









## RESEARCH ARTICLE

## Forest disturbance and recovery in Peruvian Amazonia

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## Abstract

Amazonian forests function as biomass and biodiversity reservoirs, contributing to climate change mitigation. While they continuously experience disturbance, the effect that disturbances have on biomass and biodiversity over time has not yet been assessed at a large scale. Here, we evaluate the degree of recent forest disturbance in Peruvian Amazonia and the effects that disturbance, environmental conditions and human use have on biomass and biodiversity in disturbed forests. We integrate tree-level data on aboveground biomass (AGB) and species richness from 1840 forest plots from Peru's National Forest Inventory with remotely sensed monitoring of forest change dynamics, based on disturbances detected from Landsat-derived Normalized Difference Moisture Index time series. Our results show a clear negative effect of disturbance intensity tree species richness. This effect was also observed on AGB and species richness recovery values towards undisturbed levels, as well as on the recovery of species composition towards undisturbed levels. Time since disturbance had a larger effect on AGB than on species richness. While time since disturbance has a positive effect on AGB, unexpectedly we found a small negative effect of time since disturbance on species richness. We estimate that roughly 15% of Peruvian Amazonian forests have experienced disturbance at least once since 1984, and that, following disturbance, have been increasing in AGB at a rate of 4.7 Mgha<sup>-1</sup> year<sup>-1</sup> during the first 20 years. Furthermore, the positive effect of surrounding forest cover was evident for both AGB and its recovery towards undisturbed levels, as well as for species richness. There was a negative effect of forest accessibility on the recovery of species composition towards undisturbed levels. Moving forward, we recommend that forest-based climate change mitigation endeavours consider forest disturbance through the integration of forest inventory data with remote sensing methods.

## KEYWORDS

aboveground biomass (AGB), disturbance intensity, National Forest Inventory (NFI), species richness, time since disturbance, tropical forests

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## 1 | INTRODUCTION

Tropical forests are a major terrestrial component of the carbon cycle, functioning as carbon reservoirs and sinks (Pan et al., 2011). Over the last 20 years, it is estimated that tropical forests in the Amazon Basin have been functioning as a net carbon sink of approximately  $-0.1 \text{ Gt CO}_2\text{e year}^{-1}$ , considering removals from forest growth and emissions from deforestation and other disturbances (Harris et al., 2021 *but also see* Gatti et al., 2021). This estimate suggests that, while forests in Amazonia are being affected by disturbances, overall they are actively removing  $\text{CO}_2$  from the atmosphere, and therefore contributing to climate change mitigation. This mitigating role is underpinned by the rich biodiversity found in Amazonian forests, making them resilient to disturbances and climate change (Levine et al., 2016; Thompson et al., 2009).

Tropical forests are intrinsically dynamic, and thus experience disturbance constantly. Disturbance, which has previously been defined as “a relatively discrete event causing a change in the physical structure of the environment” (Clark, 1990), is often divided into natural and human disturbances. On the one hand, natural disturbances in forests originate from events such as proliferation of pathogens, droughts, strong winds, lightning or hurricanes, causing tree damage and/or tree mortality, which lead to the creation of canopy gaps with varying size in forest ecosystems (Asner, 2013; Chambers et al., 2013; Espírito-Santo et al., 2014; Gora & Esquivel-Muelbert, 2021). On the other hand, human disturbances in forests originate from anthropogenic activities which range from selective logging practices to human-induced fires and clear-cuts, leading to the partial or complete removal of trees (Chazdon, 2014; Lewis et al., 2015; Malhi et al., 2014; Rappaport et al., 2018). However, in reality forest disturbances cannot be easily divided into these two distinct categories, as human and natural disturbances tend to be intertwined and difficult to separate (Chazdon, 2014). For example, disturbances such as droughts, wildfires, and the spread of pathogens are amplified by human-induced climate change through the increase of warmer and drier conditions (Seidl et al., 2017; Van Loon et al., 2016).

Another way to categorise forest disturbances is by the magnitude of their effect on a forest's physical structure (Pickett & White, 1985). For example, a disturbance of high intensity, such as a clear-cut, results in the total (or near-total) loss of tree living mass (that is, biomass). Other events are less intense, such as selective logging or a drought event which leads to the mortality of a few trees, and result in a partial loss of forest biomass. Similar to the classification of forest disturbances by their origin, their classification by their intensity is not discrete. For example, forest degradation—defined

as the reduction of a forest's ability to provide ecosystem services (FAO, 2011), is difficult to quantify and often overlooks what happens after ecosystem services are reduced (Ghazoul et al., 2015; Vásquez-Grandón & Donoso, 2018).

After a disturbance, forests generally have the ability to recover in terms of biomass and biodiversity, towards pre-disturbance levels or alternative states (Anderson-Teixeira et al., 2013; Didham et al., 2005). Both disturbance and recovery dynamics are essential components of tropical forest ecosystems where natural and human disturbances are predominant across large forest landscapes (Bullock, Woodcock, Souza, et al., 2020; Espírito-Santo et al., 2014; Phillips et al., 2009; Pugh et al., 2019). Forest stands recovering from lower-intensity disturbances, such as selectively-logged forests, have the potential to recover in biomass (de Avila et al., 2018; Rutishauser et al., 2015). But also secondary forests, which are forests that recover after larger-intensity, stand-replacing disturbances, have the potential to recover in biomass and biodiversity towards pre-disturbance levels (Chazdon, 2014; Poorter et al., 2016; Rozendaal et al., 2019).

While disturbance/recovery cycles in secondary forests are accounted for in climate change mitigation schemes such as REDD+, the effect of lower-intensity disturbance/recovery cycles on carbon stocks and biodiversity in degraded forests remains seldom accounted for (Berenguer et al., 2014; Bustamante et al., 2016; Edwards et al., 2010; Gardner et al., 2012; Sasaki et al., 2011), given the challenge of characterizing forest degradation (Ghazoul et al., 2015; Goslee et al., 2020).

Furthermore, we currently do not know to what extent local factors such as environmental conditions and human use have an effect on biomass, biodiversity and their recovery across forests experiencing varying levels of disturbance intensity in the Amazon Basin. In managed, logged and secondary forests, disturbance intensity has a negative effect on biomass and biodiversity (de Avila et al., 2018; Gibson et al., 2011; Rutishauser et al., 2015; Vidal et al., 2016). In logged and secondary forests, time since disturbance has a positive effect on biomass (Heinrich et al., 2021; Meli et al., 2017; Poorter et al., 2016; Rutishauser et al., 2015) as well as on biodiversity (Rozendaal et al., 2019). In secondary forests, biomass is driven by environmental conditions, generally increases with increasing water availability and soil fertility (Heinrich et al., 2021; Li et al., 2017; Poorter et al., 2016) and is generally lower at higher intensities of previous and current land use and at higher levels of human accessibility (Chazdon, 2003; Crk et al., 2009; Jakovac et al., 2015). In undisturbed and degraded forests, slope and distance to nearest forest edge also had a positive effect on biomass (Berenguer et al., 2014). In parallel, biodiversity in secondary forests is larger at higher levels of surrounding forest cover, as well as with higher levels of water availability (Rozendaal et al., 2019).

One of the main challenges of assessing forest disturbance and recovery in the Amazon Basin lies in data availability. Repeated measurements of permanent plots in seemingly undisturbed and logged forests have elucidated the effects of disturbance on biomass accumulation in these forests (Berenguer et al., 2018; Phillips et al., 2009; Rutishauser et al., 2015). However, the assessment of the effects of disturbances in large-scale studies of Amazonian forest is limited (Chambers, Negrón-Juárez, et al., 2009; Espírito-Santo et al., 2014; Fisher et al., 2008). A robust and representative setup of permanent forest plots in disturbed forests in the Amazon Basin would enable assessing forest recovery from partial to complete tree loss across large scales while at the same time accounting for the effect of broad gradients in environmental conditions and degrees of human use. While several efforts are currently underway (Laurance et al., 2011; Málaga et al., 2021; Poorter et al., 2016; Sist et al., 2015), such information does not fully capture fine-scale variations in disturbance intensity as well as gradients in environmental conditions and human use.

In the tropics, national forest monitoring capabilities have greatly improved in quality and extent over the last years, with 62 countries using National Forest Inventory (NFI) data obtained within the last 10 years for greenhouse gas (GHG) reporting, and when possible reporting at Tier 2 or Tier 3 level (Nesha et al., 2021). One of these countries, Peru, is currently carrying out an NFI led by its Forest and Wildlife Service (SERFOR). Using a consistent methodology, Peru's NFI plots are a representative sample of the country's forests, covering broad environmental and human use gradients. However, information on time of disturbance or disturbance intensity has not been quantitatively recorded in these plots.

Remote sensing has enabled the study of forest disturbance and recovery across large scales. However, while it has enabled the detection of deforestation events, detecting forest degradation has been a recurrent challenge (DeVries, Decuyper, et al., 2015; Herold et al., 2011). Dense satellite time series have proved useful in the detection of small-scale disturbances, including forest degradation (Bullock, Woodcock, & Olofsson, 2020; Bullock, Woodcock, Souza, et al., 2020; DeVries, Decuyper, et al., 2015; DeVries, Verbesselt, et al., 2015; Hamunyela et al., 2020). However, these methodologies require an initial training period to establish an undisturbed forest baseline and detect only one disturbance event, therefore not fully capturing longer-term forest change dynamics. Recent remote sensing methods (Decuyper et al., 2022) have shown that it is possible to continuously monitor forest change dynamics by using nearby forests throughout the entire period as a reference baseline. In addition to accounting for the natural variability of the annual phenological cycle in a given forest, this baseline enables the quantification and analysis of disturbance intensity by comparing the baseline vegetation index with that present at the time of disturbance. Thus, while the differentiation of disturbance types remains an ongoing challenge, the integration of current advancements in remote sensing with plot data provides the opportunity to assess general forest disturbance intensity as well as forest recovery across large scales (Bustamante et al., 2016; Requena Suarez et al., 2021).

