### **ENVIRONMENTAL RESEARCH**

**LETTERS** 



**TOPICAL REVIEW • OPEN ACCESS** 

# Climate benefits of Amazon secondary forests—recent advances and research needs

To cite this article: Jessica C A Baker et al 2025 Environ. Res. Lett. 20 043001

View the article online for updates and enhancements.

### You may also like

- Impact of the magnetic horizon on the interpretation of the Pierre Auger Observatory spectrum and composition data

A. Abdul Halim, P. Abreu, M. Aglietta et al.

The Trans-Neptunian Object (84922) 2003
 <u>VS</u><sub>2</sub> through Stellar Occultations
 Gustavo Benedetti-Rossi, P. Santos-Sanz,
 J. L. Ortiz et al.

- <u>Multi-messenger Observations of a Binary</u> Neutron Star Merger

B. P. Abbott, R. Abbott, T. D. Abbott et al.



### **ENVIRONMENTAL RESEARCH**

**LETTERS** 



#### **OPEN ACCESS**

#### RECEIVED

7 October 2024

#### REVISED

15 January 2025

#### ACCEPTED FOR PUBLICATION 24 February 2025

PUBLISHED

14 March 2025

Original content from this work may be used under the terms of the Creative Commons Attribution 4.0 licence.

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.



### **TOPICAL REVIEW**

# Climate benefits of Amazon secondary forests—recent advances and research needs

Jessica C A Baker<sup>1,\*</sup>, Marcos Adami<sup>2</sup>, Celso H L Silva-Junior<sup>3,4</sup>, Luis W R Sadeck<sup>5,6</sup>, Callum Smith<sup>1</sup>, Viola H A Heinrich<sup>7,8</sup>, Jos Barlow<sup>9</sup>, Joice Ferreira<sup>10</sup>, Henrique L G Cassol<sup>11</sup>, Liana O Anderson<sup>12</sup>, Celso Von Randow<sup>13</sup>, Arthur P K Argles<sup>14</sup>, Rita C S Von Randow<sup>15,16</sup>, Fernando Elias<sup>17</sup>, Luiz E O C Aragão<sup>2,19</sup>, Stephen Sitch<sup>18</sup> and Dominick V Spracklen<sup>1</sup>

- School of Earth and Environment, University of Leeds, Leeds LS2 9JT, United Kingdom
- <sup>2</sup> Earth Observation and Geoinformatics Division, National Institute for Space Research, São José dos Campos, SP, Brazil
- Instituto de Pesquisa Ambiental da Amazônia—IPAM, Brasília, DF, Brazil
- 4 Programa de Pós-graduação em Biodiversidade e Conservação, Universidade Federal do Maranhão—UFMA, São Luís, Brazil
- <sup>5</sup> Graduate Program in Environmental Sciences, Federal University of Pará, Belém, PA, Brazil
- <sup>6</sup> Amazon Space Coordination, National Institute for Space Research, Belém, PA, Brazil
- <sup>7</sup> GFZ Helmholtz Centre for Geosciences, Potsdam, Germany
- School of Geographical Sciences, University of Bristol, Bristol, United Kingdom
- <sup>9</sup> Lancaster Environment Centre, Lancaster LA1 4YQ, United Kingdom
- Embrapa Amazonia Oriental, C. Postal 48, 66017-970, Belem, PA, Brazil
- Bluebell Index, Alameda Vicente Pinzon, 54, 7° andar, São Paulo, Brazil
- $^{12}\,$  National Center for Monitoring and Early Warning of Natural Disasters—Cemaden, São José dos Campos, Brazil
- Impacts, Adaptation and Vulnerability Division, National Institute for Space Research, São José dos Campos, SP, Brazil
- Met Office Hadley Centre, FitzRoy Road, Exeter EX1 3PB, United Kingdom
- $^{15}\,\,$  Physics Institute, University of São Paulo (USP), São Paulo, Brazil
- $^{16}~$  Faculty of Technology of São Paulo State (FATEC), Jacareí, Brazil
- <sup>17</sup> Universidade Federal Rural da AmazôniaCapitão Poço, Pará, Brazil
- $^{18}\,$  University of Exeter, Exeter EX4 4QE, United Kingdom
- <sup>19</sup> Department of Geography, Faculty of Environment, Science and Economy, University of Exeter, Exeter EX4 4QE, United Kingdom
- \* Author to whom any correspondence should be addressed.

E-mail: J.C.Baker@Leeds.ac.uk

Keywords: secondary forests, Amazon, tropical forests, forest-climate interactions, land-atmosphere interactions, reforestation

### Abstract

A quarter of the deforested Amazon has regrown as secondary tropical forest and yet the climatic importance of these complex regenerating landscapes is only beginning to be recognised. Advances in satellite remote-sensing have transformed our ability to detect and map changes in forest cover, while detailed ground-based measurements from permanent monitoring plots and eddy-covariance flux towers are providing new insights into the role of secondary forests in the climate system. This review summarises how progress in data availability on Amazonian secondary forests has led to better understanding of their influence on global, regional and local climate through carbon and non-carbon climate benefits. We discuss the climate implications of secondary forest disturbance and the progress in representing forest regrowth in climate models. Much remains to be learned about how secondary forests function and interact with climate, how these processes change with forest age, and the resilience of secondary forest ecosystems faced with increasing anthropogenic disturbance. Secondary forests face numerous threats: half of secondary forests in the Brazilian legal Amazon were 11 years old or younger in 2023. On average, 1%–2% of Amazon secondary forests burn each year, threatening the permanence of sequestered carbon. The forests that burn are predominantly young (in 2023, 55% of burned secondary forests were <6 years old, <4% were over 30 years old). In the context of legally binding international climate treaties and a rapidly changing political backdrop, we discuss the opportunities and challenges of encouraging tropical forest restoration to mitigate anthropogenic climate change. Amazon

secondary forests could make a valuable contribution to Brazil's Nationally Determined Contribution provided there are robust systems in place to ensure permanence. We consider how to improve communication between scientists and decision-makers and identify pressing areas of future research.

### 1. Background

Between 1988 and 2023, approximately 850 000 km<sup>2</sup> of Amazon forest had been deforested (data from Instituto Nacional de Pesquisas Espaciais, INPE, 2024) of which around a quarter has regrown (Smith et al 2021). We define these regrowing forests as 'secondary' forests, i.e. forests naturally regrowing on land historically covered by forest that has experienced a land cover change (i.e. no longer forest), and subsequent abandonment (Almeida et al 2016a). Amazon secondary forests form important carbon sinks (Heinrich et al 2021), provide a buffer against primary forest loss (Wang et al 2020), improve forest connectivity and protect old-growth forests from edge effects (Smith et al 2023a) and help to protect and restore biodiversity (Matos et al 2020). Preserving old-growth forests should be the number one conservation priority (Cook-Patton et al 2021) as their value in terms of biodiversity, carbon and water cycling, and other environmental benefits is unmatched (Gibson et al 2011, Watson et al 2018). Secondary forests may accomplish similar characteristics within a few decades to centuries if kept undisturbed (Poorter et al 2021a) and promoting tropical forest regrowth is crucial for climate change mitigation and adaptation efforts (Locatelli et al 2015). However, secondary forests are distinctive from oldgrowth primary forests and differ widely in successional stage, species composition, structure, and functionality (Almeida et al 2016a, Lennox et al 2018, Rozendaal et al 2019, Leite et al 2023). Understanding the underlying variability in secondary forests is therefore vital when considering how these ecosystems interact with the Earth system.

Secondary forest age varies spatially in the Brazilian Amazon (figure 1), which contains around 75% of Amazon secondary forests (Smith et al 2021). Forest age is related to the rate of deforestation, with younger forests in more heavily deforested areas (Neeff et al 2006, Almeida 2009, Almeida et al 2016a, Wang et al 2020, da Silva et al 2023a). Brazil has the highest potential for tropical forest restoration through natural regeneration, according to a recent analysis (Williams et al 2024). Brazil has committed to restoring 120 000 km<sup>2</sup> of forest by 2030 as part of their intended Nationally Determined Contributions (NDCs) under the Paris Agreement (Federative Republic Of Brazil 2016, 2022, 2023). The aim of this agreement is to limit the rise in global mean temperatures to well under 2 °C, with forest restoration and sustainable forest management an essential part

of the mitigation strategy to reduce greenhouse gas emissions (UNFCCC 2015). Reforestation of previously deforested lands offers a way to sequester atmospheric carbon dioxide and increase terrestrial carbon stocks, on the understanding that it must be done in conjunction with preserving old-growth forests.

Analysis of land cover changes in the Brazilian Amazon between 1985 and 2019 revealed complex temporal patterns of loss-regrowth-loss, demonstrating high levels of disturbance in secondary forest ecosystems (Wiltshire et al 2022). This explains the dominance of young (<20 years) secondary forests in the region (figure 1). The rate of natural regeneration following the abandonment of agricultural land can vary widely in the Amazon, with aboveground biomass (AGB) recovering within a few decades to well over a century (Gehring et al 2005, D'Oliveira et al 2011, Heinrich et al 2021, Poorter et al 2021a), depending on the land use history (see section 3). Secondary forests in Rondônia, Southwest Amazonia had recovered 40%-60% of primary forest biomass after 18 years (Alves et al 1997), but rapid recovery is not guaranteed, and much lower rates have been observed in some of the most deforested regions (Elias et al 2020) or after mining (Kalamandeen et al 2020). Repeated cycles of forest clearance reduce carbon accumulation rates, particularly when fires have occurred (Heinrich et al 2021) and have implications for soil health and tree species composition (Villa et al 2018, Bauters et al 2021).

Restoration of species diversity is more challenging (Jakovac et al 2024), with at least 30 years before pioneer species are replaced by late-successional species and more than a century to reach the tree species composition of old-growth forests (Poorter et al 2021a, Rosenfield et al 2023). Faunal taxa (e.g. dung beetles and birds) recover across similar timescales, with high-conservation-value forest species increasing when forest biomass recovery exceeds 75 Mg  $ha^{-1}$ (Lennox et al 2018). Functional diversity may recover within just a few years to decades of regrowth, with one study of avian communities in 44 secondary forest sites reporting similar levels of ecosystem functioning to nearby primary forests (Sayer et al 2017). However, this aspect of diversity is less studied in the Amazon and responses may differ between taxa (e.g. Farneda et al 2018).

Smallholder shifting cultivation (where small patches of land are periodically cleared to grow crops before being abandoned) is an important land-management system throughout the Amazon, with many people depending on it for their livelihoods

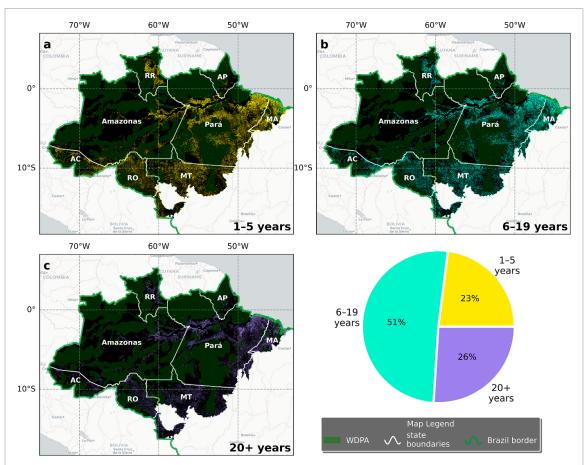


Figure 1. Map showing the distribution of Amazon secondary forests (<38 years old) in the Brazilian Legal Amazon (black background) in 2023 as detected by the MapBiomas version 9 product. (a) Forests 1–5 years old are shaded in yellow, b) forests 6–19 years old are shaded in cyan, and (c) forests 20–36 years old are shaded in purple. The distribution of Amazon secondary forests in the three age classes is shown in the pie chart. Dark green shading in panels A-C shows protected areas (data from World Database on Protected Areas, WDPA). The figure was produced using Collection 9 of MapBiomas Brasil (https://brasil.mapbiomas.org/en/colecoes-mapbiomas). Data are available at: https://github.com/celsohlsj/gee\_brazil\_sv. Abbreviations for Amazonian states are as follows: RR = Roraima, AP = Amapá, MA = Maranhão, AC = Acre, RO = Rondônia, MT = Mato Grosso. Figure credit: Ben Silver.

(Van Vliet et al 2013, Curtis et al 2018). This practice contributes to the gradual conversion of intact primary forest to secondary forest in areas that are not already protected. Successive cycles of clear cuts under shifting cultivation can reduce forest resilience (Jakovac et al 2015), resulting in an alternative stable state (Magnuszewski et al 2015). Secondary forests are often targeted for clearance as young forests are easier to cut and are not subject to the same legal protections as old-growth primary forests (Nunes et al 2020). In the state of Pará, secondary forests older than 20 years must be conserved (Vieira et al 2014) and Mato Grosso state has also approved a bill protecting secondary forests (Secretaria de Estado de Meio Ambiente, SEMA 2016), but no other Brazilian Amazon states legislate to protect secondary vegetation (Wang et al 2020).

