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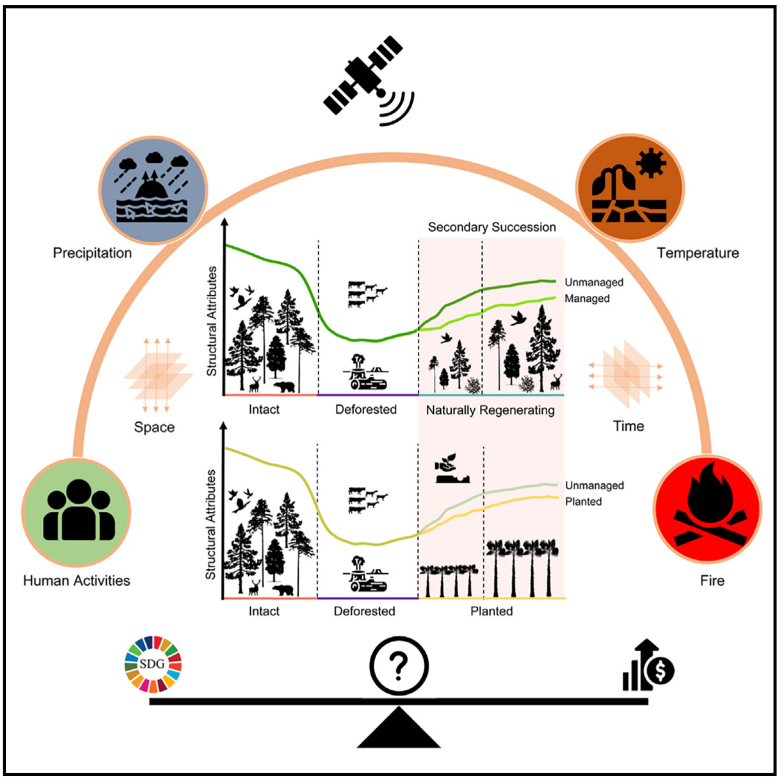
Unmanaged naturally regenerating forests approach intact forest canopy structure but are susceptible to climate and human stress

Graphical abstract



Highlights

- Multidimensional canopy structure of near-global regenerating forests was assessed
- Unmanaged naturally regenerating forest structure more resembles that of intact ones
- Managed naturally regenerating forests face a greater re-clearance rate
- Unmanaged naturally regenerating forests are vulnerable to climate and human stress

Authors

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In brief

Given the increasing global efforts in reforestation and tree planting, it is vital to understand structural dynamics of global regenerating forests under different management regimes and how they progress toward attaining intact structure. We show that unmanaged naturally regenerating forests approach intact forest canopy structure but are susceptible to climate and human stress. Meanwhile, managed naturally regenerating forests face substantial re-clearance. We highlight the importance of targeted efforts in protecting their persistence given their unique ecological values.

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Article

Unmanaged naturally regenerating forests approach intact forest canopy structure but are susceptible to climate and human stress

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SCIENCE FOR SOCIETY Regenerating forests hold significant potential for ecosystem restoration and climate-change mitigation, but their global regrowth and re-clearance patterns in canopy structure and associated relations with human management remain poorly understood. Utilizing satellite remote sensing, we assess canopy structure of global regenerating forests and their progress toward attaining intact forest structure under different human management. Our results show that unmanaged naturally regenerating forests develop a canopy structure approaching that of intact forests, much more so than managed naturally regenerating and planted forests. However, they are more susceptible to climate and human stress. Meanwhile, managed naturally regenerating forests face a higher re-clearance rate. These findings indicate that using natural regeneration as a tool for global forest restoration presents daunting challenges. Notably, safeguarding the persistence of global naturally re-growing forests becomes an urgent necessity.

SUMMARY

Maintaining newly re-established forests is an important policy and challenge for ecosystem restoration and climate-change mitigation. However, a global assessment of canopy structure in regenerating forests under different management and whether they are developing toward that of intact forests is lacking, impeding the understanding of their roles in carbon cycling and biodiversity recovery. Here we present the first near-global assessment of regenerating forest canopy structure at a 1-km resolution and its progress toward attaining intact forest characteristics. We show that canopy structure in unmanaged naturally regenerating forests more closely resemble intact forests than managed naturally regenerating forests and planted forests, but they are more susceptible to climate and human stress. Meanwhile, managed naturally regenerating forests experience substantial re-clearance. Our findings underscore the high ecological recovery potential of naturally regenerating forests and call for urgent action to enhance socio-ecological conditions for their persistence, unlocking their potential in sustainable development.

INTRODUCTION

Global efforts to protect the key functions of forests in mitigating human-driven climate change[1] and as crucial ecosystems for Earth's biodiversity are increasing.[2] Through the last decades to millennia many forested areas have been degraded or lost to deforestation. The establishment of regenerating forests, defined as forests growing via spontaneous tree recruitment or

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artificial planting in areas where complete deforestation had occurred, has potential to recover some of these losses[3–5] with high accumulation rates of aboveground biomass.[6,7] Fortunately, such recoveries have been happening across the world in recent decades as so-called forest transitions, defined as shifts from net deforestation to net reforestation.[8,9] However, it has also been reported that regenerating forests are often likely to be re-cleared under various human management schemes, e.g., in the Brazilian Atlantic Forest and European natural areas, due to changes in land tenure and government regulations as well as natural disturbances.[10–13] If widespread, such reversals would greatly impede the contribution of regenerating forests to ecosystem restoration and climate-change mitigation.[9,14] This highlights critical uncertainties regarding their persistence and contribution to carbon sequestration[6,15] and biodiversity improvements. For instance, the Kunming-Montreal Global Biodiversity Framework,[16] along with associated global targets such as the United Nations (UN) Sustainable Development Goals (SDGs),[17] plays an essential role in adapting policies and interventions effectively.

Intact forests, defined as large and continuous natural old-growth forests with no signs of significant human impact and fragmentation, are usually treated as a benchmark for assessing the quality in structure and functioning of recovering young forests.[13,18–20] However, a consistent and quantitative assessment of the multidimensional canopy structure of regenerating forests and whether they are developing structurally toward intact forests is lacking on a global scale. A global assessment of the canopy structural dynamics in regenerating forests is crucial for a deeper and broader understanding of their role in global carbon cycling and as repositories of biodiversity recovery to inform global and national biodiversity, forest, and climate policies. For example, it helps in shaping forest carbon trade mechanisms encouraged by the Paris Agreement[21] for planning sustainable forest management and restoration. It also aids in conservation activities[22] and helps meet the UN 2030 targets for ecosystem restoration. Since maintenance of forest regeneration is an important but difficult and complex policy challenge,[12] such an assessment will also provide scientists and policymakers with crucial information on the contribution of regenerating forests to global commitments such as the Glasgow Leaders' Declaration on Forests[23,24] and the SDG for life on land (SDG-15).[17]

Regenerating forests are often characterized by unpredictable successional trajectories.[15] Comprehensive and multidimensional assessments of forest canopy structure conducted over time can help alleviate this unpredictability by revealing with unprecedented coverage how forests are changing in relation to external human and non-human drivers. Such integrated assessments would help decision-makers, managers, and local users take adequate and timely action to counteract potential negative reversals. For an extrapolation of past trends to better predict future changes, forest canopy structure has shown its potential as a good indicator of such change by being a key component of secondary succession in previously deforested areas.[15] Emphasizing this potential, a recent study based on chronosequences reported that spontaneously arising tropical regenerating forests are recovering multidimensionally in terms of structure, species diversity, and species composition, highlighting the important role of spontaneous regeneration as a natural solution for ecosystem restoration.[25] Further, forest canopy structure attributes (e.g., maximum tree size and structural heterogeneity) were shown to be robust indicators of forest structure recovery.[25] They usually present more rapid and easily measurable changes following disturbances compared to other structural aspects such as species composition.[26–28]

