Chapter 24

Resilience of the Amazon forest to global changes: Assessing the risk of tipping points

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About the Science Panel for the Amazon (SPA)

The Science Panel for the Amazon is an unprecedented initiative convened under the auspices of the United Nations Sustainable Development Solutions Network (SDSN). The SPA is composed of over 200 preeminent scientists and researchers from the eight Amazonian countries, French Guiana, and global partners. These experts came together to debate, analyze, and assemble the accumulated knowledge of the scientific community, Indigenous peoples, and other stakeholders that live and work in the Amazon.

The Panel is inspired by the Leticia Pact for the Amazon. This is a first-of-its-kind Report which provides a comprehensive, objective, open, transparent, systematic, and rigorous scientific assessment of the state of the Amazon's ecosystems, current trends, and their implications for the long-term well-being of the region, as well as opportunities and policy relevant options for conservation and sustainable development.

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Graphical Abstract

Figure 24.A Simplified diagram illustrating the drivers of change that can lead to tipping points in Amazonian rainforests. Drivers of change refer to direct (i.e., higher global temperatures) and indirect (i.e., longer dry season and more frequent and intense extreme drought events) large-scale climate change effects, followed by regional to local scale wildfires and deforestation. If tipping points are crossed in current drivers of change, either individually or in a compound way, the depicted cascading chains of impacts resembling a domino effect, called feedback mechanisms, are key to trap rainforests into three different potential states already registered and documented within Amazonian rainforest: white-sand savanna (or "Amazonian *campinas*"), open-canopy degraded forest or closed-canopy degraded secondary forest.

Resilience of the Amazon Forest to Global Changes: Assessing the Risk of Tipping Points

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Key Messages

- Five tipping points described in the literature comprise disturbances triggered by changes in climatic conditions and human activities, and associated large-scale feedback mechanisms. Nevertheless, the heterogeneity in forest responses throughout the Amazon basin (i.e., how resistant and recoverable different forests are) seem to be key in determining the systemic resilience of the entire Amazon system, and should be a research priority.
- Based on empirical evidence, there are four potential ecosystem configurations that Amazonian forests could shift to: (i) a closed-canopy seasonally dry tropical forest state; (ii) a native savanna state; (iii) an open-canopy degraded state; and (iv) a closed-canopy secondary forest state. Due to the existence of novel feedbacks associated with invasive plants and human-modified landscapes, we consider the open-canopy degraded state and the closed-canopy secondary forest state as more likely to occur over broad areas, particularly across the 'arc of deforestation'.
- Further studies are needed to understand how past underlying conditions (e.g., soil fertility and rainfall regimes) affect resilience and how different species cope with the same amount of disturbance. This is key to unveiling how response heterogeneity may either increase or dampen the systemic resilience of Amazonian ecosystems.
- The likelihood of crossing tipping points within Amazonian ecosystems has been best studied so far with the use of models. Despite continuous model improvements and reductions in uncertainty, there is a lack of observational (field and remote sensing) and experimental evidence to improve these models and evaluate their results. As such, there is no reasonable/strong scientific agreement, from a modeling perspective, on the likelihood of crossing an Amazonian tipping point in the future. However, the likelihood can be expected to increase with higher levels of climate change and/or direct deforestation/degradation. Priority areas for model-data integration are understanding the CO_2 fertilization effect, soil nutrient limitations, recruitment/mortality dynamics, plant functional diversity, and reducing uncertainty in Amazonian rainfall projections.

Abstract

Here we review and discuss existing evidence of ongoing changes in the Amazon forest system that may lead to resilience loss and the crossing of tipping points beyond which the ecosystem may shift persistently to an alternative state. Grounded on the theory of complex dynamical systems, we analyze the state

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of the Amazon forest and its potential trajectories in the 21st-century, aiming to provide support for a science-based management scheme for enhancing systemic resilience. This review is based on five systemic tipping points for which there is evidence; four climate-related: (1) annual rainfall value below 1,000-1,500 mm/yr, (2) dry season length above seven months, (3) for Amazon lowlands, a maximum cumulative water deficit above 200 mm/yr, (4) a global increase of 2°C on the equilibrium temperature of the Earth; and one associated with human-induced changes: (5) 20-25% accumulated deforestation of the whole basin. Evidence suggests that, depending on varying combinations of stressing conditions, disturbances, and feedback mechanisms, current forest configurations could be replaced at local scales by: (i) a closed-canopy seasonally dry tropical forest; (ii) a native tropical savanna state; (iii) an open-canopy degraded state; and (iv) a closed-canopy secondary forest. Local-scale forest collapses could trigger cascading effects on rainfall recycling, intensifying dry seasons and wildfire occurrence, and leading to massive forest loss at continental scales, particularly in the southwest of the basin. The probability of crossing such tipping points depends largely on heterogeneities across the system, including geological, physical, chemical, and cultural processes that influence connectivity and the likelihood of contagious disturbances. Biodiversity patterns were historically shaped over the past 60 million years by these processes and still today influence forest adaptive capacity and resilience. Thus, maintaining biodiversity is critical for enhancing resilience and reducing the risk of systemic forest collapse in the near future.

Keywords: tipping points, resilience, biodiversity, heterogeneity, connectivity, climate change, land-use change.

24.1 Introduction

The Amazon is a complex dynamical system that has been constantly changing for at least 60 million years ago (Ma), with geological, hydrological, and evolutionary processes shaping the system that we know today (Hoorn *et al.*, 2010; Chapters 1-7; Figure 24.1). While the Amazon River was formed around 10 – 4.5 Ma (see Chapters 1 and 2), forests expanded over non-forest habitats, and during the same time, massive wetlands retreated at the western parts of the basin. This process altered the courses of most rivers, causing new geographical barriers to emerge, altering the distribution of species, and creating the conditions for diversification and speciation (Hoorn *et al.* 2010, see also Chapters 1 and 2). More recently, around 12,000 years ago, humans arrived in the Amazon (Potsch *et al.* 2018, see also Chapter 8) and began to contribute to further changes in the landscapes and alter plant species distributions (Levis *et al.* 2017, see also Chapters 8 and 10).

As a result of the interplay between these processes (both natural and anthropogenic) operating at different spatial and temporal scales, the Amazon is currently an extremely heterogeneous and biodiverse system (see Chapters 3 and 4, and Figure 24.1b). Forest tree communities across the basin are formed by different sets of species with contrasting functional traits selected by continental to local environmental conditions, the main drivers of this heterogeneity including soil (Quesada *et al.* 2012), climate (Davidson *et al.* 2012; ter Steege *et al.* 2013; Esquivel-Muelbert *et al.* 2017), topography (Oliveira *et al.* 2019), and microclimate (Barros *et al.* 2019). Savannas also occur along the fringes of the Amazon basin and as "islands" within the dominant forest habitat (Prance 1996). The varying types of forest and non-forest habitats that exist are connected through a rich web of ecological interactions, which have contributed to maintaining the whole system for the past 45 ka. Such resilience has been observed even under the extremely dry conditions of the Last Glacial Maximum (LGM) around 20 ka (Wang *et al.* 2017).

In the last century, however, the Amazon system began to change faster, mostly due to local, regional, and global human activities that intensified particularly since the 1970s (See Chapters 14-21, and Figs. 24.2c-e). Within the last two decades, extreme droughts have become more frequent, and extremes in precipitation during the wet and dry
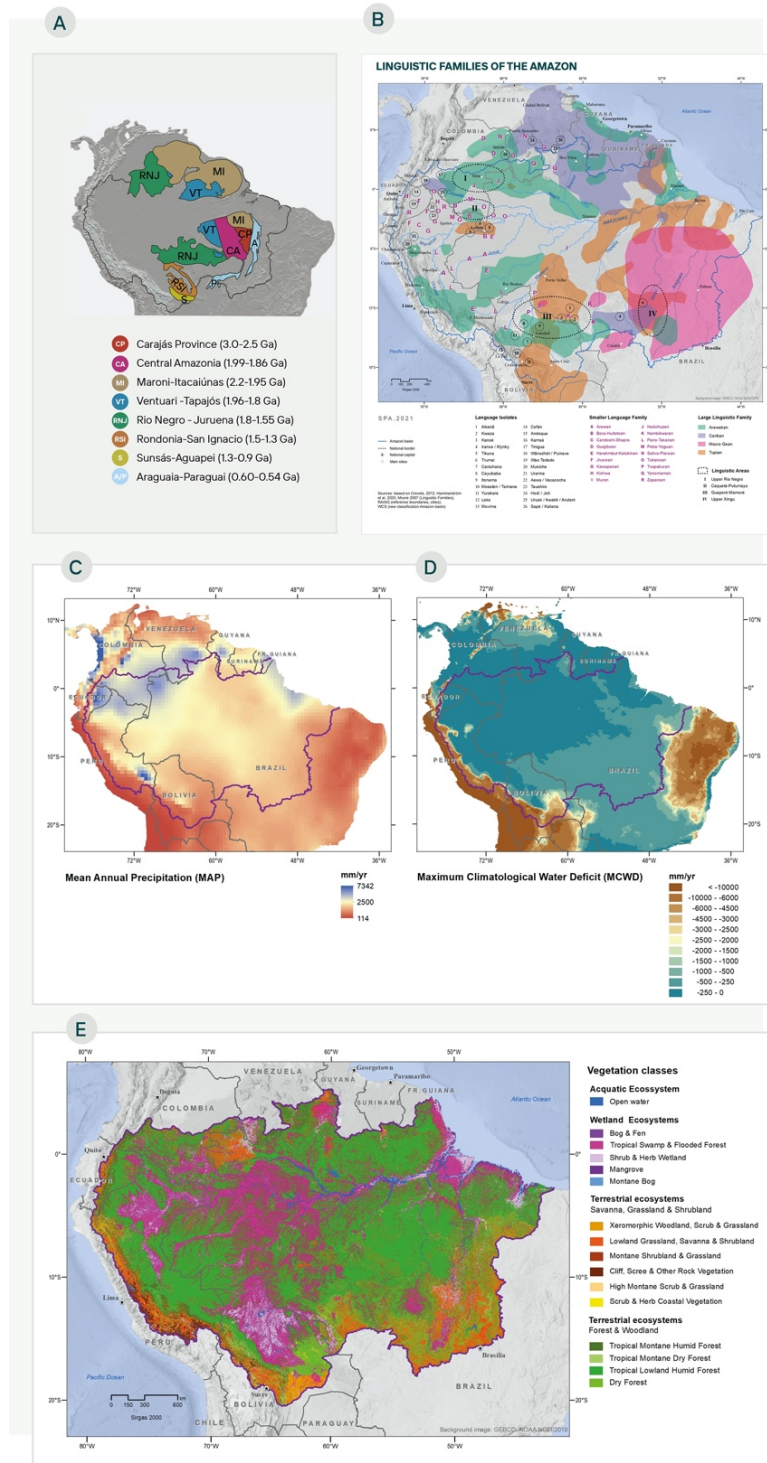
24.1 Heterogeneity in abiotic and biotic conditions throughout the Amazon system, which shaped a range of plant community assemblages within different time and spatial scales. (a) geochronological map of South America with the main provinces of the Amazon Craton (see Chapter 1); (b) past cultural diversity (to be defined either early ceramics complexes or Holocene ceramic complexes - still to be built by the map team) (see Chapter 8); (c) current climatological mean annual precipitation (MAP, mm/yr, mean value for the period from 1981 to 2010) from CHIRPS dataset (Funk *et al.* 2015); (d) current maximum climatological water deficit (MCWD, mm/yr, mean value for the period from 1981 to 2010) from CHIRPS dataset (Funk *et al.* 2015); (e) wetland and terrestrial ecosystems of the Amazon to show the tremendous biodiversity embedded within the system (See Chapter 4).

