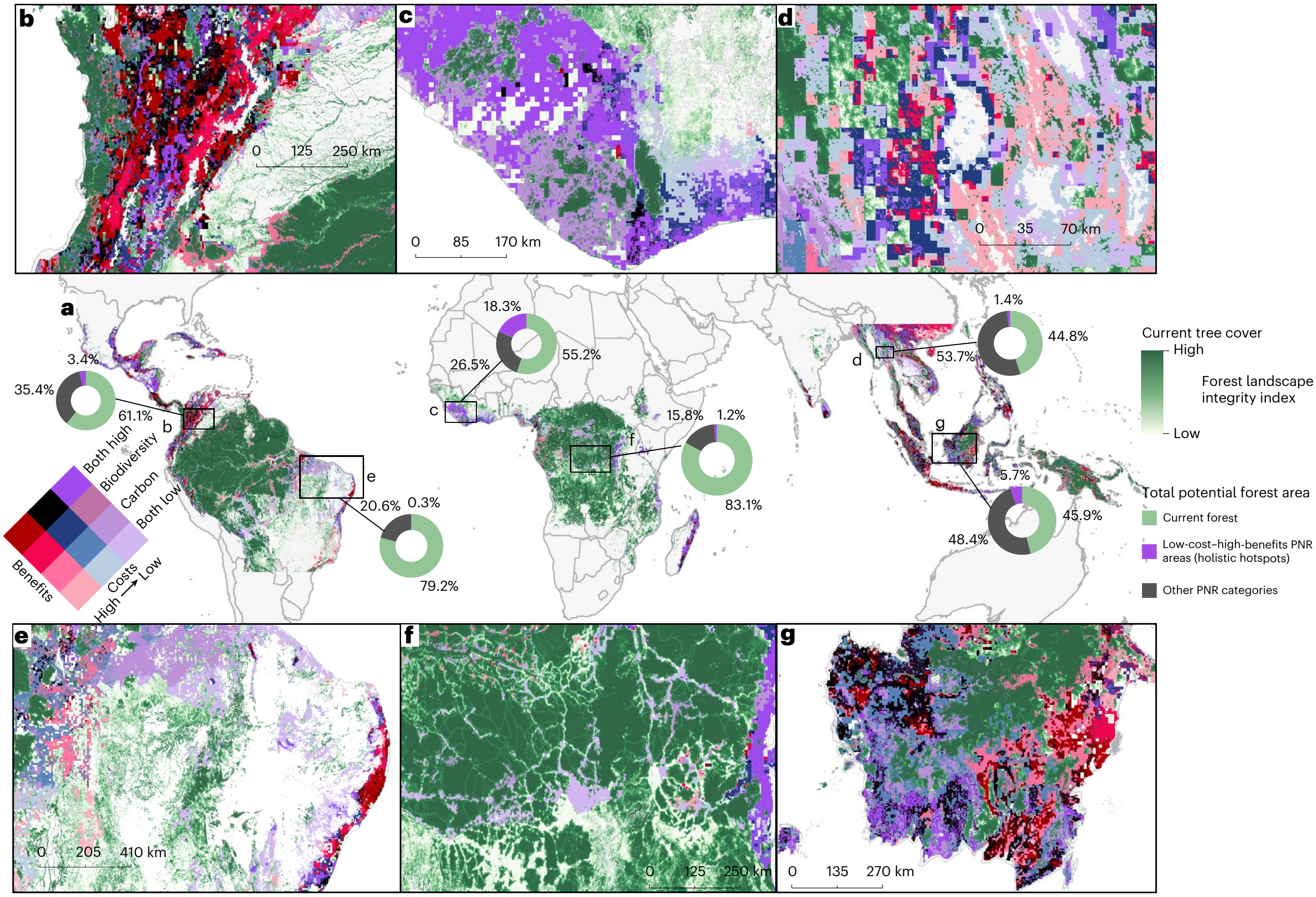

Fig. 2 | PNR cost–benefit categories. **a**, Examples across the tropics. **b**, Colombia; **c**, Liberia; **d**, Thailand; **e**, Brazil; **f**, the Democratic Republic of Congo; **g**, Indonesia. Costs are represented on a gradient from high (red) to low (purple), and benefit levels increase with darker shades within each colour scheme. The holistic hotspot category represents areas characterized by low regeneration costs and high carbon accumulation and biodiversity conservation benefits, highlighted in neon purple (9.67% of the total spatial area of potential for natural tropical forest regeneration). Currently forested areas are shown in the light to dark green gradient reflecting the forest landscape integrity index[91], with darker green indicating higher forest landscape integrity. The doughnut charts illustrate the total potential forest area, with current forest cover[93] represented in light green, the holistic hotspot in purple and all other potential for natural tropical forest regeneration cost–benefit categories in dark grey.

Results

Building on the areas recently identified by Williams and colleagues[23] with suitable biophysical conditions for natural regeneration to occur, we mapped the spatial distribution of regeneration costs and benefits across a study area bounded at ±25° latitude, spanning all or part of 71 tropical forested countries (see Supplementary Table 1 for the full list). Our analysis provides a spatially explicit, pantropical estimate of the extinction-risk reduction achievable through natural regeneration. In the study region, natural regeneration could reduce the overall extinction risk for forest-dependent species by about 31% relative to a baseline (a mean reduction of 0.084 on the 0–1 extinction-risk scale; 95% confidence interval (CI): 0.082–0.086). The analysed 7.49 million km^2 across the tropics could become profitable after approximately 13 years at carbon price of US$50 per t$CO_2$ (ref. 20) (6 years at US$100; reflecting net carbon gain only, with future revenue discounted at 5% per year) at a median natural-regeneration cost (including implementation and opportunity cost) of US$41,616 per km^2 (range: US$3,895–1,349,267 per km^2) and a median carbon accumulation rate of 2.36×10^{-8} Gt C per km^2 per year. The total potential carbon accumulation amount across the study area is approximately 0.32 Gt C per year over a 30-year period, equivalent to about 2.8% of current annual anthropogenic CO_2 emissions (11.45 ± 0.82 Gt C per year)[34]. Our study estimates a different amount of carbon potentially accumulated in regenerated forests compared to the ref. 23 result, representing an overestimation due to the coarser resolution of our chosen PNR dataset (1 km) compared to their finer-resolution analysis (30 m) (see the Methods section 'Implementation costs' for why we opted for this coarser resolution dataset), and we used a more recent carbon accumulation dataset[25].