However, most previous global studies have paid limited attention to how planted forests deviate from naturally regenerating forests in the assessment of canopy structure successional development. Spatial mixing of naturally regenerating and planted forests increases uncertainties in the assessment of regional and global contributions of secondary forests to carbon sequestration.[14,29] Besides predictability, a comparison between the two regeneration types is also economically relevant for enhancing efficiency in forest restoration and biodiversity recovery, since natural regeneration is much less costly than active tree planting.[30,31] Further, planted forests are not always used for restoration purposes but are often established mainly for timber production, e.g., in Europe.[32] Compared to intact forests, monoculture plantations usually have limited value for both biodiversity and various ecosystem services, e.g., robust climate-change mitigation.[33] Thus, a more nuanced picture is desired in the light of the increasing global commitments to tree planting, forest restoration, avoided deforestation, biodiversity conservation, and carbon sequestration.[14,21,30,34]

The successional development of regenerating forests could be influenced by climate and human activities as well as their combined effects (e.g., fire). Such succession, along with recovery of canopy structure attributes such as canopy height and cover, often occurs following land abandonment stemming from the societal dynamics such as rural out-migration,[35] market-driven land-use changes, and declining productivity of lands caused by agriculture intensification.[36–38] However, the mechanisms of such forest transitions[8,39] vary in importance and are still poorly understood due to the complicated interactions among various influencing factors, such as climate, socio-economic factors, fire, and topo-edaphic conditions.[1,26,40–42] The complicated stressor interactions make it still challenging to balance the economic benefits from forest and agriculture production (i.e., timber, fruits, and other cash crops) and sustainable ecosystem restoration despite the ongoing increasing efforts in forest reforestation in many areas.[41,43–46] Thus, a better understanding of not just the recovery of forest canopy structure but also the drivers can inform relevant policy responses for current and future forest management, e.g., achieving SDG-15 for biodiversity recovery.

Here, we present the first near-global contemporary assessment of the multidimensional canopy structure of three types of regenerating forests at a high resolution of 1 km using satellite remote sensing: naturally regenerating forests without management, naturally regenerating forests with management, and planted forests (Table S1).[22] We investigate: (1) the extent to which the contemporary structure of regenerating forests approaches intact forests; (2) whether regenerating forests are at risk of re-clearance and re-degradation, and whether any such re-clearance differs in intensity between naturally regenerating and planted forests; and (3) how the contemporary structural variations in regenerating forests are linked to climate, human activities, and their combined effect under different forest management regimes. We show that unmanaged naturally regenerating forests exhibit higher canopy structural similarities to intact forests than managed naturally regenerating forests and planted forests. Meanwhile, managed naturally regenerating forests are experiencing extensive re-clearance globally. Importantly, we found that the re-clearance of regenerating forests is not limited to specific regions but is a widespread phenomenon on a global scale, indicating a global interplay between recovery, re-clearance, and restoration potential. Path analysis demonstrates that naturally regenerating forests, especially in areas without management, are particularly vulnerable to anthropogenic pressures and climate stress worldwide. Our results highlight the urgent need to protect the persistence of naturally regenerating forests at a global scale.

RESULTS AND DISCUSSION

Global patterns in regenerating forest canopy structure

We use satellite remote sensing, including active GEDI (Global Ecosystem Dynamics Investigation) laser scanning and passive MODIS (Moderate Resolution Imaging Spectroradiometer) satellites, to depict the multidimensional canopy structure of forests and to quantify forest structural density and its heterogeneity at near-global coverage. The satellite data were extracted between April 2019 and December 2020. Here, structural density is defined as an integrative canopy structure index (CSI) depicting the overall multidimensional canopy structure in 1-km × 1-km equal-area grid cells derived from four GEDI metrics and the MODIS kernel Normalized Difference Vegetation Index (kNDVI).[47] The selected GEDI metrics include maximum canopy height (100% relative height [RH100], m), plant area index (PAI, m^2/m^2), canopy cover (CC), and foliage height diversity (FHD), which captures vertical structural complexity.[48,49] The kNDVI metric represents an additional proxy for canopy structure, leaf pigment content, and plant photosynthetic potential.[50] As these metrics are positively correlated, the CSI metric integrates these dimensions with a higher value representing generally higher values across all structural dimensions.[47] Further, we quantified heterogeneity of structural density (CSIcv) as the summation of the coefficient of variation (CV) of all the individual structure metrics within each 1-km × 1-km grid cell. We used a map of forest management for the year 2015 as the baseline for the management types (intact forests, naturally regenerating forests with and without management, and planted forests) (Figure 1 and Table S1)[22] and linked it to the current forest canopy structure. Here, the structure of intact forests without substantial tree-cover loss ($\geq$0.1 km^2) between 2001 and 2019 was used as a benchmark to evaluate whether regenerating forests develop toward intact old-growth forest structure. Pairwise comparisons in the forest structure attributes were conducted between forest management types via analysis of variance (ANOVA) and Tukey's honest significant difference (HSD) test. Analysis of covariance (ANCOVA) was also conducted to further address potential confounding effects of forest age and geographic locations on the pairwise comparisons. The planted forests in this study were categorized into those planted for timber production (rotation >15 years and rotation $\leq$15 years) and for other uses (i.e., palm plantations and agroforestry)[22] (Figure 1 and Table S1). Oil palms and agroforestry were considered in the structure comparison but were excluded in the assessment of re-clearance because they are subject to intense management away from a forest state.

We found significant canopy structural differences among intact forests, naturally regenerating forests, and planted forests across different biomes, with forests of fewer human alterations showing higher values across all structural attributes (RH100, FHD, CC, PAI, kNDVI; Figure S1). ANCOVA and Tukey's HSD tests show that those structural differences remain statistically significant after taking the potential confounding effects of forest age and geographic locations into account (Figure 1). For instance, intact forests and naturally regenerating forests without management generally showed higher canopy height and vertical structural complexity (represented by RH100 and FHD) than naturally regenerating forests with management and planted forests across different biomes. Planted forests with rotation year >15 years generally showed a higher structure attribute values than planted forests with rotation year $\leq$15 years. This pattern is well reflected in the integrative metrics of canopy structure density and its spatial heterogeneity (Figures 2A, 2B, and S1). Specifically, intact forests and naturally regenerating forests without management in the tropical rainforest areas generally showed the highest structural density followed by those in temperate areas in the Northern Hemisphere (Figures 2C and 2D). Regenerating forests in southeastern South America and eastern Africa—dry forest regions—showed a relatively lower structural density (Figures 2C and 2D). Significant differences in the spatial heterogeneity of structural density were found among forests with different management types, especially in the tropical biome with forests in a more natural environment, with less anthropogenic land transformation pressure showing lower spatial heterogeneity of structural density (Figure 2B). Further, planted forests showed generally higher spatial heterogeneity of structural density than intact forests and naturally regenerating forests, particularly in tropical and temperate biomes.

Overall, the canopy structure of both naturally regenerating forests and planted forests are approaching the canopy structure of intact forests. Importantly, naturally regenerating forests without management are more closely approaching intact forests in canopy structure compared to naturally regenerating forests with management and planted forests globally, both in structural density and heterogeneity. This is particularly evident in tropical areas, which occupy ~54% of the forest grid cells within the GEDI observational extent (Figures 2C and 2D). A similar distribution pattern was also found within each tropical forest biomes including tropical moist broadleaf, dry broadleaf, and conifer forests (Figure S2). Structural density of naturally regenerating forests decreased along with the distance to the nearest intact forests, with those without management exhibiting a clearer response (more significant slope of the fitted regression line) than those with management and planted forests (Figure 3A). However, there was no obvious relationship between local spatial heterogeneity of structural density for regenerating forests and their distance to intact forests (Figure 3A).