Current methods for mapping large-scale secondary vegetation areas and estimating their ages rely on optical remote sensing (Almeida *et al* 2016a, Silva Junior *et al* 2020). Significant advances have also been

made in remote sensing involving RADAR (RAdio Detection And Ranging) and LiDAR (Light Detection And Ranging), among others. These advances have been used to monitor forest formation, afforestation, degradation and secondary vegetation (Bispo *et al* 2019, Milenković *et al* 2022, Fawcett *et al* 2023, Cooley *et al* 2024). However, these resources do not yet have a sufficiently long time series or complete coverage of the area to be monitored. Current approaches for mapping large-scale areas of Amazon secondary vegetation and estimating their ages therefore still rely on optical remote sensing, and we focus on these in this review.

This article summarises the key advances in secondary forest research in the Brazilian Amazon. We review recent progress in satellite remote sensing and in situ data collection in Amazon secondary forests (section 2). These improvements in data availability have led to better understanding of how Amazon secondary forests impact climate at global, regional and local scales, through providing carbon

and non-carbon benefits (sections 3 and 4). We explain how these secondary forest-climate interactions are influenced by drivers of disturbance (section 5) and the importance of accurately modelling forest regrowth for future climate prediction (section 6). We describe two case studies from the Brazilian state of Pará that demonstrate how effective collaboration between scientists and policymakers can lead to successful conservation (section 7). These examples provide a guide for scaling up secondary forest conservation efforts across Brazil and beyond to the wider Amazon. Finally, we look to the future of Amazon secondary forest research and highlight some of the most exciting avenues for further work (section 8).

## 2. Advances in understanding from satellite and in situ data

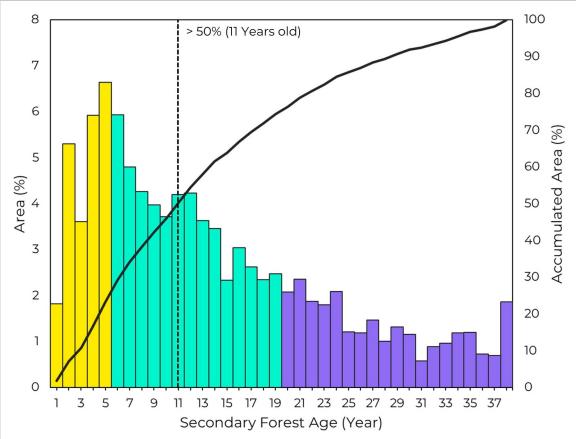
Our understanding of Amazon secondary forests comes from two key sources: satellite remote sensing and field observations. With increasing availability of satellite-based products of land-use and landcover change, it is now possible to map the extent and ages of Amazon secondary forest (Wang et al 2019, Nunes et al 2020, Silva Junior et al 2020, Smith et al 2020, Heinrich et al 2021, Vancutsem et al 2021), enabling quantification of their role in the global carbon cycle (Harris et al 2021, Smith et al 2021, Fawcett et al 2023, Heinrich et al 2023a, Chen et al 2024). The European Commission Joint Research Centre has recently mapped global forests, including Amazon secondary forests, in the year 2020 at 10 m resolution, which will enable them to be studied in unprecedented detail (Bourgoin et al 2024). Satellite datasets offer spatially comprehensive information, often spanning several decades, but some variables are difficult to measure remotely and calibrating against field data is essential. Detailed information on forest dynamics, including growth rates and compositional changes requires intensive ground data collection at the tree and stand level, but monitoring occurs over smaller areas than possible with remote sensing. In this section, we summarise the importance of satellite datasets for mapping Amazon secondary forests and the vital role of field data for evaluating regrowth rates, ecological succession and climate interactions.

The most challenging aspect of mapping secondary forest is determining whether the area has already been deforested to distinguish it from old-growth primary vegetation. Although it has been possible to identify deforestation and map secondary vegetation with satellite images since the 1970s (Landsat), the data series only became consistent from the mid-1980s with the launch of the Landsat Thematic Mapper sensor (Markham *et al* 2004). Therefore, most satellite-based secondary forest maps are limited to this timeframe. Ongoing efforts using machine

learning to incorporate satellite information with biomass maps, forest inventory data and climate variables may extend secondary forest maps beyond the satellite era in the future (Besnard *et al* 2024).

Brazil has annually mapped primary deforestation since 1988 using optical satellite images through PRODES (Programa de Monitoramento de Desflorestamento na Amazônia Legal), its satellite monitoring program for the Brazilian Amazon. In PRODES, deforestation is defined as the suppression of areas of old growth forest by anthropogenic actions (Almeida et al 2021). Usually, its overall accuracy is greater than 90% (Maurano et al 2019). To maintain consistency with the historical series, PRODES deforestation rates are calculated for areas larger than 6.25 ha (Kalamandeen et al 2018), though since 2017, Brazil's National Institute for Space Research (INPE), has also mapped deforestation smaller than 6.25 ha for Brazil's national Forest Reference Emission Level (data available via the TerraBrasilis Portal). PRODES contributes to the governance and development of policies that seek sustainable production in the Amazon (see section 7) and provides a reliable basis for mapping secondary vegetation.

There have been several attempts to map secondary forests across the Amazon with different methodologies resulting in some differences between data products (Nunes et al 2020). The Terraclass project uses the PRODES deforestation map as a base and identifies secondary vegetation using visual interpretation. This is a labour and time-consuming process but remarkably accurate (Almeida et al 2016a). Other projects have developed methodologies to estimate secondary forest age based on the MapBiomas map (Silva Junior et al 2020). MapBiomas uses fully automated mapping, which reduces the time to obtain the map but does not always show temporal consistency between mapping versions (Souza Jr et al 2020). Other methodologies involve machine and deeplearning algorithms to improve the ability to differentiate targets over time (Santos et al 2021). Such analysis has only recently become possible with advances in processing infrastructure including cloud computing and storage (e.g. Google Earth Engine, Gorelick et al 2017, Amazon Web Services, Chen et al 2017; Microsoft Azure and Microsoft Planetary Computer, Luers 2021; and government initiatives such as the Brazil Data Cube, Ferreira et al 2020). Nevertheless, improvements in detecting the timing of regrowth are necessary, and satellite-based maps may not reliably detect ground-based restoration (Begliomini and Brancalion 2024). In this review, we present data from MapBiomas Collection 9 (figures 1, 2 and 4), which has a lower area value for secondary forest in the Brazilian Amazon than previous MapBiomas collections (Nunes et al 2020, Silva Junior et al 2020), likely due to an updated classification approach including better recognition of flooded forests (Mapbiomas 2024). For this reason, it is important to only consider



**Figure 2.** Histogram showing the age distribution of Amazon secondary forests in 2023. The solid black line indicates the accumulated area (righthand axis). The vertical dashed black line represents the age threshold at which more than 50% of secondary forests are represented. Colours indicate forests 1–5 years old (yellow), 6–19 years old (cyan) and >20 years old (purple), reflecting different categories of protection status in the Brazilian state of Pará (see section 7). Figure produced using the method developed by Silva-Junior *et al* (2020) and Collection 9 of MapBiomas Brasil (https://brasil.mapbiomas.org/en/colecoesmapbiomas); Data available at: https://github.com/celsohlsj/gee\_brazil\_sv.

data within a single collection when evaluating temporal variability. A consistent validation of Amazon secondary forest maps with reference data derived from remote sending and ground data is urgently required.

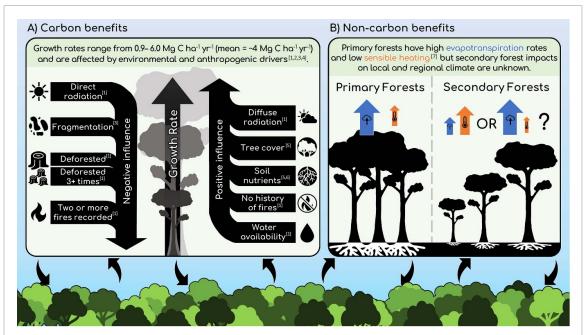
Ground data complement and enhance the insights that can be gained from satellites and are also essential to validate satellite-based maps (Barros et al 2018). Secondary forest field inventories and flux tower measurements provide vital information on forest structure, floristic composition, growth rates and climate interactions (see Alves et al 1997, Feldpausch et al 2005, Silva et al 2016, Bentos et al 2017, Von Randow et al 2020, Heinrich et al 2021, Poorter et al 2021a and references therein). Secondary forests of different ages that share environmental and soil characteristics are often studied as a chronosequence (i.e. using space-for-time substitution) to assess regrowth rates and forest succession (Feldpausch et al 2007, Silva et al 2016, Poorter et al 2021b). A typical approach is to survey all trees within a sampling plot of known area, recording information such as tree identification, diameter at breast height and tree height, which are used to estimate AGB and carbon accumulation rates (Alves et al 1997, Araújo

et al 2005, Feldpausch et al 2005). Heinrich et al (2021) compiled data from 30 field campaigns located across the Amazon and combined this information with six environmental and anthropogenic disturbance drivers to quantify the carbon uptake potential of Amazon secondary forests (see section 3).

An alternative to the chronosequence approach is long-term monitoring at a single location. For example, this may be through repeated plot inventories (Araújo *et al* 2005), or via flux tower measurements (Von Randow *et al* 2020). However, there is only a single flux tower over secondary forest in the Brazilian Amazon. Additional flux tower measurements in forests of different regrowth stages and in different Amazon regions would help to better understand the spatial variability in Amazon secondary forest water recycling and provide valuable ground-truthing for satellite evapotranspiration products (Baker *et al* 2021b).

# 3. Carbon-related climate benefits of Amazon secondary forests

Amazon secondary forests have an important influence on global climate by sequestering and storing



**Figure 3.** Schematic summarising the carbon (A) and non-carbon (B) climate benefits of Amazon secondary forests. Environmental and anthropogenic factors that influence growth are shown and remaining knowledge gaps on how secondary tropical forests interact with local-to-regional climate are highlighted. The schematic is supported by data from [1] Heinrich *et al* (2021), [2] Cook-Patton *et al* (2020), [3] Chen *et al* (2024), [4] Cassol (2018), [5] Chen *et al* (2023), [6] Davidson *et al* (2004), and [7] Spracklen *et al* (2018). Figure credit: Robin Hayward.

carbon, and could play a key role in climate change mitigation efforts (Heinrich et al 2021). Figure 2 shows the age distribution of secondary forests in the Brazilian Amazon in 2023. Most of these forests are young, with  $\sim$ 50% younger than 11 years and 90% younger than 29 years. An analysis of 1500 plots in South and Central America found secondary tropical forests took an average of 66 years to achieve 90% of the AGC of old-growth forests (Poorter et al 2016). The study found that secondary forests accumulated carbon approximately 11 times faster than old-growth forests, with an uptake rate of 3 Mg C ha<sup>-1</sup> yr<sup>-1</sup> after 20 years (Poorter et al 2016). Tropical forest restoration could therefore be important for mitigating climate change (Edwards et al 2021). However, carbon accumulation in secondary forests is not uniform across the tropics, with local geography, climate and anthropogenic disturbances influencing regrowth (Cook-Patton et al 2020). In this section we summarise the main environmental and anthropogenic factors influencing secondary forest growth variation. These factors are summarised in figure 3. We focus on aboveground carbon (AGC) dynamics as they have been more extensively studied than belowground carbon in Amazon secondary forests.

Variation in environmental conditions is an important driver of variability in secondary forest regrowth rates across the Amazon (Elias *et al* 2020, da Silva *et al* 2023a). In general, AGC accumulation rates are higher in warmer and wetter areas than cooler and drier areas (Cook-Patton *et al* 2020). Regrowth rates of young Amazon secondary forests (<20 years) can

vary by a factor of two with faster regrowth in wetter western regions (3.0 Mg C  $ha^{-1} yr^{-1}$ ) compared to drier eastern regions (1.3 Mg C ha<sup>-1</sup> yr<sup>-1</sup>) (Heinrich et al 2021). Heinrich et al (2021) identified shortwave (SW) radiation as the most important climatic control on growth rate, with higher growth in areas of the Amazon with lower SW radiation, and vice versa. This may be because areas with low SW radiation had high cloud cover and therefore more diffuse radiation, which increases plant productivity (Rap et al 2015). Surrounding tree cover and soil fertility also positively influence secondary forest growth (Chen et al 2023), while fragmentation has the reverse effect (figure 3). Houghton et al (2000) observed uptake rates ranging from 1.5 Mg C ha<sup>-1</sup> yr<sup>-1</sup> for Amazon forests with initial biomass of less than 100 Mg C ha<sup>-1</sup>, to about 5.5 Mg C ha-1 yr-1 for forests with initial biomass of more than 190 Mg C ha<sup>-1</sup>. A recent meta-analysis of 452 Amazon secondary forest plots in chronosequence (forests aged between 1-70 years) found carbon stocks ranging from 0.1 to 295 Mg C ha<sup>-1</sup> (Cassol 2018) and a mean growth rate of 4 Mg C  $ha^{-1}$   $yr^{-1}$  (CV = 77%). These findings are similar to those of Chen et al (2024), who reported an average regrowth rate equivalent to  $3.89 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$  for the Brazilian Amazon.