In this study, we evaluate the degree of general forest disturbance in Peruvian Amazonia during the years of 1984–2019, by integrating forest plot data from Peru's NFI with Landsat-based time series analysis of forest change dynamics. Next, we assess the effects that disturbance intensity, time since disturbance, environmental conditions and human use have on aboveground biomass (ABG) and on tree species richness. We address the following questions:

1. What is the degree of general forest disturbance in Peruvian Amazonia?
2. What are the effects of disturbance intensity and time since disturbance on ABG, tree species richness and their relative recovery towards undisturbed levels?
3. In disturbed forests, what are the effects of environmental conditions and human use on ABG, tree species richness and their relative recovery towards undisturbed levels?

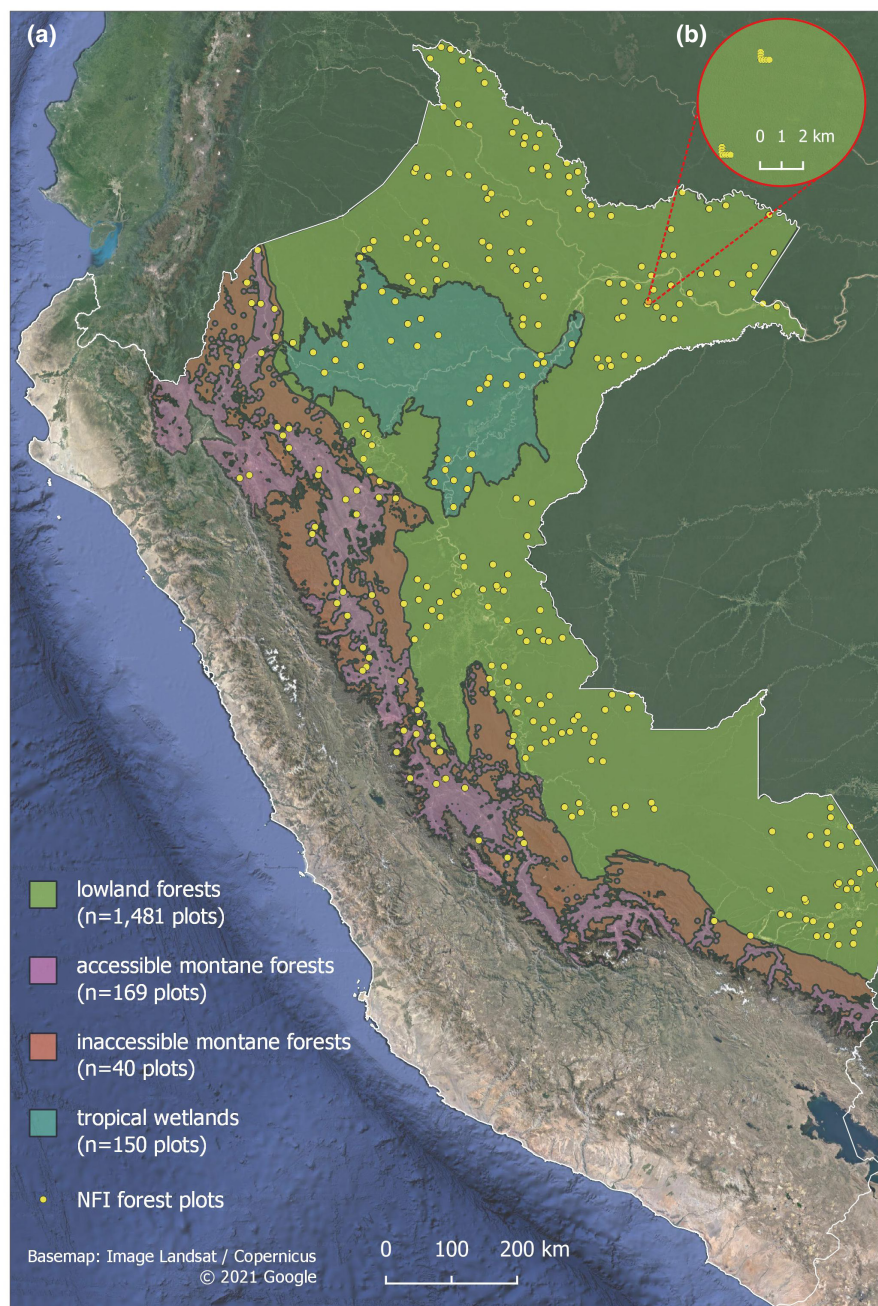
## 2 | METHODS

To address our research questions, we (1) calculated ABG and tree species richness for all NFI plots in Peruvian Amazonia; (2) derived metrics of disturbance intensity and time since disturbance for plot locations, using the Landsat archive for the period of 1984–2019 and available high-resolution imagery; (3) estimated the percentage of recovery for ABG and tree species richness in disturbed forest plots, using levels of ABG and tree species richness in nearby forests plots that were not disturbed during the study period, based on a chronosequence approach; and (4) applied a mixed-effects modeling framework to assess the effect of disturbance intensity, time since disturbance, and gradients in environmental conditions and human use on disturbed forests in Peruvian Amazonia.

### 2.1 | Forest plot data

Forest plot data are part of SERFOR's ongoing Peruvian National Forest and Wildlife Inventory. The Inventory considers six forest types, four of which are located in Peruvian Amazonia: lowland forests, accessible montane forests, inaccessible montane forests and tropical wetlands (Figure 1a). These forest types were defined based on biophysical and accessibility criteria (MINAGRI, 2016). Peru's NFI follows a non-aligned systematic sampling design, where clusters are randomly located within grid cells whose size varies per forest type. Approximately, 30% of the total sample had been completed by the time of our study, with samples being uniformly distributed along each forest type. The sampling strategy has been explained in detail by MINAGRI and MINAM (2016) and further elaborated by Málaga et al. (2022). Given that the Peru's NFI is a probabilistic sample of the entire Peruvian Amazonian forest lands, it captures a wide range of natural and human disturbance histories. Of the plots used in this study, 66% had signs of human disturbance, and 34% had signs of natural disturbance. Quantitative information on the time





**FIGURE 1** Cluster locations in Peruvian Amazonia and overview of the L-shaped cluster design. (a) Distribution of clusters in lowland forests, accessible montane forests, inaccessible montane forests, and tropical wetlands in Peruvian Amazonia. (b) Inset of map showing the L-shaped disposition of plots. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

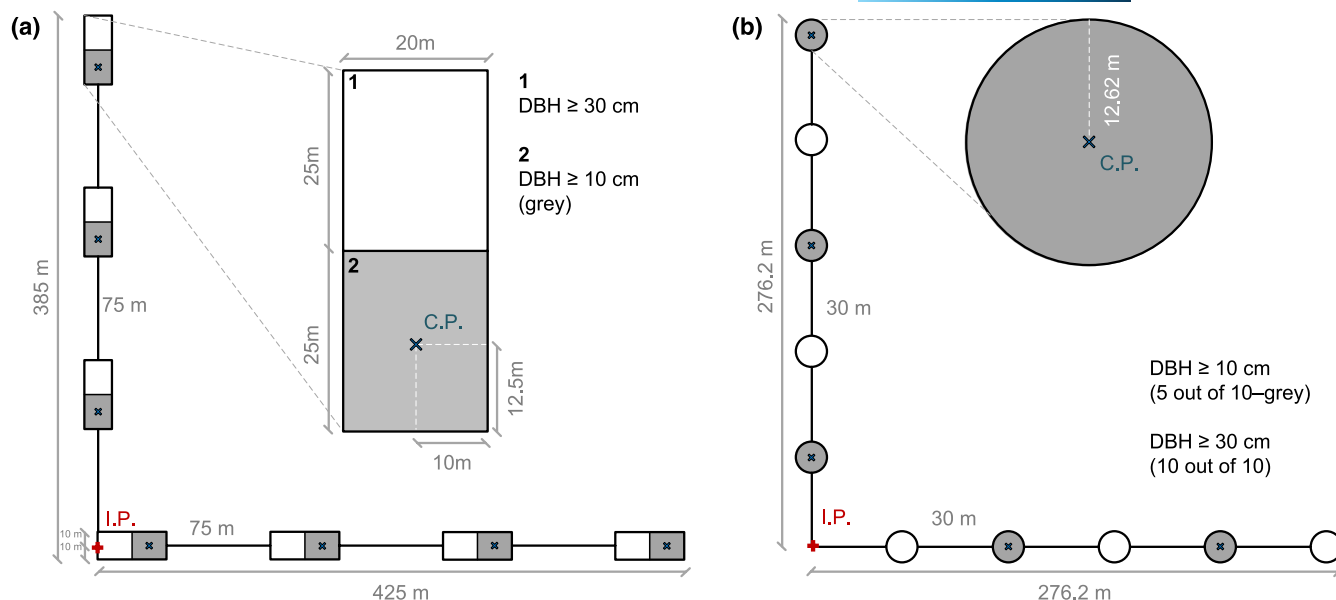
or intensity of disturbance was not available. No re-measured plots were included in this study.

Plot cluster configuration varied per forest type. Clusters within the lowland forests consisted of seven rectangular 0.1 ha plots arranged in the form of a L (Figure 2a). In the remaining forest types, L-shape clusters consisted of ten 0.05-ha circular plots (Figure 2b). For the purpose of this study, we consistently focused on the sampling units where all trees with a diameter at breast height (DBH) of  $\geq 10$  cm were measured. Hence, within the lowland forests we used only half of the seven plots (0.05 ha) and for the remaining forest

types, 5 out of 10 plots (0.05 ha) within a cluster. A total of 1840 0.5-ha plots embedded in 306 clusters were included in this study.

For all included plots, the DBH was measured and their taxonomic identification was recorded. Taxonomic identification was done by trained botanists acquainted with the tree flora of region under evaluation, aided by botanical collections and photographic documentation of unknown species, as specified in the Inventory field guide (SERFOR, 2019). When possible, trees were identified up to species level. Tree species data consisted of 58% trees identified up to species level, 32% trees up to genus level, and 6% up to family





**FIGURE 2** Cluster configuration for (a) lowland forests and (b) accessible montane forests, inaccessible montane forests and tropical wetlands, adapted from MINAGRI and MINAM (2016). Red cross-shaped marks indicate cluster initial points (I.P.) and blue x-shaped marks indicate plot center points (C.P.). Rectangular plots in (a) are divided into two units. For both (a) and (b), only areas in grey (with a DBH  $\geq 10$  cm) were included in this study. DBH, diameter at breast height.

level. When present, DBH (or diameter at ground level) for dead standing trees and stumps with a DBH of  $\geq 10$  cm was measured.