The generally higher canopy structure heterogeneity in planted forests is likely linked to intensive management such as rotational harvesting with clear-felling.[51,52] This suggests that the remotely sensed CSIcv metric developed in this study may

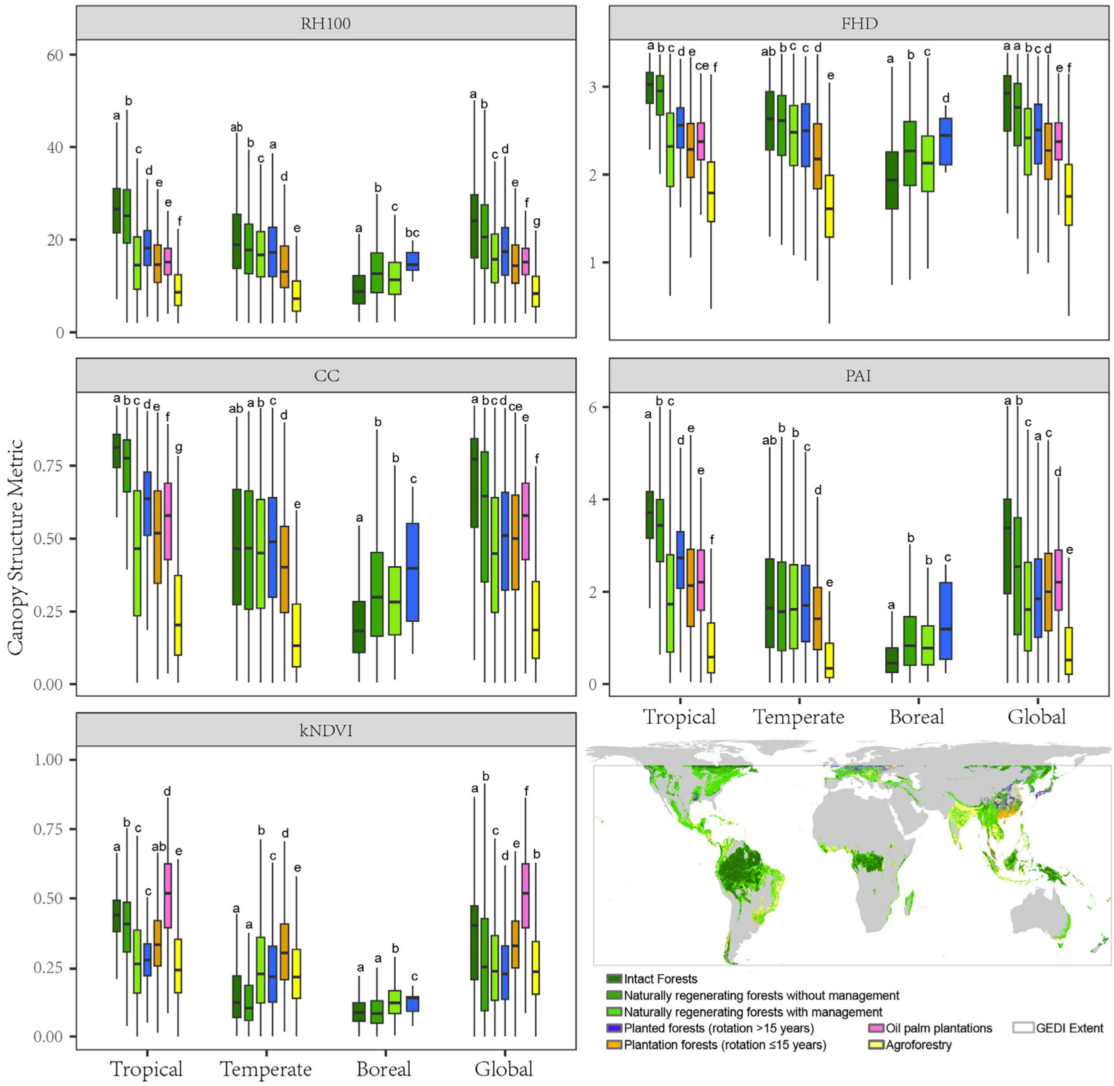

Figure 1. Forests including intact forests and naturally regenerating forests with fewer human alterations and management showing higher canopy structural attributes across different biomes globally

The forest canopy structure is depicted from multiple dimensions by GEDI structure metrics, namely, canopy height (RH100), foliage height diversity (FHD), canopy cover (CC), plant area index (PAI), and MODIS-derived kernel Normalized Difference Vegetation Index (kNDVI). The biomes include tropical, temperate, and boreal biomes. Different colors of the box plots represent different forest management types shown by the global map of forest management types in the lower right panel. The horizontal lines in the middle of the box plot represent the median values, and the lower and upper edges represent the 25th and 75th percentiles, respectively. The bottom and top whiskers represent the minimum and maximum values, respectively. For each biome, box plots not sharing any letter are significantly different among mean values tested by ANCOVA and Tukey's HSD tests at the 5% level of significance. Potential confounding effects of forest age and geographic locations were accounted for in the ANCOVA (see experimental procedures). The gray box represents the observational extent of the GEDI satellite.

have potential in capturing the differences in forest canopy structure composition caused by forest management, which is usually more challenging to detect than deforestation.[53] The greater canopy structural approximation of unmanaged naturally regenerating forests to intact forests than managed naturally regenerating forests and planted forests suggests that a more natural tree composition and ecological dynamics are more favorable for the recovery of forest canopy structure toward an intact old-growth status.[20,26,54,55] The negative correlation between structural density in regenerating forests and their distance to the nearest intact forests further suggests that proximity of the existing intact forests facilitates secondary succession. This is likely due to enhanced seed dispersal by nearby seed sources and presence of seed-dispersing fauna,[54,56,57] alongside positive environmental effects such as climate moderation provided by existing forests.[58] Such a proximity relationship can guide decision-makers, managers, and local users to consider deforested areas with high proximity to remaining forest fragments during the assessment and prediction of forest restoration potential.[59] Thus, future forest restoration commitments, via either