To examine finer spatial variation in restoration costs, we developed an approach to scale the ref. 20 implementation cost data (provided at state/province scale) to 1-km spatial resolution based on the ref. 23 PNR data. We then coupled this with the ref. 20 opportunity-cost data to account for natural-regeneration costs such as site preparation, protection and land opportunity costs, with all costs reported in 2020 US dollars (see Methods for details). We first classified the total costs into three categories (low, medium and high) (Fig. 2). To assess tradeoffs with ecosystem services, we then combined costs with the carbon accumulation and biodiversity conservation benefits. These were then categorized under each of the three cost categories into four subgroups: low-carbon–low-biodiversity, high-carbon–low-biodiversity, low-carbon–high-biodiversity and high-carbon–high-biodiversity (see Methods for classification calculation), resulting in 12 (3 × 4) categories. Of the total PNR area, 724,164 km^2

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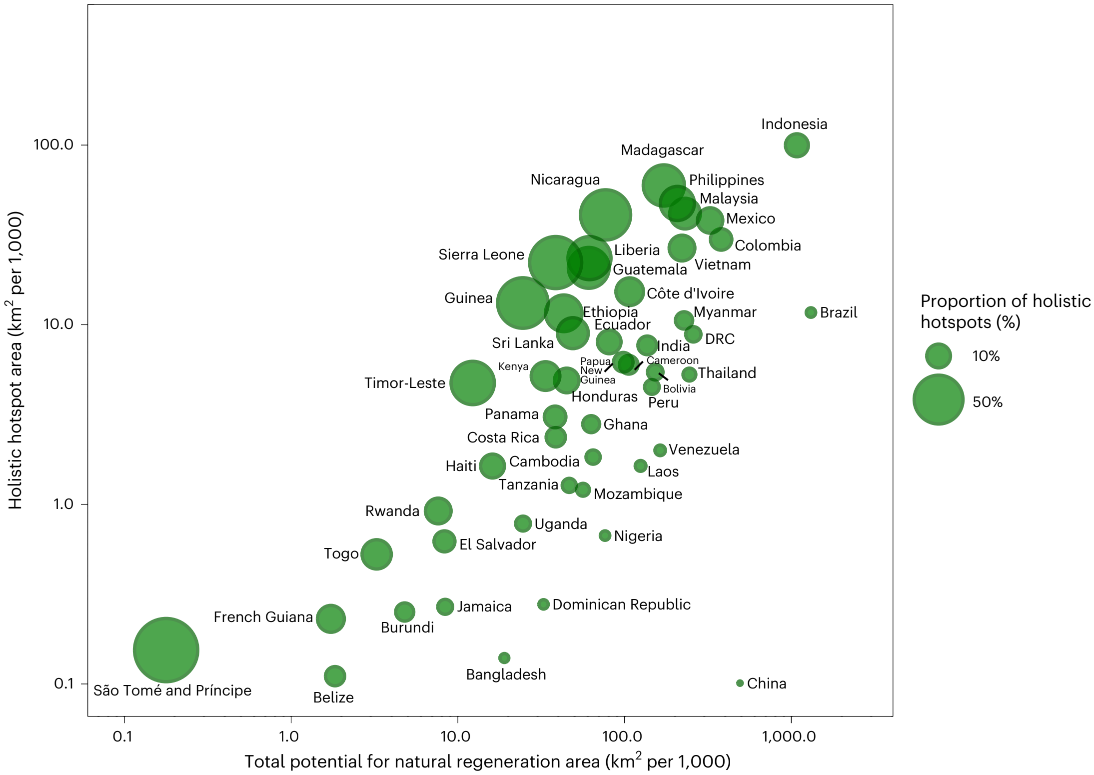

Fig. 3 | Total potential for natural tropical forest regeneration area versus holistic hotspot area. Countries shown have >100 km^2 holistic hotspots. Bubble size is the proportion of holistic hotspots in total potential for natural tropical forest regeneration; São Tomé and Príncipe (87.27%), Nicaragua (56.97%), Sierra Leone (56.33%), Guinea (52.03%) and El Salvador (46.14%) are the five countries with the largest proportion of holistic hotspot areas. Bubble positions are on $\log_{10}$ scale for visualization.

(9.67%) are classified as holistic hotspots (low-cost–high-carbon–high-biodiversity areas), which are distributed across different realms (see Fig. 2).

Patterns of costs and benefits across the tropics

The distribution of natural-regeneration opportunities varies among the three major tropical forest realms (Neotropics, Afrotropics and Indomalayan tropics), reflecting distinct patterns in both costs and ecological benefits (Fig. 2). All percentages reported herein represent proportions of the total PNR area (7.49 million km^2) (see Supplementary Table 1 for full details). We found the Indomalayan tropics to be the region containing the largest PNR area (42.96%), as well as the largest holistic hotspots (311,735 km^2, 4.15% of total PNR area). This realm provides the most cost-effective opportunities for carbon and biodiversity co-benefits of natural regeneration, although implementation faces inevitable socioeconomic barriers in this densely populated region[29]. The Neotropics has exceptional potential for carbon accumulation at low costs, with 190,244 km^2 of low-cost–high-carbon areas in this realm (2.54%), partly due to the deforestation and fire in the Amazon basin and Brazilian Atlantic Forest (see Supplementary Fig. 1 for input carbon data)[35,36]. Additionally, this realm has substantial biodiversity conservation potential, with the largest area of low-cost–high-biodiversity potential (243,606 km^2, 3.25%), as species here have lost relatively more habitat, making natural regeneration particularly effective at reducing their extinction risk. Although the Afrotropics has a relatively low area of holistic hotspot (207,183 km^2, 2.77%), carbon benefits there are exceptional, with 158,052 km^2 identified as low-cost–high-carbon areas (2.11%).

National opportunities

Natural-regeneration opportunities vary substantially in both scale and cost-effectiveness among the analysed 71 tropical forested countries. Five countries account for nearly half (47.88%) of the global PNR: Brazil (1.3 million km^2, 17.44% of total PNR area), Indonesia (1.1 million km^2, 14.48%), China (493,159 km^2, 6.59%), Colombia (376,516 km^2, 5.03%) and México (324,601 km^2, 4.34%) (see Fig. 3). This pattern differs from the distribution of holistic hotspots. Of the total identified 724,164 km^2 of holistic hotspot area, five countries—Indonesia (113,316 km^2, 15.65% of total holistic hotspots), Madagascar (71,760 km^2, 9.91%), Philippines (50,666 km^2, 7.00%), México (44,810 km^2, 6.19%) and Malaysia (44,299 km^2, 6.12%)—include nearly half (44.86%) of the total holistic hotspot areas (Figs. 3 and 4).

Relative to each country's total PNR area, São Tomé and Príncipe (87.27%), Nicaragua (56.97%), Sierra Leone (56.33%), Guinea (52.03%) and El Salvador (46.14%) contain the highest proportion of holistic hotspot areas (Fig. 3). An additional 45 countries contain more than 100 km^2 of holistic hotspot area (see Supplementary Table 1 for full details), indicating notable opportunities for cost-effective natural regeneration offering both biodiversity conservation (reduction of species' extinction risk) and carbon removal (Fig. 3).