seasons have intensified (see Chapter 22; Marengo *et al.* 2011; Gloor *et al.* 2013; Jiménez-Muñoz *et al.* 2016). Mean, maximum, and minimum temperatures have also risen (see Chapter 22; Jiménez-Muñoz *et al.* 2013), particularly on fragmented landscapes due to deforestation (Zeppetello *et al.* 2020). As a result, mature Amazonian forests are now losing drought-sensitive species and becoming more dominated by drought-tolerant species (Esquivel-Muelbert *et al.* 2016, 2019; see also Chapter 23), with higher mortality rates for drought-sensitive species taking place particularly along the southern fringes of the Amazon (Esquivel-Muelbert *et al.* 2020). In the central Amazon, interactions between extremely wet and dry periods are increasing tree mortality rates and reducing growth (Aleixo *et al.* 2019; Esteban *et al.* 2021).

Moreover, human-induced wildfires are intensifying (Alencar *et al.* 2015, see also Chapter 22), causing unprecedented levels of tree mortality (Brando *et al.* 2014). The expansion of cattle production has introduced invasive alien grasses, increasing the flammability of degraded and regenerating forests (Cochrane 2003). Moreover, deforestation disrupts forest-rainfall interactions across the Amazon by interrupting the moisture recycling by forest trees (see Chapter 7), and consequently the east-west moisture flow; a process that may accelerate forest loss (Zemp *et al.* 2017; Staal *et al.* 2020). Wildfires and deforestation also threaten species located along the southern edge of the system (Steege *et al.* 2015), particularly where forests are likely to be more resilient to climate change (Ciemer *et al.* 2019). On the other hand, changes in wildfire regimes may affect areas away from the southern edges, given that species may have fewer adaptations to thrive under more frequent and intense wildfire events (Staver *et al.* 2020). In the case of Brazil, the Amazonian country that holds the largest deforestation rates (see Chapter 19), rates had been slowing down but began to rise again starting in 2012, due to political changes that led to the weakening of Brazilian environmental governance (Levis *et al.* 2020; Rajão *et al.* 2020, see Chapters 14 and 17). All these changes imply that the Amazon

now has to deal with unprecedented levels of stressing conditions and disturbance regimes.

A topic that has raised concern is the potential existence of an ecological tipping point that could affect the stability of the Amazon, causing large-scale forest dieback or collapse (Box 24.1). Despite increasing evidence of tree mortality caused by extreme rainfall events (both dry and wet), fire, deforestation, and the potential of their combined effects (Cochrane *et al.* 1999; Aragão *et al.* 2007, 2008; Phillips *et al.* 2009; Brando *et al.* 2014; Nobre *et al.* 2016; Esquivel-Muelbert *et al.* 2020; Staal *et al.* 2020; Esteban *et al.* 2021), the actual behavior of the Amazon system remains uncertain. For instance, with increasing water-deficit levels and aridity, the Amazon forest may not necessarily shift abruptly across the whole basin, but instead shift gradually with the least-resilient forests affected first, followed by the more resilient ones (Levine *et al.* 2016; Figure 24.1). On the other hand, human-induced changes are likely to occur faster than the time forest communities would need to recover. Moreover, a long-lasting hypothesis is that the Amazon forests that collapse may undergo a "savannization" process, i.e., forests would be replaced by savanna-like vegetation (Nobre *et al.* 1991). Nevertheless, evidence suggests that native savannas are unlikely to replace all portions of the Amazon forest, since most stressors are associated with human activities that would introduce invasive alien grasses instead of native savanna species (Veldman and Putz 2011), trapping forests in a degraded and early successional stage (Barlow and Peres 2008).

Grounded on the theory of complex dynamical systems, we review and discuss existing evidence of ongoing changes that may reduce forest resilience and potentially lead to tipping points (Box 24.1), in which the Amazon forest may shift into other configurations. By analyzing the state of the Amazon forest and its potential trajectories in the 21st-century, we expect to provide critical information that will support a science-based management scheme for enhancing the resilience of this iconic system.
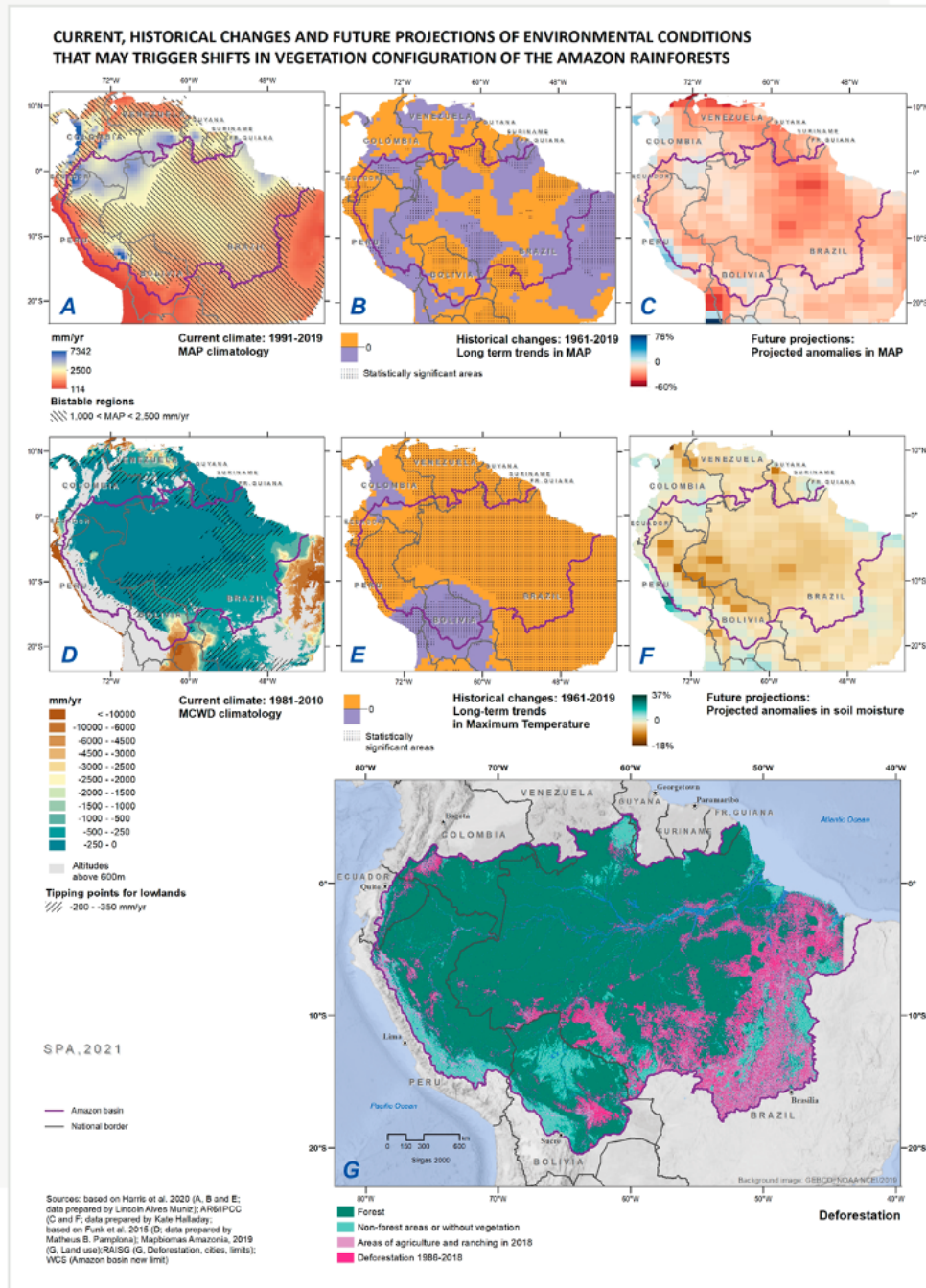
Figure 24.2 Tipping points (section 2) and disturbances/perturbations which may affect the resilience of the Amazon. (A) 1991 - 2019 climatology of mean annual precipitation (MAP, mm/yr) showing bistable areas for tipping point range (tipping point 1) using CRU 4.04 dataset (Harris *et al.* 2020); (B) historical changes from 1961 to 2019 in MAP (hatched areas are statistically significant) using CRU 4.04 (Harris *et al.* 2020); increases in MAP (larger than 0) shown in orange, and decreases in MAP (lower than 0) shown in purple; (C) projected relative changes in MAP at 4°C global warming with the UKESM1 climate model (Sellar *et al.* 2019) for the period 2070-2100; future increases in MAP shown in blue and future decreases in red; (D) 1981-2010 MCWD climatology showing tipping points (-200 and -350 mm/yr for lowlands) (tipping point 3); (E) historical changes from 1961 to 2019 in maximum temperatures (hatched areas are statistically significant) using CRU 4.04 dataset (Harris *et al.*, 2020); increases in T$_{max}$ (larger than 0) shown in orange, and decreases (lower than 0) in T$_{max}$ in purple; (F) projected relative changes in soil moisture at an extreme 4°C global warming with the UKESM1 climate model (Sellar *et al.* 2019) for the period 2070-2100; future increases in soil moisture shown in green and future decreases in brown; (G) deforestation according to MapBiomas.