## 2.2 | Estimation of disturbance intensity and time since disturbance

For each plot cluster, data on forest disturbance were obtained through satellite time series analysis of Landsat-derived Normalized Difference Moisture Index (NDMI) spatio-temporal cubes for the study period of 1984–2019 (Figure 3). Time series analysis was performed using the Anomaly Vegetation Change Detection algorithm (coined AVOCADO; Decuyper et al., 2022).

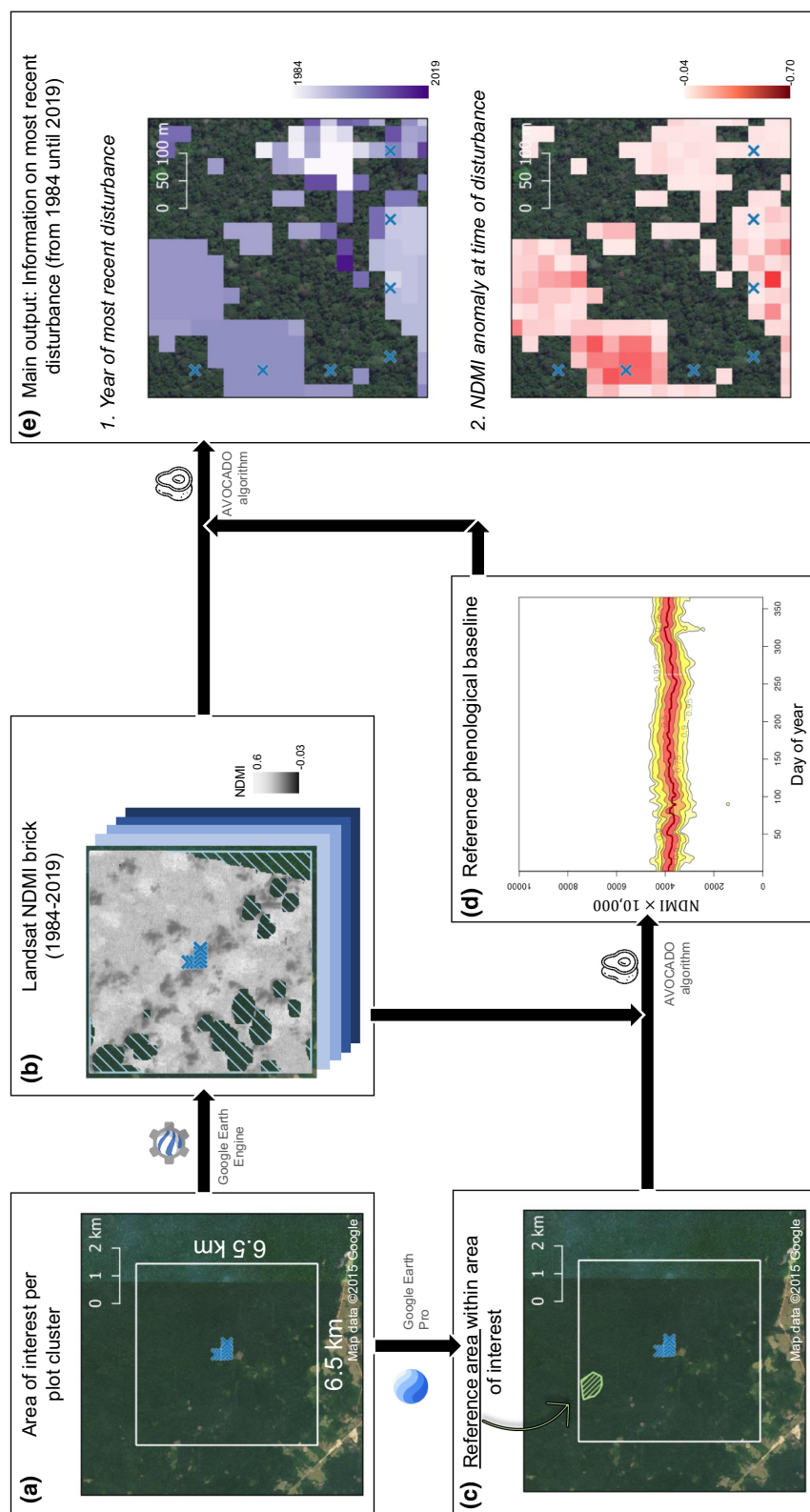
We chose NDMI (Gao, 1996; Wilson & Sader, 2002) due to its high sensitivity for canopy moisture content (Jin & Sader, 2005), and therefore its reliability for detecting forest disturbance events (Goodwin et al., 2008; Jin & Sader, 2005; Wilson & Sader, 2002). NDMI was calculated by combining Landsat's near-infrared (NIR) and shortwave infrared (SWIR) spectral bands (Equation 1),

$$\text{NDMI} = \frac{\text{NIR} - \text{SWIR}}{\text{NIR} + \text{SWIR}} \quad (1)$$

NDMI accounts for the moisture content of canopy vegetation, and thus is sensitive to changes in forest structure. Because of this, NDMI has previously been used to quantify disturbances at different levels of intensity, ranging from non-stand replacing disturbances, such as beetle outbreaks, to stand-replacing disturbances, such as harvesting (Goodwin et al., 2008). In tropical forest ecosystems, including Peruvian Amazonia, this index has been used to reliably quantify disturbance-regrowth dynamics (Chen et al., 2021; Decuyper

et al., 2022; DeVries, Decuyper, et al., 2015; Hayes, 2007; Murillo-Sandoval et al., 2018). Due to the nature of our method and the aforementioned complexities related to distinguishing natural and human disturbances, we were unable to classify disturbances by type.

Year and intensity of disturbance were determined for square-shaped areas of interest per plot cluster (Figure 3a). To begin this process, NDMI spatiotemporal cubes using the entire Landsat archive at the time (1984–2019) were pre-processed and downloaded from Google Earth Engine for a 6.5 km  $\times$  6.5 km area around each cluster (Figure 3b). In order to construct a local phenological reference baseline, small undisturbed forest patches with similar characteristics to the forests coinciding with the plot centre points were delineated within the square-shaped areas (Figure 3c). For this, we visually assessed historical imagery available in Google Earth Pro for each square-shaped area from 1984 until 2019. These patches were used in combination with the full Landsat NDMI time-series to construct robust probabilistic estimations of the annual phenology (i.e. reference phenological baseline) for each square-shaped area (Figure 3d), using kernel density estimations of NDMI across space and time within the reference area (Decuyper et al., 2022). Following this, the reference phenological baseline was used over the spatiotemporal NDMI time series in the square-shaped area to detect forest disturbance over the entire timeframe. A disturbance was detected when three or more consecutive NDMI values were located out of the reference baseline (including likelihood boundaries), which was set as 95% of the reference frequency distribution (yellow, orange and red band in Figure 3d). The two main outputs of this process were (1) year of most recent disturbance and (2) NDMI anomaly at the time of disturbance (Figure 3e). The latter corresponds to the difference between the NDMI value at the time of



**FIGURE 3** (a–d) Workflow used to derive remote sensing based information on most recent disturbance between 1984 until 2019 for a given plot cluster. Main outputs (e) consist of (1) Year of most recent disturbance and (2) NDMI anomaly at the time of disturbance. Note that NDMI anomalies are originally obtained as negative values. NDMI, Normalized Difference Moisture Index.

disturbance and its corresponding temporal value within the reference phenological baseline (red line in Figure 3d).

The resulting spatially explicit information was overlaid with the locations of plot center points (C.P. in Figure 2) to distinguish disturbed forest plots from undisturbed forest plots. For the purpose of this study, we define *disturbed forests* as forests plots located in a pixel with at least one disturbance detected during the study period (from 1984 until the year of field measurement) and *undisturbed forests* as forests plots located in a pixel with no detected disturbance during the study period. In disturbed forest plots, disturbance intensity was estimated as the absolute NDMI anomaly ( $\Delta\text{NDMI}$ ) and time since disturbance was calculated as the number of years between the latest disturbance and the year of plot measurement.

### 2.3 | Estimation of AGB, tree species richness and their recovery

To evaluate biomass and its recovery, we calculated AGB and percent recovery of AGB towards values found in nearby undisturbed forests (hereafter AGB [%r]). DBH and species-specific wood density (WD) were used to calculate AGB, using the pantropical allometric equation of Chave et al. (2014). WD estimates were extracted from the Global Wood Density database (Chave et al., 2009; Zanne et al., 2009) on August 2022. Species-level WD was assigned for 38% of all trees, genus-level WD estimates were assigned to 47%, and plot-level means were used for the remaining 16%. This was done in R v.3.6.1 (R Core Team, 2019), using BIOMASS (Réjou-Méchain et al., 2017). Next, we calculated AGB [%r] as the percentage of AGB present in a disturbed forest plot in comparison with undisturbed forest plot(s) in the same cluster. If more than one undisturbed forest plot was present within the same cluster, AGB [%r] was calculated using the average AGB of all undisturbed forest plots in that cluster. AGB [%r] was not calculated for disturbed forest plots in clusters with no undisturbed forest plots.

To evaluate species richness and its recovery, rarefied tree species richness (hereafter *species richness*; i.e. number of species per 10 stems) was calculated, and percent recovery of species richness towards values found in nearby undisturbed forests (hereafter *species*

*richness* [%r]). For species richness, we calculated rarefied richness in R using *vegan* (Oksanen et al., 2019) for all plots with  $\geq 10$  stems. Next, species richness [%r] was calculated as the percentage of species richness present in a disturbed forest plot in comparison with species richness in undisturbed forest plot(s) in the same cluster. If more than one undisturbed forest plot with  $\geq 10$  stems was present within the same cluster, species richness [%r] was calculated using the average value of species richness in all undisturbed forest plots with  $\geq 10$  stems in that cluster. Species richness [%r] was not calculated for disturbed forest plots in clusters with no undisturbed forest plots with  $\geq 10$  stems.