Low-cost areas offering maximum carbon benefits do not totally coincide with those that offer maximum biodiversity benefits. Of the 524,811 km^2 of low-cost–high-carbon areas, which account for 7.01% of the total PNR area, the top five countries are Brazil (144,048 km^2, 1.92% of total PNR area), Indonesia (74,728 km^2, 1.00%), Democratic Republic of the Congo (42,805 km^2, 0.57%), Liberia (35,497 km^2, 0.47%) and Myanmar (30,833 km^2, 0.41%). Of the 524,283 km^2 of low-cost–high-biodiversity areas, which account for 7.00% of the total PNR area, the five countries with the largest area are México (94,238 km^2, 1.26%), Myanmar (30,419 km^2, 0.41%), Indonesia (29,415 km^2, 0.39%), Tanzania (26,302 km^2, 0.35%) and Democratic Republic of the Congo (25,307 km^2, 0.34%). Given that cost-effective opportunities for biodiversity conservation and for carbon benefits do not always overlap (which aligns with previous finding for tropical rainforests in ref. 37), decision-makers

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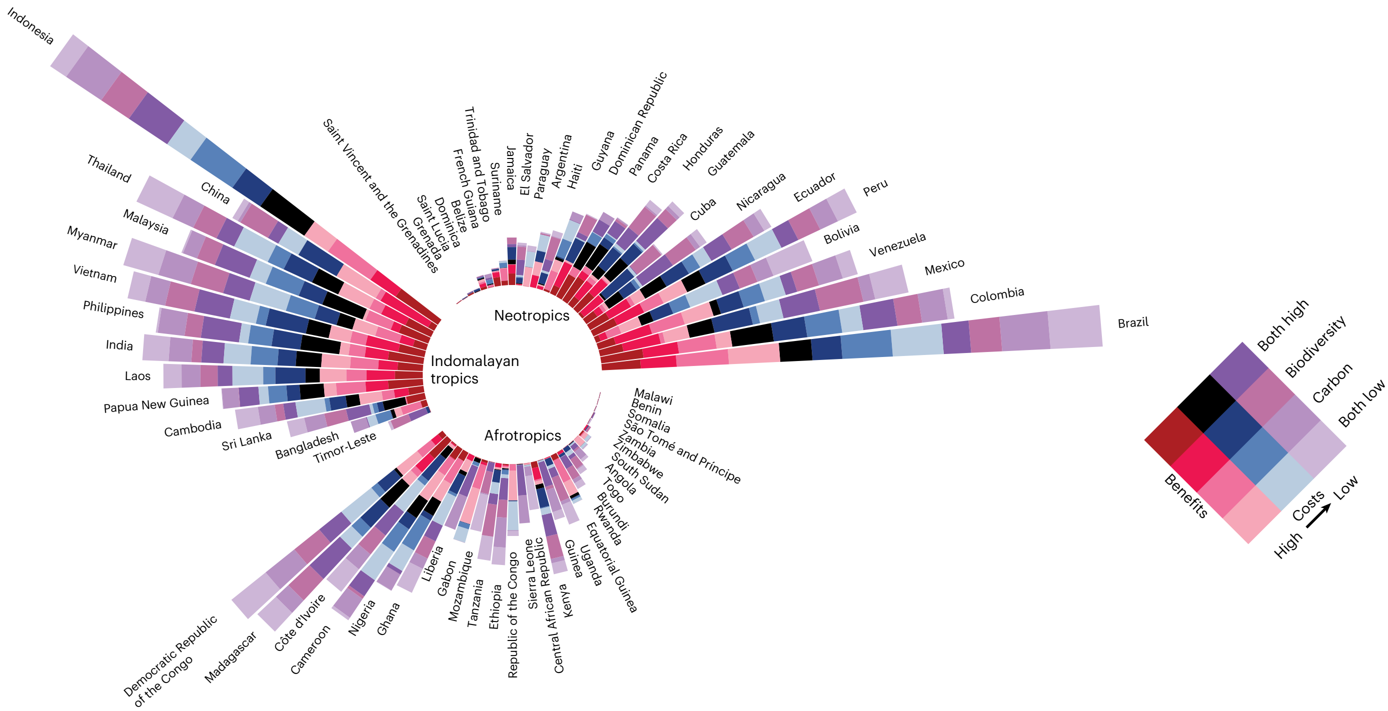

Fig. 4 | Summary of 12 cost–benefit categories. The circular barplot shows 12 cost–benefit categories for all countries in the study area, with countries ordered from smallest to largest total natural tropical forest regeneration area within each tropical realm. Categories are arranged from low-cost–low-benefit (outer ring) to high-cost–high-benefit (inner ring). For the circular barplot showing only holistic hotspots versus other natural tropical forest regeneration area cost–benefit categories (Supplementary Section 4 and Supplementary Fig. 9). Scale: $\log_{10}(x/1{,}000+1)$.

who prioritize either carbon or biodiversity will target different areas for restoration.

We conducted two sensitivity analyses: one excluding opportunity costs from the total cost calculation (Supplementary Section 2 and Supplementary Table 2) and one using Jenks natural breaks rather than median values to classify benefit subgroups (Supplementary Section 3 and Supplementary Table 3). Spatial patterns varied substantially between classification methods. Under natural breaks, the highly skewed biodiversity distribution resulted in only one country (México) exhibiting holistic hotspots, compared to all 71 countries under the median-based approach used in the main analysis. The choice of classification method therefore is important for identifying cost-effective regeneration areas and should be tailored to decision-making objectives and local context.

Country-level normalized analyses addressing potential bias in global threshold classifications are presented in Supplementary Section 8 and Supplementary Table 6. Beyond costs and ecological benefits, we also examined the social context of PNR areas. Approximately 52.1% of PNR areas currently coincide with active agricultural land, and 60% overlap with areas currently inhabited by 0.77 billion people (see Supplementary Section 9 for full analysis and discussion).

Discussion

Evaluation of economic costs and ecological benefits is required to fully take advantage of broad-scale PNR opportunities. In this study, we present a comprehensive pantropical assessment that integrates natural-regeneration costs with both carbon-removal and biodiversity conservation benefits. By synthesizing spatial patterns, we reveal important cost-effective restoration opportunities where tropical forests can deliver substantial ecological benefits. We found the Indomalayan tropics contain substantial proportions of holistic hotspots, where natural regeneration can deliver notable co-benefits for both carbon accumulation and biodiversity conservation at a low cost. With quantile-based classification in the main analyses, we identified 9.67% of the pantropical PNR area as holistic hotspots: these areas provide promising opportunities and impactful outcomes for exploring the feasibility of restoration projects based on natural regeneration of forests. Overall, these holistic hotspots indicate key opportunities for different markets (carbon and biodiversity markets) to incentivize the implementation of natural regeneration synergistically.