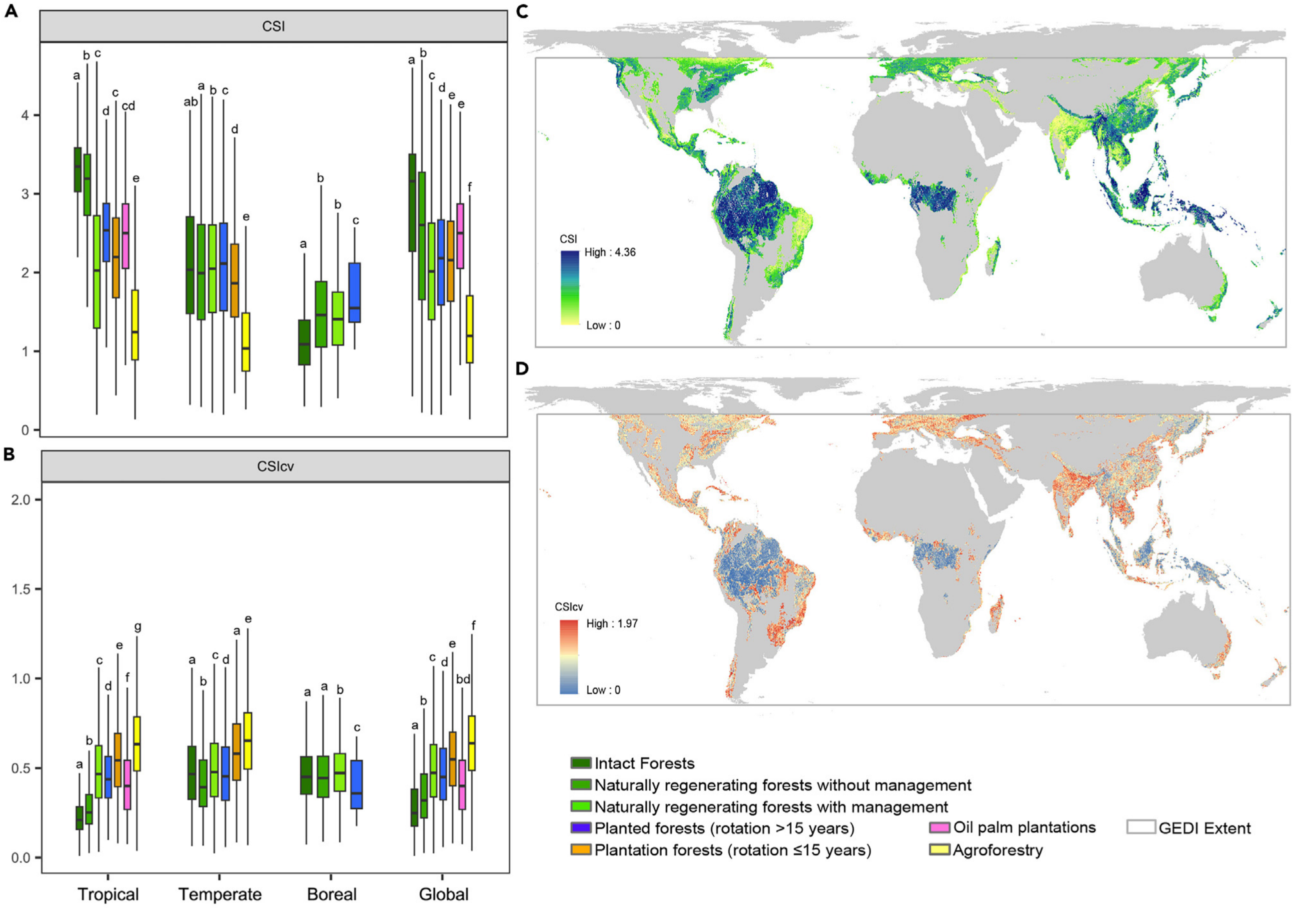

Figure 2. Naturally regenerating forests without management more resemble intact forests in canopy structural density and spatial heterogeneity than naturally regenerating forests with management and planted forests

Distribution of (A) canopy structural density and (B) its spatial heterogeneity in regenerating forests under different management types compared to intact forests, and (C and D) their spatial patterns at 1-km resolution. Structural density and its spatial heterogeneity were quantified by the integrative canopy structural index (CSI) and its coefficient of variation (CSIcv), respectively. The horizontal lines in the middle of the box plot represent the median values, and the lower and upper edges represent the 25th and 75th percentiles, respectively. The bottom and top whiskers represent the minimum and maximum values, respectively. For each biome, box plots not sharing any letter are significantly different among mean values tested by ANCOVA and Tukey's HSD tests at the 5% level of significance. Potential confounding effects of forest age and geographic locations were accounted for in the ANCOVA. The gray boxes in (C) and (D) represent the observational extent of the GEDI satellite.

natural regeneration or tree planting, should take advantage of and promote a more natural and biodiverse environment for regenerating forests. This should include, for instance, cessation of agricultural or pastoral land use, prevention of human-caused fires and intense livestock grazing,[54] and active promotion of diverse, native-rich tree assemblages rather other than monoculture plantations[14,60] alongside other ecosystem components,[61] e.g., overcoming defaunation legacies via trophic rewilding with wild large-bodied fauna.[62,63]

Accelerating re-clearance of regenerating forests

We also investigated the re-clearance rate and associated potential re-degradation by quantifying tree-cover loss during the 2001–2019 period in the regenerating forests using simple linear regression and the time-series 30-m Global Tree Cover product.[64] Assessing re-clearance rate is important for informing timely policies for forest recovery, biodiversity conservation, and climate-change mitigation. Effects of preceding re-clearance on regenerating forest canopy structure were evaluated along the year when tree-cover loss happened, differentiating naturally regenerating and planted forests. We found accelerating tree-cover loss in regenerating forests globally within the GEDI satellite observation domain between 2001 and 2019. There were approximately 2.53 million hectares (Mha) of naturally regenerating forests without management and 8.72 Mha of naturally regenerating forests with management lost overall with an annual loss rate of ca. 0.007 Mha/year and 0.018 Mha/year, respectively (Figures 4A and 4B). In contrast, tree-cover loss in planted forests (excluding oil palm plantations and agroforestry) showed the lowest increasing trend, with a total loss of about 2.19 Mha and an annual loss rate of ca. 0.006 Mha/year. Most of the tree-cover loss was found in Africa, Asia, and North America, while Europe and Australia showed the least loss (Figure 4B). Widespread tree-cover loss was found in the two types

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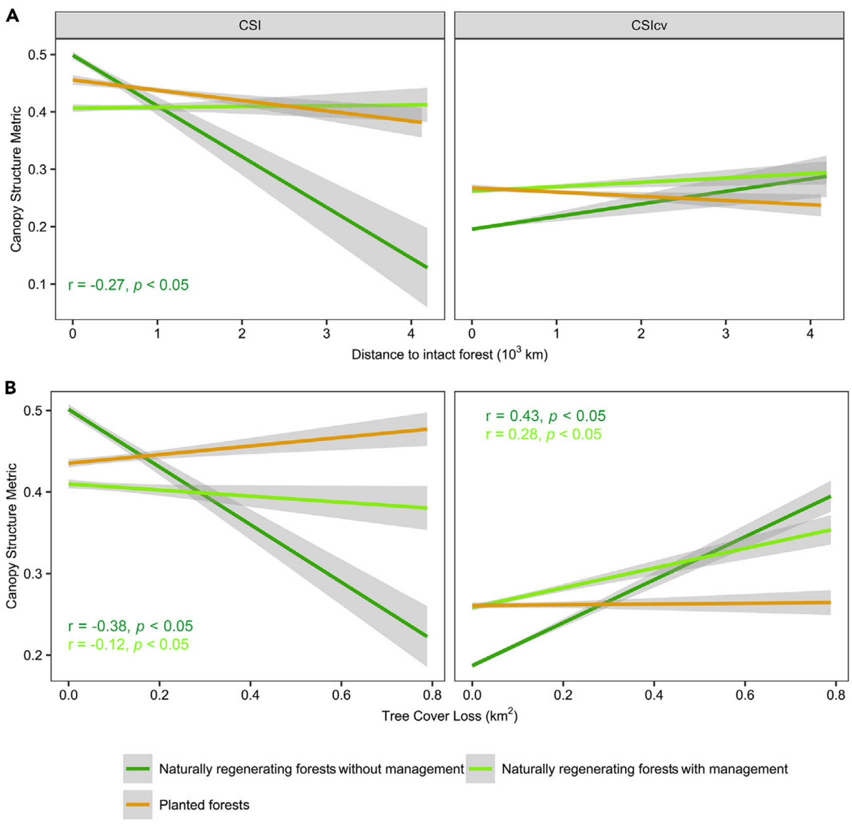

Figure 3. Response of regenerating forest canopy structure to the distance to intact forests and to tree-cover loss

(A) Structural density of naturally regenerating forests without management decreases along the distance to intact forests.

(B) Preceding tree-cover loss between 2001 and 2019 resulted in reduced canopy structural density and increased heterogeneity in regenerating forests worldwide, particularly in naturally regenerating forests without management. Forest structure presented by structural density and heterogeneity are quantified by the integrative canopy structural index (CSI) and its coefficient of variation (CSIcv), respectively. Lines in the plots are regression lines fitted using simple linear regression. Shadings indicate the 95th percentile empirical confidence intervals. Pearson's correlation coefficients (*r*) with significance at $p < 0.05$ level are shown and colored according to corresponding forest management type. The CSI and CSIcv values were normalized for better visualization.

of naturally regenerating forests, particularly in the managed ones (Figure S3). Areas in naturally regenerating forests without management where substantial tree-cover loss (≥ 0.1 km^2) happened before 2012 showed much lower contemporary structural density (CSI) and higher associated spatial heterogeneity (CSIcv) (dark-green lines in Figure 4C). This suggests a low tree-cover recovery after re-clearance in those areas. Areas in planted forests with rotations (excluding oil palms and agroforestry) where substantial tree-cover loss happened before 2008 showed a distinctively opposite response relationship between canopy structural density (heterogeneity) and the year when tree-cover loss happened. Those planted forests with preceding tree-cover loss before 2008 showed a relatively high contemporary structural density, which suggests that they experienced fast tree-cover recovery by active planting after re-clearance. Areas in naturally regenerating forests with management, where substantial tree-cover loss happened before 2008, showed similar lower contemporary structural density to naturally regenerating forests without management. However, their spatial heterogeneity of canopy structural density is much lower than naturally regenerating forests without management, likely linked to intense forest management. A consistent pattern was observed for each type of forest before and after the year 2015 when the forest management map was produced (gray line in Figure 4C). Generally, increasing tree-cover loss resulted in naturally regenerating forests with reduced canopy structural density and increased spatial heterogeneity, particularly in naturally regenerating forests without management (Figure 3B). The upward trend of canopy structure density in naturally regenerating forests along with the year of tree-cover loss (dark-green and light-green lines for CSI metric in Figure 4C) suggests that tree-cover re-clearance is spatially expanding into high-quality naturally regenerating forests with high structural density.