In addition, to evaluate the recovery of species composition towards undisturbed levels (hereafter *species composition* [%r]), we calculated similarity in species composition between disturbed and undisturbed forests. For this, we calculated Chao's dissimilarity index (Chao et al., 2004), which uses species abundance information to identify shared species between two locations and evaluate how dissimilar these locations are in species composition. This index was obtained for the differences between each disturbed forest plot and each undisturbed forest plot in the same cluster using *vegan*, obtaining dissimilarity values ranging from 0 to 1, which we then subtracted from 1 to obtain similarity values. Average similarity values were calculated for disturbed plots with more than one undisturbed plot in the same cluster. To account for the natural dissimilarity among nearby undisturbed forests, we averaged the within-cluster similarity in 268 clusters with at least two undisturbed forest plots, obtaining an overall average of 0.37 (SD=0.17). The similarity value of 0.37 was therefore considered as the maximum attainable reference value and thus, as 100% recovery of species composition.

### 2.4 | Data on environmental conditions and human use

To identify the main environmental and human use drivers of AGB, AGB [%r], species richness, species richness [%r] and species composition [%r], we included predictors of climate, topography, soil and human use for all plot locations (Table 1). The

TABLE 1 Summary of environmental and human use predictors for all disturbed forest plots.

Covariate	Unit	Minimum	Maximum	Mean	SD	Original source	Original resolution
Climatic water deficit (CWD)	mm year <sup>-1</sup>	-588.5	0	-111.7	124.1	2.5'	Chave et al. (2014)
Slope	°	0.0	15.5	1.7	3.4	90m	Jarvis et al. (2008)
Total nitrogen (N) content	g kg <sup>-1</sup>	223.0	608.0	335.3	88.9	250m	ISRIC (2020)
Surrounding tree cover	%	31.7	100.0	92.0	9.8	30m	Hansen et al. (2013)
Distance to nearest navigable waterway or road	km	0.0	27.2	5.8	6.7	-	OpenStreetMap Contributors (2020), Schielein (2017)



effect of climate was evaluated by including Climatic Water Deficit (CWD, in  $\text{mm year}^{-1}$ ; Chave et al., 2014), which is the annual evaporative demand during dry months, and thus includes both precipitation and temperature during dry periods. Given that CWD is one of the parameters used for calculating AGB using the allometric equation developed by Chave et al. (2014), we tested for correlations between CWD and AGB. Considering both plot and tree-level AGB estimates, correlations with CWD were no higher than 0.2. The effect of topography was evaluated by including slope ( $^{\circ}$ ), calculated from 90-m resolution elevation data (Jarvis et al., 2008). Soil fertility was assessed by including total Nitrogen (N) content, through extracted gridded predictions from SoilGrids250m 2.0 (in  $\text{g kg}^{-1}$ ; ISRIC, 2020). In line with previous studies (Poorter et al., 2016; Requena Suarez et al., 2021; Rozendaal et al., 2019), we included surrounding tree cover and human accessibility as proxies for degree of human use. Surrounding tree cover was calculated as the mean percent tree cover in 2010 (Hansen et al., 2013) within 0.5, 1 and 5 km radii around each plot. Ideally, using tree cover percentage values at the year of disturbance would have been preferred, however such information is only available for 2000 and 2010. The later year was ultimately chosen as it is closer to the years in which the plots were measured. Accessibility was calculated as the Euclidean distance (km) of each plot to the nearest navigable waterway (Schielein, 2017) or road (OpenStreetMap Contributors, 2020). Predictor values were extracted or calculated for all plot locations using *raster*, *spatialEco* and *rgeos* (Bivand & Rundel, 2017; Evans, 2018; Hijmans, 2019) in R.

## 2.5 | Statistical analysis

Linear mixed-effects models were used to test whether there was a significant difference between disturbed and undisturbed forest plots, with plot category included as a fixed effect. To further evaluate this difference, we tested whether there was a significant difference in the relative number and basal area of dead trees and stumps, including plot category as a fixed effect (Figure S1). We also used linear mixed-effects models to identify the drivers of (1) AGB, (2) AGB (%r), (3) species richness, (4) species richness (%r) and (5) species composition (%r). Per variable, we included disturbance intensity, time since disturbance, CWD, slope, soil N content, surrounding tree cover and distance to nearest road or navigable waterway as fixed effects. To select the final surrounding tree cover radius (0.5, 1 or 5 km), we compared models using Akaike's information criterion. Models that included surrounding tree cover based on a 5 km radius performed best; therefore, we included surrounding tree cover within a 5 km radius in the final models. Time since disturbance was ln-transformed for AGB and AGB (%r), to account for the nonlinear increase in AGB and AGB (%r) over time.

In all models, plot clusters were included as random intercepts, to account for the effect of proximity between plots within a cluster.

Predictors were standardised and model fits were evaluated based on the conditional (fixed and random effects) and marginal (only fixed effects)  $R^2$  (Nakagawa & Schielzeth, 2013). We used *lme4* and *lmerTest* (Bates et al., 2015; Kuznetsova et al., 2017) to fit all mixed-effects models in R.

## 3 | RESULTS

### 3.1 | Levels of disturbance

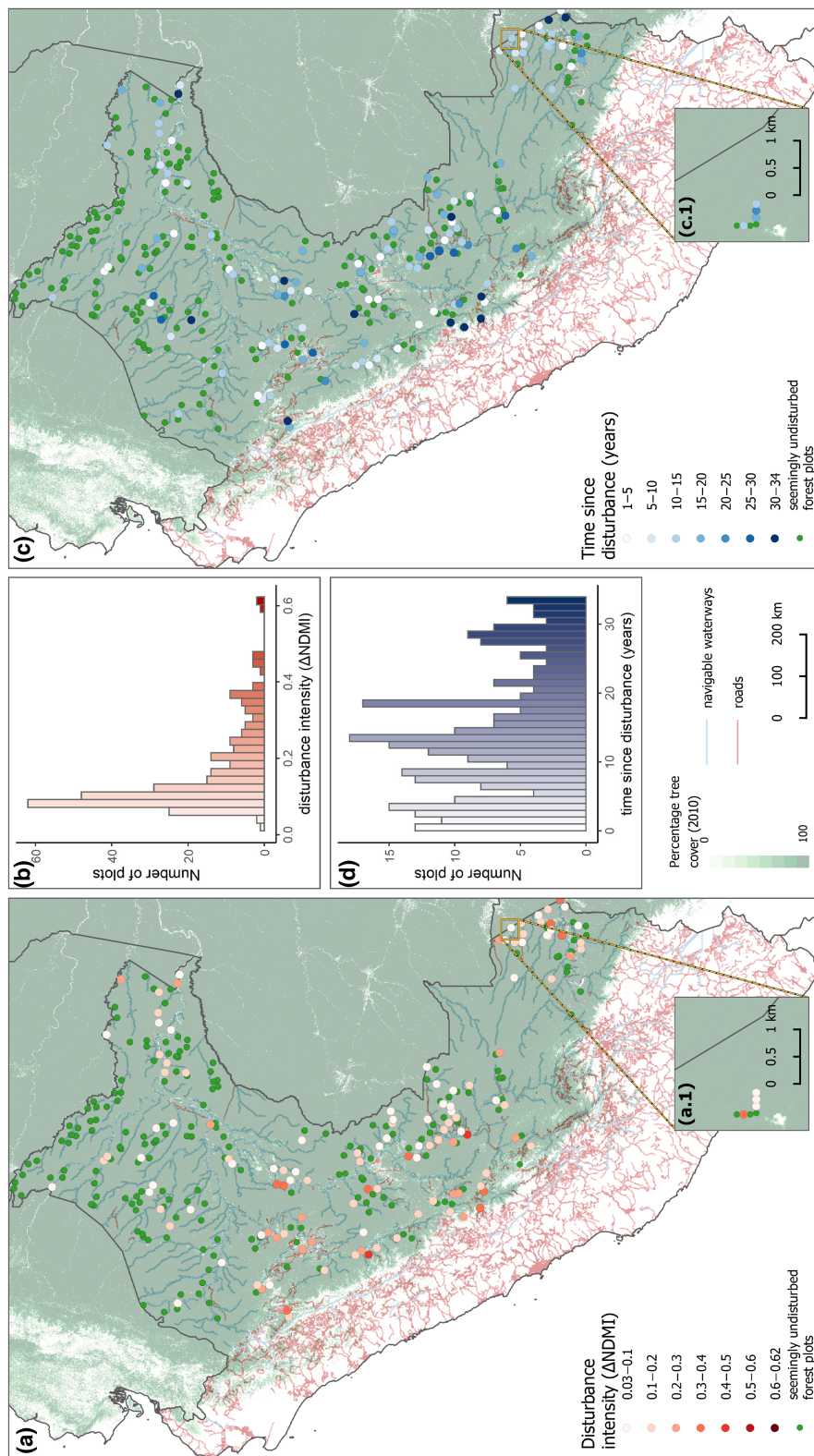
Out of all plots considered in this study (1840), 283 were in areas with detected disturbance. Within these plots, disturbance intensity skewed towards lower disturbance intensities (Figure 4b). The majority of disturbed forest plots (241) had one disturbance event, 38 plots had two events and 4 plots had three events of disturbance during the study period. Time since the latest disturbance in these plots ranged from 1 to 34 years, with a mean of 14.5 years (Figure 4d).

Overall, mean AGB and species richness were lower in disturbed forest plots than in undisturbed forest plots. Mean AGB (Figure 5a) in disturbed forest plots across all clusters was  $165.3 \text{ Mg ha}^{-1}$  ( $\text{SD} = 177.9$ ), which approximately 60.7% of the mean biomass in undisturbed forest plots across all clusters ( $272.5 \text{ Mg ha}^{-1}$ ,  $\text{SD} = 355.5$ ). Overall, species richness in disturbed forest plots with  $\geq 10$  stems (213 plots) was 87.5% of what was observed in undisturbed forest plots with  $\geq 10$  stems (1488 plots), with a mean value of 7.2 ( $\text{SD} = 2.0$ ) in comparison to 8.2 ( $\text{SD} = 1.2$ ) in undisturbed forest plots (Figure 5c). Both the relative number as well as the relative basal area of dead trees and stumps were higher in disturbed forests than in undisturbed forests (Figure S1).