Land use history and the magnitude of disturbance are major factors affecting regeneration and biomass accumulation in Amazon secondary forests. Disturbance magnitude is measured by the spatial extent, duration, frequency and severity of use before abandonment (Waide and Lugo 1992, Chazdon 2014). Major anthropogenic disturbances,

such as the conversion of forests to agricultural areas and pastures, have more severe effects on the regeneration of forests than areas abandoned immediately after cutting without cultivation, e.g. due to soil degradation (Moran et al 2000, Zimmermann et al 2006). Studies have shown that the type of land use (agricultural, pasture, silviculture, or no use), the frequency of clear cuts (number of cycles), and the method used for forest removal (mechanized, with/without fire) can all influence carbon accumulation rates in Amazon secondary forests (Uhl et al 1988, Steininger 2000, Wandelli and Fearnside 2015). Abandoned pastures reportedly have slower regrowth rates than other land uses due to the frequent use of fire and higher predation of seeds and seedlings in these areas (Uhl et al 1988, Fearnside and Guimarães 1996, Sorrensen 2000). In the central Amazon, secondary forests regenerating on pastures accumulated 25-50% AGB of primary forests in the first 12-14 years (Feldpausch et al 2004). Secondary forests growing after a single slash-and-burn cycle showed rapid growth rate saturation, taking an estimated 25 years to reach 50% primary forest AGB and 175 years to restore 75% AGB (Gehring et al 2005).

The knowledge of such variation in forest regrowth is important for estimating carbon accumulation potential in secondary forests. Carbon assimilation models often use unrealistically fixed carbon regrowth rates for secondary tropical forests. In their global stocktake, Pan et al (2024) estimated carbon uptake in South America tropical regrowth forests to be 4.13 Mg C ha<sup>-1</sup> yr<sup>-1</sup> over a 30 year period, with uncertainty in carbon stocks of around 43%. Cook-Patton et al (2020) mapped spatial variation in carbon uptake rate for secondary forests globally, based on 66 environmental covariates and assumed fixed growth rates over the first 30 years of regeneration. They estimated carbon uptake rates of up to 6.0 Mg C ha<sup>-1</sup> yr<sup>-1</sup> with South American rainforest having the highest average uptake rate of 41 ecozones analysed. These studies provide a valuable benchmark for assessing the climate change mitigation potential of reforestation. However, it is important to note that Amazon secondary forest regrowth rates are not linear but decay exponentially with time, and it cannot be assumed that secondary forests will return to the same AGB as primary forests (Gehring et al 2005). A long-term repeated assessment in the Eastern Amazon shows 60-year-old forests accumulating just  $1.08 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  (Elias et al 2020). Research has shown the loss of resilience of Amazon secondary forest areas due to the intensification of land-use practices (Jakovac et al 2015, Chazdon et al 2016, Poorter et al 2016). Heinrich et al (2021) showed carbon accumulation rates may saturate sooner than 30 years, with fire and repeated deforestation substantially limiting regrowth rates (see section 5). The slowest regrowth rates are in Amazon regions with the longest history of deforestation, where there are

almost no primary forests left to provide seed sources (Elias *et al* 2020).

The geographic complexity of regrowth rates in Amazon secondary forest has implications for policies focused on maximising climate mitigation potential whilst enabling secondary forests to be used sustainably. If the current area of secondary forest in the Brazilian Amazon is maintained to the year 2030, the carbon sink could contribute 5.5% of Brazil's NDCs from the Paris Agreement of the United Nations Framework Convention on Climate Change (Heinrich et al 2021). Given that in 2017, the area of secondary forests in the Brazilian Amazon ( $\sim$ 136 000 km<sup>2</sup>) was equivalent to 1.6% of Brazil's land area, the mitigation contribution is proportionally large ( $\sim$ 30%, Heinrich et al 2021). Due to the dominance of young (<10 years) secondary forest stands in Brazil (figure 2), preserving only mature (>20 years) secondary forests to 2030 would reduce the mitigation contribution to <1% of Brazil's NDC (Heinrich et al 2021). Across the Brazilian Amazon, the Amazon biome and indeed the pantropics, secondary forest carbon regrowth only balances 9%-14% of the carbon lost from ongoing deforestation and degradation (Harris et al 2021, Heinrich et al 2021, Smith et al 2021).

Amazon secondary forests could also contribute to country-level commitments under the Global Biodiversity Framework (Convention on Biological Diversity (CBD) 2022) and are fundamental for achieving the aim of restoring 30% of degraded areas. While secondary forests may take centuries to acquire the largest trees and structural complexity of old growth forests, the colonisation of species of higher conservation value accelerates when they surpass 75 Mg C ha<sup>-1</sup>, which can happen on decadal time scales (Lennox et al 2018). Furthermore, even young forests can be important for biodiversity by enabling species movement and gene exchange across the landscape, and one analysis across the Amazon suggests over 2 million fragments are connected by some form of secondary forest (Smith et al 2023). Further landscape-level benefits are accrued from the buffering of over 40% of exposed forest edges (Smith et al 2023), potentially helping mitigate the edge effects that are a pervasive driver of vertebrate declines (Pfeiffer et al 2017) and diminish aboveground carbon stocks (Berenguer et al 2014). Keeping pledges on protecting forests, particularly old-growth forests, made on global geopolitical stages remains a priority for addressing the climate and biodiversity emergencies.

# 4. Non-carbon climate benefits of Amazon secondary forests

Old-growth tropical forests are well known to modulate local and regional climate through mediating exchanges of water and energy between the land and the atmosphere and altering the surface energy balance (Bonan 2008). Amazon forests, including secondary vegetation, have a lower albedo than pasture and croplands (~2% lower), so absorb more incoming solar radiation (Bastable et al 1993, Gash and Nobre 1997, Campos et al 2021). However, forests also have high rates of evapotranspiration and high surface roughness, which promote the transfer of heat and moisture from the land to the atmosphere, resulting in low sensible heat fluxes and a net cooling at the surface (Gash and Nobre 1997, Von Randow et al 2004, Da Rocha et al 2009, Spracklen et al 2018). Research estimating the effect of natural regeneration on local temperatures suggested tropical reforestation could cause annual cooling of 2 °C (Alibakhshi et al 2024), though this work was based on an analysis of climate variables over intact forests only.

In the Amazon, 24%-41% of precipitation is sourced from evapotranspiration from within the basin (Baker and Spracklen 2022). When the Amazon is deforested these land-atmosphere interactions are disrupted causing substantial surface warming (<2 °C) and precipitation reductions (Alkama and Cescatti 2016, Bright et al 2017, Spracklen et al 2018, Baker and Spracklen 2019, Cohn et al 2019, Smith et al 2023b). The regional impacts on temperature are extensive, with a recent analysis showing Amazon deforestation causes warming up to 100 km from the site of deforestation (Butt et al 2023). The impacts of deforestation on precipitation are scale dependent (D'Almeida et al 2007, Lawrence and Vandecar 2015). Small patches of deforestation may increase precipitation over or near to the location of forest loss due to convection initiation (Garcia-Carreras and Parker 2011, Khanna et al 2017). At larger scales, deforestation reduces precipitation (Spracklen and Garcia-Carreras 2015, Smith et al 2023b) through reduced moisture recycling (Zemp et al 2017, Staal et al 2018). In addition, air pollution associated with biomass burning, e.g. across the arc of deforestation, exposes nearby secondary forest trees to high ozone levels. These fast growing, high stomatal conductance tree species are likely highly susceptible to ozone air pollution, reducing plant productivity and regrowth (Cheesman et al 2024, Brown et al submitted).

Amazon secondary forests differ in important ways from primary forests in terms of species composition, structure and hydrological functioning (Peña-Claros 2003, Feldpausch *et al* 2005, Poorter *et al* 2016, Von Randow *et al* 2020), so we might expect that secondary forests would also interact differently with local and regional climate. Fast-growing pioneer tree species that dominate in secondary forests tend to have lower wood densities and invest less in water conservation measures than slower-growing tree species that are better protected against drought (Poorter *et al* 2010). A comparison of flux tower measurements in a primary forest and a 20-year-old secondary forest in Central Amazonia revealed important differences

in land-atmosphere interactions between the two sites (Von Randow et al 2020). Over four years of measurements, evapotranspiration was 20% higher in the secondary forest (3.6 mm  $d^{-1}$ ) than in the primary forest (3.1 mm day<sup>-1</sup>), while gross primary productivity was only 5% higher (8.1 gC m<sup>-2</sup> d<sup>-1</sup> in the secondary forest, 7.8 gC  $m^{-2}$   $d^{-1}$  in the primary forest). The differences in evapotranspiration between primary and secondary forest sites were attributed to higher transpiration rates of the secondary forest tree species. This conclusion is supported by the findings of Kunert et al (2015) who observed higher leaf-scale transpiration rates in secondary tree species than in old-growth species in the same region. Von Randow et al (2020) estimated that stomatal resistance was 40% lower in the secondary forest than in the primary forest site, highlighting the higher drought vulnerability of secondary forests.

In contrast, a study in the southern Amazon based on remote sensing data reported lower evapotranspiration and higher land surface temperature in secondary compared to intact forest sites, particularly in the dry season (Rangel Pinagé *et al* 2023). They found secondary sites had lower structural complexity (a proxy for surface roughness), and as such transfers of heat and moisture from the land to the atmosphere would be lower than over intact forests. The southern Amazon region has a longer and more severe dry season than the flux tower sites in the central Amazon measured by von Randow *et al*, possibly explaining the differences in secondary forest evapotranspiration between the two studies.

Two studies based on MODIS land surface temperature estimates have drawn opposite conclusions about the relative influence of forest loss and forest gain on surface temperature. Su et al (2023) analysed areas that remained classified as 'forest' but experienced fine-scale (sub-grid) changes in tree cover. They reported that the cooling from tree gain in the tropics was stronger than the warming due to tree loss, such that grid cells where areas of gain and loss were equal saw an overall cooling effect of—0.58 °C. They concluded that this was caused by increases in evapotranspiration from tree cover gains being higher than the decreases in evapotranspiration from tree loss. In contrast, Zhang et al (2024) reported a cooling of—0.10 °C due to tropical forest gain compared to a warming of +0.56 °C caused by tropical forest loss. These authors used a slightly different approach whereby 30 m tree cover data were aggregated to a larger grid and grid cells were categorised as forest (tree cover >60%) or non-forest (tree cover <60%) in each year to identify forest gains and losses. This study may have included areas with larger reductions in forest, as they did not limit their analysis to areas that remained classified as forest. Both studies were limited to a period of about a decade (2000-2012 in Su et al 2023 and 2003-2013 in, Zhang et al 2024), and therefore may not fully capture the climate

interactions of regrowing secondary forests. Overall, the lack of agreement on how regrowing secondary forests influence the local-to-regional climate system and how these interactions change as forests age highlights a need for further research in this area (figure 3).

### 5. Drivers of secondary forest disturbance

Understanding drivers of secondary forest disturbance is crucial, as they impact the dynamics of forest regrowth, carbon sequestration and forest-climate interactions. Currently, there is a lack of information on selective logging in Amazon secondary forests and use of non-wood materials. Although their impacts on forest dynamics are still poorly understood, fires, droughts and repeated deforestation after regrowth are perhaps the most studied drivers of secondary forest disturbance in the Amazon due to the availability of satellite-derived products and we focus our discussion on these here. The impacts of fire, deforestation and water availability on secondary forest growth are summarised in figure 3.