Our results showed an overall negative impact on regenerating forest canopy structure from tree-cover loss and associated re-degradation in naturally regenerating forests across the globe. We note that this tree-cover loss is not always outright deforestation but also includes, e.g., industrial timber harvest in planted forests. However, we interpret the substantial tree-cover loss in naturally regenerating forests without management as likely re-degradation. The re-clearance of planted forests found in this study is likely related to rotational management systems (i.e., clear-felling and re-planting) with short fallow periods in ranching and agriculture in tropical countries such as Brazil and Argentina.[29,65] We found that the re-clearance of naturally regenerating forests without management not only happened in the tropics[10,11] but is a widespread phenomenon globally. This indicates a global interplay between natural recovery and re-degradation processes.[26] The re-clearance of regenerating forests with management include activities allowed by law, especially within private properties, and activities to reduce the pressure over primary forests including intact forests in the Brazilian Amazon.[66] It is reported that the clearance of secondary forests has surpassed the clearance of primary forests in the Amazon region.[12,14] Such re-clearance echoes results of previous local studies that secondary forest loss can hinder its role for climate-change mitigation and forest ecosystem restoration due to its often ephemeral nature.[10,12,54,67] It further proves that major challenges exist for realizing the potential of natural regeneration as a tool for global forest restoration,[54] even though it is much less costly compared to intensively managed plantations.[31] The sometimes higher structural density of planted forests is likely linked to intensive human management

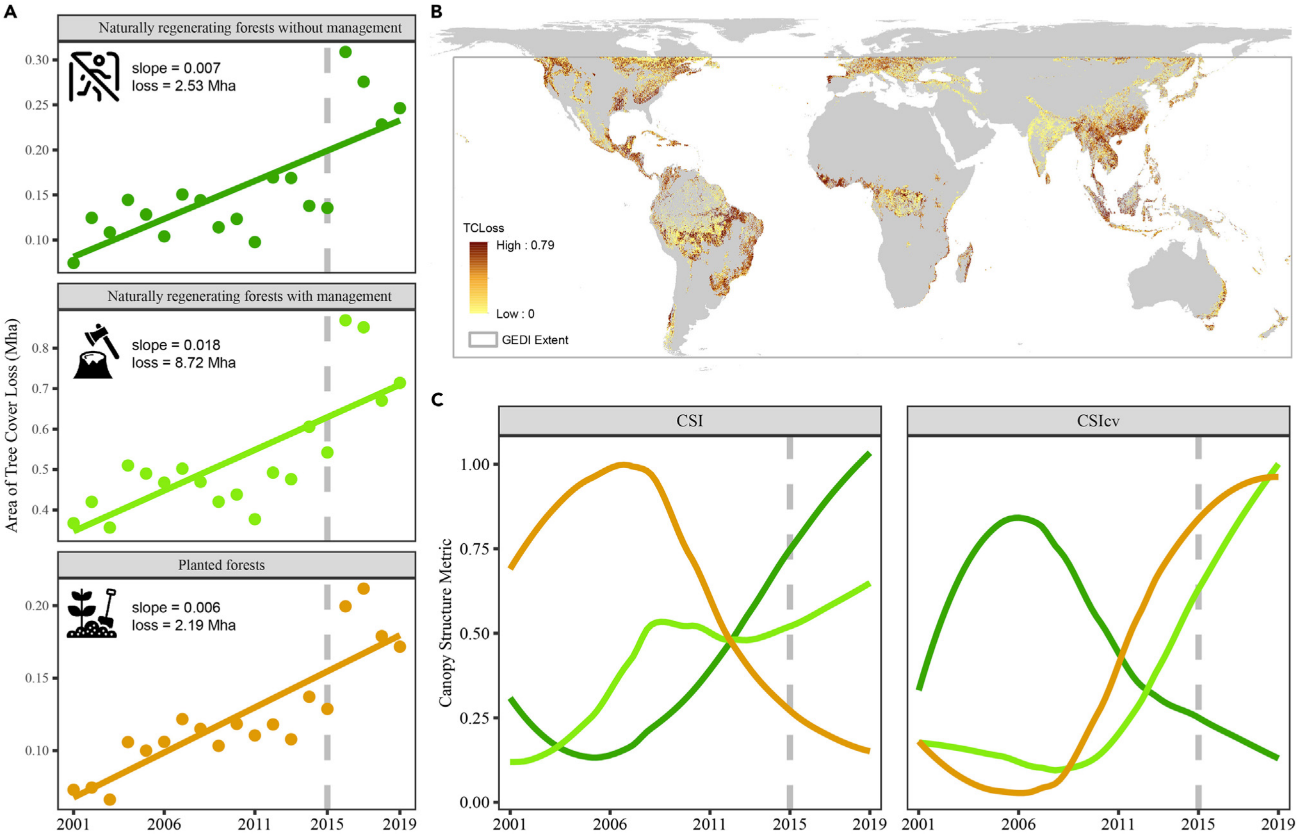

Figure 4. Increasing re-clearance of regenerating forests between 2001 and 2019

(A) Total area of tree-cover loss (converted to Mha) observed for naturally regenerating forests without management (dark green) and with management (light green), as well as planted forests excluding oil palms and agroforestry (brown) per year (n = 19).

(B) Map of total tree-cover loss (TCLoss, km^2) observed in near-global regenerating forests between 2001 and 2019.

(C) Average canopy structural density and its heterogeneity (the year 2019–2020) in areas where substantial tree-cover loss was observed (here only referring to the presence of loss ≥ 0.1 km^2) in preceding years for naturally regenerating forests with management and without management, as well as planted forests (same color legend as A). The lines represent the smoothed trend lines fitted using the LOESS function. The x axis represents the year when substantial tree-cover loss happened that was provided by Hansen's tree-cover product. Structural density and heterogeneity were quantified by the integrative canopy structural index (CSI) and its associated coefficient of variation (CSIcv), respectively. CSI and CSIcv values were normalized for better visualization. The gray lines in (C) represent the year of forest management type map.

and protection for wood production, e.g., regular cycles of replanting and protection from livestock grazing.[11] While this pattern may indicate increased protection of planted forests, this is not necessarily beneficial for biodiversity.[33] It may also increase the risk of catastrophic fires,[68] e.g., in the case of dense planted forests in naturally semi-open woodland ecosystems.[69,70] Nevertheless, the lower canopy structure recovery found in naturally regenerating forests without management where tree-cover loss happened before 2012 (Figure 4C) suggests that current environmental forest restoration and conservation policies should be designed and enforced to ensure the persistence of natural forest recovery with favorable conditions.[12,14,71] Ensuring such persistence for regional and global natural forest regeneration is also paramount for achieving critical UN SDGs (SDG-12: ensure sustainable consumption and production patterns; SDG-13: take urgent action to combat climate change and its impacts; SDG-15: halt and reverse land degradation and halt biodiversity loss) by mitigating climate change and reducing biodiversity loss.[17,72]

Climate and human influence

We investigated how structural density and heterogeneity in regenerating forests are linked to climate, human activities, and fire using structural equation modeling (SEM) and assessed how these relations vary with forest management. The climatic factors included annual mean precipitation (MAP), precipitation seasonality (PreS), and mean annual temperature (MAT). We used the human modification index (HMI) as proxy of the intensity of human activities.[73] Annual total fire frequency (FireFreq) was used to represent the fire regime, itself modulated by both climate and human activities. In this study, we only consider the impacts from climate, human activities, and fire, since they are major drivers of current and near-future forest dynamics globally.[46,74–76] However, this does not mean that other factors such as soil properties, hurricanes, and biotic disturbances (wildlife grazing, herbivore or pathogen attacks) are not important in various settings,[26,54] but they are less feasible to be spatial-explicitly quantified at the global scale with this high resolution.