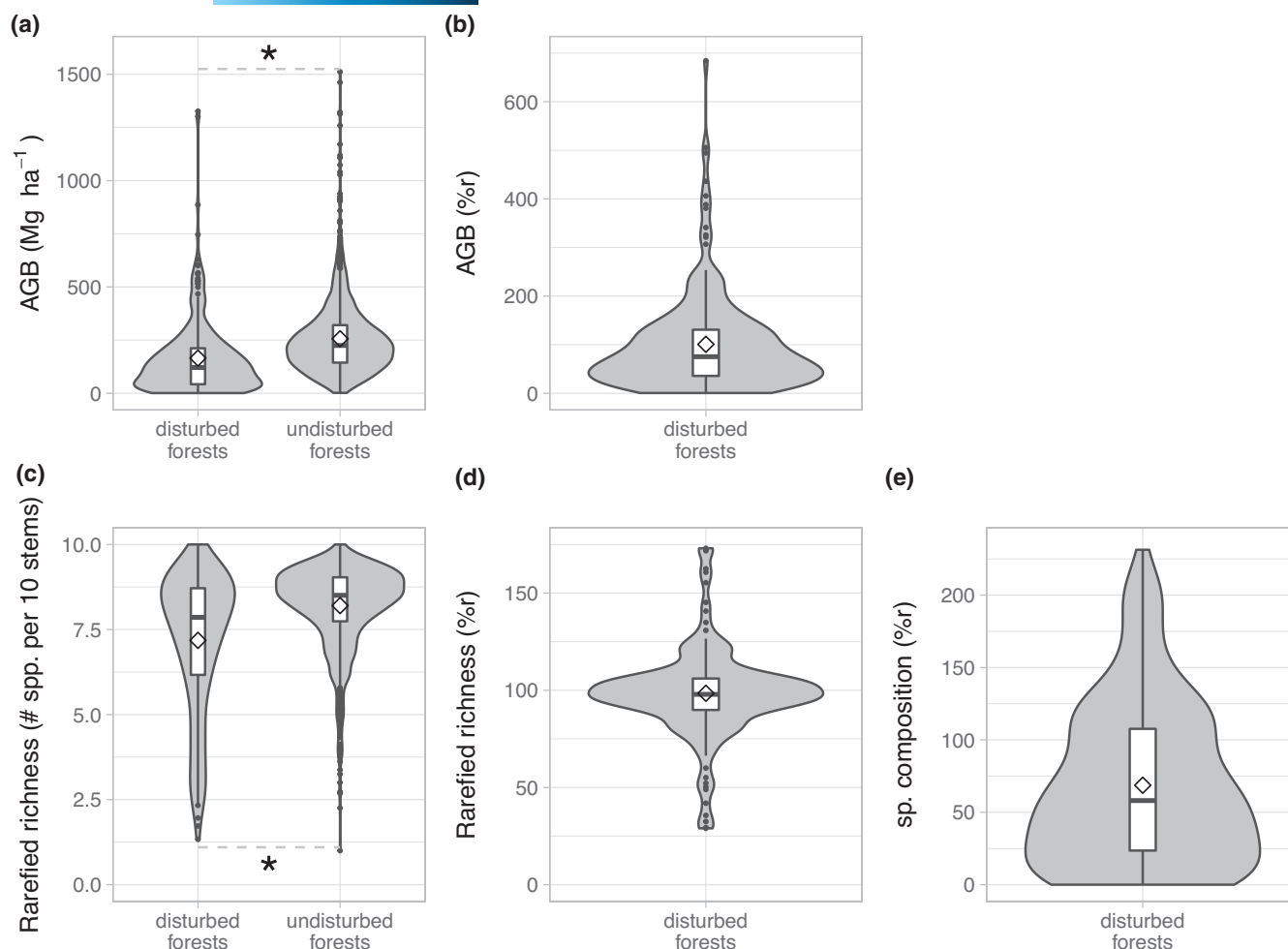
Two-hundred and eight disturbed forest plots had at least one undisturbed forest plot in the same plot cluster, which enabled evaluating percent recovery of AGB (AGB [%r]) and recovery of species composition relative to undisturbed levels (species composition [%r]). For percent recovery of species richness (species richness [%r]), 165 plots with  $\geq 10$  stems had at least one undisturbed forest plot with  $\geq 10$  stems for comparison. When compared to nearby undisturbed forest plots (i.e. within the same cluster), disturbed forests had on average 100.7% of the AGB (%r) (Figure 5b) and 98.4% of species richness (%r) (Figure 5d) of undisturbed forests, and a 68.7% recovery of species composition relative to undisturbed forests (Figure 5e).

### 3.2 | Effects of disturbance intensity and time since disturbance on AGB and species richness

We found a significant negative effect of disturbance intensity on species richness, but not on AGB (Figure 6a,c). AGB tended to decrease with disturbance intensity (Figure 6a). Rarefied species richness decreased throughout the entire disturbance intensity range from 8.0 to 5.9 species per 10 stems.



**FIGURE 4** Levels of disturbance of National Forest Inventory plots. Distribution (a) and number of plots (b) per disturbance intensity ( $\Delta\text{NDMI}$ ), including closeups of plot clusters (a.1 and c.1); and distribution (c) and number of plots (d) per time since disturbance (years). In (a) and (c), undisturbed forest plots are shown as hollow circles; navigable waterways (Schielein, 2017) and roads (OpenStreetMap Contributors, 2020) are indicated with blue and red lines, respectively; and 2010 percentage tree cover (%) from Hansen et al. (2013) is displayed in green. Note that not all plots are visible in (a) and (c), due to the proximity of plots within clusters. Map lines delineate study areas and do not necessarily depict accepted national boundaries. NDMI, Normalized Difference Moisture Index.



**FIGURE 5** (a) Aboveground biomass (AGB), (b) its recovery (AGB [%r]), (c) species richness (rarefied species richness up to 10 stems), (d) its recovery (species richness [%r]), and (e) recovery of species composition (species composition [%r]). AGB values for six plots in undisturbed forests plots (1634.5, 1790.7, 2243.6, 6811.3, 6983.8 and 7702.5  $\text{Mg ha}^{-1}$ ) are not shown in (a), but included in further analysis. Star signs in (a) and (c) indicate significant differences between disturbed and undisturbed forest plots ( $p < .05$ ).

There was a positive significant effect of time since disturbance on AGB (Figure 6b). AGB increased by  $7.6 \text{ Mg ha}^{-1}$  per year, during the first 10 years after disturbance, slowing to an increase of  $2.0 \text{ Mg ha}^{-1}$  per year between 11 and 20 years after disturbance,  $1.2 \text{ Mg ha}^{-1}$  per year between 21 and 30 years, and  $0.9 \text{ Mg ha}^{-1}$  per year between 31 and 34 years after disturbance. According to our AGB model, and keeping all other variables constant at the mean, AGB at 34 years since disturbance would be  $243.4 \text{ Mg ha}^{-1}$ , 89% of the overall mean AGB in undisturbed forests. There was a small but significant inverse effect of time since disturbance on species richness (Figure 6d), indicating that species richness decreased slightly with time during the first 34 years since disturbance. Species richness declined at a rate of  $-0.02$  species per 10 stems per year, from 8.1 to 7.3 species per 10 stems after 34 years following a disturbance.

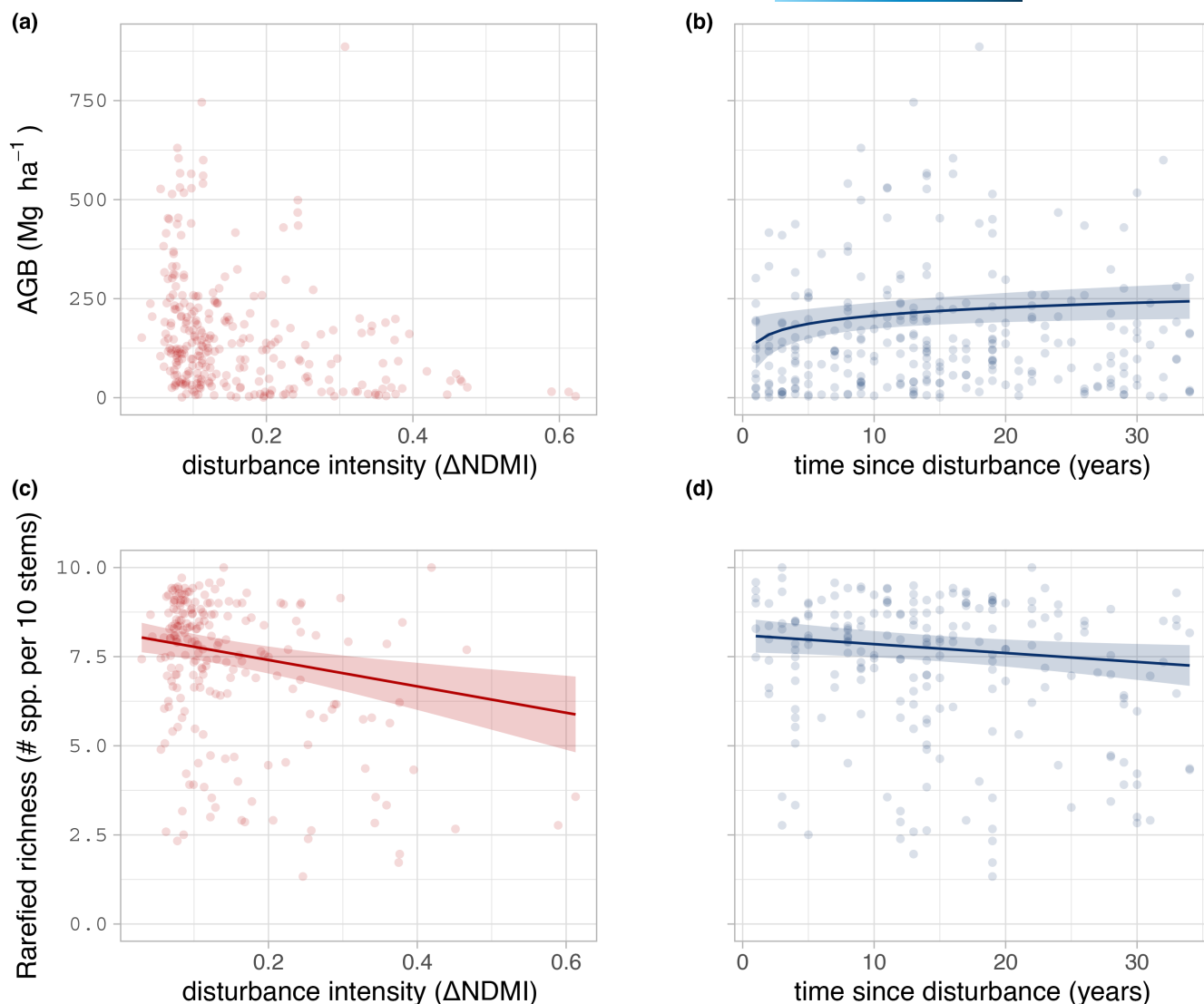
There was a significant effect of disturbance intensity on AGB (%r), species richness (%r) and species composition (%r) (Figure 7a,c,e). Across the range in disturbance intensity that was observed, AGB (%r) decreased from 127.1% to 11.2% of AGB in