24.2 Potential Tipping Points and New Configurations

The tipping points that have been proposed for the Amazon rainforests so far are: (1) annual rainfall totals below 1,000 mm/yr, inferred from satellite observations of tree cover distributions (Hirota *et al.* 2011; Staver *et al.* 2011; Figs. 24.2a-d) or 1,500 mm/yr inferred from global climate models (Malhi *et al.* 2009), (2) dry season length longer than seven months, inferred from satellite observations of tree cover distributions (Staver *et al.* 2011), (3) for the Amazon lowlands, maximum cumulative water deficit values larger than 200 mm/yr or 350 mm/yr, inferred from different analyses with global climate models (respectively, from Malhi *et al.* 2009; Zelazowski *et al.* 2011; Figure 24.2e); (4) an increase of 2°C on the equilibrium temperature of the Earth, inferred from a coupled climate–vegetation model (Jones *et al.* 2009; for instance, with consequences shown in Figs. 24.2d,g), and (5) surpass 20-25% accumulated deforestation, inferred from a combination of environmental changes (i.e., increases in dry season length, see Chapter 22), climate projections for the most pessimistic pathway of the Intergovernmental Panel on Climate Change (IPCC; Figs. 24.2d,g), and human-induced degradation via deforestation (Figure 24.2h) (Nobre *et al.* 2016; Lovejoy and Nobre 2019). The main concern is that beyond these possible tipping points, the system would enter a loop of rainfall reduction, fire, and forest mortality.

Given the challenges in acquiring sufficiently long time series to effectively and directly account for temporal changes, their impacts on vegetation cover, and consequent tipping points (Box 24.1), the ones mentioned above have been inferred and proposed by different types of modeling and observational approaches. The first two use a space-for-time substitution method, which replaces temporal information on changing conditions and
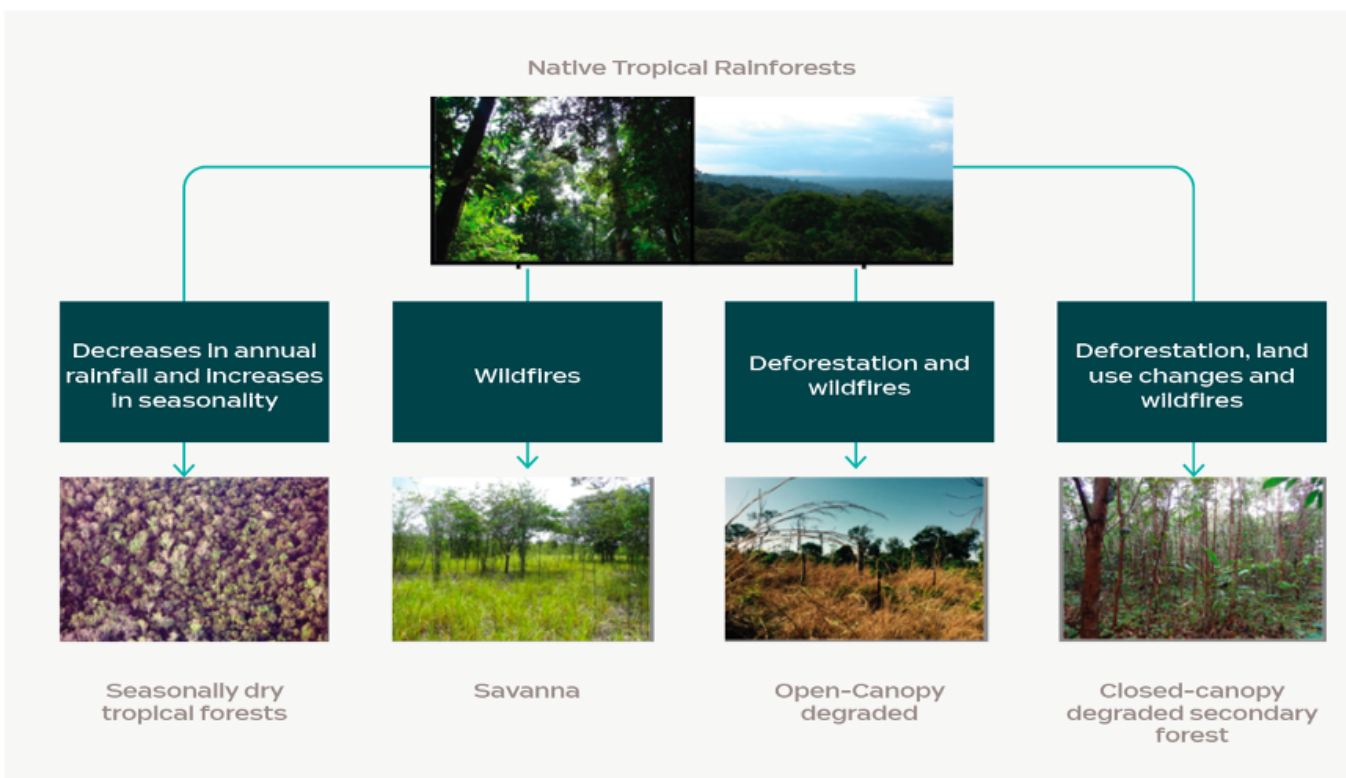
Figure 24.3 Potential alternative configurations and drivers. Photo credits: Native tropical rainforests at ZF2 Station (AM, Brazil) by Marina Hirota; seasonally dry tropical forests at Maracá Island (RR, Brazil) by Marcelo Trindade Nascimento; savanna at Barcelos (AM, Brazil) by Bernardo M. Flores; open-canopy degraded at Fazenda Tanguro (MT, Brazil) by Paulo Brando; closed-canopy degraded secondary forest at Tefé (AM, Brazil) by Catarina Jakovac.

their impacts (e.g., changes in precipitation intensity leading to changes in vegetation cover) by observational data of vegetation status (canopy closure using tree cover values) along a gradient of precipitation (e.g., 1,000 to 2,500 mm/yr) at a single snapshot in time. Tipping points (3) to (5) are based on coupled climate-vegetation models, which are able to simulate long time series with their integrative structure, but depend on a set of parameterizations that may fail to adequately represent soil-plant-atmosphere interactions. Thus, even having a glimpse of thresholds that may trigger irreversible changes, the trajectories leading to stable and transient configurations of the Amazon basin need to be further explored and studied by a combination of experimental and modeling studies. For instance, a recent study has shown that, given the large uncertainty and variability inv olved in projecting future climate conditions, after correcting for models' biases identified using observational data, a basin-wide Amazon dieback is unlikely to occur, even under the most pessimist IPCC pathway (Chai *et al.* 2021).

Based on existing evidence, we identify four main configurations Amazonian forests may shift to and persist in due to self-reinforcing feedbacks (Figure 24.3): (i) a closed-canopy seasonally dry tropical forest, with increasing abundance of deciduous tree species; (ii) a tropical savanna state, dominated by native grass and tree species; (iii) an open-canopy degraded state, dominated by invasive alien grasses and native fire-tolerant tree species; and (iv) a closed-canopy secondary forest, dominated by native early successional tree and other plants species. In the following subsections, we explain how current environmental changes in the Amazon system (see Chapters 14-22 and Figure 24.2) may alter forest dynamics, as well as feedback mechanisms (Box 24.1) that could arrest Amazonian ecosystems in the configurations (i) to (iv), and illustrate these trajectories with evidence on past and current changes.

24.2.1 Forest shift to a closed-canopy, seasonally dry tropical forest

Considering the observed trends towards a drier climate in some parts of the Amazon (see Chapter 22), there is a possibility that forests over nutrient-richer soils may shift into a closed-canopy state that resembles, in terms of structure and functioning, a seasonally dry tropical forest (SDTF) (Malhi *et al.* 2009; Dexter *et al.* 2018), dominated by fast-growing deciduous trees, with high tolerance to drought conditions, and a higher demand for nutrients. This type of semi-deciduous forest (i.e., with varying abundances of deciduous species) is very common in the transitional zones along the Amazon's boundaries, and under drier climatic conditions (Silva de Miranda *et al.* 2018) could expand over wet Amazonian forests (Dexter *et al.* 2018). For instance, drought-tolerant species are widely distributed across the Amazon region (Esquivel-Muelbert *et al.* 2017), and a shift in the climate regime would allow them to dominate (Esquivel-Muelbert *et al.* 2019). However, drought-tolerance is not only expressed in terms of deciduousness, and alternative phenotypes may include trees with more resistant water-transporting systems (Barros *et al.* 2019) and/or deeper-rooted species. Nonetheless, a shift to a semi-deciduous forest would probably not follow catastrophic non-linear dynamics, with associated tipping points (Box 24.1, Figure 24.B1) because rainforests and STDFs occupy separate climatic niches (Silva de Miranda *et al.* 2018), implying that tree species may have to migrate long geographical distances. Hence, such changes might occur smoothly and more gradually with increasing aridity and seasonality (Oliveira *et al.* 2021.).

24.2.2 Forest shift to a native savanna state

The Amazon forest is often assumed to shift into a savanna-like state, once it passes tipping points such as the ones described above (Cox *et al.* 2004; Jones *et al.* 2009; Hirota *et al.* 2011; Staver *et al.* 2011; Lovejoy and Nobre 2019). However, evidence

Box 24.1 Main concepts and definitions based on the theory of dynamical systems

The theory of dynamical systems suits as a model to any type of system that evolves in time. The dynamics of such systems may have linear, nonlinear, chaotic, and complex behaviors, depending on the underlying conditions or the control/explanatory variables, and the response or state variable (Strogatz 2015). For ecosystems such as the Amazon, conditions would be, for instance, the total amount of precipitation or nutrient availability; the state variable would represent the status of vegetation cover, e.g., tree cover percentage or productivity. When the system presents nonlinear dynamics, we can have a steep but still gradual shift from one ecosystem state to another (Figure 24.B1, left panel b), meaning that for each condition there is one and only one ecosystem state associated; and a more abrupt or catastrophic shift (Figure 24.B1, left panel c), when two (or more) ecosystem states can exist under the same set of conditions (the reason why the sigmoid from panel b turns into an s-shaped curve in panel c). The two possible configurations (continuous red line on left panel c) represent stability and are called alternative stable states or attractors; and the dashed red line in the middle represents the transient behavior of the system and is called the unstable states or repellors (from there the system could move either upwards to the higher stable state or downwards to the lower state - see green arrows pointing up and downwards).