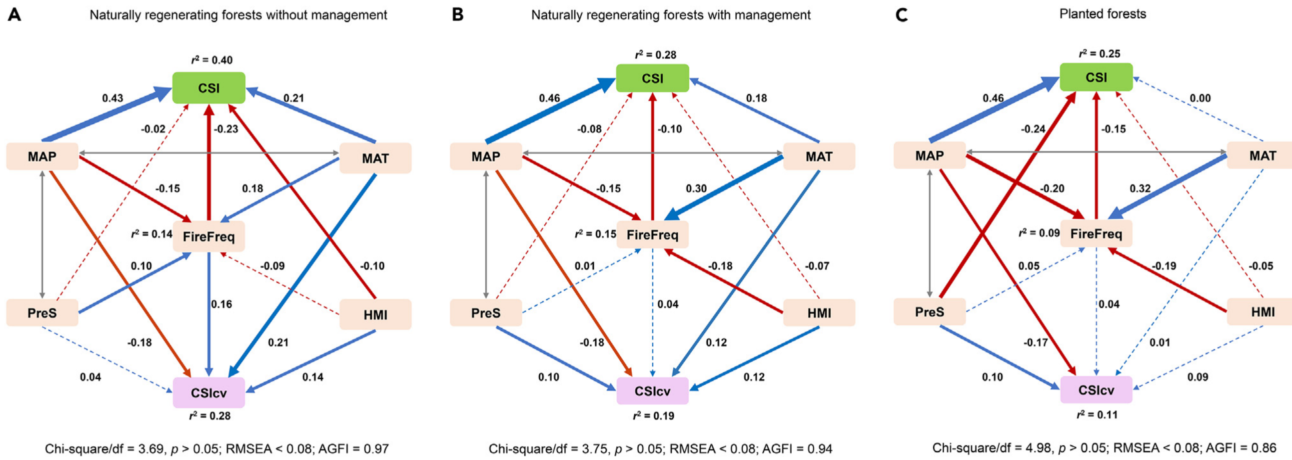

Figure 5. Pathways showing the linkages of structural density and its heterogeneity of regenerating forests to climatic and anthropogenic factors

Structural equation models (SEMs) were built for three types of regenerating forests: (A) naturally regenerating forests without management, (B) naturally regenerating forests with management, and (C) planted forests. Structural density and heterogeneity were quantified by the integrative canopy structural index (CSI) and its coefficient of variation (CSIcv), respectively. The controlling factors included annual mean precipitation (MAP) and its seasonality (PreS), annual mean temperature (MAT), human modification index (HMI), and fire frequency (FireFreq). Blue and red single-headed arrows indicate the hypothesized direction of causation with positive and negative relationships, respectively. Solid lines represent relationships that are statistically significant ($p < 0.05$), and dashed lines represent relationships that are statistically insignificant ($p > 0.05$). Arrow thickness is proportional to the strength of the relationship except for insignificant relationships. r^2 represents explained variance of the response variables in the model. Double-headed gray arrows indicate covariance between variables. The SEMs were evaluated by chi-squared/df, the adjusted goodness-of-fit index (AGFI), and the root-mean-square error of approximation (RMSEA). Chi-squared values were obtained from a chi-squared test; df represents degrees of freedom, indicating the number of paths omitted from the model.

The SEM analyses showed that climate and human factors have a much stronger influence on structural density and associated spatial heterogeneity of naturally regenerating forests without management than on naturally regenerating forests with management and planted forests (Figure 5). The SEMs explained a much higher fraction of variance in CSI (40% vs. 28% and 25%) and CSIcv (28% vs. 19% and 11%) for the former vs. the latter two forest types. Among the factors, MAP showed a significant positive influence on CSI in all three regenerating forests, with a stronger contribution than PreS and MAT. HMI showed a significantly positive impact on CSIcv of naturally regenerating forests, likely reflecting human-driven degradation and fragmentation.[77] Fire frequency acted as an important mediator by indirectly shaping the influence on the regenerating forest canopy structure by climate and human factors with a significant negative contribution to CSI and positive contribution to CSIcv. Overall, the SEM analyses suggested that planted forests are less affected by climate and human impacts than naturally regenerating forests. These patterns are consistent with active management reducing the role of environmental influences and unwanted human pressures.[78] They also indicate more uniform management for planted forests than naturally regenerating forests. An overall stronger contribution of climatic factors to SEM with higher interactions with fire was found in explaining the fraction of CSI for naturally regenerating forests vs. planted forests. This suggests that natural regeneration is strongly influenced by climate and repeated stand-level disturbances such as fire.[79] Meanwhile, a consistently significant contribution of HMI on the structure of three types of regenerating forests indicates a strong response of regenerating forest canopy structure to human impacts, e.g., forest clearing and non-forest land use.[26,47,54] This agrees with previous studies showing that secondary succession, particularly natural regeneration, is strongly shaped by changing socio-ecological processes.[79,80] While forests are being restored and protected at various scales in both developed and developing countries, this requires long-term support from financing and governmental commitments and actions.[31] The more evident forest structure-human-fire interactions found in naturally regenerating forests without management echoes previous studies emphasizing that relationships between forest and people, who inhabit and share the landscape with it, are crucial for sustainable forest restorations.[31,81] We highlight that naturally regenerating forests are at higher risk from rising anthropogenic pressures and climate stress than planted forests. The persistence of naturally regenerating forests should receive greater attention given their much higher value for biodiversity than tree plantations.[60] Such attention, together with control practices, could also reduce the negative impact from fire outbreaks and thus can further enhance the persistence of secondary succession from early to mature stage.[82–85]

Caveats

We are aware that potential uncertainties may exist in our analysis. For instance, there is a time gap of 4 years between the forest management map and structure data, which may cause some uncertainties in the assessment of regenerating forest canopy structure. However, we believe that any such uncertainty is unlikely to be a major concern for our analysis, since a consistent variation trend of forest dynamic impact on canopy structure was observed after 2015 when the forest management map was produced (Figure 4C). Due to the absence of detailed global maps depicting forest management types as of 2001, this study acknowledges potential uncertainties in assessing the re-clearance of regenerating forests. Specifically, there may have been changes in the management of some forests between 2001 and 2015, especially in those less than 14 years old. To better account for these management shifts, future research should focus on creating detailed time-series maps of forest management types. Such efforts should be supported by a thorough validation process incorporating historical forest inventory data and local mapping resources. Given the time gap between the canopy structure and forest age data, we removed the forest grid cells with significant total tree-cover loss ($\geq$1 km^2) between 2001 and 2019 before the ANCOVA to reduce the influence on forest age caused by tree-cover loss since 2010. Despite high overall classification accuracy, caveats in relation to the forest management map used in this study still exist as mentioned by the production team, e.g., underestimation of planted forests at some localities.[22] However, we believe these caveats are unlikely to influence the general pattern on forest canopy structure of regenerating forests at the global scale, with the map specifically being recommended for global and supra-regional applications.[22]

Implications

Our analysis showed that naturally regenerating forests without management across the world more closely approach intact forests in canopy structural density and heterogeneity than naturally regenerating forests with management and planted forests. At the same time, managed naturally regenerating forests experienced greater and accelerating tree-cover loss rates between 2001 and 2019, resulting in negative effects on canopy structural density and increased spatial heterogeneity. Path analyses showed a significantly higher influence of climate, human activities, and fire on the canopy structure of naturally regenerating forests than that of planted forests, particularly in unmanaged areas, suggesting greater sensitivity to anthropogenic and environmental pressures. Spontaneous forest regeneration provides an inexpensive, nature-based solution to restore biodiversity as well as key ecosystem services such as carbon sequestration.[14,25,54] In consequence, the worrying re-degradation risks of these forests is a key challenge for these benefits and other forest-related sustainable development goals. Since naturally regenerating forests are more diverse structurally than planted forests and have potentially high socio-ecological value, it is crucial to ensure the persistence of existing and emerging naturally regenerating forests via targeted, enforced, and inclusive land-use policies globally.[11,13] The consistently high human impacts on regenerating forests at a near-global level found in this study suggest the need to promote more effective, contextually grounded conservation of these forests to realize and safeguard their important roles.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Wang Li (liwang@aircas.ac.cn).