nearby undisturbed forests; species richness (%r) decreased from 100.9% to 69.3% of species richness in nearby undisturbed forests; and species composition (%r) decreased from 79.0% to 40.2%. There was no significant effect of time since disturbance on AGB (%r), species richness (%r) nor species composition (%r) (Figure 7b,d,f).

### 3.3 | Effects of gradients in environmental conditions and human use

When looking at the combined effect of all potential drivers, AGB was significantly, in order of increasing importance, positively associated with time since disturbance and surrounding tree cover (Figure 8a). In the same order of importance, AGB (%r) was significantly negatively associated with disturbance intensity and positively associated with surrounding tree cover and with slope (Figure 8b). Neither CWD, soil N content, nor distance to nearest waterway or road were significantly associated with AGB or with AGB (%r). Species richness was, in order of increasing importance, significantly negatively





**FIGURE 6** Effect of disturbance intensity and time since disturbance on aboveground biomass [AGB; (a, b)] and species richness [Rarefied richness; (c, d)] in disturbed forest plots. Solid lines indicate significant effects, and bands indicate confidence intervals (CI, 95%). For all panels, all other predictors were kept at the mean. Symbols represent observed AGB and species richness in disturbed forest plots. For (a), the AGB value of two points ( $1301.5$  and  $1326.7 \text{ Mg ha}^{-1}$ ) were excluded from this graph but kept in the analysis.

associated to time since disturbance, disturbance intensity and CWD; and significantly positively associated to surrounding tree cover (Figure 8c). Species richness (%r) was significantly, negatively associated to disturbance intensity only (Figure 8d). Species composition (%r) was significantly negatively associated to disturbance intensity, positively associated to distance to nearest waterway/road, and negatively associated to slope (Figure 8e).

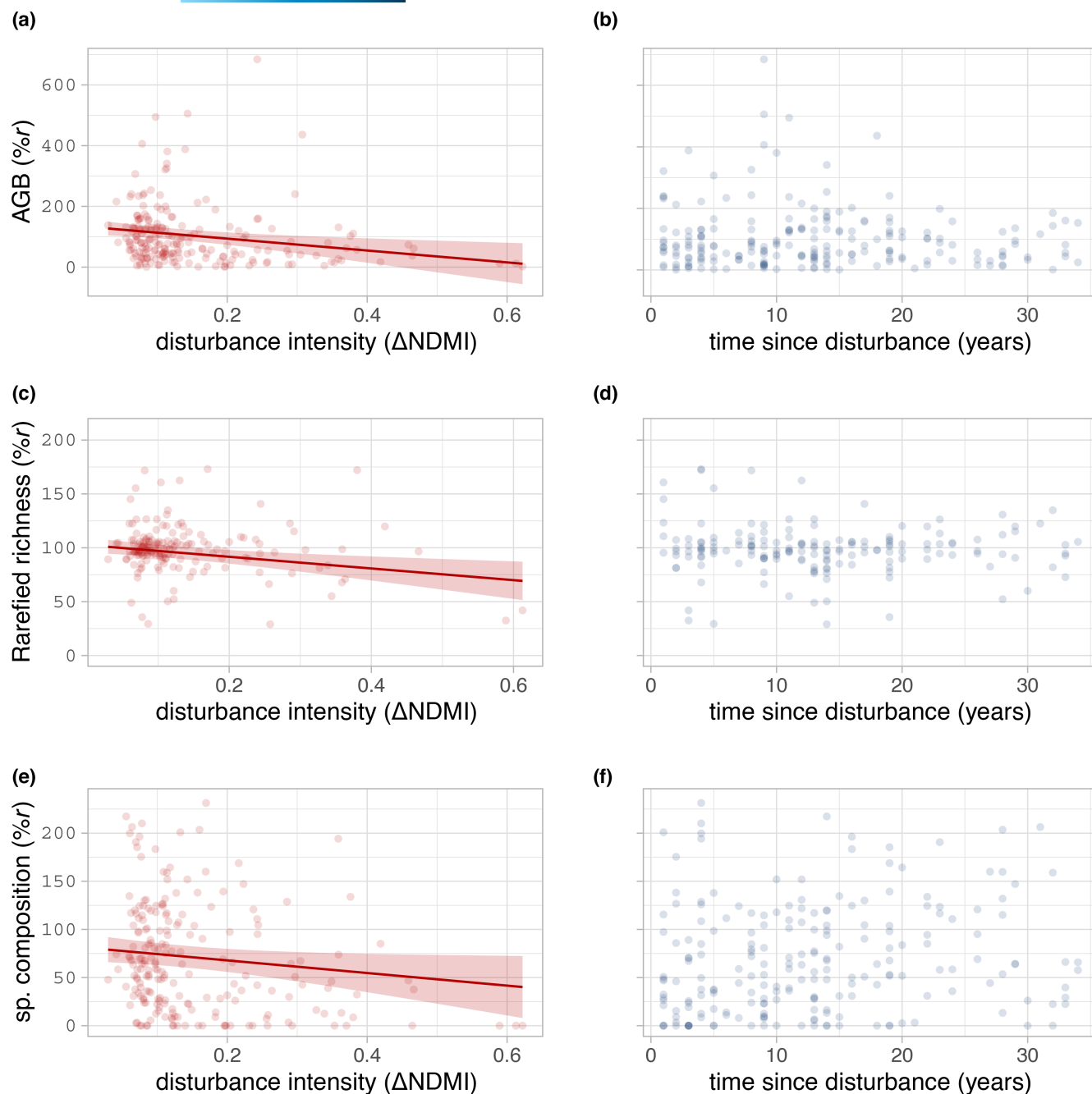
The amount of variation explained by the predictors (fixed effects) and by cluster-to-cluster variation (random effects) varied. For AGB and AGB (%r), fixed effects explained 11% and 12% of the variation, respectively. Large part of the variation was explained by cluster-to-cluster variation, as fixed and random effects together explained 52% and 29% of the variation, respectively. For species richness and species richness (%r), fixed effects explained 36% and 8% of the variation, respectively. Similarly, large part of the variation in

species richness and species richness (%r) was explained by cluster-to-cluster variation, as fixed and random effects together explained 76% and 58% of the variation, respectively. For recovery of species composition, fixed effects explained 16% of variation and 61% was explained by fixed and random effects together.

## 4 | DISCUSSION

### 4.1 | Extent and degree of disturbance in Peruvian Amazonia

We found that 283 of the evaluated forest plots were located in forests recovering from recent human or natural disturbances, with 210 of them having a disturbance intensity lower than  $0.2 \Delta\text{NDMI}$