We identified a spatial mismatch between cost-effective areas for carbon accumulation versus biodiversity conservation for leading PNR containing countries. This was largely driven by tropical America and Southeast Asia having a higher carbon accumulation potential, whereas species in Central Africa and tropical North America experienced a higher reduction in extinction risk due to recent habitat loss. Most countries with substantial holistic hotspot areas share common characteristics of degraded lands, complex land-use patterns[38], smaller-scale landholdings and diversified livelihoods[39,40], which could contribute to lower opportunity costs for regeneration. However, this overlap with smallholder farming areas raises important considerations for implementation (Supplementary Section 9), necessitating careful planning to avoid displacing rural populations dependent on these lands for their livelihoods. Hence, differentiated financing strategies are required depending on whether carbon accumulation or biodiversity conservation is the primary restoration objective. It is now well recognized that enhancing biodiversity in restoration planning and delivery is integral to deliver other long-term restoration aims, such as carbon sequestration[41,42]. It is therefore concerning that many restoration efforts focus solely on carbon benefits—for example, through monocultures or inappropriate species placement—at the expense of biodiversity[43,44]. Natural regeneration is less prone to such tradeoffs as it allows ecosystems to recover through natural processes[22]. Nevertheless, we emphasize that markets should avoid focusing exclusively on financial, carbon-driven outcomes. Our results can inform where the carbon and biodiversity benefits from natural-regeneration overlap and, importantly, where restoration in these holistic hotspot areas can be implemented at low cost. However, this does not exclude other

https://doi.org/10.1038/s41559-026-03154-7

areas as candidates for biodiversity-focused restoration efforts, which should be a central objective of all forest restoration, particularly for ecological restoration.

The emergence of distinct market mechanisms, such as carbon-removal credits (representing a growing segment of the US$95 billion annual carbon credit market[45]) and new biodiversity-positive investment frameworks[46], could enable targeted investments in regions based on their specific ecological strengths (however, implementation requires addressing land-tenure complexities in regions where private land ownership is limited[47]). Although substantial integrity concerns have been raised about carbon markets, such as studies finding that some REDD+ projects[48] and forest regeneration offset projects[49] have not delivered claimed benefits, we here suggest that carbon markets could potentially provide large-scale funding to expansive, carbon-rich areas but should represent supplementary rather than primary funding drivers. Other than carbon markets, biodiversity frameworks could potentially direct focused investments to areas with high concentrations of threatened species or critical habitats at risk of further degradation. These market mechanisms, when combined with equitable benefit sharing, can support restoration across different cost–benefit contexts. Diversified funding approaches are particularly important for LMICs, where resource constraints often limit large-scale restoration efforts[50], enabling these nations to align ecological restoration with economic development objectives. Understanding the specific opportunities and limitations of these market mechanisms is crucial for realizing their potential in incentivizing tropical forest restoration.

Beyond ecological and economic considerations, natural regeneration also carries important social implications. PNR areas overlap with areas currently inhabited by approximately 0.77 billion people and substantial areas of cropland and pastureland, raising important considerations around local livelihoods, land tenure and equitable benefit sharing. These include risks such as displacement of rural populations dependent on agricultural land, as well as opportunities including employment, sustainable harvesting of forest products and timber revenues for local communities and governments. A full discussion of these social dimensions, including livelihood opportunities and land-tenure challenges across key countries, is provided in Supplementary Section 9.4.

Our analysis is potentially limited by the inherent uncertainties associated with the datasets used. First, the ref. 23 PNR dataset may underestimate its true potential, as regeneration is a dynamic, positive-feedback process that can expand beyond initially suitable areas. This conservative estimate could indicate that we are identifying fewer areas with natural-regeneration opportunities than actually exist. Second, we may not fully capture the dynamics of forest carbon accumulation: we employed total carbon accumulation potential of regrowing forests over 30 years, but actual accumulation may vary due to future climate-change impacts on both removal rates and carbon-storage durability, including disturbance frequency, change in CO_2 fertilization and temperature-driven changes in respiration[24,25]. Additionally, this carbon dataset does not account for seed-dispersal disruption by declining animal populations, which can reduce forest carbon accumulation by up to 75% in areas with disrupted seed-disperser communities[25,51]. Third, the Global Forest Watch (GFW) tree-cover dataset[52] used for our habitat baseline does not distinguish natural forest from plantations (including rubber, oil palm and non-native timber monocultures), which might not act as suitable ‘forest’ habitat for many forest-dependent species. Including plantations therefore overestimates the habitat a species already retains, which may make our estimates of the natural-regeneration benefit conservative.

Beyond the input data, our use of the quantile method for classifying benefits subgroups is subjective, and the varying thresholds of ‘high’ or ‘low’ carbon and biodiversity values could be useful among countries based on their internal distributions rather than absolute global values (see Supplementary Section 8 for country-level normalized analysis). Local decision-makers will need to determine meaningful thresholds based on their specific contexts and restoration objectives. Finally, the dataset does not specify the intervention required for successful restoration outcomes and assumes that a suite of assisted natural-regeneration interventions may be required. Therefore, the costs used in the analysis may not perfectly align with on the ground implementation needs.

Several cost-related limitations exist in our analysis. Our implementation costs, adjusted from ref. 20, approximate the costs of interventions including site evaluation and protection measures such as fencing and guards, but local contexts must be considered for implementation, where there may be additional costs. These may include weed suppression, enrichment planting, fertilization, protection from burning or grazing[53] and logistical costs related to site remoteness and travel time to regeneration areas[54]. Areas with the lowest costs may represent locations already undergoing cyclical natural regeneration, where converting to persistent forest recovery requires interventions ranging from early-stage fencing to later-stage policy frameworks and formal protection measures. Additionally, although our adjustments to the ref. 20 data represent the best available near-global dataset of natural-regeneration implementation costs, they are based on relatively few observations (several hundred across all LMICs), are subject to considerable uncertainty and typically cover only the first three years of implementation, thereby underestimating long-term costs associated with ongoing annual maintenance, monitoring and protection[53,55].

Furthermore, we used a static cost estimation to categorize the cost, but restoration costs are dynamic and influenced by fluctuating land prices and labour markets[55]. Given these limitations, we echo calls for greater investment in collecting and reporting restoration cost data across tropical and even global contexts, which would substantially improve the accuracy and applicability of future restoration analyses. This limitation also means that decision-makers should consider local land-pricing trends when translating our findings into implementation strategies. Regenerating areas also face threats of being recleared when perceived as unused land that is not providing direct economic benefits. Protecting these young forests may require both physical measures (firebreaks, fencing, patrolling)[56] and policy interventions (incentives, legislation, enforcement)[23].

Finally, we did not account for land-tenure and -ownership patterns[57–60], which are important factors that can influence the success of natural regeneration. Future research could incorporate land-tenure arrangements and property-rights data to better understand how ownership structures shape specific opportunities and limitations of carbon and biodiversity market mechanisms.