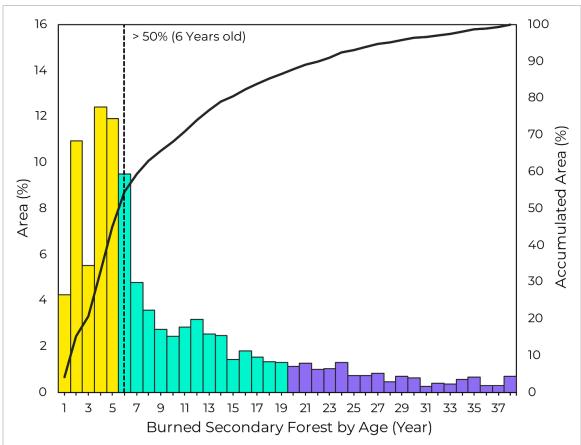
In the humid forests of the Amazon, fire is an anthropogenic driver of secondary forest disturbance and a major source of carbon emissions (Silva et al 2020). A recent analysis showed that between 2003 and 2020 on average approximately 79 500 km<sup>2</sup> of land burned annually in the Amazon (including forests, savannas, grasslands and agricultural lands), of which approximately 2% (1862 km<sup>2</sup>) occurred in areas of secondary tropical forest (Silveira et al 2022). This represents less than 1% of Amazon secondary forests by area. Most Amazon secondary forest burning occurs in Brazil (89%), where 1%-2% of secondary forests burned each year (Silveira et al 2022). In 2023, for example,  $\sim$ 2% of Brazilian secondary forests burned, the majority of which were young forests (55% were <6 years old, figure 4) where the highest carbon uptake rates are found. More mature secondary forests formed a smaller proportion of the burned area, with only 12% of fires occurring in forests older than 20 years and <4% in forests older than 30 years (figure 4). These results have relevance when considering the contribution of secondary forests to NDCs, since permanence is a key requirement when accounting emission reductions (NDC Synthesis Report 2022). With young Amazon secondary forests more likely to burn, safeguards will be required to ensure reforestation for climate change mitigation is effective.

Amazon fire activity in 2020 was the highest in the two first decades of this century with a total burned area of 91 250 km<sup>2</sup> (Silveira *et al* 2022). Major fire events in the Amazon are often associated with extreme meteorological conditions such as droughts (Aragão *et al* 2018, Li *et al* 2021a, 2021b), including the intensive burning of old-growth forests in 2023 (Mataveli *et al* 2024). However, the fires in 2020 were associated with deforestation rather than water

deficit anomalies (Silveira et al 2022). Butt et al (2022) demonstrated strong positive associations between deforestation and fire across the Brazilian Amazon. An analysis of large fires in Brazil found nearly 30% occurred in near-normal meteorological conditions (Li et al 2021b). This highlights the dominance of human activity on the Amazon fire regime (Aragão et al 2014). Amazon secondary forests that experienced repeated fire events showed AGC accumulation rates 50%-75% lower than forests with no burning history (figure 3), and long-term reductions in maximum accumulated AGC (Zarin et al 2005, Heinrich et al 2021). Furthermore, fires can substantially alter microclimatic conditions, hindering regeneration and in some cases completely preventing forest recovery (Almeida et al 2016b, Smith et al

Droughts are another important driver of change in the carbon balance of tropical forests. In oldgrowth forests, droughts affect tree species composition and lead to reductions in biomass (Phillips et al 2009, Esquivel-Muelbert et al 2019). We might reasonably expect secondary forests to be even more susceptible to drought stresses. Young trees may lack the deep roots known to support old-growth forests (Nepstad et al 1994, Broedel et al 2017); pioneer species that dominate secondary forests tend to have lower wood density, which is associated with higher drought-driven mortality (Phillips et al 2009, Poorter et al 2010, Uriarte et al 2016); and pioneers are also more vulnerable to stem cavitation (Markesteijn et al 2011). Recent work has shown that Amazon forests with more fast-growing tree species take greater hydraulic risks and consequently have higher drought-induced mortality rates than forests with more slow-growing species (Tavares et al 2023). On the other hand, if the shift in species composition seen in old-growth forests towards species associated with dry environments (Esquivel-Muelbert et al 2019) is also occurring in secondary forests, then the latter may become more resilient to drought. However, secondary forests are often found in regions with little surrounding old-growth forest cover (Silva Junior et al 2020) and compositional changes may be limited by seed bank availability.

A growing body of evidence suggests that Amazon secondary forests are indeed vulnerable to drought stress, but via a different mechanism to primary forests (Poorter *et al* 2016, Elias *et al* 2020, Heinrich *et al* 2021). Evidence from repeated forest inventories in the Brazilian Amazon shows that droughts reduce the carbon balance of secondary forests by reducing growth (Elias *et al* 2020). This differs from primary forests, where droughts impact the carbon balance through increased tree mortality (Phillips *et al* 2009). A study using a space-for-time analysis of secondary forests found carbon uptake rates were 44% lower in secondary forests experiencing very high water deficits (>-350 mm yr<sup>-1</sup>)



**Figure 4.** Burned areas of Amazon secondary forest in 2023 stratified by forest age. The solid black line indicates the accumulated area (righthand axis). The vertical dashed black line represents the age threshold at which more than 50% of burned secondary forests are represented. Colours indicate forests 1–5 years old (yellow), 6–19 years old (cyan) and >20 years old (purple), reflecting different categories of protection status in the Brazilian state of Pará (see section 7). Figure produced from the data of figure 2 superimposed on the burned areas mapped by Collection 3 of MapBiomas Fogo in 2023 (https://brasil.mapbiomas.org/en/colecoes-mapbiomas).

compared to those experiencing very low water deficits  $(<-180 \text{ mm yr}^{-1})$  (Heinrich et al 2021). A previous study assessing the impact of 2015 El Niño suggested Amazon secondary forests may be resilient to oneoff drought or fire events, reporting elevated regrowth rates in the aftermath of the drought. However, the authors cautioned that their focus on stem growth across a 2.5 year period could overlook longer-term carbon losses (Berenguer et al 2018). Meanwhile, repeated drought events are reported to cause canopy damage and reductions in photosynthetic capacity in Amazon secondary forests (Anderson et al 2018). With droughts increasing across all tropical continents (Dunn et al 2020), these findings are a cause for concern and highlight the importance of understanding the differences in primary and secondary forest responses.

All secondary forests grow on land that was once deforested, but in the Amazon repeated deforestation following regrowth is common, contributing to the predominance of young secondary forests (>50% <11 years old, figure 2). By 2014, clearance of secondary forest accounted for over 70% of Amazon deforestation (Wang *et al* 2020). Repeated deforestation has slightly smaller consequences for

Amazon secondary forest regrowth rates than fire and droughts, reducing regrowth by 20%–55% (Heinrich et al 2021). However, when repeated deforestation and fire are combined growth rates are reduced up to 80% and maximum carbon accumulation is suppressed (Heinrich et al 2021). In addition to affecting the carbon balance, these anthropogenic disturbances reduce seed availability, impact nutrient dynamics and lower biodiversity resulting in increasingly depleted and dysfunctional ecosystems (Uhl et al 1988, Hughes et al 2000, Faria et al 2023).

### 6. Representation of secondary tropical forests in climate models

Reliable predictions of future climate require accurate representation of secondary forest regrowth, forest resilience and forest-climate interactions in climate models. Regrowth is modelled using Dynamic Global Vegetation Models (DGVMs), which simulate vegetation dynamics within land-surface schemes and Earth system models. The Amazon has an estimated  $\sim\!16\,000$  Amazon tree species (Ter Steege et~al~2013), though only around 1% account for 50% of carbon uptake and storage (Fauset et~al~2015). By

necessity, DGVMs condense this vegetation diversity into a handful of plant functional types (PFTs)—broad groupings of plants that attempt to capture key differences in vegetation structure and function. For example, in the UK land-surface model JULES-TRIFFID, the number of tree PFTs was recently increased from five to nine (Harper *et al* 2016). At present PFTs do not distinguish between primary and secondary forests. A key knowledge gap is whether secondary forests are functionally different from primary forests, and if so, which key traits (e.g. wood density, bark thickness, evapotranspiration rate etc) need to be differentiated when describing primary and secondary forest PFTs.

DGVMs employ a variety of methodologies to simulate forest mortality, competition, and recruitment (Fisher et al 2018, Argles et al 2022) and regrowth dynamics are often represented in an oversimplified way (Hanbury-Brown et al 2022). Underestimating forest regrowth rates in JULES-TRIFFID has been shown to affect the resilience of tree PFTs to fires, with implications for modelled vegetation cover (Burton et al 2019). Furthermore, demographic-dependent disturbances such as drought mortality increasing with tree size (Gora and Esquivel-Muelbert 2021, Oliveira et al 2021), are often not fully implemented into landsurface models. Some models have recently incorporated plant hydraulics (Eller et al 2018), and the ORCHIDEE land surface model has been updated to explicitly include drought mortality (Yao et al 2022). Results show improved simulation of temporal trends and variability in the carbon cycle over Amazonia (Yao et al 2023).

To simulate secondary forest regrowth, models need to represent forest demography and variation in tree size through time as prerequisite. Increasingly, land-surface models are representing forest demography through use of cohort DGVMs (Haverd et al 2014, Fisher et al 2015, Argles et al 2020, Weng et al 2022). These models partition PFTs into size classes to capture the variation of forest size-structure, and/or rely on using patch age classes to represent spatial variation of forest. Cohort DGVMs have the potential to capture heterogeneous sub-grid processes for evaluation at the landscape scale to improve our understanding of forest ecosystem resilience. The cohort DGVM has been used to investigate important dynamics, such as forest-fire-fragmentation feedbacks (Longo et al 2019) and the impact of rooting depth on tree hydraulic water-stress and mortality (Chitra-Tarak et al 2021).

Although implementing forest demography in models is challenging, changes in forest cover have an important effect on climate through energy partitioning and land-atmosphere moisture fluxes (see section 5). Modelling studies have shown the major impact of Amazon deforestation scenarios on the regional water cycle, with reductions in

evapotranspiration impacting precipitation, runoff and river discharge (D'Almeida *et al* 2006, Costa and Pires 2010, Júnior *et al* 2015, Spracklen and Garcia-Carreras 2015, Guimberteau *et al* 2017, Baker and Spracklen 2022, Luo *et al* 2022). Errors in model representation of forest-climate interactions can result in unrealistic climate projections under future land-use-change scenarios (Baker *et al* 2021a, Robertson 2019). The CMIP6 climate models showed substantial variability in their ability to capture increases in temperature and decreases in precipitation caused by historical tropical deforestation, with some models simulating the opposite response to observations (Smith *et al* 2023c).

A modelling study examined the potential effects of Amazon secondary forest growth on regional climate and hydrology (Von Randow et al 2019). The authors simulated future discharge in the Tocantins river basin in Brazil under multiple climate and land-use-change scenarios. In their model, reductions in river discharge caused by climate change were exacerbated when secondary regrowth scenarios were included, due to the high evapotranspiration of secondary forests. It is important to note that the model simulations used in this study considered the direct effects of climate and land-use change on discharge but did not include feedbacks between forest change and rainfall production. For instance, deforestation (reforestation) might impact regional climate in the long term by reducing (increasing) precipitation recycling in the region, which may then feedback reducing (increasing) discharge (Lima et al 2014). An analysis of rain gauge data from Europe found realistic reforestation could increase summer rainfall by 7.6%, partially offsetting reductions due to climate change (Baker 2021, Meier et al 2021). These studies highlight that accurate representation of secondary forests in fully coupled Earth system models would improve climate predictions in areas expected to see large future changes in forest cover, such as the Amazon (Marengo et al 2018).

# 7. Applying scientific knowledge to policy for conserving secondary forests

Large-scale restoration of tropical secondary forests has the potential to deliver high ecological benefits at low economic cost (Crouzeilles *et al* 2017), but currently this potential remains largely unrealized. Despite favourable ecological conditions for natural regeneration across much of the Amazon, the absence of robust regional governance to protect secondary forests undermines their permanence within the landscape (Vieira *et al* 2014). In this section we discuss two case studies from the Brazilian state of Pará in the eastern Amazon (figure 1), where evidence from scientific research has directly influenced landuse policies relating to secondary forest conservation. We use these jurisdictional-level cases to explore the

role of science in shaping policy and discuss lessons that can be applied to scale efforts to the regional level.

# 7.1. Case study 1: clarifying legal definitions of secondary forests for conservation

In 2014, the Pará State Environment Secretariat (Secretaria de Estado de Meio Ambiente do Pará, SEMAS) identified a significant public issue: the lack of clarity in state legislation regarding the legal status of secondary forests. This ambiguity was causing conflicts between landowners, the federal monitoring agency, and SEMAS. According to Pará's land zoning regulations, 'late-stage' secondary forests were prohibited from being clearcut. However, there was no clear definition of what constituted 'late-stage', leaving landowners, decision-makers, and enforcement agencies uncertain about how to apply the rule. To address this issue, the Green Municipality Programme invited a scientific working group coordinated by Embrapa (the Brazilian Agricultural Research Corporation) and the Sustainable Amazon Network (RAS), an international consortium of researchers focused on improving the sustainability of tropical land use and fostering dialogue between scientists and policymakers (Gardner et al 2013). The team compiled ecological data across Pará by bringing together local institutions and researchers working in Brazil and internationally.