The two black open circles (F1 and F2) are named bifurcation points, tipping points, or critical thresholds. In this sense, such tipping points exist only when two or more alternative stable states occur (Scheffer et al. 2001). Tipping points can be reached if either disturbances (changes in conditions), or perturbations (changes in the state), or both occur (Fig. 24.B1, right panels) (Van-Nes et al. 2016). First, if conditions change and F2 is crossed (Fig. 24.B1, right panel a), a sudden drop (downwards) can occur towards a different state. Interestingly, to return to the original state, the system would need to undergo a much stronger change in conditions, in this case, to reach the other bifurcation point F1, which could lead the system upwards again. This path-dependence behavior is called hysteresis. Such a feature defines the likelihood of irreversibility after crossing a tipping point. Eventually, it is so challenging to return conditions to F1 levels, and thus return to the original state, that reaching a tipping point can indeed cause irreversible changes. In the case of Amazon rainforests, climate change translated into extreme drought events or increases in dry season length could represent changes in one of the underlying conditions that maintain Amazonian ecosystems in the current configuration. Secondly, if changes occur in the ecosystem state, e.g., decreases in tree cover after deforestation and/or wildfire events, the system could reach the instability region (red dashed line), causing either a return to the original state or a (irreversible) change in the system configuration.

In either case what drives the accelerated shift to a new state are **positive** *feedback mechanisms* (DeAngelis *et al.* 1986), determined by the internal dynamics of the system in a closed loop, i.e., the initial perturbation is self-reinforced and amplified. For instance, deforestation leads to less tree cover, which, in turn, leads to less evapotranspiration, less precipitation, and thus less tree cover; i.e., in this case, the initial perturbation is reinforced and amplified. On the other hand, (**negative**) **stabilizing** *feedback mechanisms* occur when they dampen the initial disturbance/perturbation (DeAngelis *et al.* 1986). Therefore, in broader context, *tipping points* can refer "to any situation where accelerating change caused by a positive feedback drives the system to a new state" (Van-Nes *et al.* 2016).

The connection between *tipping points* and *resilience* is more easily observed when building *stability landscapes* (or ball-in-a-cup diagram) using the concept of *basins of attraction* (Fig. 24.B2a, b) (Scheffer *et al.* 2001; Strogatz 2015). In this sense, theoretically *resilience* can be qualitatively understood as the size of the *basin of attraction* (valleys on Fig. 24.B2a). Each cross-section of the ecosystem state *vs.* conditions
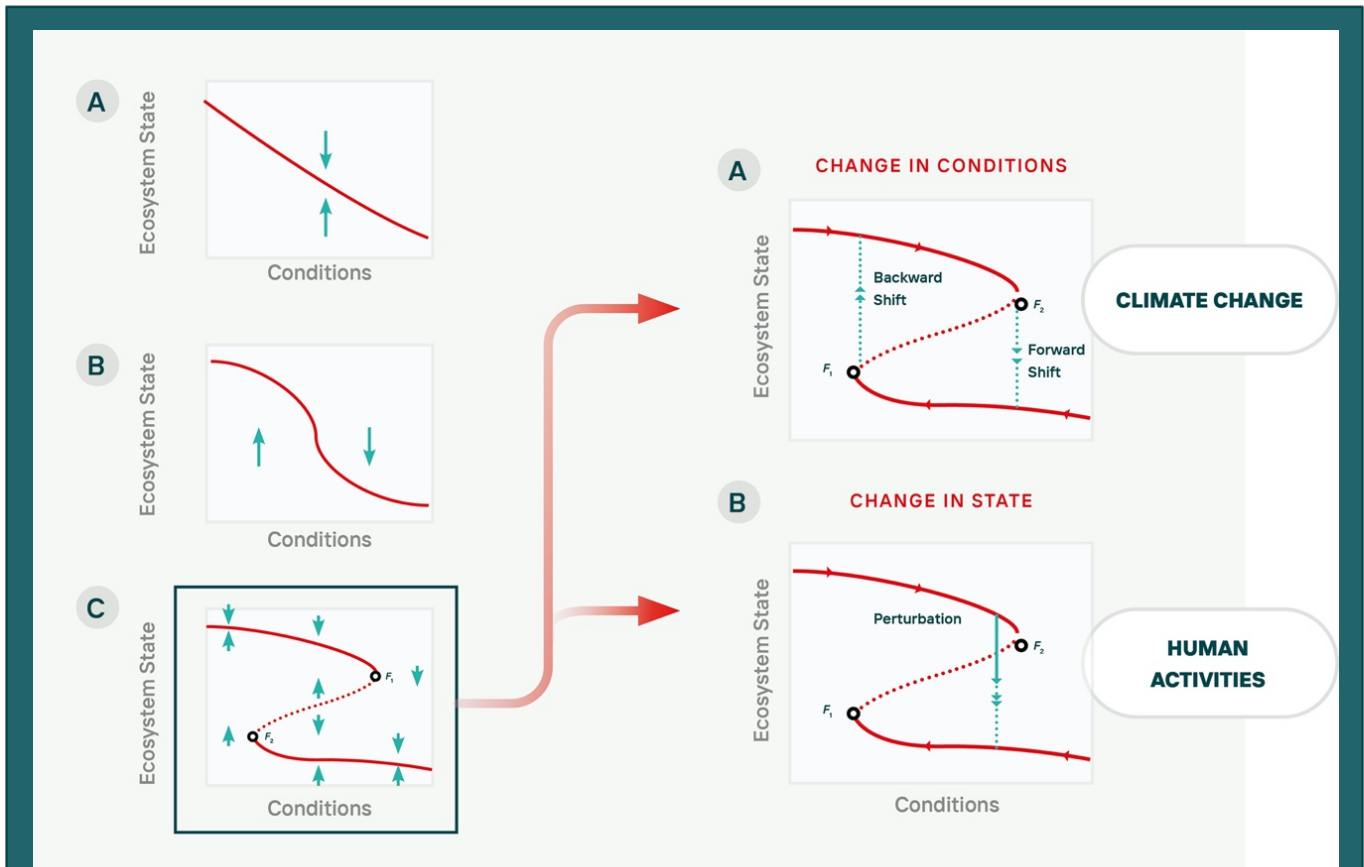
Figure 24.B1 (Left panels) Linear and nonlinear responses of ecosystem state (y-axis) depending on underlying conditions (x-axis). (Right panels) Illustration of how catastrophic shifts can occur under changes in conditions (e.g., climate changes) and in the state variable (e.g., human activities). Modified from Scheffer *et al.* (2001).

graph corresponds to a different *stability landscape*, showing potential *alternative stable states* and the **size** of the *basin of attraction* separating them. Particularly, for tropical forests, Fig. 24.B2b shows five condition cross-sections (for increasing precipitation): 1) only a treeless state, i.e., only one *basin of attraction* representing one state possible; 2) two *alternative stable states*, namely treeless and savanna, with a higher resilience (deeper valley) associated with the treeless state; 3) and 4) forests and savannas as *alternative states* with higher forest resilience related to higher levels of precipitation; 5) only forests as a stable state with the highest levels of precipitation. Note that this diagram shows only precipitation as a driving condition. We can go further and think about changes in the conditions or in the ecosystem state (Fig. 24.B1) using this type of diagram (Figs. 24.B2c-e).

For instance, increases in the frequency of extreme droughts and/or in dry season length could **erode** the *basin of attraction* of the forest state, i.e., forests lose resilience up to a point that a relatively lower-intensity drought could trigger a shift towards another *basin of attraction* easier than if climate change impacts would not occur (Fig. 24.B2d). Human-induced changes affecting the ecosystem state directly (e.g., wildfires or deforestation) would provoke a state flip independently on whether forests had lost resilience or not (Fig. 24.B2e).
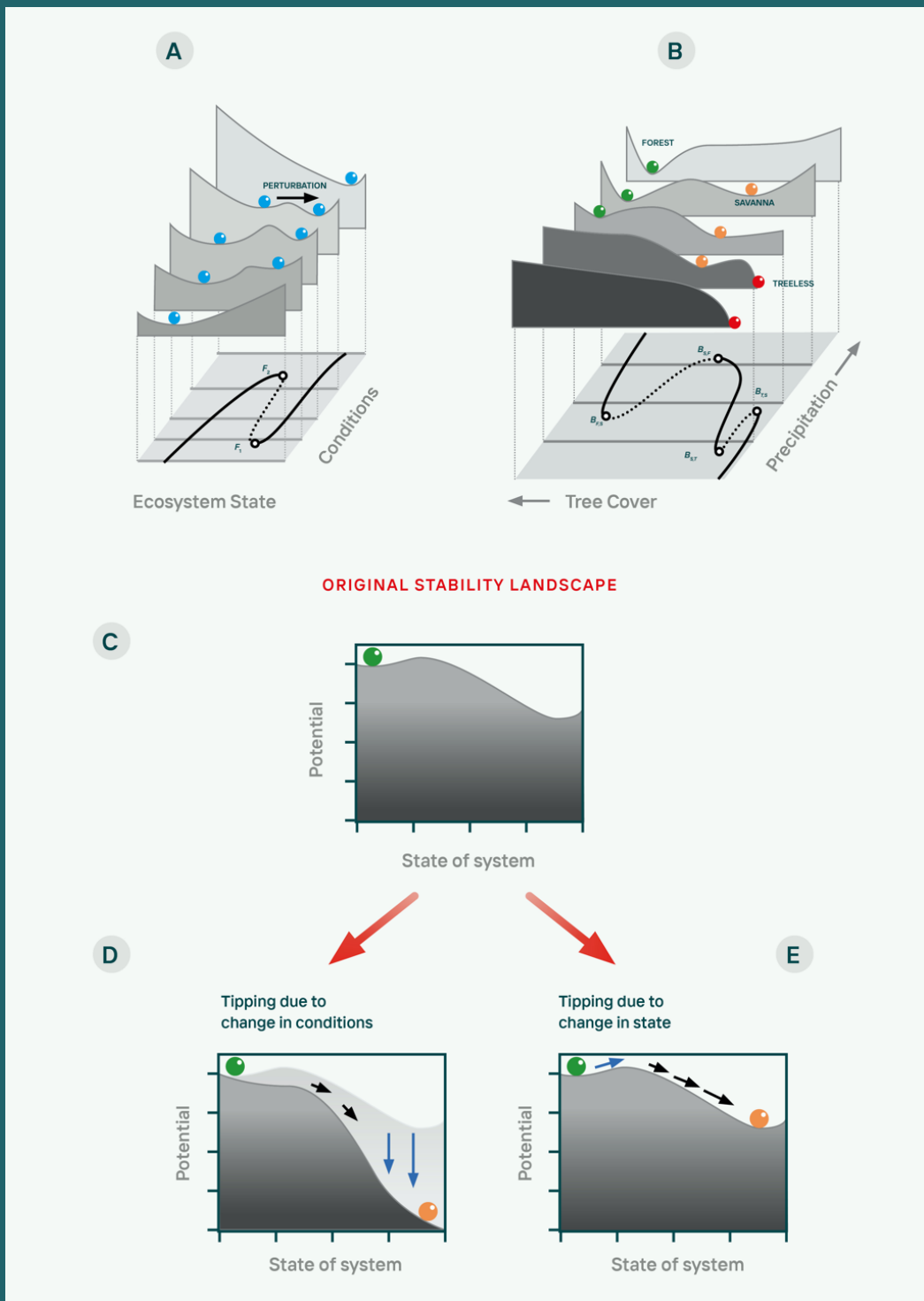
Figure 24.B2 The connection between *tipping points* and *resilience* using *stability landscapes*. Modified from Scheffer *et al.* (2001); Hirota *et al.* (2011); van Nes *et al.* (2016).