Materials availability

This study did not generate new unique materials.

Data and code availability

- All data needed to evaluate the conclusions in the paper are open access and are present in the paper and/or the supplemental information. GEDI data are freely available at https://lpdaac.usgs.gov/. The forest management map is available at https://zenodo.org/record/4541513. The intact forest landscape map is available at https://intactforests.org/. The forest biome and ecoregion information extracted from the RESOLVE Ecoregions dataset is available at https://ecoregions2017.appspot.com/. The global forest age map is available at https://www.bgc-jena.mpg.de/geodb/projects/FileDetails.php. All the other environmental data are publicly available in the data catalog of Google Earth Engine at https://developers.google.com/earth-engine/datasets/catalog.
- Codes that support the main findings in this study are available at the Zenodo repository: https://doi.org/10.5281/zenodo.11078200.
- Any additional information required to re-analyze the data reported in this paper is available from the lead contact upon request.

Method overview

Forest structural density and its heterogeneity of the near-global (within -52° and 52° latitude) forests were quantified using data from GEDI Level 2B (version 2) product and MODIS kNDVI acquired between April 2019 and December 2020. We used a map for the year 2015 produced by Lesiv et al.[22] as a baseline for global forest management types. We then investigated the re-clearance and potential re-degradation of regenerating forests using the Global Tree Cover product from Hansen et al.[64] Finally, SEM was conducted to explore the direct and indirect pathways of how climate, human, and fire factors influence regenerating forest structural density and heterogeneity. All the spatial analyses were conducted in equal-area Behrmann projection at 1-km × 1-km resolution.

Forest management type

The forest management map at 100-m resolution for the year 2015 categorized the global forest into six classes, namely "Naturally regenerating forests without management, including primary forest (class 11)," "Naturally regenerating forests with management (class 20)," "Planted forests (rotation >15 years) (class 31)," "Plantation forests (rotation $\leq$15 years) (class 32)," "Oil palm plantations (class 40)," and "Agroforestry (class 53)."[22] A detailed definition of each forest management type is presented in Table S1.[22] The forest management map is a spatially explicit map, developed on the basis of a large reference dataset built by many experts, crowdsourcing campaigns, and PROBA-V satellite imageries, which was independently validated by following the procedure proposed by Olofsson et al.[86] The map obtained an overall classification accuracy of approximately 82%.[22] We aggregated the forest management map into 1-km resolution to be consistent with the rasterized forest canopy structure data derived from GEDI and MODIS satellites. We believe such an aggregation into 1-km resolution can still represent the forest management types as suggested by the user notes from the production team of the map.[22] In this study, we reclassified class 11 by separating intact forests (class 10) from it as a benchmark class for regenerating forests to investigate to what extent regenerating forests develop structurally toward a more natural, intact, and old-growth status in different biomes. The global intact forest landscapes (IFL) map as polygons for the year 2020 was used to depict the boundaries of remaining forest landscapes where only limited human activity or habitat fragmentation has occurred.[87] We rasterized the IFL polygons into 30-m resolution in ArcGIS (version 10.6; Esri), whose resolution was identical to that of Landsat data used to produce the IFL map. We then aggregated the 30-m IFL map into 1-km resolution by generating another raster with its pixel values defined as the proportions of 30-m IFL pixels. We finally overlaid the 1-km IFL map with the Lesiv map and reclassified the class 11 pixels with a proportion of 30-m IFL pixels $\geq$90% as intact forest class (class 10).

Forest structural density and heterogeneity

We used data from GEDI and MODIS satellites to quantify the multidimensional structural density and heterogeneity of global forests.

GEDI data

The GEDI Level 2B (version 2) data were used to quantify the multidimensional forest canopy structure of all available near-global forested areas.[88] We collected all the GEDI Level 2B data with a 25-m footprint-level dataset of structural metrics acquired between April 2019 and December 2020. Four GEDI structure metrics including the 100th relative height (RH100), CC, PAI (one-half of the total plant area projected per unit ground surface), and FHD (the vertical heterogeneity or variations of foliage profile) with unique ecological meanings were used in this study. No further validation on the GEDI structure metrics was conducted, since comprehensive validation on the GEDI data Level 2B product was conducted by the product providers using an extensive airborne lidar and field-measured dataset,[88,89] which has been supported by recent studies on global forest mapping.[47,90] Following our previous study,[47] we conducted a similar data filtering by excluding footprints with low signal-to-noise ratio and those collected during the night and leaf off season.

GEDI metrics rasterization

We rasterized the 25-m footprint-level GEDI metrics into a raster with an equal-area spatial resolution of 1 km for each individual GEDI structure metric. The 1-km resolution is believed to reduce the influence from the GEDI geolocation uncertainty.[91] The average structure value for all footprints within the grid cell obtained during each month were calculated for each 1-km grid cell. An annual median dataset for the year 2019–2020 was obtained by a monthly median composition on the data collected during the 21 months. During the rasterization, only footprints representing forested areas were selected by overlaying the center coordinates of the footprints with the global forest management type map described above, representing the contemporary canopy structure of forests under different management types. We only selected the forest grid cells with GEDI laser shot density greater than 10 points/km^2 to further ensure the data quality and to avoid outliers. GEDI data processing was performed using the R software's key packages *rGEDI*[92,93] and *rhdf5*.[94]

Kernel Normalized Difference Vegetation Index

The kNDVI, defined as nadir bidirectional reflectance imagery from MODIS (MCD43A4) satellite at 500-m resolution, was used as an additional proxy for canopy structure, leaf pigment content, and plant photosynthetic potential.[50] Monthly and annual median compositions were conducted on all the reflectance imagery from the MODIS imagery obtained between April 2019 and December 2020, obtaining a time series of monthly and an annual kNDVI imagery. The monthly composited kNDVI imagery was further used to quantify the heterogeneity of structural density. The annually composited kNDVI imagery was then aggregated to 1-km resolution.

Structural density

We developed an integrative CSI to represent the overall multidimensional structure of forest canopies or structural density based on the five GEDI and MODIS structure metrics (RH100, CC, PAI, FHD, and kNDVI) based on our previous study.[47] The CSI metric represents an overall proxy of multidimensional structure that reflects the height and three-dimensional density of the forest canopy structure. To calculate the CSI metric, we firstly normalized each single structure metric to a value ranging from 0 to 1 based on the values from all the forest grid cells, then added up their values for each grid cell to represent the CSI value with equal weight.[47] Giving an equal weight to each metric not only keeps their original ecological information but also assumes that no one metric of the five metrics is better or more important than the others.[47]

Structural heterogeneity

Forest structural heterogeneity at the grid cell level was also quantified during the structural metrics calculation and temporal composition. We first calculated the CV of each single structure metric based on all the 25-m GEDI footprints or 500-m kNDVI pixels within each 1-km × 1-km grid cell for each month. Annual temporal median composition on the CVs of the metrics was then conducted respectively. Like CSI, the CV of each single structure metric (RH100cv, CCcv, PAIcv, FHDcv, and kNDVIcv) was normalized to a value ranging from 0 to 1 based on the values from all forest grid cells. We finally added up all the five normalized CV values for each grid cell, obtaining another integrative metric representing the overall coefficient of variation or heterogeneity of the multidimensional canopy structure (here denoted as CSIcv).