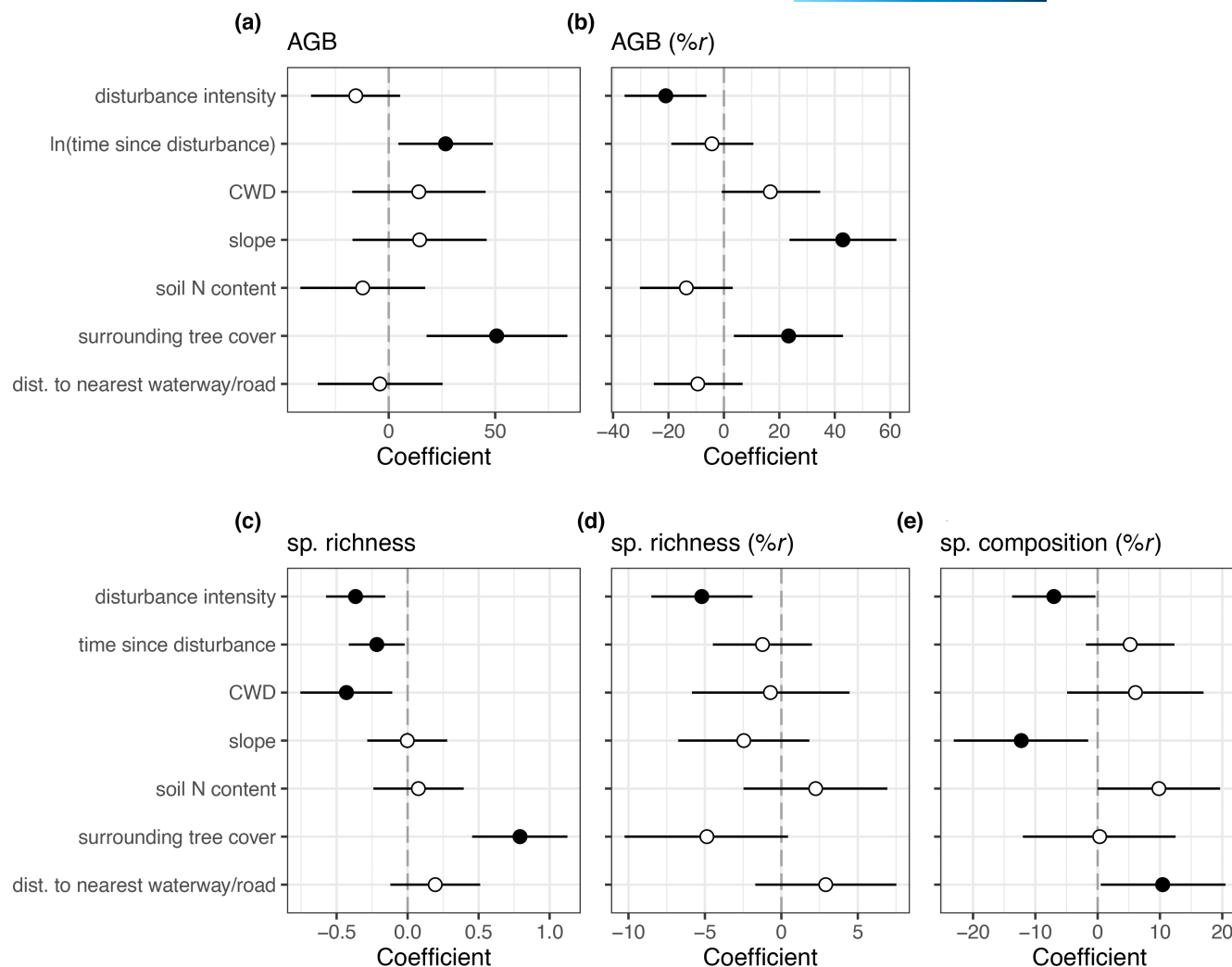


**FIGURE 7** Effect of disturbance intensity and time since disturbance on (a, b) AGB (%r), (c, d) species richness (%r), and (e, f) species composition (%r). Disturbance intensity and time since disturbance values are indicated in red and blue, respectively. Solid lines indicate significant effects, and bands indicate confidence intervals (CI, 95%). For all panels, all other predictors were kept at the mean. AGB, aboveground biomass.

(Figure 4). By extrapolating our results to the reported forest extent of 2019 (Plataforma Geobosques, 2021), taking into consideration the forest types defined by SERFOR, approximately 15% (roughly 105,306 km<sup>2</sup>) of Peruvian Amazonia has experienced natural and/or human disturbances at least once during the study period of 34 years, with a rate of 0.45% per year. Our results include disturbed forests recovering from varying intensities of disturbance (i.e. partial to full removal of forest cover), and thus account for the combined

effect of human and natural disturbances (Easterling & Apps, 2005; Fischlin et al., 2009).

Both AGB and species richness were significantly lower in disturbed forest plots than in undisturbed forest plots (Figure 5a,c). AGB (%r) and species richness (%r) had mean values close to 100%, suggesting that the differences between disturbed and undisturbed values for AGB and species richness were not evident. This is expected, given the predominance of natural and human



**FIGURE 8** Effects of disturbance, environmental conditions and human use on (a) AGB, (b) AGB (%r), (c) species richness, (d) species richness (%r) and (e) species composition (%r) in disturbed forests. Significant predictors are shown as filled, black symbols; non-significant predictors are shown as open symbols. Whiskers represent confidence intervals (CI, 95%). AGB, aboveground biomass.

disturbances noted in the Inventory, and in the Amazon Basin in general (Chambers et al., 2013; Clement et al., 2015; Espírito-Santo et al., 2010; Levis et al., 2017). Therefore, while no disturbance was detected through remote sensing during the last 34 years in areas where undisturbed plots were located, these could likely still be recovering from undetected disturbances before the study period. The absence of differences in AGB (%r) and species richness (%r) could also be due to the chronosequence approach employed in this study, which we used in the absence of data from repeatedly measured plots (discussed further in Section 4.5). For the clusters with disturbed plots, 86% of them had two or more undisturbed plots, which were averaged to constrain local variability.

## 4.2 | Effect of disturbance intensity

The significant, negative effect of disturbance intensity on AGB (%r) coincides with previous studies in logged forests in the region

(de Avila et al., 2018; Rutishauser et al., 2015; Vidal et al., 2016), where silvicultural practices with low disturbance intensities, such as reduced-impact logging (RIL), resulted in forests with higher remaining biomass compared to forests under higher-impact silvicultural practices, such as conventional logging (Karsten et al., 2013; Longo et al., 2016; Rutishauser et al., 2015; Vidal et al., 2016). In a similar manner, the intensity of human-induced fires was also found to have a negative effect on forest structure (Rappaport et al., 2018). Furthermore, the intensity of natural disturbances, such as windthrow severity, has been found to result in tree damage and/or mortality (Brando et al., 2019; Negrón-Juárez et al., 2011, 2018; Rifai et al., 2016; Urquiza Muñoz et al., 2021).

Disturbance intensity also negatively influenced species richness and species richness (%r), however both measures remained relatively high even at the highest disturbance intensities (Figures 6c and 7c). There was also a negative influence of disturbance intensity on the recovery of species composition towards undisturbed forest levels (Figure 7e). Our results coincide with studies in logged forests under



silvicultural practices of varying intensities (Putz et al., 2012), and studies on effects of disturbance in human-disturbed forests (Gibson et al., 2011), as well the effects of natural disturbances of varying intensities (Chambers, Robertson, et al., 2009; Rifai et al., 2016; Slik, 2004). While not explored here, many studies have looked into the effects of natural and human disturbances on species richness in various animal taxa (Barlow et al., 2016; Burivalova et al., 2014; França et al., 2017; Gibson et al., 2011; Moura et al., 2013; Perry et al., 2016; Viljur et al., 2022), showing that higher disturbance intensities lead to higher reductions in animal species richness when compared to undisturbed levels. Assessments of taxa more sensitive to disturbances can provide insights into the effect of minor disturbances on biodiversity which cannot be fully captured by evaluating only tree species (Gibson et al., 2011; Putz et al., 2012).

The range of disturbance intensity was broad (Figure 4b), but the high frequency of lower disturbance intensity values suggests that minor-intensity disturbances were the more predominant disturbance events. This is supported by the larger effects of disturbance intensity on AGB (%r) in comparison to the effects on species richness, species richness (%r) and recovery of species composition (Figures 6 and 7). The larger relative effects of disturbance intensity on AGB (%r) compared with its smaller effects on species richness (%r) are in line with studies in logged forests, which suggest that these disturbances affect structure more than tree species richness, with high percentages of tree and animal diversity remaining (Gibson et al., 2011; Putz et al., 2012).

#### 4.3 | Effect of time since disturbance

Our results show that, as expected, after disturbance forests have been increasing in AGB over time; however, unexpectedly, this effect was not captured when recovery in AGB towards values in nearby undisturbed forests (AGB [%r]) was evaluated. This could be due to the high AGB variability in undisturbed forest plots (Figure 5a), although variation was constrained by the cluster average of undisturbed plots as reference value. Additionally, while no disturbance was detected for undisturbed plots since 1984, undisturbed forest plots could still be recovering from disturbances prior to 1984. This is supported by the qualitative data on human and natural disturbance collected. However, this data did not provide the exact time of disturbance, and thus could not be included in our analysis.

Until now, large-scale studies of  $\Delta$ AGB in disturbed forests had not been carried out throughout Peruvian Amazonia. During the first 20 years after disturbance,  $\Delta$ AGB rates were  $4.7 \text{ Mgha}^{-1} \text{ year}^{-1}$ . Our rate is consistently lower compared to rates found in forests recovering from stand-replacing disturbances, that is secondary forests: 20% lower than the 2019 IPCC rate for young secondary forests in North and South America ( $5.9 \text{ Mgha}^{-1} \text{ year}^{-1}$ ; Requena Suarez et al., 2019), 23% lower than for Neotropical secondary forests ( $6.1 \text{ Mgha}^{-1} \text{ year}^{-1}$ ; Poorter et al., 2016), and 22% lower than for secondary forests in western Brazil ( $6.0 \text{ Mgha}^{-1} \text{ year}^{-1}$ ; Heinrich et al., 2021). When comparing to  $\Delta$ AGB in forests recovering from

forest degradation, this result is consistently greater: 74% larger than in logged forests across the Brazilian Amazon ( $2.7 \text{ Mgha}^{-1} \text{ year}^{-1}$ ; Rutishauser et al., 2015) and 370% and 96% larger than in forests under conventional logging and RIL respectively in Para, Brazil ( $1.0$  and  $2.4 \text{ Mgha}^{-1} \text{ year}^{-1}$ ; Vidal et al., 2016). Our  $\Delta$ AGB estimate is 18% greater than what was found for terra-firme forests recovering from windthrows in the Central Amazon ( $4.0 \text{ Mgha}^{-1} \text{ year}^{-1}$ ; Magnabosco Marra et al., 2018). While previous studies have looked at  $\Delta$ AGB rates in secondary forests or degraded forests, we have quantified  $\Delta$ AGB in forests recovering from disturbances ranging in intensity and representative for Peruvian Amazonia. In this respect, we provide a broader context of net AGB change in Amazonian disturbed forests.

Previous large-scale studies suggest that recovery of tree species richness is a slower process than biomass recovery (Martin et al., 2013; Meli et al., 2017), with secondary forests often taking more than 50 years to recover in species richness following major disturbances (Rozendaal et al., 2019). Windthrow events, which are common in northwestern Amazonia (Chambers et al., 2013; Negrón-Juárez et al., 2018; Urquiza Muñoz et al., 2021), tend to have a positive effect on tree species richness (Marra et al., 2014). However, recovery of species richness over time is not observed in disturbed forests in Peruvian Amazonia. The significant but weak inverse effect of time since disturbance on absolute species richness suggests a slight impoverishment of tree species richness during the first 34 years following a disturbance (Figure 6d). This degradation in species richness could be due to the combination of different stressors, such as fragmentation and windthrows (Silvério et al., 2019), or to the long-term disturbance history prior to 1984 (McMichael, 2021), which was not assessed in this study. Furthermore, the absence of recovery in species richness could be due to the predominance of disturbances that had a larger effect on AGB (%r) than on species richness (%r) (Figure 7a,c). Thus, forests recovering from disturbances—which had no large effects on species richness—did not recover in species richness over time. The negative effect of time of disturbance was not observed on species richness (%r).