We emphasize that natural regeneration requires and complements the protection of existing forest ecosystems, including small fragments. As ref. 61 highlights, effective tropical forest management requires both conservation and restoration approaches. This integration is important because intact tropical forest ecosystems harbour the majority of global terrestrial biodiversity, support complex ecological processes and provide critical habitat for wide-ranging species and large-bodied vertebrates that require vast contiguous areas to maintain viable populations[62]. Regaining these values once lost is expensive, and most can never be fully restored[63]. Furthermore, the success of natural regeneration is closely linked to the persistence of existing forests. Williams and colleagues[23] found that distance to forest and forest density have a positive association with regeneration potential, consistent with Bello and colleagues[64] finding that frugivorous birds contributed more to seed dispersal with higher carbon-storage deposition and potential biomass accumulation, but only in landscapes with high forest cover. Furthermore, 81% of tropical trees depend on animals for seed dispersal, meaning that habitat disruption and reduced animal mobility can significantly constrain the carbon-accumulation

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potential of regenerating forests[51]. Together, these studies highlight how intact forests act as essential seed sources and biodiversity reservoirs for regeneration.

Our analysis is best suited for international decision-makers providing finance, such as non-governmental organizations or international governing bodies seeking to effectively invest in restoration, whereas country-specific tailored approaches within specific economic and ecological contexts would be required for local decisions. As tropical-forest-containing nations work to meet their restoration commitments under Target 2 of the Global Biodiversity Framework, this spatial understanding of cost–benefit relationships can inform the strategic deployment of limited resources while ensuring that crucial opportunities for both climate mitigation and biodiversity conservation are not overlooked.

Methods

To quantify the spatial variation in regeneration opportunities across Earth, we classified landscapes with PNR based on costs and benefits. We synthesized four published datasets that map spatial variation in carbon accumulation potential, opportunity costs, implementation costs and PNR. The carbon-accumulation-potential dataset estimates the carbon-accumulation capacity of the possible regenerating forests over the first 30 years[25]. We created a dataset to assess biodiversity conservation benefits based on assessing how natural regeneration could reduce species-extinction risk by increasing their available habitat[65]. The opportunity-cost data[20] represent the portion of annual agricultural profits attributed to land used for crop or livestock production, summed and discounted over a 30-year period, which reflects the economic value of keeping the land in its current agricultural use[20]. Additionally, we included the implementation cost data, which is also taken from ref. 20, representing the implementation costs of natural regeneration, including expenses related to site evaluation and protection from herbivores and human encroachment.

Study area

Our study region spans 7.49 million km^2, which encompasses all areas with PNR based on ref. 23. We refined the data frame by removing cells with PNR scores of 0 (unsuitable for natural regeneration, requiring active planting instead) and cells with NA values (28.61%) due to missing information in other datasets. The study area includes tropical and subtropical dry broadleaf forests, tropical and subtropical moist broadleaf forests and tropical and subtropical coniferous forests located within ±25° latitude. These biomes harbour more than half of the world's biodiversity and have the greatest capacity for rapid carbon accumulation compared to any other forest type[1,66]. Our study region includes deforested areas available for restoration, excluding water bodies, urban areas, sparse vegetation, existing forest cover and areas that naturally regenerated or were used for forestry activities between 2000 and 2016. As most nations with emerging economies are concentrated in the tropical region[67], restoration efforts offer opportunities to generate financial benefits through carbon credits while contributing to ecological improvements, which could support and sustain local livelihoods by enhancing food security and promoting economic sustainability in the study area[68]. Our study region is larger than the reported 2.15 million km^2 with area available for natural regeneration by Williams and colleagues[23], because they report a weighted-area value that scales area by natural-regeneration potential scores.

Benefits

Climate-change mitigation (carbon accumulation). We adopted global carbon-accumulation maps generated from Chapman–Richards (CR) growth-curve parameters developed by Robinson and colleagues[25], which estimate carbon accumulation potential in naturally regenerating forests (see Supplementary Fig. 1 for input data). This dataset integrates 109,708 georeferenced field measurements from national and provincial forest inventories and literature sources with 66 environmental covariates, including climate, soil properties, radiation, topography and biome characteristics. Multiple random-forest models were trained on this integrated dataset to generate global age-specific predictions of aboveground live carbon density. The resulting predictions cover naturally regenerating forest stands at approximately 1-km resolution across 5-year age intervals spanning 1–100 years.

To align with the 30-year period applied in the ref. 20 cost analysis and provide near-future policy-relevant carbon accumulation estimates, we employed the CR growth functions from the ref. 25 dataset, which models nonlinear forest growth patterns. For each 1-km^2 grid cell, CR functions were fitted with the following equation:

$$y = A \times \left(1 - be^{-kt}\right)^{\frac{1}{(1-m)}}$$

where y denotes accumulated carbon at time t (years); A represents the asymptotic carbon accumulation limit (MgC ha^{-1}); b impacts the initial carbon density; k signifies the growth rate; m is a shape-controlling parameter fixed at 0.67 (refs. 25,69) and e is the base of the natural logarithm.

To calculate the 30-year carbon accumulation potential by natural regeneration, we first computed y_{30} by setting $t = 30$ in the CR equation using the spatially explicit A, k and b parameter dataset[25] and then subtracted y_0 ($t = 0$) to derive net carbon gain:

$$\text{Netcarbon gain} = y_{30} - y_0$$

To calculate the potential carbon that could be accumulated, we summed the carbon value of each cell and weighted it by the PNR score. Our carbon accumulation estimates differ from values reported by Williams and colleagues[23], as we opted for different carbon-accumulation datasets: this paper employed a dataset from ref. 25, whereas Williams and colleagues chose datasets from ref. 24. Given our research question focused on categorizing the costs and benefits of PNR using the best data available, rather than determining exact carbon accumulation from natural regeneration, this is reasonable.

We also show the global PNR cost–benefit categories employing maximum carbon-accumulation rates (Supplementary Section 6 and Supplementary Table 4), which may be more relevant for decision-makers seeking to achieve rapid carbon-removal targets within shorter policy timeframes.

Biodiversity conservation benefits. A range of metrics could represent the biodiversity benefits of natural regeneration, such as species richness, abundance, diversity or area-based measures[70]. To capture this benefit at the species level, we instead quantified the reduction in extinction risk for forest-dependent species achieved by recovering lost habitat. This measure reflects the nonlinear relationship between habitat area and species persistence, as a given area of restored habitat provides more benefits for species with small ranges or that have lost much of their habitat[71,72].

Reducing species-extinction risk. We created a species-extinction risk layer following the approach created by Eyres and colleagues[71] in the LIFE (Land-cover change Impacts on Future Extinctions) metric, which quantifies the reduction in species-extinction risk achievable by restoring pasture and arable land to their natural state. We did not employ the LIFE dataset directly because (1) it does not account for the proportional 0–1 value representing PNR in each cell, and (2) it does not cover our entire study region. Instead, we applied the same species–area relationship to our potential natural-regeneration layer across the full study area, for comparison and sensitivity analysis; we present our results using the LIFE metric (for the parts of our study region that it covers) in Supplementary Section 5.