The working group developed ecological criteria to define 'Early', 'Intermediate' and 'Late' stage forest regeneration, allowing the state to licence the re-use of forests with the lowest ecological value and protect the most ecologically important forests. Specifically, the working group compiled evidence from a range of research to identify when secondary forests begin to hold much higher levels of biodiversity. The final analysis suggested that: all forests above 20 years old should be protected; forests less than 5 years old could be cleared; and forests between 5 and 20 years old should be protected if their basal area sits above a certain threshold (between 5 and 10  $\text{m}^2$   $\text{ha}^{-1}$ ). Forests in these three categories of protection status are indicated in figures 1, 2 and 4. The precise basal area threshold used to decide whether 5-20 year-old forests should be protected is linked to the level of forest cover in the municipality, accounting for the slower growth rates in the most deforested regions.

This analysis formed the basis of a new law that was published in three revisions; in the final revision (Instrução Normativa N°08, dated 28 October 2015) the working group clarified the measurement criteria for field-based assessments of carbon stocks, refined the thresholds between basal area and forest cover at the municipality level, and added clauses to ensure that the legislation guards against perverse outcomes, such as secondary forests being deliberately degraded prior to carbon assessments. As a result of this legislation, secondary forests in Pará older than 20 years

must be conserved (Vieira et al 2014). If Pará's legislation were applied to all secondary vegetation in the Brazilian Amazon, around a quarter would be protected at the present (figure 1). The licensing detailed by this law allows farmers to return low-value secondary forests to agricultural use whilst ensuring those with the highest carbon stocks and highest biodiversity values are protected (Vieira et al 2014).

### 7.2. Case study 2: the importance of accurate carbon assessments for climate change mitigation

In 2020, members of RAS were invited by SEMAS to provide scientific guidance about the carbon accumulation rates of secondary forests in the eastern Amazon to help formulate the 'State Plan for Amazonia Now' (Plano Estadual Amazonia Agora; PEAA—State Decree no. 941 from the 3rd of August 2020), which aims to achieve carbon neutrality in Pará by 2035. Under the PEAA, the state is planning to reforest over 500 000 km<sup>2</sup> of land, representing almost half of Brazil's NDC. The researchers provided up-to-date and regionally appropriate assessments of the carbon accumulation rates of secondary forests (e.g. Elias et al 2020, Lennox et al 2018). These were substantially lower than the rates that were initially proposed, which were based on data from other regions of the Amazon. The change therefore increased the extent of secondary forest required to reach carbon neutrality. Forest restoration plans from PEAA are being implemented through the Pará Forest Restoration Plan, launched in 2023, following a comprehensive participatory process in which local institutions and stakeholders have been actively involved.

### 7.3. Lessons for policymaking in the wider Amazon context

These two case studies underscore the importance of creating institutional spaces for sharing knowledge and policy solutions, both within individual Amazonian countries and across the region (Vieira et al 2024). Ideally, these spaces should be fostered not merely through the translation of scientific findings but through processes of co-construction, participation, and active engagement (Toomey et al 2017). Communication across the science-policy interface is a fundamental challenge, and improving it is key to developing evidence-based decision making and avoiding the potential disregard of available knowledge by policymakers (Bertuol-Garcia et al 2018). In the cases above, successful engagement required agility on the part of the researchers; policymakers identified an explicit and time-sensitive need for scientific guidance and local researchers were willing to engage at short notice, work collaboratively, and meet those needs. By highlighting these examples, we aim to inspire more researchers to proactively collaborate with decision-makers, contributing to and strengthening evidence-based policymaking.

Scaling to the rest of the Amazon will require resolving pervasive disparities in knowledge production that persist across the region (e.g. Carvalho and Resende et al 2023). For example, a metanalysis of 362 articles (da Silva et al 2023b) found that Brazil, particularly the state of Pará, dominated the number of restoration studies (292 articles), while countries like Peru and Colombia lagged behind (37 and 15 articles, respectively) despite having significant areas of secondary forest recovery (Smith et al 2021). Venezuela, French Guiana, Guyana, and Suriname had only 11 restoration articles between them. The success of Brazil's PRODES program, which monitors land-use changes via satellite (see section 2), highlights the importance of robust monitoring systems in fostering knowledge production and enabling effective policy measures. PRODES has supported a range of conservation initiatives, including the soy moratorium and Payment for Ecosystem Services programs (e.g. Rudorff et al 2011, Nepstad et al 2014, Wong et al 2022). There have been efforts to improve forest monitoring capacity outside Brazil. From 2010 to 2017, INPE delivered training in satellite-based forest monitoring techniques to nearly 700 participants from 60 tropical countries through the Capacitree Project (INPE 2021). Establishing a basin-wide monitoring system under the Amazon Cooperation Treaty Organization (ACTO) could greatly enhance integrated research and improve conservation across the Amazon.

### 8. Outlook

Amazon secondary forest research has advanced rapidly in the past decade and this trend promises to continue. We have summarised the climatic importance of secondary forests at global through to local scales, through feedbacks on the carbon and water cycles. However, key knowledge gaps remain. There is a pressing need to provide a consistent validation of secondary forest maps using ground and remote-sensing data, to identify areas of agreement and understand why discrepancies arise (Nunes et al 2020, Silva-Junior et al 2020). Reliable forest monitoring is essential for conservation and a prerequisite for Amazon secondary forests to contribute to climate change mitigation efforts (Heinrich et al 2021). Careful consideration of secondary forest definitions, robust systems to ensure permanence, and transparent methods for reporting land carbon emissions are also required (Wiltshire et al 2022, Heinrich et al 2023b). Research on Amazon secondary forests outside of Brazil remains scarce (da Silva et al 2023b), in part due to insufficient secondary vegetation mapping. Establishing a robust forest monitoring framework under ACTO would improve our understanding of secondary forest dynamics across the whole Amazon and support policies for their conservation.

Further research is also needed to better understand local-to-regional forest-climate interactions and how they change as forests age. Current approaches that predict the impact of tropical forest restoration on local temperature based on relationships with intact forest (Alibakhshi et al 2024), or through evaluating relatively short time series (Su et al 2023, Zhang et al 2024) may overlook the distinct nature of Amazon secondary forest-climate interactions (e.g. Von Randow et al 2020) and their unknown responses to succession. Future work should address these crucial unknowns, focussing on how secondary forests modulate local and regional temperatures in space and time, their influence on the water cycle, and understanding secondary forest resilience to long-term climate change.

A new network of permanent monitoring plots in Amazon secondary forests is being established as part of Amazon-SOS: a Safe Operating Space for Amazonian Forests initiative, which will provide valuable new insights about forest regrowth and resilience in a changing environment. Results from Amazon-SOS will help to improve climate model representation of secondary forests, including the potential to describe a new secondary tropical forest PFT. This work is essential to improve predictions of how large-scale tropical forest restoration will influence regional temperature projections. Additional ground observations, including eddy covariance flux tower measurements in different Amazon regions and in forests at different stages of regrowth, and measurements of belowground carbon would further enhance our knowledge of secondary forest functioning and provide essential validation for remotesensing studies.

The rapid pace of anthropogenic changes in the Amazon threatens the future viability of the ecosystem and urgent action is needed to protect what forest remains (Albert et al 2023, Lapola et al 2023, Flores et al 2024). Since 1985, carbon accumulation in Amazon secondary forests has offset less than 10% of the emissions from destruction of primary old-growth forests, highlighting that strengthening primary forest protection must be a priority to stabilise the basin carbon balance (Smith et al 2020). Furthermore, climate models predict the Amazon dry season will become hotter and drier with increased risk of fires (Marengo et al 2018), threatening secondary forest growth rates. Better integration of forest conservation and restoration strategies with societal needs could deliver enhanced social and ecological outcomes (Chazdon 2019). Local Amazon populations require access to livelihoods that do not rely on deforestation, for example, by a shift towards sociobioeconomies that support sustainable forest use and restoration (Garrett et al 2024). Revolutionising agricultural practices to improve food production while enhancing environmental benefits would optimise the use of already-deforested landscapes (Maeda

et al 2023). In conclusion, protecting remaining oldgrowth forests and increasing the area of secondary forests will enhance biodiversity, improve ecosystem resilience and help ensure the persistence of the Amazon ecosystem for decades and centuries to come.

### Acknowledgments

This paper originated following a workshop on Amazon Secondary Forests held in São José dos Campos in Brazil 2022. The workshop was funded by the European Research Council under the European Union's Horizon 2020 research and innovation program (Grant Ref. 771492). The authors sincerely thank Ben Silver for processing MapBiomas version 9 and producing figure 1. The authors also gratefully acknowledge the contributions of Robin Hayward, who designed and produced the schematic shown in figure 3, following a suggestion from a reviewer. The work was supported by a UK Research and Innovation Future Leaders Fellowship (awarded to JCAB, Grant Ref: MR/X034097/1) and the Newton Fund, through the Met Office Climate Science for Service Partnership Brazil. At the time of the workshop, VH was supported by the RECCAP2 project which is part of the ESA Climate Change Initiative (Contract No. 4000123002/18/I-NB) and the H2020 European Institute of Innovation and Technology (4C; Grant No. 821003). VH was also supported by the CGIAR MITIGATE+ project, the WRI Land and Carbon Lab, and the Open EarthMonitor Project funded by the European Union (Grant Agreement No.101059548). CHLS-J was supported by funding from the National Council for Scientific and Technological Development (CNPq) under the project 'YBYRÁ-BR: Space-Time Quantification of CO2 Emissions and Removals by Brazilian Forests' (CNPq Process 401741/2023-0). FE was supported by the Serrapilheira Institute fellowship/FAPESPA (grant number – R-2401–46863).

### **ORCID** iDs

Jessica C A Baker https://orcid.org/0000-0002-3720-4758

Marcos Adami https://orcid.org/0000-0003-4247-4477

Celso H L Silva-Junior https://orcid.org/0000-0002-1052-5551

Luis W R Sadeck https://orcid.org/0000-0002-2337-8634

Callum Smith https://orcid.org/0000-0002-2705-8398

Jos Barlow https://orcid.org/0000-0003-4992-

Liana O Anderson 6 https://orcid.org/0000-0001-9545-5136 Celso Von Randow https://orcid.org/0000-0003-1045-4316

Fernando Elias https://orcid.org/0000-0001-9190-

Dominick V Spracklen https://orcid.org/0000-0002-7551-4597

### References

Albert J S *et al* 2023 Human impacts outpace natural processes in the Amazon *Science* 379 eabo5003

Alibakhshi S, Cook-Patton S C, Davin E, Maeda E E, Araújo M B, Heinlein D, Heiskanen J, Pellikka P and Crowther T W 2024 Natural forest regeneration is projected to reduce local temperatures *Commun. Earth Environ.* 5 577

Alkama R and Cescatti A 2016 Biophysical climate impacts of recent changes in global forest cover *Science* 351 600–4

Almeida C A D, Coutinho A C, Esquerdo J C D M, Adami M, Venturieri A, Diniz C G, Dessay N, Durieux L and Gomes A R 2016a High spatial resolution land use and land cover mapping of the Brazilian Legal Amazon in 2008 using Landsat-5/TM and MODIS data *Acta Amaz.* 46 291–302

Almeida C A 2009. Estimativa da área e do tempo de permanência da vegetação secundária na amazônia legal por meio de imagens LANDSAT/TM 2008
IBI:8JMKD3MGP8W/346KGA2. (INPE-15651-TDI/1429)
(Dissertação (Mestrado em Sensoriamento Remoto)—Instituto Nacional de Pesquisas Espaciais) p 129 (available at: http://urlib.net/ibi/8JMKD3MGP8W/346KGA2)

Almeida C A, Maurano L E P, De Morisson Valeriano D, Camara G, Vinhas L, Gomes A R, Monteiro A M V, De Almeida Souza A A, Rennó C D and Silva D E 2021 Methodology for forest monitoring used in PRODES and DETER projects CEP 12 1–29

Almeida D R A D, Nelson B W, Schietti J, Gorgens E B, Resende A F, Stark S C and Valbuena R 2016b Contrasting fire damage and fire susceptibility between seasonally flooded forest and upland forest in the Central Amazon using portable profiling LiDAR *Remote Sens. Environ*. 184 153–60

Alves D, Soares J V, Amaral S, Mello E, Almeida S, Da Silva O F and Silveira A 1997 Biomass of primary and secondary vegetation in Rondônia, Western Brazilian Amazon Glob. Change Biol. 3 451–61

Anderson L O, Neto G R, Cunha A P, Fonseca M G, Moura Y M D, Dalagnol R, Wagner F H and Aragão L E O E C D 2018

Vulnerability of Amazonian forests to repeated droughts

Phil. Trans. R. Soc. B 373 20170411

Aragão L E O C *et al* 2018 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions *Nat. Commun.* 9 536

Aragão L E O C, Poulter B, Barlow J B, Anderson L O, Malhi Y, Saatchi S, Phillips O L and Gloor M 2014 Environmental change and the carbon balance of Amazonian forests *Biol. Rev.* **89** 913–31