Forest biomes and ecoregions

We investigated the distribution of forest structural density and heterogeneity at biome level and compared the structure of naturally regenerating and planted forests to that of intact forests in development. We extracted the main biomes and ecoregions where the three forest management types existed and associated each grid cell with the corresponding biome and ecoregion. Information from the forest biomes and ecoregions was extracted from the RESOLVE Ecoregions dataset updated in 2017.[95] Forest grid cells only in biomes with labels containing "forests" were selected and regrouped into three main biomes (boreal, temperate, and tropical) according to their definitions. The forest grid cells of all the three main biomes were denoted as a global group for comparison. Comparisons in canopy structure were also conducted among forests with different management types across the three tropical forest biomes, since different secondary successions exist in moist and dry forests in the tropics, which may influence the forest structure.[96,97]

Regenerating forest re-clearance

The 30-m global tree-cover product provided by Hansen et al. was used to check the tree-cover loss during the period 2001–2019.[64] The period of tree-cover estimation represented in Hansen's product is in line with that of GEDI and MODIS data used in this study. Here, we only used the tree-cover loss data ("loss year") to quantify the re-clearance and potential re-degradation of regenerating forests, since they are expected to contribute to tree-cover gain and our focus is to assess their re-clearance rate. We counted the areas of tree-cover loss in km^2 or Mha within each 1-km × 1-km regenerating forest grid cell for each year. The relationship between forest canopy structure and total tree-cover loss for all of the forest grid cells was fitted using simple linear regression. The slope of the fitted regression models was used to describe the annual re-clearance rate of each type of regenerating forest. We grouped the regenerating forest grid cells according to the year when tree-cover loss was observed by Hansen's product and defined the regenerating forest grid cell with a total tree-cover loss ≥ 0.1 km^2 as a substantial loss. Tree-cover loss in planted forests is more likely linked to forestry cycles of felling and replanting. Thus, we interpreted the substantial tree-cover loss in naturally regenerating forests as potential re-degradation.

We averaged the contemporary structural density and heterogeneity for the regenerating forest grids where substantial preceding tree-cover loss happened. We investigated the relationship between the contemporary structure and the year when preceding tree-cover loss happened. Such a relationship helps to show how natural and planted forests deviate from each other in contemporary structure since tree-cover loss happened. The averaged structural density and heterogeneity were normalized and matched with the loss year between naturally regenerating and planted forests, since they may have different structural dynamic trajectories after tree-cover loss. We believe that differences among the three types of regenerating forests in the responses of contemporary structure to loss year are highly influenced by potential natural disturbances and human management. For instance, planted forests where tree-cover loss happened in an earlier year are likely to have a relatively higher contemporary structural density if intensive human management such as replantation was applied, which might be unlikely to happen in naturally regenerating forests without management. During the re-clearance assessment, oil palm plantation and agroforestry were not considered, since they are subject to intense management away from a forest state. The two types of planted forests with different rotation years (class 31 and class 32) were grouped into one category for simplicity during the comparison.

Forest age

The global forest age map at 1-km resolution was produced by Besnard et al. using a machine-learning approach trained with forest inventories, biomass, and climate data.[98] It represents the most up-to-date product of global forest age distribution circa 2010. We categorized the continuous forest age values into different age groups with an interval of 20 years and used the categorical age group as one type of prior knowledge in the random stratified sampling for the statistical analysis.

Statistical analysis

To compare the statistical differences in forest canopy structure between management types, one-way ANOVA was conducted based on a linear regression model between forest structure attribute and management type. Mean structure attribute values of different pairs of management types within each biome were compared via Tukey's HSD tests at the 5% level of significance based on the ANOVA results. The *aov* and *TukeyHSD* functions from the *stats* base package in the R software suite were used in the pairwise comparisons.[93] To account for potential confounding effects of forest age and geographic locations on both forest canopy structure and management type, we conducted an additional ANCOVA by adding forest age and geolocation factors (longitude, latitude, and ecoregion type) as covariates in the linear models. We fitted the ANCOVA model with type III of sums of squares. We tested the statistical significance of the covariance model using the general linear hypotheses *glht* function from the *multcomp* package and *TukeyHSD* function in R.[99] Since the forest age map represents circa 2010, there is a 10-year time gap compared to the contemporary forest canopy structure data in 2019–2020. Tree-cover loss has very likely happened since 2010, thus changing the forest ages. To reduce the influence on forest age caused by tree-cover loss since 2010, we removed the forest grid cells with significant tree-cover loss ($\geq$1 km^2) before the ANCOVA. To reduce the influence of the potential confounding effect caused by forest age and geographic locations, we conducted a stratified random sampling on the forest grid cells by randomly sampling 1% of grid cells from each forest age group and ecoregion, which resulted in weak spatial autocorrelations in the forest canopy structure attributes that assessed using Moran's I index using the *spdep* R package.[100] The randomization ensures that each grid cell has an equal chance of being selected, thereby distributing confounding factors equally among the chosen samples. This aids in mitigating the influence of potential confounding effects before conducting ANCOVA.

Climate, human, and fire

Climatic factors including MAP, PreS (CV for monthly precipitation), and MAT between 2000 and 2019 were calculated using the TerraClimate dataset.[101] The TerraClimate dataset incorporates high-spatial-resolution climatological normals from the WorldClim dataset with coarser spatial resolution and time-varying data from CRU Ts4.0 and the Japanese 55-year reanalysis (JRA55) at a resolution of 5.5 km. We used the HMI, representing a cumulative measure of human modification of lands to depict human influence.[73] Fire frequency was quantified by using the MODIS burned area product (MCD64A1) by summing the number of fire occurrences for each 500-m pixel from 2001 to 2019.[102] The annual total fire frequency for each pixel per year was counted, which was then used to calculate the mean annual FireFreq for the period between 2001 and 2019. The HMI and FireFreq raster layers were then aggregated to a 1-km resolution.

Structural equation modeling

We used SEM to assess the direct and indirect pathways of how climate, human, and fire factors influence regenerating forest structural density and heterogeneity. SEM is a multivariate statistical method that provides strong pointers to underlying deterministic processes.[103] We selected the maximum-likelihood estimation method that synthesized with path and different factors for the SEM and built the model for naturally regenerating and planted forests, respectively. The overall fit of the SEMs was assessed using a chi-squared test (chi-squared/df, df representing degrees of freedom indicating the number of paths omitted from the model), the adjusted goodness-of-fit index, and the root-mean-square error of approximation.[104] The *p* value for the chi-squared test was also used to indicate the model performance. A *p* value of >0.05 for the chi-squared test indicates that the hypothesis of a perfect fit cannot be rejected.[105] We randomly sampled 1,000 forest grid cells for each SEM for naturally regenerating forests without management, naturally regenerating forests with management, and planted forests, respectively. We selected the sample size of 1,000 mainly because the chi-squared value is very sensitive to sample size, and a relatively moderate sample size can support the assessment of the random effect in the statistic regression and the interpretations of *p* values for the coefficients. It also reduces the influence from spatio-autocorrelation from a big population of samples. We conducted SEM analysis using AMOS (version 26.0) software (Amos Development, Chicago, IL, USA).

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2024.05.002.

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AUTHOR CONTRIBUTIONS

W.L. and J.-C.S. designed the research. W.L. performed the research with help from W.-Y.G., Z.N., L.W., F.C., Y.Q., H.Q., and J.-C.S. M.P. assisted with the contribution framing and political implications of the study. W.L. wrote the first draft of the manuscript with contributions from J.-C.S. All authors contributed to subsequent versions of the paper.

DECLARATION OF INTERESTS

J.-C.S. is a member of the advisory board of *One Earth*.

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