We modelled the change in extinction risk at 5 km for 4,145 mammals, 4,578 amphibians, 8,120 birds and 6,052 reptiles (totalling 22,895 species) identified as forest dependent based on International Union for the Conservation of Nature (IUCN) habitat classification. Species were classified as forest dependent by filtering against IUCN taxonomy records specifying forest as a habitat type. Species-distribution maps were accessed from the IUCN Red List[73] and ref. 74. We also included a similar analysis using a broader dataset of all species whose ranges contain at least some currently forested areas in the tropics (24,929 species), presented in Supplementary Section 10.

To estimate the potential benefits of natural regeneration to biodiversity, we quantified the reduction in the extinction risk of each species resulting from increases in its area of habitat. We used a function based on the species–area relationship that estimates extinction risk (r) for each species on the basis of the ratio between its current and original habitat extent[33,75–80]: $r = 1 - (x/A_0)^z$, in which A_0 is the original area of habitat to the focal species, x is the current area of habitat (which can be increased by restoration, derived from the GFW tropical tree-cover dataset[52], including plantations such as rubber, oil palm and non-native timber monocultures; see Supplementary Section 1.2.1 for details). The power z describes the rate of diminishing returns in value of additional area of habitat at reducing extinction risk. This application of the species–area relationship assumes that likelihood of extinction is a function of the proportion of original habitat remaining for a species and is silent on absolute amount of habitat and so may underestimate extinction risk for naturally restricted-range species and overestimate it for widespread ones[81]. We evaluate reductions in extinction risk using a z value of 0.25, following refs. 33,71,72,75–80. The created metric represents the summed species extinction-risk reduction that would occur if natural regeneration occurred in each individual pixel (Supplementary Fig. 2).

To quantify how natural regeneration could reduce extinction risk, we masked baseline and post-natural-regeneration extinction-risk datasets to our study area and calculated the reduction in extinction risk for each forest-dependent species individually. These reductions were summed across species within each grid cell to map biodiversity benefit and summarized across species as the mean per-species reduction and the aggregate reduction relative to baseline. Across all 22,895 forest-dependent species analysed, restoring all potential natural-regeneration areas could reduce species-level extinction risk by an average of 0.084 (95% CI: 0.082–0.086, s.d. = 0.158), a relative 31% reduction compared to baseline. Among these, 19,510 species have PNR areas overlapping their ranges, for which the mean extinction-risk reduction is higher at 0.099 (95% CI: 0.097–0.101, s.d. = 0.167), a relative 57% reduction compared to baseline. Full details and taxon-level estimates are provided in Supplementary Section 1.2.1.

Threatened-species ranges. We also employed a distinct approach to measure biodiversity outcomes, focusing specifically on how natural regeneration can increase habitat range overlap for threatened species, which are the target of many restoration initiatives[37]. To account for post-regeneration biodiversity benefits, we used the threatened-species richness dataset from the IUCN, which represents potential areas of species occurrence[65] at 30-km resolution (Supplementary Section 7). These occurrence data include amphibians ($n = 1339$), birds ($n = 1354$), mammals ($n = 1848$) and reptiles ($n = 2876$) categorized as critically endangered, endangered or vulnerable[82]. This dataset was resampled to 1-km resolution to align with other input datasets. For reporting purposes, we estimated the potential biodiversity conservation benefits of natural regeneration by determining how many additional threatened-species distributions could overlap with regenerated forest areas. Importantly, IUCN threat assessments explicitly incorporate habitat loss, population distribution and demographic changes[83], making threatened-species richness a meaningful proxy for extinction risk that remains accessible to decision-makers (see Supplementary Section 7 and Supplementary Table 5 for the results of using this proxy).

To quantify potential biodiversity conservation benefits, we first established a baseline of current tree cover using data from ref. 52. We created a binary forest map by classifying areas with ≥30% tree cover as forest (value = 1) and <30% as non-forest (value = 0), following ref. 84. This map was then constrained to our study region: tropical and subtropical forests (including dry broadleaf, moist broadleaf and coniferous forests) within 80 countries between ±25° latitude. Using this forest map, we calculated the current overlap between existing forest areas and threatened-species distributions. We then estimated the potential increase in species habitat by overlaying areas of potential natural regeneration (weighted by PNR scores) with species-distribution data. The difference between current and potential future overlap with species distributions provides an estimate of how forest regeneration could increase forest coverage within existing threatened-species ranges (not expanding the species' distributions themselves). To make this clear, we (1) calculated current overlap: the percentage of threatened-species distributions that currently overlap with existing forests; and (2) calculated future overlap: the percentage that would overlap if natural regeneration occurred in all potential areas; and then (3) took the difference at a 11.34% increase. Regions with greater species richness are thus classified as having higher conservation significance.

Costs

Although assisted natural regeneration incurs lower costs due to its minimal need for human intervention, it is not without some associated expenses, such as fencing to remove threats and opportunity costs from the loss of potential agricultural revenue[33,85]. We assumed that natural regeneration is more likely to be effectively implemented and sustainably maintained in regions where (1) land opportunity costs are lower, making land conversion to forests more viable when agricultural returns are minimal, increasing the probability of repurposing land for the regeneration of second-growth native forests[37]; and (2) regeneration implementation costs are low, which means natural-regeneration potential is high, requiring less human effort and financial investment[23].

Opportunity costs. To estimate opportunity costs, which refer to annual agricultural profit (annual net income from crop or livestock production) foregone due to land conversion to forest, we adopted the dataset from ref. 20. This dataset provides updated cropland and pastureland opportunity-cost data in 2020 in US dollars per hectare at 1-km resolution (values vary at a 5-arcmin (~10 km at the equator) resolution) (Supplementary Section 1.3). This dataset uses revenue information from the MapSPAM datasets, reflecting real crop locations, yields and values, and incorporates household surveys to more accurately represent true land opportunity costs than previous studies[85]. Where cropland and pastureland values intersect, we used the higher value at each location, thereby ensuring that our analysis captures the maximum possible opportunity cost.

Implementation costs. For implementation costs, we adjusted the ref. 20 data to map spatial variation in implementation costs at a finer resolution (that is, 1 km as opposed to state/province scale). This dataset represents implementation costs for unassisted natural forest regeneration (ref. 20 term 'passive natural regeneration'), which includes minimal human interventions for site evaluation to assess natural seed source adequacy and protection measures to protect regenerating trees from herbivore predation and human encroachment (Supplementary Section 1.4). Busch and colleagues[20] developed a linear regression model that accurately predicts costs in 2020 US dollars per hectare by applying machine learning to 355 regeneration-cost observations from 99 source documents, including World Bank documents and both peer-reviewed and grey literature. We scaled these implementation costs using the ref. 23 PNR dataset, meaning that areas with higher natural-regeneration potential correspondingly have lower implementation costs. The PNR dataset provides a continuous metric ranging from 0 to 1, where higher values indicate greater potential or likelihood of successful natural regeneration. This metric was developed using a random-forest model based on biophysical variables[23].