Araújo M M, Tucker J M, Vasconcelos S S, Zarin D J, Oliveira W, Sampaio P D, Rangel-Vasconcelos L G, De Assis Oliveira F, De Fatima Rodrigues Coelho R and Aragão D V 2005 Successional pattern and process in secondary forests of different ages in the eastern amazon *Cienc. Florest.* 15 343–57

Argles A P K, Moore J R, Huntingford C, Wiltshire A J, Harper A B, Jones C D and Cox P M 2020 Robust ecosystem demography (RED version 1.0): a parsimonious approach to modelling vegetation dynamics in Earth system models *Geosci. Model Dev.* 13 4067–89

Argles A P, Moore J R and Cox P M 2022 Dynamic global vegetation models: searching for the balance between demographic process representation and computational tractability *PLoS Clim.* 1 e0000068

- Baker J C A 2021 Planting trees to combat drought Nat. Geosci. 14 458–9
- Baker J C A, Garcia-Carreras L, Buermann W, Castilho De Souza D, Marsham J H, Kubota P Y, Gloor M, Coelho C A S and Spracklen D V 2021a Robust Amazon precipitation projections in climate models that capture realistic land–atmosphere interactions *Environ. Res. Lett.* **16** 074002
- Baker J C A, Garcia-Carreras L, Gloor M, Marsham J H, Buermann W, Da Rocha H R, Nobre A D, De Araujo A C and Spracklen D V 2021b Evapotranspiration in the Amazon: spatial patterns, seasonality, and recent trends in observations, reanalysis, and climate models *Hydrol. Earth* Syst. Sci. 25 2279–300
- Baker J C A and Spracklen D V 2019 Climate benefits of intact Amazon forests and the biophysical consequences of disturbance *Front. For. Glob. Change* **2** 47
- Baker J C A and Spracklen D V 2022 Divergent representation of precipitation recycling in the Amazon and the Congo in CMIP6 models Geophys. Res. Lett. 49 e2021GL095136
- Barros M N R, Pinheiro A F, Morais V M C, Santos L B, Dos Santos Coelho A, Sadeck L W R, Adami M, Gomes A R and Da Silva Narvaes I 2018 Validation of TerraClass mapping for the Municipality of Paragominas state of Pará *Int. J. Adv. Eng. Res. Sci.* 5 264215
- Bastable H G, Shuttleworth W J, Dallarosa R L G, Fisch G and Nobre C A 1993 Observations of climate, albedo, and surface radiation over cleared and undisturbed amazonian forest *Int. J. Climatol.* 13 783–96
- Bauters M et al 2021 Soil nutrient depletion and tree functional composition shift following repeated clearing in secondary forests of the Congo Basin *Ecosystems* 24 1422–35
- Begliomini F N and Brancalion P H S 2024 Are state-of-the-art LULC maps able to track ecological restoration efforts in Brazilian Atlantic Forest? *IGARSS 2024–2024 IEEE Int.* Geoscience and Remote Sensing Symp. (7–12 July 2024) pp 4748–52
- Bentos T V, Nascimento H E M, Vizcarra M D A and Williamson G B 2017 Effects of lightgaps and topography on Amazon secondary forest: changes in species richness and community composition For. Ecol. Manage. 396 124–31
- Berenguer E, Ferreira J, Gardner T A, Aragão L E O C, De Camargo P B, Cerri C E, Durigan M, Oliveira Junior R C D, Vieira I C G and Barlow J 2014 A large-scale field assessment of carbon stocks in human-modified tropical forests *Glob. Change Biol.* **20** 3713–26
- Berenguer E, Malhi Y, Brando P, Cardoso Nunes Cordeiro A, Ferreira J, França F, Chesini Rossi L, Maria Moraes De Seixas M and Barlow J 2018 Tree growth and stem carbon accumulation in human-modified Amazonian forests following drought and fire *Phil. Trans. R. Soc.* B 373 20170308
- Bertuol-Garcia D, Morsello C, N El-Hani and Pardini R 2018 A conceptual framework for understanding the perspectives on the causes of the science–practice gap in ecology and conservation *Biol. Rev.* **93** 1032–55
- Besnard S et al 2024 Global Age Mapping Integration (GAMI) (GFZ Data Services)
- Bispo P D C et al 2019 Mapping forest successional stages in the Brazilian Amazon using forest heights derived from TanDEM-X SAR interferometry Remote Sens. Environ. 232 111194
- Bonan G B 2008 Forests and climate change: forcings, feedbacks, and the climate benefits of forests *Science* **320** 1444–9
- Bourgoin C *et al* 2024 Mapping global forest cover of the year 2020 to support the EU regulation on deforestation-free supply chains
- Bright R M, Davin E, O'Halloran T, Pongratz J, Zhao K and Cescatti A 2017 Local temperature response to land cover and management change driven by non-radiative processes *Nat. Clim. Change* 7 296–302
- Broedel E, Tomasella J, Cândido L A and Von Randow C 2017 Deep soil water dynamics in an undisturbed primary forest

- in central Amazonia: differences between normal years and the 2005 drought *Hydrol. Process.* **31** 1749–59
- Brown F, Sitch S, Folberth G, Cheesman A, Mercado L and Barningham S Fire activity and drought increases ozone-plant damage to the Amazon rainforest submitted (https://doi.org/10.21203/rs.3.rs-4802855/v1)
- Burton C, Betts R, Cardoso M, Feldpausch T R, Harper A, Jones C D, Kelley D I, Robertson E and Wiltshire A 2019 Representation of fire, land-use change and vegetation dynamics in the Joint UK Land environment simulator vn4.9 (JULES) *Geosci. Model Dev.* 12 179–93
- Butt E W, Baker J C A, Bezerra F G S, Von Randow C, Aguiar A P D and Spracklen D V 2023 Amazon deforestation causes strong regional warming *Proc. Natl Acad. Sci.* **120** e2309123120
- Butt E W, Conibear L, Smith C, Baker J C A, Rigby R, Knote C and Spracklen D V 2022 Achieving Brazil's deforestation target will reduce fire and deliver air quality and public health benefits *Earth's Future* 10 e2022EF003048
- Campos M S, Adami M and Araújo A C D 2021 Analysis of surface albedo in oil palm and differents land use and land cover in The Eastern Amazon *Rev. Bras. Meteorol.* **36** 15–21
- Carvalho R L et al 2023 Pervasive gaps in Amazonian ecological research Curr. Biol. 33 3495–504.e4
- Cassol H L G 2018 Aplicação dos dados polarimétricos ALOS/PALSAR-2 para modelagem de biomassa em florestas secundárias da Amazônia considerando o histórico de uso Thesis for PhD in Remote Sensing (National Institute for Space Research (INPE))
- CBD (Convention on Biological Diversity) 2022 Decision Adopted by the Conference of the Parties to the Convention on Biological Diversity 15/4 (Kunming-Montreal Global Biodiversity Framework)
- Chazdon R L 2014 Second Growth (University of Chicago Press)
  Chazdon R L et al 2016 Carbon sequestration potential of
  second-growth forest regeneration in the Latin American
  tropics Sci. Adv. 2 e1501639
- Chazdon R L 2019 Towards more effective integration of tropical forest restoration and conservation *Biotropica* 51 463–72
- Cheesman A W *et al* 2024 Reduced productivity and carbon drawdown of tropical forests from ground-level ozone exposure *Nat. Geosci.* 17 1003–7
- Chen N, Tsendbazar N-E, Requena Suarez D, Silva-Junior C H L, Verbesselt J and Herold M 2024 Revealing the spatial variation in biomass uptake rates of Brazil's secondary forests *ISPRS J. Photogramm. Remote Sens.* **208** 233–44
- Chen N, Tsendbazar N-E, Requena Suarez D, Verbesselt J, Herold M, Pettorelli N and Abdi A 2023 Characterizing aboveground biomass and tree cover of regrowing forests in Brazil using multi-source remote sensing data *Remote Sens*. *Ecol. Conserv.* **9** 553–67
- Chen X, Huang X, Jiao C, Flanner M G, Raeker T and Palen B 2017 Running climate model on a commercial cloud computing environment: a case study using community earth system model (CESM) on Amazon AWS *Comput. Geosci.* 98 21–25
- Chitra-Tarak R *et al* 2021 Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest *New Phytol.* **231** 1798–813
- Cohn A S, Bhattarai N, Campolo J, Crompton O, Dralle D, Duncan J and Thompson S 2019 Forest loss in Brazil increases maximum temperatures within 50 km *Environ*. *Res. Lett.* 14 084047
- Cook-Patton S C *et al* 2020 Mapping carbon accumulation potential from global natural forest regrowth *Nature* 585 545–50
- Cook-Patton S C *et al* 2021 Protect, manage and then restore lands for climate mitigation *Nat. Clim. Change* 11 1027–34
- Cooley S S *et al* 2024 Combining spaceborne lidar from the Global Ecosystem Dynamics Investigation with local knowledge for monitoring fragmented tropical landscapes: a case study in the forest–agriculture interface of Ucayali, Peru *Ecol. Evol.* **14** e70116

- Costa M H and Pires G F 2010 Effects of Amazon and Central Brazil deforestation scenarios on the duration of the dry season in the arc of deforestation *Int. J. Climatol.* 30 1970–9
- Crouzeilles R, Ferreira M S, Chazdon R L, Lindenmayer D B, Sansevero J B B, Monteiro L, Iribarrem A, Latawiec A E and Strassburg B B N 2017 Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests *Sci. Adv.* 3 e1701345
- Curtis P G, Slay C M, Harris N L, Tyukavina A and Hansen M C 2018 Classifying drivers of global forest loss *Science* 361 1108–11
- D'Almeida C, Vörösmarty C J, Hurtt G C, Marengo J A, Dingman S L and Keim B D 2007 The effects of deforestation on the hydrological cycle in Amazonia: a review on scale and resolution *Int. J. Climatol.* **27** 633–47
- D'Almeida C, Vörösmarty C J, Marengo J A, Hurtt G C, Dingman S L and Keim B D 2006 A water balance model to study the hydrological response to different scenarios of deforestation in Amazonia *J. Hydrol.* 331 125–36
- D'Oliveira M V N, Alvarado E C, Santos J C and Carvalho J A 2011 Forest natural regeneration and biomass production after slash and burn in a seasonally dry forest in the Southern Brazilian Amazon For. Ecol. Manage. 261 1490–8
- Da Rocha H R *et al* 2009 Patterns of water and heat flux across a biome gradient from tropical forest to savanna in Brazil *J. Geophys. Res. Biosci.* 114 1–8
- Da Silva C M, Elias F, Do Nascimento R O and Ferreira J 2023a The potential for forest landscape restoration in the Amazon: state of the art of restoration strategies *Restorat*. *Ecol.* **31** e13955
- Da Silva G M, Adami M, Galbraith D, Nascimento R G M, Wang Y, Shimabukuro Y E and Emmert F 2023b Spatial distribution of secondary forests by age group and biomass accumulation in the Brazilian Amazon *Forests* 14 924
- Davidson E A, Reis de Carvalho C J, Vieira I C, Figueiredo R D, Moutinho P, Yoko Ishida F, Primo dos Santos M T, Benito Guerrero J, Kalif K, Tuma Sabá R 2004 Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest *Ecol. Appl.* 14 150–63
- Dunn R J H *et al* 2020 Development of an updated global land in situ-based data set of temperature and precipitation extremes: hadEX3 *J. Geophys. Res. Atmos.* 125 e2019ID032263
- Edwards D P, Cerullo G R, Chomba S, Worthington T A, Balmford A P, Chazdon R L and Harrison R D 2021 Upscaling tropical restoration to deliver environmental benefits and socially equitable outcomes *Curr. Biol.* 31 R1326–41
- Elias F *et al* 2020 Assessing the growth and climate sensitivity of secondary forests in highly deforested Amazonian landscapes *Ecology* **101** e02954
- Elias F et~al 2020 Assessing the growth and climate sensitivity of secondary forests in highly deforested Amazonian landscapes Ecology~101~e02954
- Eller C B *et al* 2018 Modelling tropical forest responses to drought and El Niño with a stomatal optimization model based on xylem hydraulics *Phil. Trans. R. Soc.* B 373 20170315
- Esquivel-Muelbert A *et al* 2019 Compositional response of Amazon forests to climate change *Glob. Change Biol.* **25** 39–56
- Faria D *et al* 2023 The breakdown of ecosystem functionality driven by deforestation in a global biodiversity hotspot *Biol. Conserv.* **283** 110126
- Farneda F Z, Rocha R, López-Baucells A, Sampaio E M, Palmeirim J M, Bobrowiec P E D, Grelle C E V and Meyer C F J 2018 Functional recovery of Amazonian bat assemblages following secondary forest succession *Biol. Conserv.* 218 192–9
- Fauset S et al 2015 Hyperdominance in Amazonian forest carbon cycling Nat. Commun. 6 6857