Based on the ball-in-a-cup diagram, we use the qualitative definition of resilience as the capacity of the Amazon region to persist as a tropical rainforest, maintaining similar interactions and functioning, despite being constantly pushed away from its stable states by disturbances and perturbations (Holling 1973).

for such shifts at the local scale is lacking, mostly because disturbed forests are commonly invaded by alien grasses (see section 22.2.3) instead of native grass species from South American savannas (Veldman 2016). This happens particularly in landscapes where forest is converted into pastures; invasive grasses escape and become dominant in disturbed forests. Nonetheless, far from the agricultural frontier ("arc of deforestation"), and far from small-scale pastures at the core of the Amazon forest system, black water floodplain forests disturbed by wildfires are being replaced by native savanna vegetation (Flores and Holmgren 2021) (Figure 24.3). In floodplain landscapes of the Rio Negro, fires are highly destructive, killing practically all trees, and allowing the ecosystem to shift to a savanna state within only 40 years. After the first wildfire, soils start to change from clayey to sandy, while tree composition shifts from forest to white-sand savanna species, and the herbaceous community remains dominated by native opportunistic plants (Flores and Holmgren 2021). This local abrupt shift from forest to white-sand savanna seems to be driven by repeated wildfires and a strong flood erosion mechanism that alters plant-soil interactions, favoring savanna species. Previous analyses at the basin scale have shown that these floodplain forests are less resilient than upland forests (Flores *et al*. 2017), including in the watersheds of large white-water rivers, such as the Madeira and Solimões. Hence, as in other forest-savanna transition zones, evidence suggests that savannas of the Amazon system may expand and persist due to feedback mechanisms involving repeated wildfires and soil erosion processes (Flores *et al*. 2020; Flores and Holmgren 2021).

24.2.3 Forest shift to an open-canopy, degraded state

When forests are repeatedly disturbed and native savanna species are not able to colonize, the ecosystem often becomes trapped in an open-vegetation state, dominated by fire-tolerant tree and palm species that usually occur in the forest, together with invasive alien grasses and opportunistic herbaceous plants (Perz and Skole 2003; Veldman and Putz 2011), as well as vines and lianas (Tymen *et al*. 2016; Maia *et al*. 2021; Medina-Vega *et al*. 2021) (Figure 24.3). Below, we describe the feedback mechanisms that have been proposed to explain how the ecosystem can be trapped in this state.

Numerous disturbances that open the forest structure immediately increase light availability at ground level, allowing herbaceous plants to invade (Cochrane and Schulze 1999; Silvério *et al*. 2013; Longo *et al*. 2020). Satellite observations of fire occurrences from across the global tropics reveal that when tree cover is reduced below 50%, ecosystem flammability rises steeply (van Nes *et al*. 2018). Because most trees in the Amazon forest are fire-sensitive, repeated fires often kill most of the tree community (Cochrane and Schulze 1999; Barlow and Peres 2008; Balch *et al*. 2011; Brando *et al*. 2012; Staver *et al*. 2020), particularly the younger individuals, reducing tree recruitment (Balch *et al*. 2011). As a result, disturbances that reduce forest cover below this threshold may cause the ecosystem to be trapped in an open-canopy state by repeated wildfires. Such consequences have been reported in multiple studies in the Amazon, showing that shifts to an open-canopy degraded state are already occurring (Barlow and Peres 2008; Brando *et al*. 2012; Flores 2016).

Other feedback mechanisms are also known to contribute to this ecosystem shift at the landscape scale. For instance, the expansion of invasive alien grasses may also directly reduce tree recruitment due to light competition with young seedlings (Hoffmann *et al*. 2004), which maintains low tree cover and grass dominance. Forest loss, degradation, and fragmentation inhibit the movement of many mobile animal species, particularly the ones that are sensitive to open habitats (Laurance *et al*. 2004), causing many species to disappear from the system (Barlow *et al*. 2016). In the case of frugivore species, by avoiding the use of open disturbed habitats, tree seed dispersal in those sites may become limited, reducing tree recruitment and forest regrowth. This dispersal limitation feedback is expected to be stronger where disturbances are most severe (Turner *et al.* 1998). Evidence from the trop-

ical Atlantic Forest suggests that 30% tree cover could be a threshold in which many forest adapted animal species disappear, and are replaced by disturbance-adapted species (Banks-Leite *et al.* 2014), potentially disrupting plant-animal interactions that are critical for forest recovery.

The current expansion of open-canopy degraded ecosystems across vast portions of the southeastern Amazon forest is triggering other types of feedback mechanisms at the regional and global scales. Forests play a major role in maintaining the rainfall regime of the Amazon by allowing moisture that originates in the Atlantic Ocean to be transported across the basin; a process that may involve up to seven cycles of rainfall and re-evapotranspiration (Spracklen *et al.* 2012; Zemp *et al.* 2017; Staal *et al.* 2018; see also Chapter 7). Hence, by interrupting this process, deforestation and forest degradation will likely reduce rainfall at the central and western Amazon, with stronger potential impacts, particularly during the dry season. This process also involves a feedback between drought and deforestation that is already strengthening with accumulated deforestation, in which the more forest area is lost, the stronger the dry seasons will be, further increasing deforestation rates (Staal *et al.* 2020) and forest fires (Xu *et al.* 2020). In addition to its effects on precipitation, deforestation also affects regional temperatures, with fragmented landscapes being considerably hotter than non-fragmented ones (Zeppetello *et al.* 2020). Due to this large-scale feedback, a tipping point (5) has been proposed to cause major forest dieback within the Amazon basin (Nobre *et al.* 2016; Lovejoy and Nobre 2019). A previous model study had estimated this deforestation tipping point at 40% (Sampaio *et al.* 2007), yet, recent evidence based on a climate-vegetation model that accounts for the combined effects of climate change, deforestation and wildfires (Nobre *et al.* 2016; Lovejoy and Nobre 2019), suggests that this threshold might indeed be closer to 20-25%. In sum, considering these broad-scale interactions, the more Amazonian forests become trapped in an open-canopy degraded state, the more likely that a 20-25% threshold is sufficient to accelerate a critical sys-

temic transition.

24.2.4 Forest shift to a closed-canopy, secondary forest state

Different from the previous cases, in which the forest is trapped in a contrasting open-canopy state, here, disturbed forests recover their closed-canopies but do not progress towards a mature forest state. Instead, they persist in an early successional stage, trapped by different feedback mechanisms (Figure 24.3). Such secondary forests may not be identified through satellite monitoring of canopy conditions, as high levels of greenness and leaf area index may be interpreted as if the ecosystem has recovered its original forest state; however, aspects such as biodiversity and carbon storage would remain at much lower values (Poorter *et al.* 2016; Rozendaal *et al.* 2019). In the Brazilian Amazon, for example, around 23% of previously deforested land is currently covered by secondary forests (INPE and EMBRAPA 2016), but the ecological state of regrown vegetation is unknown.

Under optimal conditions, during regrowth, environmental conditions in the understory gradually change along with species taxonomic and functional composition, in a transition from an open-canopy state with light-demanding species towards a closed-canopy state with mature-forest species. With time, species diversity increases and plant-animal interactions recover complexity and biomass (Poorter *et al.* 2016; Rozendaal *et al.* 2019). Nonetheless, secondary forests are almost two times more likely to be cleared for land use than mature forests, possibly due to lower governmental restrictions and higher accessibility (Wang *et al.* 2020). As a result, most secondary forests are cleared again before 20 years of regrowth (Chazdon *et al.* 2016; Jakovac *et al.* 2017; Schwartz *et al.* 2020). Such feedback causes secondary forests to persist in the landscape only at an early-successional state (Barlow and Peres 2008).

A combination of socio-economic and biophysical factors defines where and when forests recover their previous state in terms of structure and com-

position. Within the traditional shifting cultivation systems that dominate riverine landscapes of the Amazon, forest regrowth constitutes the fallow period that supports repeated crop yields, being an essential element of the rotational system. In contrast, throughout the extensive pasturelands that dominate Amazonian landscapes in the "arc of deforestation", forest regrowth constitutes an obstacle to pasture productivity and is often managed with prescribed burning. Eventually, regrowth may occur in abandoned areas when landowners do not have the means to continue managing the land or when land productivity is reduced by soil degradation (Vieira *et al.* 2014; Nanni *et al.* 2019). Therefore, feedback mechanisms between social and ecological elements partly determine whether the ecosystem will become arrested in a closed-canopy secondary forest state.

The capacity of secondary forests to fully recover depends on the management practices applied prior to the abandonment and on the landscape context where it occurs (Jakovac *et al.* 2021). Repeated fire use to clean pastures and fertilize cropping fields reduces soil fertility and consequently the rates of forest recovery, particularly when return-intervals between slash-and-burn events are shortened (Zarin *et al.* 2005; Jakovac *et al.* 2015; Heinrich *et al.* 2020). Under a high disturbance regime, survival strategies are favored over growth strategies and a plant community with conservative traits is more likely to thrive. Survival traits include high sprouting ability and low nutrient demand (Jakovac *et al.* 2015), high wood density and high leaf toughness (Fernandes Neto *et al.* 2019), all of which are traits associated with resistance to disturbance and often with slow growth rates (Poorter *et al.* 2010). Lianas and grasses are also favored by disturbances (Roeder *et al.* 2010; Veldman and Putz 2011), contributing to arrest succession by competing with trees and leading to reduced growth rates and higher tree mortality (Schnitzer and Bongers 2002). Combined, these feedbacks impede forest succession, maintaining lower basal area, biomass, canopy height, and species diversity, as well as higher density of stems, lianas in the canopy, and grass cover in the understory (see also

Chapter 19).