We used the 1 km × 1 km resolution PNR dataset[23], which represents the proportion of area in each pixel that has the potential for natural regeneration. We opted for this coarser resolution because it aligns with the resolution of available costs (1 km resolution) and benefits datasets (carbon 1 km, biodiversity 5 km), thus minimizing discrepancies that could arise from integrating datasets at significantly different resolutions. Specifically, for example, downscaling a coarse-resolution dataset (for example, 5 km) to a much finer resolution (for example, 30 m) can give rise to misleading results by introducing uncertainties and biases[86]. We did not apply a minimum threshold for regeneration potential; instead, our cost formula below incorporates PNR values (continuous between 0–1) so that areas with lower potential incur higher costs, enabling decision-makers to target restoration areas based on their objectives and budgets.

Cost calculation. We calculated the total cost (including both opportunity and implementation costs) of natural forest regeneration using the method described by ref. 87. This calculation was used to generate the cost categories in Fig. 2:

$$C = (1 - \mathrm{PNR} \times 0.6) \times I/0.4 + O$$

where C represents the cost of natural regeneration, PNR refers to the PNR score, I represents the implementation costs and O represents the opportunity costs. The scaling factor of 0.6 is derived from the implementation cost differential between restoration approaches identified by Busch and colleagues[20], which their results indicate is, on average, 40% lower for unassisted (passive) natural regeneration than for assisted natural regeneration ($\exp(-0.916) = 0.40$ based on their lasso regression results). Therefore, we applied a 0.6 scaling factor here to ensure that the cost reduction reflects this relationship rather than suggesting that there are no implementation costs when there is full PNR, as unassisted natural regeneration typically requires interventions such as site evaluation, monitoring, protection measures, fencing and patrols to ensure long-term success[88].

The division by 0.4 converts the implementation cost dataset from ref. 20 (which represents unassisted or passive natural regeneration) to the costs for assisted natural regeneration, establishing our cost range. When PNR = 1 (full natural-regeneration potential), implementation costs equal the original unassisted (passive) natural-regeneration cost. When PNR approaches 0 (little natural-regeneration potential), implementation costs are scaled up by a factor of 2.5 (1/0.4) to represent assisted natural-regeneration costs.

We estimated the approximate time for a natural-regeneration project to become profitable, which is when accumulated carbon revenue offsets restoration cost. We calculated the average annual carbon revenue from the median 30-year carbon accumulation, spread evenly over 30 years and valued at each carbon price (US$50 and 100 per tCO_2; converting C to CO_2 using a factor of 44/12). We then calculated the discounted payback period, which is the number of years of this revenue needed to cover the median restoration cost (implementation plus opportunity cost), with each year's revenue discounted at 5%. This is a rough, best-case estimate that values carbon at the full price without accounting for carbon-crediting costs (for example, monitoring, reporting, verification and registration) or time-varying accumulation rates.

Categories of costs and benefits. Using the calculated costs of natural regeneration, we employed a hierarchical classification approach. First, we classified areas into three cost categories based on quantile thresholds (low, medium and high). Within each cost category, we further classified areas into benefit subgroups using the median number in each carbon and biodiversity dataset, thus resulting in four subgroups: (1) both high, (2) high-carbon–low-biodiversity, (3) low-carbon–high- biodiversity and (4) both low. This hierarchical classification resulted in 12 distinct categories of restoration opportunities (see Supplementary Table 1 for the full names of the 12 categories). This categorization allows decision-makers to tailor their regeneration strategies based on specific objectives: for instance, invest in areas with high carbon benefits alone if climate mitigation is the primary goal, without necessarily requiring high biodiversity benefits.

Sensitivity analysis

Impact of opportunity costs on natural-regeneration costs. To assess the sensitivity of the total cost of natural regeneration to opportunity costs, we carried out a sensitivity analysis using the formula

$$C = (1 - \mathrm{PNR} \times 0.6) \times I/0.4$$

Where C is the cost of natural regeneration, PNR refers to the PNR score and I is the implementation cost. This formula evaluates how the results would change if opportunity costs were not considered. Our analysis reveals that opportunity costs constitute a substantial component of the total natural-regeneration cost, contributing a mean of 53.37% to the total cost (for full results of this sensitivity analysis, see Supplementary Section 2 and Supplementary Table 2). Including opportunity costs increases the median total cost to US$41,616 per km^2 (range: US$3,895–1,349,266 per km^2), compared to US$22,894 per km^2 (range: US$1,587–72,707 per km^2) when excluding them.

The substantial contribution of opportunity costs aligns with typical patterns in land-based restoration, where land price often represents the largest expense[20]. In areas with high natural-regeneration potential, opportunity costs can comprise up to 99% of total costs, as no implementation expenses are needed. Although absolute values differ between analyses with and without opportunity costs, the spatial patterns of PNR cost–benefit categories also shifted, while holistic hotspots remained largely consistent. This sensitivity analysis suggests that opportunity costs substantially influence the total expense of natural regeneration and are often the primary cost driver.

Sensitivity to classification thresholds. We conducted a sensitivity analysis using Jenks natural-breaks classification method values to separate the carbon and biodiversity values under every cost category, rather than using median values as the classification method presented in the main analysis (see Supplementary Section 3 and Supplementary Table 3 for this full analysis). This optimization method tends to minimize within-class variance while having a maximum difference between classes[89]. The results indicate that different classification methods can produce different spatial patterns of cost–benefit categories, and the choice of approach may affect how many areas are classified as holistic hotspots (areas with both high carbon and high biodiversity benefits at low cost). Decision-makers should consider which classification method with meaningful thresholds best aligns with their specific objectives, budget constraints and local context when making small-scale or local regeneration decisions.