- Fawcett D *et al* 2023 Declining Amazon biomass due to deforestation and subsequent degradation losses exceeding gains *Glob. Change Biol.* 29 1106–18
- Fearnside P M and Guimarães W M 1996 Carbon uptake by secondary forests in Brazilian Amazonia *For. Ecol. Manage.* **80** 35–46
- Federative Republic Of Brazil 2016 Federative Republic of Brazil intended nationally determined contribution towards achieving the objective of the United Nations framework convention on climate change (available at: https://www4.unfccc.int/sites/submissions/INDC/Published%20
  Documents/Brazil/1/BRAZIL%20iNDC%20english%20
  FINAL.pdf) (Accessed 1 August 2022)
- Federative Republic Of Brazil 2022 Federative Republic of Brazil
  Paris Agreement Nationally Determined Contribution
  (NDC) Second Update (available at: https://unfccc.int/
  sites/default/files/NDC/2022-06/Updated%20-%20First%
  20NDC%20-%20%20FINAL%20-%20PDF.pdf) (Accessed 1
  August 2022)
- Federative Republic Of Brazil 2023 Federative Republic of Brazil Nationally Determined Contribution (NDC) to the Paris Agreement under the UNFCCC 2023 Adjustment (available at: https://unfccc.int/sites/default/files/NDC/2023-11/Brazil%20First%20NDC%202023%20adjustment.pdf) (Accessed 13 September 2024)
- Feldpausch T R, Prates-Clark C D C, Fernandes E C M and Riha S J 2007 Secondary forest growth deviation from chronosequence predictions in central Amazonia *Glob. Change Biol.* 13 967–79
- Feldpausch T R, Riha S J, Fernandes E C M and Wandelli E V 2005 Development of forest structure and leaf area in secondary forests regenerating on abandoned pastures in Central Amazônia Earth Interact. 9 1–22
- Feldpausch T R, Rondon M A, Fernandes E C M, Riha S J and Wandelli E 2004 Carbon and nutrient accumulation in secondary forests regenerating on pastures in Central Amazonia Ecol. Appl. 14 164–76
- Ferreira K R *et al* 2020 Earth observation data cubes for Brazil: requirements, methodology and products *Remote Sens*. 12 4033
- Fisher R A *et al* 2015 Taking off the training wheels: the properties of a dynamic vegetation model without climate envelopes, CLM4.5(ED) *Geosci. Model Dev.* 8 3593–619
- Fisher R A *et al* 2018 Vegetation demographics in Earth system models: a review of progress and priorities *Glob. Change Biol.* 24 35–54
- Flores B M *et al* 2024 Critical transitions in the Amazon forest system *Nature* **626** 555–64
- Garcia-Carreras L and Parker D J 2011 How does local tropical deforestation affect rainfall? *Geophys. Res. Lett.* 38 1–6
- Gardner T A *et al* 2013 A social and ecological assessment of tropical land uses at multiple scales: the sustainable Amazon network *Phil. Trans. R. Soc.* B **368** 20120166
- Garrett R *et al* 2024 Transformative changes are needed to support socio-bioeconomies for people and ecosystems in the Amazon *Nat. Ecol. Evol.* 8 1815–25
- Gash J H C and Nobre C A 1997 Climatic effects of amazonian deforestation: some results from ABRACOS Bull. Am. Meteorol. Soc. 78 823–30
- Gehring C, Denich M and Vlek P L G 2005 Resilience of secondary forest regrowth after slash-and-burn agriculture in central Amazonia J. Trop. Ecol. 21 519–27
- Gibson L et al 2011 Primary forests are irreplaceable for sustaining tropical biodiversity Nature 478 378–81
- Gora E M and Esquivel-Muelbert A 2021 Implications of size-dependent tree mortality for tropical forest carbon dynamics *Nat. Plants* 7 384–91
- Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D and Moore R 2017 Google Earth Engine: planetary-scale geospatial analysis for everyone *Remote Sens. Environ*. 202 18–27

- Guimberteau M *et al* 2017 Impacts of future deforestation and climate change on the hydrology of the Amazon Basin: a multi-model analysis with a new set of land-cover change scenarios *Hydrol. Earth Syst. Sci.* 21 1455–75
- Hanbury-Brown A R, Ward R E and Kueppers L M 2022 Forest regeneration within Earth system models: current process representations and ways forward New Phytol. 235 20–40
- Harper A B, Cox P M, Friedlingstein P, Wiltshire A J, Jones C D, Sitch S, Mercado L M, Groenendijk M, Robertson E and Kattge J 2016 Improved representation of plant functional types and physiology in the Joint UK land environment simulator (JULES v4. 2) using plant trait information Geosci. Model. Dev. 9 2415–40
- Harris N L et al 2021 Global maps of twenty-first century forest carbon fluxes Nat. Clim. Change 11 234–40
- Haverd V, Smith B, Nieradzik L P and Briggs P R 2014 A stand-alone tree demography and landscape structure module for Earth system models: integration with inventory data from temperate and boreal forests *Biogeosciences* 11 4039–55
- Heinrich V H A *et al* 2021 Large carbon sink potential of secondary forests in the Brazilian Amazon to mitigate climate change *Nat. Commun.* 12 1785
- Heinrich V H A *et al* 2023a The carbon sink of secondary and degraded humid tropical forests *Nature* **615** 436–42
- Heinrich V *et al* 2023b Mind the gap: reconciling tropical forest carbon flux estimates from earth observation and national reporting requires transparency *Carbon Balance Manage*. 18 22
- Houghton R A, Skole D L, Nobre C A, Hackler J L, Lawrence K T and Chomentowski W H 2000 Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon *Nature*  $403\ 301-4$
- Hughes R F, Kauffman J B and Cummings D L 2000 Fire in the Brazilian Amazon Oecologia 124 574–88
- INPE 2021 Institutional Courses (available at: https://www.gov.br/ inpe/pt-br/area-conhecimento/unidade-amazonia/ capacitree/cursos-institucionais) (Accessed 16 December 2024)
- INPE 2024 Deforestation data provided by TerraBrasilis data portal: Incrementos ds desmataento Amazônia Legal Estados (incluir agregado) [Online] (available at: https://terrabrasilis.dpi.inpe.br/app/dashboard/deforestation/biomes/legal\_amazon/increments) (Accessed 1 June 2024)
- Jakovac C C, Peña-Claros M, Kuyper T W, Bongers F and Gibson D 2015 Loss of secondary-forest resilience by land-use intensification in the Amazon J. Ecol. 103 67–77
- Jakovac C et al 2024 Meta-analysis of carbon stocks and biodiversity outcomes across Brazilian restored biomes Sci. Total Environ. 906 167558
- Júnior J L S, Tomasella J and Rodriguez D A 2015 Impacts of future climatic and land cover changes on the hydrological regime of the Madeira River basin Clim. Change 129 117–29
- Kalamandeen M et al 2020 Limited biomass recovery from gold mining in Amazonian forests J. Appl. Ecol. 57 1730–40
- Kalamandeen M, Gloor E, Mitchard E, Quincey D, Ziv G, Spracklen D, Spracklen B, Adami M, Aragão L E O C and Galbraith D 2018 Pervasive rise of small-scale deforestation in Amazonia Sci. Rep. 8 1600
- Khanna J, Medvigy D, Fueglistaler S and Walko R 2017 Regional dry-season climate changes due to three decades of Amazonian deforestation *Nat. Clim. Change* 7 200
- Kunert N, Aparecido L M T, Higuchi N, Santos J D and Trumbore S 2015 Higher tree transpiration due to road-associated edge effects in a tropical moist lowland forest Agric. For. Meteorol. 213 183–92
- Lapola D M et al 2023 The drivers and impacts of Amazon forest degradation *Science* 379 eabp8622
- Lawrence D and Vandecar K 2015 Effects of tropical deforestation on climate and agriculture Nat. Clim. Change 5 27–36
- Leite M F A et al 2023 Microbiome resilience of Amazonian forests: agroforest divergence to bacteria and secondary

- forest succession convergence to fungi *Glob. Change Biol.* **29** 1314–27
- Lennox G D, Gardner T A, Thomson J R, Ferreira J, Berenguer E, Lees A C, Mac Nally R, Aragão L E, Ferraz S F and Louzada J 2018 Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests Glob. Change Biol. 24 5680–94
- Li S, Rifai S, Anderson L O and Sparrow S 2021b Identifying local-scale meteorological conditions favorable to large fires in Brazil *Clim. Resil. Sustain.* 1 e11
- Li S, Sparrow S N, Otto F E L, Rifai S W, Oliveras I, Krikken F, Anderson L O, Malhi Y and Wallom D 2021a Anthropogenic climate change contribution to wildfire-prone weather conditions in the Cerrado and Arc of deforestation *Environ*. *Res. Lett.* 16 094051
- Lima L S, Coe M T, Soares Filho B S, Cuadra S V, Dias L C P, Costa M H, Lima L S and Rodrigues H O 2014 Feedbacks between deforestation, climate, and hydrology in the Southwestern Amazon: implications for the provision of ecosystem services *Landscape Ecol.* **29** 261–74
- Locatelli B, Catterall C P, Imbach P, Kumar C, Lasco R, Marín-Spiotta E, Mercer B, Powers J S, Schwartz N and Uriarte M 2015 Tropical reforestation and climate change: beyond carbon *Restorat. Ecol.* 23 337–43
- Longo M *et al* 2019 The biophysics, ecology, and biogeochemistry of functionally diverse, vertically and horizontally heterogeneous ecosystems: the ecosystem demography model, version 2.2—part 1: model description *Geosci. Model Dev.* 12 4309–46
- Luers A L 2021 Planetary intelligence for sustainability in the digital age: five priorities *One Earth* 4 772–5
- Luo X, Ge J, Guo W, Fan L, Chen C, Liu Y and Yang L 2022 The biophysical impacts of deforestation on precipitation: results from the CMIP6 model intercomparison *J. Clim.* 35 3293–311
- Maeda E E, Aragão L E O C, Baker J C A, Balbino L C, De Moura Y M, Nobre A D, Nunes M H, Silva Junior C H L and Dos Reis J C 2023 Land use still matters after deforestation Commun. Earth Environ. 4 29
- Magnuszewski P, Ostasiewicz K, Chazdon R, Salk C, Pajak M, Sendzimir J, Andersson K and Adam P 2015 Resilience and alternative stable states of tropical forest landscapes under shifting cultivation regimes *PLoS One* **10** e0137497
- Mapbiomas 2024 MapBiomas general "handbook" algorithm theoretical basis document (ATBD) collection 9
- Marengo J A, Souza C M, Thonicke K, Burton C, Halladay K, Betts R A, Alves L M and Soares W R 2018 Changes in climate and land use over the Amazon region: current and future variability and trends *Front. Earth Sci.* 6 228
- Markesteijn L, Poorter L, Paz H, Sack L and Bongers F 2011 Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits *Plant Cell Environ.* 34 137–48
- Markham B L, Storey J C, Williams D L and Irons J R 2004 Landsat sensor performance: history and current status *IEEE Trans. Geosci. Remote Sens.* 42 2691–4
- Mataveli G, Jones M W, Carmenta R, Sanchez A, Dutra D J, Chaves M, de Oliveira G, Anderson L O, Aragão L E 2024 Deforestation falls but rise of wildfires continues degrading Brazilian Amazon forests *Glob. Change Biol.* **30** e17202
- Matos F A R *et al* 2020 Secondary forest fragments offer important carbon and biodiversity cobenefits *Glob. Change Biol.* **26** 509–22
- Maurano L E P, Escada M I S and Renno C D 2019 Padrões espaciais de desmatamento ea estimativa da exatidão dos mapas do PRODES para Amazônia Legal Brasileira *Cienc. Florest.* **29** 1763–75
- Meier R, Schwaab J, Seneviratne S I, Sprenger M, Lewis E and Davin E L 2021 An observation-based estimate of precipitation changes from forestation in Europe *Nat. Geosci.* 14 473–8