Furthermore, forest fragmentation associated with deforestation limits tree seed dispersal, reducing tree recruitment (Arroyo-Rodríguez *et al.* 2015), representing another amplifying feedback that can hinder secondary forest succession. The seed rain in such landscapes is mainly composed of early successional pioneers dispersed by wind or by generalist seed dispersers such as bats and birds that are able to cross large extents of pasture or cropping fields (Cubiña and Aide 2001; Wieland *et al.* 2011). Overhunting in degraded forests embedded within human-modified landscapes further contributes to reduce the availability of animal dispersers and increase dispersal limitation (Bagchi *et al.* 2018). The slow inputs of seeds from mature forests results in consistently slow species accumulation over time and therefore a slow species turnover during regrowth (Mesquita *et al.* 2015).

In sum, different combinations of drivers and feedback mechanisms can cause Amazonian forests to be trapped in different configurations, some of which are alternative states (Box 24.1). Shifts to the abovementioned alternative configurations may occur locally, but depending on the scale of the feedbacks, they may become contagious and spread disturbances across large parts of the basin, increasing the probability of a systemic forest dieback. Moreover, other types of configurations are possible, such as the bamboo-dominated (*Guadua sarcocarpa*) forests of the southwestern Amazon that self-perpetuate facilitated by fire feedback; however, we have focused on four general types that are more likely to expand in the coming future.

24.3 Past Evidence of the Dynamics of Amazonian Ecosystems Since the Last Glacial Maximum (20 Ka)

Studies focusing on past vegetation changes have documented several of the forest change scenarios outlined in section 22.2 (see also Chapters 1 and 2). For instance, an expansion of savannas in the northeastern portions of the basin during a climat-

ically unstable period with increasing temperatures was registered at the beginning of the Holocene, i.e., approximately 11 ka (Rull *et al.* 2015). However, the changes observed in sedimentary archives have not always shown a change towards savannization, but depended on the nature of the environmental driver. For instance, pollen analysis revealed a rainforest expansion during the last 3,000 years in forest-savanna boundaries of the southern Amazon, driven by wetter conditions related to changes in the location of the intertropical convergence zone (Mayle *et al.* 2000). Hence, under wetter conditions, these forests have likely reached their maximum potential southern limit for the past 50 ka (Mayle *et al.* 2000), with a 22% increase in the CO_2 storage budget since the mid-Holocene (6 ka) (Mayle and Beerling 2004). Given the historical observations registered during the last decades (see Chapter 22), the climate projections forecasted for this region towards drier conditions (Magrin *et al.* 2014), and the current levels of human impacts, it is unlikely that this forest expansion and consequent increased carbon sequestration will continue. Instead, combined evidence suggests that these forests are more likely to recede, being replaced by open vegetation types.

Empirical data of long-term forest dynamics have shown the differential sensitivity to past climate change across the Amazon basin. Regions like the southern and southeastern Amazon have shifted between forest and open savanna vegetation in relatively recent periods of colder and drier LGM climate (Absy and Hammen 1976), whereas the Andean flank in the western (van der Hammen and Absy 1994) and eastern portions of the Amazon (Wang *et al.* 2017) seem to have persisted as forest. Long-term ecological data from pollen analysis have shown the prevalence of various types of rainforests, both in the southwestern cloud forests and northwestern pre-montane forests of the Amazonian highlands, showing the importance of cloud cover in buffering forests when facing climate change (Urrego *et al.* 2010; Montoya *et al.* 2018). The presence of forests with distinct composition during the LGM has also been observed in the northwestern Brazilian Amazon (Bush *et al.* 2004;

D'Apolito *et al.* 2013). This regional evidence of a persistently forested Amazon are consistent with large-scale speleothem analyses showing a remarkable stability of the Amazon rainforest for the past 45 ka, even under a 60% decrease in precipitation totals (Wang *et al.* 2017).

The Mid-Holocene Dry Event (MHDE; 9-4 ka) has been proposed as a potential past analog of current and future trends of decreased precipitation, yet there is still limited evidence covering the entire duration of MHDE throughout the basin. Currently available paleo-records, however, suggest a higher vulnerability of tropical forests to extended droughts in peripheral transitional zones (Mayle and Power 2008; Smith and Mayle 2018). In addition, changes in plant functional traits spanning the termination of the MHDE (i.e., a period of increasing rainfall amount) suggest that rainfall increases led to a replacement of slow-growing, drought-tolerant taxa by fast-growing, drought-vulnerable taxa (van der Sande *et al.* 2019). Indeed, secondary forest species usually differ in their ecological strategies from mature forest species, changing the forest functioning and stability. In southeastern Venezuela, for instance, rainforest taxa were replaced by secondary dry forests around 2.7 ka, a shift that persisted for more than 1,000 years. These secondary forests were finally replaced 1.4 ka under a period of high fire occurrence by the current vegetation consisting of open savanna (Montoya *et al.* 2011).

When a forest is disturbed, the rates of ecosystem change observed in sedimentary archives depend on the ecological scale, being abrupt (decadal) at the species level, but gradual (centennial) at the community level (Montoya *et al.* 2018, 2019). In a tropical meta-data analysis of forest recovery rates after disturbances based on pollen records, Cole *et al.* (2014) observed that South American forests required an average of 325 years to recover from disturbances (natural and human-induced). The recovery rate was calculated in terms of attaining a forest cover (expressed in % of tree pollen) similar to that prior to the disturbance, without differentiating changes in the forest composition, structure,

or function. Forests exposed to natural, large, infrequent disturbances (i.e., hurricanes or volcanic eruptions) recovered faster compared to those affected by post-climatic and human impacts. However, forests exposed to more frequent disturbances usually recovered faster, suggesting that repeated disturbances may increase forest adaptive capacity and resilience, yet over multi-centennial time scales (Cole *et al*. 2014). In the Andean Amazon region, Loughlin *et al*. (2018) studied lands that were managed by Indigenous populations, but following European conquest, forests recovered structurally (not compositionally) in only 130 years, possibly because the higher soil productivity of this region boosted tree growth. Despite differences in these estimates, both studies manifest that the temporal range required for forests to potentially recover is multi-centennial (Cole *et al*. 2014; Loughlin *et al*. 2018).

In summary, paleoecological evidence hints at two main directions. Firstly, the Amazon forests have undergone local to regional shifts to dry secondary forests or savannas depending on the disturbances at play (climate- or human-induced changes), but not a basin-wide abrupt dieback, even during intense drier and warmer periods that could well represent analogs of the hypothesized climate-related tipping points (1) – (4). Secondly, the recovery ability of Amazonian forest ecosystems depends on their disturbance histories; the more disturbance-adapted, the faster the recovery rates. Nevertheless, long-term ecological data are still limited in the basin and concentrate primarily along the Amazon's margins; more work is still needed to unravel the dynamics of such heterogeneous ecosystems (Lombardo *et al*. 2018). In addition, some important caveats need to be addressed when using paleo-data as reference for future dynamics: (1) the rates and magnitudes of the changes projected for the near future, with combined disturbance events (climatic and human-induced) acting synchronously, are unprecedented and may hamper forest recovery due to novel mechanisms; and (2) the baseline conditions we have shown are no analog of ecophysiological drivers such as the enhanced

atmospheric CO_2 concentrations of the 21st century (section 22.5.3).

24.4 Drivers of Amazon Forest Resilience

Across the Amazon forest system, biotic diversity and abiotic heterogeneity promote a huge variety of responses to disturbances such as extreme droughts and wildfires (Feldpausch *et al*. 2016; Longo *et al*. 2018). This spectrum of responses affects the balance between plant growth, survival, and mortality, and therefore, the resilience of ecosystems. Below, we discuss the main environmental factors that affect plant growth and mortality at different spatial and temporal scales.

The resilience of the Amazon forest is directly linked to the functional characteristics of individual trees and their capacity to resist adverse conditions and disturbances. Thus, processes that exert pressure on the capacity of trees to maintain their functioning and survival are critical. Water deficit associated with increasing length of the dry season or extreme droughts (i.e., related to *tipping points* (2) and (3), section 22.2), is likely to be the major climatic threat to Amazonian trees, as suggested by observational and experimental studies, showing that droughts increase tree mortality rates of individual trees (Nepstad *et al*. 2007; DaCosta *et al*. 2010; Phillips *et al*. 2010; Rowland *et al*. 2015; Zuleta *et al*. 2017; Aleixo *et al*. 2019; Janssen *et al*. 2020b). At least 50% of the Amazon forest is exposed to seasonal droughts of three months or more (Nepstad *et al*. 1994), and contrasting rainfall regimes have selected species with different drought resistance mechanisms (Oliveira *et al*. 2021; Barros *et al*. 2019; Brum *et al*. 2019). In many cases, extreme drought events may not necessarily cause the death of trees, but reduce their growth and capacity to maintain transpiration rates. However, a recent meta-analysis of field observations reveals that highly diverse Amazonian tree communities seem to buffer this effect, conferring higher ecosystem resistance in terms of evapotranspiration rates (Janssen *et al*. 2020a).

Examples of functional characteristics of Amazonian trees to cope with seasonal water deficit include: (1) investment in deep roots (Nepstad *et al.* 1994; Brum *et al.* 2019); (2) roots that allow hydraulic redistribution during the dry season (i.e., passive movement of water from deep to shallow soil through roots) (Oliveira *et al.* 2005); (3) high embolism resistance, particularly in shallow-rooted understory trees and trees over plateaus far away from the water table (Oliveira *et al.* 2019; Brum *et al.* 2019); (4) strong stomatal control in the dry season resulting in high water use efficiency (Barros *et al.* 2019; Brum *et al.* 2019); (5) leaf shedding capacity by deciduous species (Wolfe *et al.* 2016). Although these traits do not guarantee survival under the increasingly drier and variable climates of the future, in locations where the dry season has been intensified, changes in forest composition dynamics are already underway through the recruitment of more dry-affiliated species and the mortality of more wet-affiliated species (Esquivel-Muelbert *et al.* 2019). Also, life-history strategies (e.g., fast-slow continuum in growth rates) have been shown to determine species-level mortality, i.e., the faster you grow, the higher is the mortality risk (Esquivel-Muelbert *et al.* 2020).

There is also evidence that temperature changes (see Chapter 22; Figure 2e) could already be changing forest functioning. Warmer temperatures tend to reduce forest productivity rates (Sullivan *et al.* 2020), particularly by intensifying the atmospheric vapor pressure deficit (Smith *et al.* 2020), indicating that rising temperatures may eventually impact forest functioning and persistence (Araújo *et al.* 2021). Additional CO_2 is expected to buffer the effect of water stress by increasing plant water-use efficiency and accelerating tree growth (section 22.5.3). Elevated atmospheric CO_2 may be the cause of the increase in woody biomass and productivity observed across Amazonian forests (Brienen *et al.* 2015), favoring fast-growth species (Esquivel-Muelbert *et al.*, 2019). However, elevated atmospheric CO_2 driven accelerations of tree growth have come at the cost of decreasing tree longevity across the basin, further contributing to increased tree mortality rates (Brienen *et al.* 2015;

Hubau *et al.* 2020). The acceleration of the system via CO_2 fertilization may allow trees to reach the canopy earlier and be more vulnerable to death (Brienen *et al.* 2020), and particularly vulnerable to water deficits (Oliveira *et al.* 2021).