We use GADM (database of Global Administrative Areas)[90] for all country-based summaries in this analysis, and all figures in the main text and Supplementary Information use GADM administrative boundary polygons as their basemap. The analyses were conducted using R for dataset intersections and statistical evaluations, and ArcGIS Pro 2.9.5 was employed for map generation (full details of the R packages used, with version numbers, are provided in the Code Availability statement). All integrated datasets were resampled using the nearest-neighbour method to match the spatial resolution of the PNR dataset[23], with the

Mollweide equal-area projection to maintain consistent pixel sizes across the study area.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Input datasets analysed in this study are publicly available from their original sources: PNR data from Williams and colleagues[23], natural-regeneration-cost data from Busch and colleagues[20], carbon accumulation data from Robinson and colleagues[25], species range maps from the IUCN Red List[73] and BirdLife International[74], threatened-species richness data from IUCN[65], tropical tree-cover data from GFW[52], Forest Landscape Integrity Index data from Grantham and colleagues[91] and Global Administrative Areas data from GADM[90]. The raster datasets generated during this study are available via Zenodo at https://doi.org/10.5281/zenodo.20983218 (ref. 92). These comprise ~1-km resolution maps of the potential for natural regeneration (PNR) cost–benefit categories presented in Fig. 2 and in the Supplementary Information, including the opportunity-cost and classification method sensitivity analyses, the alternative carbon and threatened-species-richness inputs, the country-level normalization; and maps of the reduction in extinction risk for forest-dependent species and for the broader set of species with forest in their area of habitat. Categorical maps have integer pixel values corresponding to cost–benefit categories 1–12, with full definitions listed in the Supplementary Tables; not all categories are present in every map. The extinction-risk maps are continuous, with each pixel value representing the aggregate reduction in extinction risk from natural regeneration. Files are named after the figure they correspond to.

Code availability

R code developed for and used in this analysis is available via GitHub at https://github.com/Juli0825/NEE_Variation_in_the_costs_and_ecological_benefits_of_tropical_natural_forest_regeneration. Analyses were performed in R (v4.3.3) using terra (v1.7.78), raster (v3.6.26), sp (v2.1.4), sf (v1.0.16), exactextractr (v0.10.0), classInt (v0.4.10), dplyr (v1.1.4), scales (v1.4.0), ggplot2 (v4.0.2) and writexl (v1.5.0); spatial visualization and map production used ArcGIS Pro (v2.9.5; Esri).

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Acknowledgements

We thank J. R. Rhodes for his comments on this paper. IUCN ranges and planning units (raster cells) within them—for the extinction-risk calculation—were reprocessed by the International Institute for Sustainability (IIS) Rio team, especially G. Duarte (gabitduarte@gmail.com) and J. Krieger (joanamkrieger@gmail.com). We thank them for kindly sharing their data with us.

Author contributions

All authors contributed to the conceptualization of the study. J.L. coordinated the development of the modelling approach with the support of B.A.W. J.L. led the analysis with the support of B.A.W and M.S.L. J.L. led the writing, synthesis, figure development and coordination of manuscript drafts. B.A.W. and M.S.L. undertook supervisory roles. All of the authors provided substantial input into the development of the manuscript.

Funding

B.A.W. is supported by an Australian Research Council Discovery Early Career Researcher Award (grant no. DE260100352).

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-026-03154-7.

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Peer review information *Nature Ecology & Evolution* thanks Jeffrey Vincent and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

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Last updated by author(s): Jun 30, 2026

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Software and code

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Data collection	All data used in this study were sourced from publicly accessible published papers, as detailed in the manuscript. No computational tools were used for data collection.
Data analysis	Spatial data processing and statistical analyses were performed in R (v4.3.3) using the packages terra (v1.7.78), raster (v3.6.26), sp (v2.1.4), sf (v1.0.16), exactextractr (v0.10.0), classInt (v0.4.10; for Jenks natural-breaks classification), dplyr (v1.1.4), scales (v1.4.0), ggplot2 (v4.0.2), and writexl (v1.5.0). ArcGIS Pro (v2.9.5; Esri) was used for spatial visualisation and map production. R code developed for and used in this analysis are available on GitHub (https://github.com/Juli0825/NEE_Variation_in_the_costs_and_ecological_benefits_of_tropical_natural_forest_regeneration).

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Input datasets analysed in this study are publicly available from their original sources: potential for natural regeneration data from Williams and colleagues (https://rdcu.be/fqVAi); natural regeneration cost data from Busch and colleagues (https://rdcu.be/fqVxe); carbon accumulation data from Robinson and colleagues (https://rdcu.be/fqVym); species range maps from the IUCN Red List (https://www.iucnredlist.org/) and BirdLife International (http://datazone.birdlife.org/species/requestdis); threatened species richness data from IUCN (https://www.iucnredlist.org/resources/other-spatial-downloads); tropical tree-cover data from Global Forest Watch (https://data.globalforestwatch.org/datasets/gfw::tropical-tree-cover/about); Forest Landscape Integrity Index data from Grantham and colleagues (https://rdcu.be/fq8mK); Global Administrative Areas data from GADM (https://gadm.org/). Full citations, including DOIs where available, are provided in the reference list.

The raster datasets generated during this study are available and include: 1) spatial distribution of cost-benefit categories for the potential of natural regeneration (PNR) at ~1 km resolution, as presented in Fig. 2 of the Results section (fig2_PNR_categories.tif, 5.52 MB); 2) reduction in extinction risk for forest-dependent species as presented in Supplementary Figure 2 (sup_fig2_extinction_risk_forest_dependent.tif, 51 MB); 3) reduction in extinction risk for the broader set of species with forest in their area of habitat, as presented in Supplementary Figure 3 (sup_fig3_extinction_risk_broader_species.tif, 6.72 MB); 4) opportunity cost sensitivity analysis map, as presented in Supplementary Figure 7 (sup_fig7_sensitivity_opp.tif, 5.69 MB); 5) sensitivity analysis map using Jenks natural break as the classification method, as presented in Supplementary Figure 8 (sup_fig8_sensitivity_natural_break.tif, 5.01 MB); 6) PNR cost–benefit categories using alternative carbon dataset of max accumulation rate, as presented in Supplementary Figure 13 (sup_fig13_max_rate_annual_carbon.tif, 5.48MB); and 7) PNR cost–benefit categories using IUCN threatened species richness, as presented in Supplementary Figure 15 (sup_fig15_threatened_species_categories.tif, 6.77 MB); 8) PNR cost–benefit categories normalised at the country level, as presented in Supplementary Figure 16 (sup_fig16_country_level.tif, 19.4 MB); and 9) PNR cost–benefit categories using the reduction in extinction risk of species whose area of habitat includes forest, as presented in Supplementary Figure 19 (sup_fig19_broader_species_categories.tif, 5.54 MB). The categorical maps have integer pixel values from 1 to 12, each representing a cost–benefit category; the full category definitions are listed in each Supplementary Tables file. The two extinction-risk maps (datasets 2 and 3) are continuous, with each pixel value representing the aggregate reduction in extinction risk from natural regeneration. Data are available in the Zenodo repository (https://doi.org/10.5281/zenodo.20983218).

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Research sample	This study did not involve physical or biological samples. We worked with spatial data layers.

Sampling strategy	N/A
Data collection	We compiled publicly available spatial datasets, no new data were collected, all analyses were conducted using existing data sources.
Timing and spatial scale	N/A
Data exclusions	We excluded grid cells that lacked a potential for natural regeneration score or contained NA values (28.61% of total cells) due to missing information or non-overlapping coverage across the compiled datasets.
Reproducibility	This study did not involve experiments.
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