Across neotropical secondary forests, Rozendaal et al. (2019) found an increase of similarity in species composition over time, as well as Meli et al. (2017), pantropically. Thus, we expected to find a positive effect of time since disturbance on recovery of species composition towards undisturbed levels, however this effect was not observed. This could be due to the limited number of stems per plot (which was constrained by plot size), which limited us to calculate recovery of species composition in plots with a low number of stems.

#### 4.4 | Effects of climate, topography, soil and human use

While higher values of AGB and AGB (%r) in disturbed forests were expected in areas with higher water availability during dry periods (Álvarez-Dávila et al., 2017; Heinrich et al., 2021; Poorter et al., 2016, 2017; Sullivan et al., 2017), our results were not significant. This could

be due to a low variability in CWD within our study area. Slope, which ranged from 0 to 16° in the studied plots (Table 1), had a positive significant effect on AGB (%r), which could perhaps be associated with accessibility. Other possible drivers, such as the distance to nearest waterway or road, did not have a significant effect on AGB or on AGB (%r). The mean distance to nearest navigable waterway or road was large, 5.8 km (Table 1), which could be why we did not find an effect. However, the absence of an effect could also relate to the absence of smaller roads in the spatial dataset, even though we included primary, secondary and tertiary roads. Similarly, our results suggest that soil nitrogen content—a proxy for soil fertility—had no significant effect on AGB nor AGB (%r). Previous studies have shown AGB to be positively related to soil fertility in undisturbed forest (Sullivan et al., 2017). However, this effect has not been consistently observed in secondary nor disturbed forests (Poorter et al., 2016), which also employed gridded soil data that may not be representative of local values. Surrounding tree cover had a significant positive effect on AGB and AGB (%r). These results were expected, as surrounding forests foster natural regeneration processes by acting as a source of propagules, necessary for tree recruitment (Chazdon, 2003; Rocha et al., 2016). Moreover, though not explored here, biotic factors such as species and functional diversity have been found to influence AGB to a lesser extent in regrowing forests (Capellesso et al., 2020; Manuel Villa et al., 2020; Pyles et al., 2018).

Surrounding tree cover had a large, positive effect on species richness, but not on species richness (%r) nor on recovery of species composition. This was unexpected, but could be due to the consistently high tree cover percentages (Table 1), in combination with the effect of undetected disturbances, which could also have affected surrounding forests. Similar to AGB and AGB (%r), no effect of soil N content was observed on species richness, species richness (%r) nor species composition (%r), which also coincides with results from Rozendaal et al. (2019), who found no effect of soil fertility on species richness and its recovery, but a positive effect of water availability on species richness, to which we found opposing results. This could be due to the generally high water availability throughout the year in our study region, which may have limited our analysis in respect to water availability gradients. Distance to nearest waterway or road had a significant negative relationship to species composition (%r), suggesting that disturbed forests in less accessible areas tend to be more similar to nearby undisturbed forests. This is possibly related to higher levels of deforestation and logging in areas closer to roads and waterways (Barber et al., 2014; Laurance et al., 2009). Lastly, there was a negative effect of slope on species composition (%r), suggesting that steep slopes may slow down tree establishment and growth.

#### 4.5 | Methodological challenges

Working on the combination of NFIs with remote sensing of forest change dynamics in the tropics brings forward several challenges. For example, the geo-location error of the handheld GPS receptors at

the time of defining plot locations might contribute to misalignment between the cluster plots and Landsat pixels. Geo-location error was on average 5.8 m; thus, 0.05-ha plots with a minimum spacing of 60 m were somewhat constrained within a 0.09-ha Landsat pixel. Furthermore, given that our forest change analysis can only date back to 1984, plots classified as undisturbed could be forests recovering from disturbances prior to this year. This could be why we did not find major differences when comparing AGB and species richness in disturbed forests to values found in seemingly-undisturbed forest plots in the same cluster. Another potential reason lies behind the limitations of using Landsat imagery, which can omit small-scale and understory disturbances (Lima et al., 2019).

In addition, although cluster and plot configuration varied per forest type, we do not think that this influenced our results as plots were of the same size. Large variability of AGB and species richness values were observed among both disturbed and undisturbed forest plots, partially as a consequence of the small size of NFI plots (McRoberts & Tomppo, 2007; Requena Suarez et al., 2021). The limitations of working with small plots has been discussed in extent (Chave et al., 2004; Málaga et al., 2022; Maurya et al., 2015; Réjou-Méchain et al., 2014); therefore, we expect that the presence of large trees will lead to the overestimation of AGB, and high variability in our plot-level AGB and species richness estimates. Thus, our results should be confirmed by future studies, which use larger, repeatedly-measured plots. The use of NFI plots in this case should be regarded as an initial step towards exploring forest disturbance in regions where limited plot data is available.

Even though the comparability among plots within the same cluster is hindered by the high levels of AGB variation due spatial variability among plots within the same cluster, we consider plots within the same cluster to be comparable. Previous studies have highlighted high local variability in AGB (Réjou-Méchain et al., 2014; Wagner et al., 2010), which may result in a lack of spatial correlation among nearby plots (Chave et al., 2004). Within our plot data, spatial correlations for AGB in two of our most data-rich forest types (lowland forests and accessible montane forests) were found in plots separated up to 30 km (Supplemental Material S.2 in Málaga et al., 2022). This assumption is supported by our results, which show that large part of the variation for all variables was explained by cluster-to-cluster variation, with clusters explaining 41% of the variation observed for AGB and 40% of the total variation observed for species richness (Section 3.3).

We chose to work with NDMI; however, future studies could assess the performance of different indices (e.g. Schultz et al., 2016), as well as the possibility of characterising forest disturbance through the use of a combination of indices. Our remote sensing derived results could not be systematically validated using high-resolution imagery, given that frequent high-resolution images are not available for all sites and for the whole study period. Future studies can evaluate the performance of our RS approach in areas for which information on time and intensity of disturbance has been recorded. When looking at the relative predominance of dead trees and stumps for all plots, there was a significant difference between disturbed and undisturbed forest plots (Figure S1). While we do not know the date

of tree mortality or extraction, these observations align with our RS-derived results. Furthermore, disturbance intensity had a strong negative influence on the recovery of AGB and species richness, which is an expected result that argues for the feasibility of this approach. Previous studies have stated the challenges of accounting for phenology in tropical humid forests (Negrón-Juárez et al., 2020; Verbesselt et al., 2010), which are minimised in our approach by defining highly-local phenological baselines prior to detecting forest change.

#### 4.6 | Integration of NFI forest plots and remote sensing

Previously, no large scale study of forest disturbance and recovery using forest plot data has been undertaken in Peruvian Amazonia. By combining consistent data on biomass and tree species richness from forest plots with remote sensing of forest change dynamics, our results offer insight into the extent of disturbed forests, their ABG and species richness and recovery therein, as well as their variation across environmental and human use gradients. These insights are much-needed, not only for enhancing ecological understanding, but also for climate-change mitigation efforts (Bustamante et al., 2016). From this perspective, NFIs, providing a snapshot of a country's forests, are a valuable source of data in combination with remote sensing. NFI data are valuable not only for GHG reporting and national forest management practices, but also for ecological research, as they provide forest plot data representative of large areas, while employing a consistent methodology throughout (see Requena Suarez et al., 2021). As time passes and the Landsat archive increases in time, analyses of forest disturbance frequency and intensity, and recovery will be possible at a longer temporal scale. Moreover, as detection methods of forest disturbance improve, we might be able to assess forest recovery from different disturbance types. Finally, as countries advance in tropical forest monitoring (Nesha et al., 2021) and more NFIs become available, the opportunity to assess disturbance and recovery in other regions arises.

## 5 | CONCLUSIONS AND IMPLICATIONS

Our results highlight the negative effect of disturbance intensity on ABG and tree species richness and composition. We found a direct effect of time since disturbance on AGB, and a small but significant inverse effect of time on species richness, suggesting an increase in biomass and slight impoverishment in species richness over time. Thus, our methods show a way forward in which ongoing efforts such as NFIs can be used to explore forest disturbance and recovery throughout large areas in the tropics.

Here, we have explored the paths of forests following a disturbance in Peruvian Amazonia: for a mean-intensity disturbance, AGB increased from 131.3 Mgha<sup>-1</sup> at the time of disturbance to 243.4 Mgha<sup>-1</sup> at 34 years after a disturbance event. During the first 20 years after a disturbance, AGB has been increasing at 4.7 Mgha<sup>-1</sup>

per year. Disturbance intensities were relatively low, with 74% of disturbed plots with a disturbance intensity of up to 0.2 ΔNDMI. These insights, in conjunction with more information on type of disturbance (natural or human), can contribute towards improving GHG inventories in forest ecosystems. As a way forward, we recommend forest-based mitigation endeavours to be cognizant of the role of disturbance intensity on forest biomass and biodiversity and their potential recovery over time. Given that disturbed forests and their recovery are often overlooked in mitigation policies (Bustamante et al., 2016; Edwards et al., 2010), as well as the role of biodiversity in climate change mitigation (Gardner et al., 2012), large-scale analyses of biomass and biodiversity in disturbed forests, as well as their recovery, are an important step towards their inclusion.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest with respect to the research, authorship and/or publication of this article.

#### DATA AVAILABILITY STATEMENT

Data and code supporting the findings of this study are openly available at Data4TU at <https://doi.org/10.4121/44f7b164-d85e-49a5-b0db-64f3f71772fb>. Spatial datasets used in this study are accessible from the sources cited in Table 1. Estimation of disturbance and time since disturbance was done using the AVOCADO algorithm (Decuyper et al., 2022, <https://doi.org/10.1016/j.rse.2021.112829>), and Landsat imagery downloaded from Google Earth Engine. The underlying code for AVOCADO can be found in the following GitHub repository: <https://github.com/MDecuy/AVOCADO>, as well as a tutorial: <https://www.pucv.cl/uuaa/labgrs/proyectos/avocado>.

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