Despite the uncertainties regarding forest responses to climate change, current findings suggest that, in the absence of fire, Amazonian forests may change both compositionally and functionally in response to climatic changes, but still remain as closed-canopy forests. Furthermore, if climate-related *tipping points* (2) − (4) (section 22.2) are crossed, shifts are likely to be sparse and local because of the high heterogeneity and diversity of forest types. Increased tree mortality caused by human-induced disturbances (e.g., wildfires and deforestation), however, may contribute to destabilize the Amazon forest (Silva *et al.* 2018), increasing the likelihood that forests will be trapped in an open-canopy degraded state, and that the system as a whole will cross the *tipping point* (5) (section 22.2.3).

24.5 Uncertainties Associated with Tipping Points within the Amazon System

24.5.1 How does forest heterogeneity affect large-scale tipping points?

Amazonian forests are home to more than 15,000 tree species (ter-Steege *et al.* 2020; Chapters 3 and 4). Most of these species are rare, and many remain unknown to science (ter Steege *et al.* 2013), implying that this huge diversity imposes an enormous challenge to the understanding of how the system functions. In particular, dominant species are responsible for most of the ecosystem functions, such as carbon cycling (Fauset *et al.* 2015). Yet, the many non-dominant and rare species that exist in a forest theoretically also play a fundamental role in ecosystem resilience (Walker *et al.* 1999). When stressing conditions and disturbance regimes change, these rare species can offer new possibilities of functioning, thus increasing the capacity of the ecosystem to adapt and persist (Elmqvist *et al.* 2003). For instance, if a tree species is rare in wa-

terlogged forests, but common on drier climatic conditions, due to adaptations such as deep roots, it could emerge as a dominant species if the climate becomes drier. As a general rule, species diversity is therefore expected to increase the resilience of Amazonian ecosystems. First, because diversity has a positive impact on forest productivity (Coelho de Souza *et al.* 2019) and carbon storage (Poorter *et al.* 2015), potentially accelerating regrowth after disturbances. Moreover, as the number of species is related to the number of strategies and potential responses to disturbances, diversity increases stability at the community and ecosystem levels, and the overall forest resilience (Elmqvist *et al.* 2003; Sakschewski *et al.* 2016; Anderegg *et al.* 2018). For instance, disease and herbivore outbreaks have been causing large-scale tree mortality in temperate regions, yet such events have not been observed in the tropics, likely because the high species diversity of tropical ecosystems reduces the spread of contagious diseases. Drought-tolerant species are often distributed across a vast range of precipitation conditions, hence they may occur as rare species in the wet parts of the basin (Esquivel-Muelbert *et al.* 2016). This pattern implies that if climate becomes drier in the more diverse wet forests, drought-affiliated species may already be present and could increase in abundance, maintaining forest cover, while altering forest functioning.

Rainfall variability (intra- and inter-annual fluctuations) may also add more heterogeneity to the system, as forests that experience more variability seem to be more resilient, likely due to a training-effect after experiencing multiple wet and dry periods (Ciemer *et al.* 2019). For instance, tree communities embedded within a more seasonal rainfall regime are more diverse in terms of their tolerance strategies to cope with drought, when compared to communities within a less seasonal rainfall regime (Barros *et al.* 2019). In other words, while higher mean annual precipitation (above 2,500 mm/yr) increases forest resilience (e.g., the northwestern Amazon; Hirota *et al.* 2011; Staver *et al.* 2011), forests exposed to higher seasonality and interannual variability seem to be more resilient to

intermediate mean annual precipitation values (between 1,300 and 1,800 mm/yr), compensating the lower resilience (e.g., eastern x northwestern forests). Valley forests may also be less resistant to droughts than plateau forests due to a similar mechanism, due to a training-effect related to water table fluctuations selected for tree communities with contrasting hydraulic traits (Zuleta *et al.* 2017; Cosme *et al.* 2017; Oliveira *et al.* 2019). Nonetheless, *tipping point*s (2) and (3), related to dry season increases in length and intensity, imply that in forests where the climate is already drier, increases in rainfall seasonality could potentially cause forest loss. Also, increases in the frequency of extreme drought events may prevent proper forest recovery (Anderson *et al.* 2018; Longo *et al.* 2018).

Another heterogeneity that may affect the probability of *tipping point* (1) (1,000 mm/yr; section 22.2) is related to seasonal flooding. Amazonian floodplains cover around 14% of the basin and the forests in these ecosystems were shown to be less resilient than the dominant upland forests, with a potential tipping point of forest collapse when annual mean precipitation reaches approximately 1,500 mm/yr (Flores *et al.* 2017). Therefore, exploring the sources of heterogeneities in forest responses to different types of disturbances is key to understanding whether the Amazon could shift gradually or abruptly from local to basin-wide scales (e.g., Higgins and Scheiter 2012; Levine *et al.* 2016).

24.5.2 How does forest connectivity affect large-scale tipping points?

Spatial heterogeneity implies reduced connectivity (fewer interactions) and may have a huge influence on the systemic resilience of the Amazon, altering how the forest responds to changes in climate and human pressures (Levine *et al.* 2016; Longo *et al.* 2018). For instance, the climatic, hydrological, and biogeochemical connections between the Andes and the low-lying Amazon are undeniably key factors in determining the functioning of the entire system, current and future, on the large scale (see Chapters 5, 7 and 22; Builes-Jaramillo and Poveda 2018). Nonetheless, theoretically, connectivity

may still be high even in heterogeneous environments, with different processes linking parts of the system (Scheffer *et al.* 2012). Although forests with contrasting geomorphological, climatological, biological, and cultural histories have formed the Amazon (see Chapters 1-13; Figure 24.1), these forests can interact. For instance, biogeochemical cycles involve fluxes that transport water vapor from plateau to valley forests on a landscape scale. At broader scales, large white-water rivers transport huge loads of nutrient-rich sediments from the west to the east of the basin (see Chapters 1, 3 and 4), depositing them along floodplains where forests can grow faster. Eastern Amazonian forests are also connected to western forests through rainfall recycling (Zemp *et al.* 2017, see also Chapter 7); a mechanism that enhances the resilience of western forests but may be losing strength due to deforestation (Staal *et al.* 2020). When a forest is disturbed locally, mobile animals may transport tree seeds and propagules from surrounding forests and accelerate its recovery (Lundberg and Moberg 2003). However, mobile animals may also transport the seeds of alien invasive grasses from open areas to degraded forested landscapes, increasing their flammability. Local human populations of different Amazonian regions may share ancient knowledge of forest management practices (Levis *et al.* 2018, see also Chapters 8 and 10), potentially changing tree species composition and reshaping forest resilience.

In sum, connectivity may theoretically increase systemic forest resilience, because spatial interactions facilitate recovery of disturbed sites, but as conditions change and disturbance regimes intensify, increasing, for instance, landscape fragmentation and wildfires, disturbances may become contagious, resulting in systemic collapse (Scheffer *et al.* 2012). Managing the various processes that connect different parts of the Amazon is therefore critical for enhancing its resilience.

24.5.3 The interplay between the CO_2 fertilization effect and nutrient availability

Two of the most pressing uncertainties regarding

the resilience of the Amazon forest to climate change and other anthropogenic disturbances are the potential physiological effect of increased atmospheric CO_2 (also known as the "CO_2 fertilization effect", eCO_2; see also Chapter 23) and the hypothetical limitations to forest productivity and biomass accumulation imposed by soil nutrient constraints, notably phosphorus (P). The current generation of ecosystem models (namely standard Dynamic Global Vegetation and Earth System Models), are constrained in their ability to provide more trustful projections on the impact of climate change on the forest, due mainly to the acute lack of evidence about the existence, magnitude, and duration of a CO_2 fertilization effect and associated limitations imposed by soil nutrients (Lapola 2018).

On the one hand, the CO_2 fertilization effect could, theoretically, increase forest productivity, biomass accumulation rates (Ainsworth and Long 2005), and water use-efficiency (Kauwe *et al.* 2013). On the other hand, the lack of key nutrients for plant metabolism constrains further biomass gains under elevated CO_2 conditions (Norby *et al.* 2010). There are preliminary (i.e., short-term) indications from other phosphorus-limited forests (in sub-tropical Australia), subjected to increased atmospheric CO_2 concentrations, that did not significantly increase biomass (Jiang *et al.* 2020) given that phosphorus is needed especially for making the cell membrane, and also for energetic (ATP) and genetic (DNA and RNA) plant molecules. As such, trees might increase their photosynthetic rates under enhanced CO_2 but do not allocate these extra photosynthates to additional plant biomass, possibly simply increasing biomass turnover rates across the forest ecosystem. Nevertheless, this evidence comes from single-species forests and the response of highly diverse forests such as the Amazon to enhanced CO_2 is yet to be understood. In this sense, observational data along a P availability gradient in Panamanian tropical forests revealed that, although such P limitation exists, it does not affect different species in the same way (Turner *et al.* 2018). This latter finding is of particular relevance for the Amazon forest given that climate change

and other anthropogenic disturbances may imply significant alteration of the forest tree community composition and dominance relations, both in taxonomic and functional terms (Norby *et al.* 2016). Alternatively, it is hypothesized that Amazon forest trees could change symbiotic exchanges of carbohydrates and nutrients with mycorrhizae fungi to access currently unavailable soil P pools.

Besides the implications for the Amazonian forest carbon budget and functional diversity, the physiological effects of elevated CO_2 have the potential to interfere in the flux of humidity from trees to the atmosphere, which is especially relevant for the region, where up to 50% of the precipitation that falls within the basin is regionally recycled (Zemp *et al.* 2014). In that sense, free-air concentration enrichment (FACE) experiments in temperate forests in the United States and in an Eucalyptus-dominated woodland in Australia have found a reduction of stomatal conductance and canopy transpiration on the order of -20% (Kauwe *et al.* 2013; Gimeno *et al.* 2016). That is the same magnitude of reduction in transpiration found in recent coupled climate-vegetation modeling studies for the region, which is ultimately related to a basin-wide reduction of 15% to 20% in rainfall (Kooperman *et al.* 2018). Such a rainfall reduction possibly caused by the physiological effect of elevated CO_2 is equivalent to the rainfall reduction in a scenario with complete deforestation of the Amazon (Sampaio *et al.* 2020).