- Milenković M, Reiche J, Armston J, Neuenschwander A, De Keersmaecker W, Herold M, Verbesselt J 2022 Assessing Amazon rainforest regrowth with GEDI and ICESat-2 data Sci. Remote Sens. 5 100051
- Moran E F, Brondizio E S, Tucker J M, Da Silva-Forsberg M C, Mccracken S and Falesi I 2000 Effects of soil fertility and land-use on forest succession in Amazônia For. Ecol. Manage. 139 93–108
- Neeff T, Lucas R M, Santos J R D, Brondizio E S and Freitas C C 2006 Area and age of secondary forests in Brazilian Amazonia 1978–2002: an empirical estimate *Ecosystems*
- Nepstad D C, De Carvalho C R, Davidson E A, Jipp P H, Lefebvre P A, Negreiros G H, Da Silva E D, Stone T A, Trumbore S E and Vieira S 1994 The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures *Nature* 372 666–9
- Nepstad D, Mcgrath D, Stickler C, Alencar A, Azevedo A, Swette B, Bezerra T, Digiano M, Shimada J and Seroa Da Motta R 2014 Slowing Amazon deforestation through public policy and interventions in beef and soy supply chains Science 344 1118–23
- Nunes S, Oliveira L, Siqueira J, Morton D C and Souza C M 2020 Unmasking secondary vegetation dynamics in the Brazilian Amazon Environ. Res. Lett. 15 034057
- Oliveira R S, Eller C B, Barros F D V, Hirota M, Brum M and Bittencourt P 2021 Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems *New Phytol.* 230 904–23
- Pan Y *et al* 2024 The enduring world forest carbon sink *Nature* 631 563–9
- Peña-Claros M 2003 Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon1 *Biotropica* **35** 450–61
- Pfeifer M *et al* 2017 Creation of forest edges has a global impact on forest vertebrates *Nature* **551** 187–91
- Phillips O L, Aragão L E, Lewis S L, Fisher J B, Lloyd J, López-González G, Malhi Y, Monteagudo A, Peacock J and Quesada C A 2009 Drought sensitivity of the Amazon rainforest *Science* 323 1344–7
- Poorter L et~al~2016 Biomass resilience of Neotropical secondary forests Nature~530~211-4
- Poorter L et al 2021a Multidimensional tropical forest recovery Science 374 1370–6
- Poorter L et al 2021b Functional recovery of secondary tropical forests Proc. Natl Acad. Sci. 118 e2003405118
- Poorter L, Mcdonald I, Alarcón A, Fichtler E, Licona J C, Peña-Claros M, Sterck F, Villegas Z and Sass-Klaassen U 2010 The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species New Phytol. 185 481–92
- Rangel Pinagé E, Bell D M, Longo M, Silva C A, Csillik O and Huete A 2023 Surface energy dynamics and canopy structural properties in intact and disturbed forests in the Southern Amazon J. Geophys. Res. Biosci. 128 e2023IG007465
- Rap A *et al* 2015 Fires increase Amazon forest productivity through increases in diffuse radiation *Geophys. Res. Lett.* **42** 4654–62
- Robertson E 2019 The local biophysical response to land-use change in HadGEM2-ES J. Clim. 32 7611–27
- Rosenfield M F *et al* 2023 Ecological integrity of tropical secondary forests: concepts and indicators *Biol. Rev.* **98** 662–76
- Rozendaal D M A *et al* 2019 Biodiversity recovery of Neotropical secondary forests *Sci. Adv.* 5 eaau3114
- Rudorff B F T, Adami M, Aguiar D A, Moreira M A, Mello M P, Fabiani L, Amaral D F and Pires B M 2011 The soy moratorium in the Amazon biome monitored by remote sensing images *Remote Sens.* 3 185–202
- Santos L A, Ferreira K R, Camara G, Picoli M C and Simoes R E 2021 Quality control and class noise reduction of satellite

- image time series ISPRS J. Photogramm. Remote Sens. 177 75-88
- Sayer C A, Bullock J M and Martin P A 2017 Dynamics of avian species and functional diversity in secondary tropical forests *Biol. Conserv.* 211 1–9
- SEMA 2016 INSTRUÇÃO NORMATIVA Nº 001, DE 12 DE FEVEREIRO DE 2016 Secretaria de Estado de Meio Ambiente (SEMA) (Governo de Mato Grosso)
- Silva C V D J, Santos J R D, Galvao L S, Silva R D A D and Moura Y M 2016 Floristic and structure of an Amazonian primary forest and a chronosequence of secondary succession *Acta Amaz.* 46 133–50
- Silva C V J et al 2020 Estimating the multi-decadal carbon deficit of burned Amazonian forests Environ. Res. Lett. 15 114023
- Silva Junior C H L et al 2020 Benchmark maps of 33 years of secondary forest age for Brazil Sci. Data 7 269
- Silveira M V F, Silva-Junior C H L, Anderson L O and Aragão L E O C 2022 Amazon fires in the 21st century: the year of 2020 in evidence *Glob. Ecol. Biogeogr.* 31 2026–40
- Smith C C, Barlow J, Healey J R, De Sousa Miranda L, Young P J and Schwartz N B 2023a Amazonian secondary forests are greatly reducing fragmentation and edge exposure in old-growth forests *Environ. Res. Lett.* 18 124016
- Smith C C, Espírito-Santo F D B, Healey J R, Young P J, Lennox G D, Ferreira J and Barlow J 2020 Secondary forests offset less than 10% of deforestation-mediated carbon emissions in the Brazilian Amazon *Glob. Change Biol.* 26 7006–20
- Smith C C, Healey J R, Berenguer E, Young P J, Taylor B, Elias F, Espírito-Santo F and Barlow J 2021 Old-growth forest loss and secondary forest recovery across Amazonian countries *Environ. Res. Lett.* **16** 085009
- Smith C et al 2023c Observed and simulated local climate responses to tropical deforestation Environ. Res. Lett. 18 104004
- Smith C, Baker J and Spracklen D 2023b Tropical deforestation causes large reductions in observed precipitation *Nature* 615 270–5
- Smith M N *et al* 2023 Diverse anthropogenic disturbances shift Amazon forests along a structural spectrum *Front. Ecol. Environ.* 21 24–32
- Sorrensen C L 2000 Linking smallholder land use and fire activity: examining biomass burning in the Brazilian Lower Amazon For. Ecol. Manage. 128 11–25
- Souza C M Jr et al 2020 Reconstructing three decades of land use and land cover changes in brazilian biomes with landsat archive and earth engine *Remote Sens.* 12 2735
- Spracklen D V, Baker J C A, Garcia-Carreras L and Marsham J 2018 The effects of tropical vegetation on rainfall *Annu. Rev. Environ. Resour.* **43** 14.1–14.26
- Spracklen D V and Garcia-Carreras L 2015 The impact of Amazonian deforestation on Amazon basin rainfall *Geophys*. *Res. Lett.* 42 9546–52
- Staal A, Tuinenburg O A, Bosmans J H C, Holmgren M, Van Nes E H, Scheffer M, Zemp D C and Dekker S C 2018 Forest-rainfall cascades buffer against drought across the Amazon *Nat. Clim. Change* 8 539–43
- Steininger M K 2000 Satellite estimation of tropical secondary forest above-ground biomass: data from Brazil and Bolivia Int. J. Remote Sens. 21 1139–57
- Su Y et al 2023 Asymmetric influence of forest cover gain and loss on land surface temperature Nat. Clim. Change 13 823–31
- Tavares J V et al 2023 Basin-wide variation in tree hydraulic safety margins predicts the carbon balance of Amazon forests Nature 617 111–7
- Ter Steege H *et al* 2013 Hyperdominance in the Amazonian Tree Flora *Science* 342 1–9
- Toomey A H, Knight A T and Barlow J 2017 Navigating the space between research and implementation in conservation *Conserv. Lett.* **10** 619–25
- Uhl C, Buschbacher R and Serrao E A S 1988 Abandoned pastures in Eastern Amazonia. I. Patterns of plant succession *J. Ecol.* **76** 663–81

- UNFCCC 2015 Paris Agreement (available at: https://unfccc.int/ sites/default/files/english\_paris\_agreement.pdf) (Accessed 1 August 2022)
- UNFCCC 2022 NDC Synthesis Report (available at: https://unfccc.int/ndc-synthesis-report-2022#:~:text=Scope% 20and%20Approach-,This%20version%20of%20the%20 NDC%20synthesis%20report%20synthesizes%20 information%20from,cent%20of%20the%20total %20global)
- Uriarte M, Schwartz N, Powers J S, Marín-Spiotta E, Liao W and Werden L K 2016 Impacts of climate variability on tree demography in second growth tropical forests: the importance of regional context for predicting successional trajectories *Biotropica* 48 780–97
- Van Vliet N, Adams C, Vieira I C G and Mertz O 2013 "Slash and burn" and "shifting" cultivation systems in forest agriculture frontiers from the Brazilian Amazon *Soc. Nat. Resour.* **26** 1454–67
- Vancutsem C, Achard F, Pekel J-F, Vieilledent G, Carboni S, Simonetti D, Gallego J, Aragão L E O C and Nasi R 2021 Long-term (1990–2019) monitoring of forest cover changes in the humid tropics *Sci. Adv.* 7 eabe1603
- Vieira I C G *et al* 2024 Governance and policy constraints of natural forest regeneration in the Brazilian Amazon *Restor*. *Ecol.* e14272
- Vieira I C G, Gardner T, Ferreira J, Lees A C and Barlow J 2014 Challenges of governing second-growth forests: a case study from the Brazilian Amazonian State of Pará Forests 5 1737–52
- Villa P M, Martins S V, De Oliveira Neto S N, Rodrigues A C, Martorano L G, Monsanto L D, Cancio N M and Gastauer M 2018 Intensification of shifting cultivation reduces forest resilience in the northern Amazon For. Ecol. Manage. 430 312–20
- Von Randow C et al 2004 Comparative measurements and seasonal variations in energy and carbon exchange over forest and pasture in South West Amazonia Theor. Appl. Climatol. 78 5–26
- Von Randow R C S, Rodriguez D A, Tomasella J, Aguiar A P D, Kruijt B and Kabat P 2019 Response of the river discharge in the Tocantins River Basin, Brazil, to environmental changes and the associated effects on the energy potential *Reg. Environ. Change* 19 193–204
- Von Randow R D C S, Tomasella J, Von Randow C, De Araújo A C, Manzi A O, Hutjes R and Kruijt B 2020 Evapotranspiration and gross primary productivity of secondary vegetation in Amazonia inferred by eddy covariance *Agric. For. Meteorol.* 294 108141
- Waide R B and Lugo A E 1992 A research perspective on disturbance and recovery of a tropical montane forest Tropical Forests in Transition: Ecology of Natural and

- Anthropogenic Disturbance Processes ed J G Goldammer (Birkhäuser Basel)
- Wandelli E V and Fearnside P M 2015 Secondary vegetation in central Amazonia: land-use history effects on aboveground biomass For. Ecol. Manage. 347 140–8
- Wang Y et al 2019 Mapping tropical disturbed forests using multi-decadal 30 m optical satellite imagery Remote Sens. Environ. 221 474–88
- Wang Y, Ziv G, Adami M, Almeida C A D, Antunes J F G, Coutinho A C, Esquerdo J C D M, Gomes A R and Galbraith D 2020 Upturn in secondary forest clearing buffers primary forest loss in the Brazilian Amazon *Nat.* Sustain. 3 290–5
- Watson J E M et al 2018 The exceptional value of intact forest ecosystems Nat. Ecol. Evol. 2 599–610
- Weng E et al 2022 Modeling demographic-driven vegetation dynamics and ecosystem biogeochemical cycling in NASA GISS's Earth system model (ModelE-BiomeE v.1.0) Geosci. Model Dev. 15 8153–80
- Williams B A *et al* 2024 Global potential for natural regeneration in deforested tropical regions *Nature* **636** 131–7
- Wiltshire A J, Von Randow C, Rosan T M, Tejada G and Castro A A 2022 Understanding the role of land-use emissions in achieving the Brazilian Nationally determined contribution to mitigate climate change *Clim. Resil. Sustain.* 1 e31
- Wong P Y, Kuralbayeva K, Anderson L O, Pessoa A M and Harding T 2022 Individual pay for collective performance and deforestation: evidence from Brazil *Working paper* (Norwegian School of Economics)
- Yao Y et al 2022 Forest fluxes and mortality response to drought: model description (ORCHIDEE-CAN-NHA r7236) and evaluation at the Caxiuana drought experiment Geosci. Model Dev. 15 7809–33
- Yao Y, Ciais P, Viovy N, Joetzjer E and Chave J 2023 How drought events during the last century have impacted biomass carbon in Amazonian rainforests *Glob. Change Biol.* **29** 747–62
- Zarin D J et al 2005 Legacy of fire slows carbon accumulation in Amazonian forest regrowth Front. Ecol. Environ. 3 365–9
- Zemp D C, Schleussner C-F, Barbosa H M J, Hirota M, Montade V, Sampaio G, Staal A, Wang-Erlandsson L and Rammig A 2017 Self-amplified Amazon forest loss due to vegetation-atmosphere feedbacks *Nat. Commun.* 8 1–10
- Zhang Y, Wang X, Lian X, Li S, Li Y, Chen C and Piao S 2024 Asymmetric impacts of forest gain and loss on tropical land surface temperature *Nat. Geosci.* 17 426–32
- Zimmermann B, Elsenbeer H and De Moraes J M 2006 The influence of land-use changes on soil hydraulic properties: implications for runoff generation *For. Ecol. Manage* 222 29–38