Without an enhancement of productivity and with a reduction of forest canopy transpiration due to increased atmospheric CO_2, the actual Amazon forest and its current community compositions and functional relations are thought to become less resilient to climatic changes, deforestation, degradation, and other anthropogenic disturbances, with pervasive impacts on the regional socio-economy (Lapola 2018). Two ongoing ecosystem-scale experiments - the AmazonFACE experiment and the Amazon Fertilization Experiment (AFEX) - will soon provide valuable information about the CO_2 fertilization effect and the limitation of forest productivity and biomass stocks by soil nutrients in the Amazon forest (Hofhansl *et al.* 2016).

24.6 Modeling the Resilience and Tipping Points of the Amazon Forest

For modelling the impact of global change on vegetation at scales as large as the Amazon basin, Dynamic Global Vegetation Models (DGVMs) and Land Surface Models (LSMs) are the most used tools (Sato *et al.* 2015; Fisher and Koven 2020). Those models are capable of simulating long time series of various pressures on vegetation and are therefore key to project the future of the Amazon system (e.g., White *et al.* 1999; Cox *et al.* 2004). Often DGVMs and LSMs are the vegetation component in Earth System Models (ESMs), and their success in comprehensively representing processes of vegetation growth and interactions with other Earth System components relies on empirically-derived evidence. This means those models need to make use of the information described in section 22.4. Given the extreme complexity involved in soil-plant-atmosphere interactions at different temporal and spatial scales, selecting the most relevant processes and implementing them into models are very challenging tasks (Fisher and Koven 2020), and leads to substantial uncertainties (e.g., Rammig *et al.* 2010).

Model simulations can be performed a) offline, meaning the vegetation model is driven standalone by externally generated climate data or b) coupled, meaning that the vegetation model is part of an ESM in which different compartments of the Earth System (e.g., the vegetation and the atmosphere) can interact. Such a coupling increases the amount of accounted feedback mechanisms (Box 24.1) which are theoretically necessary to identify *classical tipping points*, besides the prerequisite that the DGVM/LSM allows for the existence of two or more alternative vegetation cover configurations under the same underlying conditions (e.g., climatic; Box 24.1). For Amazonian ecosystems, tipping point simulations performed so far rely on both offline and coupled runs (*tipping points* (4) and (5) from section 22.2). Taking the inherent limitations of simulating alternative stable states into account, below we present a summary of what such models can already tell us about dieback, thresh-

olds (Box 24.1), and resilience within the Amazon basin.

About 20 years ago, modeling studies pointed to a potential Amazon dieback under climate change (White *et al.* 1999; Cox *et al.* 2000, 2004; Cramer *et al.* 2001; Oyama and Nobre 2003). Up to now a substantial amount of literature has painted a complex picture with key uncertainties regarding the resilience and potential tipping points of the Amazon under global and regional environmental changes. The results span from the clear identification of crossing tipping points in time, as represented by decreasing levels of tree cover or biomass stock (e.g., Cox *et al.* 2004; Sitch *et al.* 2008), up to an overall increase of biomass and forest cover (Schaphoff *et al.* 2006; Lapola *et al.* 2009; Rammig *et al.* 2010; Huntingford *et al.* 2013). Such a large variety of results can be explained by: 1) whether the DGVM/LSM was coupled (e.g., Cox *et al.* 2004); 2) the existing variety of underlying model assumptions and processes; and 3) general uncertainties on future climate changes in the region. Moreover, DGVMs and LSMs represent vegetation using a limited set of plant functional types (PFTs), which are still not capable of comprising the entire range of plant strategies that confer more or less resilience to Amazonian forests (Oliveira *et al.* 2021). In this sense, a more comprehensive representation of different vegetation ecosystems is needed to improve the simulation of the gradual and abrupt shifts to alternative configurations for the Amazon forests described in section 22.2. Hence, so far, there is a fairly binary possibility simulated by current models: either the current configuration or a complete replacement of forest by another vegetation type.

The main drivers behind this original modeled forest dieback (Cox *et al.* 2004) are acute reduction in regional rainfall, and a prolonged dry period, which affects photosynthetic rates and the accompanying increase in temperature that further increases plant respiration and water demand, resulting therefore in a considerable reduction of plant productivity and growth. The effects on carbon assimilation also impact the flux of water from the surface vegetation to the atmosphere through transpiration, reinforcing the moisture limitation and ultimately leading to a shift of PFTs, from predominantly tropical broadleaf trees to C_4 grasses with about 30% of broadleaf tree cover, resembling savanna vegetation (Betts *et al.* 2004; Cox *et al.* 2004). Even without acknowledging such feedbacks through coupling within ESMs, previous offline simulations support such "savannization" processes (section 22.2.2) under future scenarios of precipitation and temperature changes (Nobre *et al.* 1991; Oyama and Nobre 2003). Importantly, the feedbacks magnify the regional climate and vegetation response, and a long-term commitment to Amazon dieback occurs at 2°C global warming, determining an actual *tipping point* (4) from section 22.2 (Jones *et al.* 2009). Therefore, it is clear that the Amazon dieback is an issue about feedbacks (i.e., interactions within a closed-loop) between the regional climate and the forest vegetation functioning. In this sense, a key component is the regional climate response to global warming and the role of non- or dysfunctional forest states in magnifying this process; in other words, whether the regional climate moves from a configuration supporting the rainforest to another, which it does not. This depends on the availability of soil moisture, which itself depends on precipitation and evaporation, both of which change with global warming (see Figure 24.2 for historical and projected changes in some of these variables). If the regional climate reaches a critical state, the resulting forest dieback magnifies the regional climate change and causes further forest dieback.

However, as in many regions of the world, the projected changes in precipitation in the Amazon due to anthropogenic climate change are highly uncertain (e.g., Jupp *et al.* 2010). While the majority of the current generation of climate models project a decrease in annual mean precipitation with global warming (see Chapter 22), the rate of the Amazon precipitation decrease in relation to global warming varies widely between the models. A family of climate models notable for their projection of severe Amazon drying, HadCM3 (Gordon *et al.* 2000), project annual precipitation in the eastern Amazon
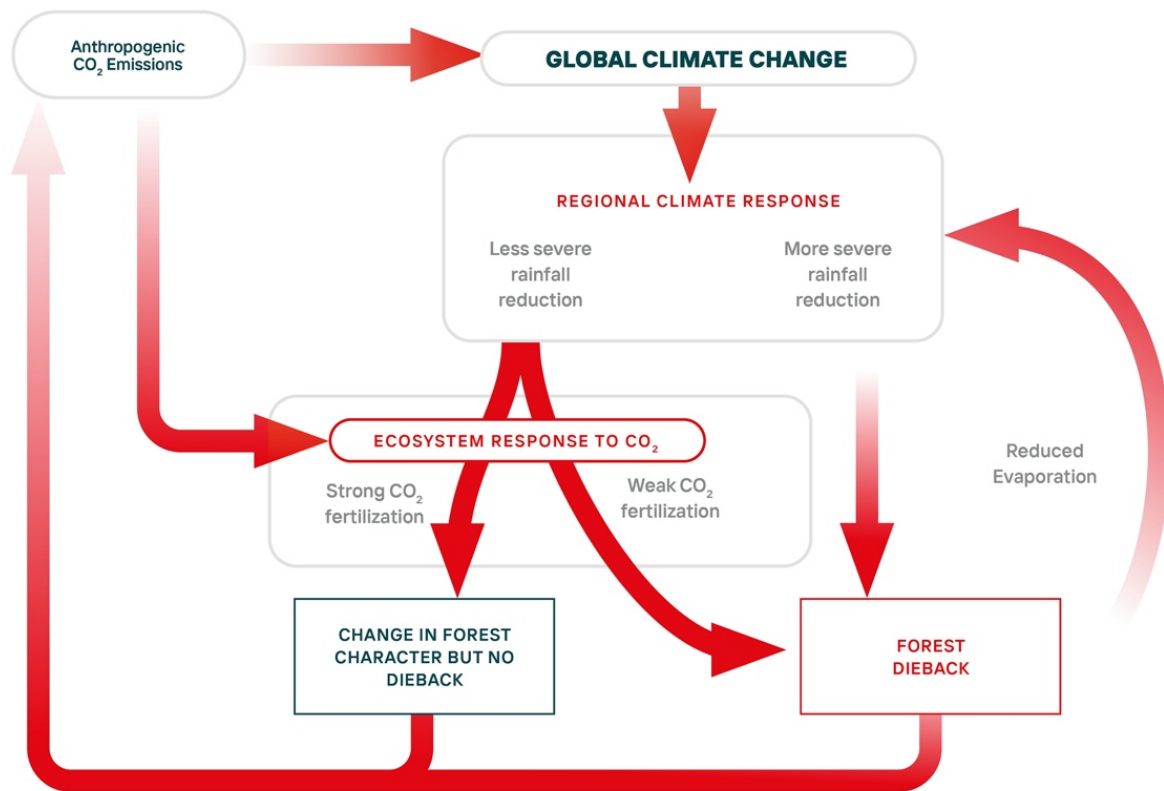
Figure 24.4 Simplified sketch of processes involved in the potential Amazon dieback tipping point due to climate change.

to fall below 1,500 mm/yr at approximately 3°C global warming (Betts *et al.* 2012). This precipitation level has been identified as one of the climatic thresholds critical to the support of rainforests (Malhi *et al.* 2009), with empirical evidence suggesting this seems to be the *tipping point* (1) for floodplain forests (Flores *et al.* 2017). The largest decrease in precipitation in the HadCM3 model family was largely a result of atmospheric circulation changes driven by particular patterns of sea surface temperature (SST) (Harris *et al.* 2008). The variation in precipitation change between the models was found to be related to the strength of the SST changes in the equatorial Atlantic (Good *et al.* 2008, 2013). Most other models also project decreased precipitation, but less severely.

On the one hand, there are three main underlying drivers to the aforementioned climatic changes that can trigger or reinforce a modeled threshold crossed in the region, even under less severe decreases in precipitation: global climatic changes

due to higher atmospheric greenhouse gas (GHG) concentration (Cox *et al.* 2004; Schaphoff *et al.* 2006; Lapola *et al.* 2009; Jupp *et al.* 2010; Huntingford *et al.* 2013), deforestation and forest degradation (Sampaio *et al.* 2007; Staal *et al.* 2020), and forest fires (Burton *et al.*; Barlow and Peres 2008; Cochrane and Barber 2009; Nobre *et al.* 2016). The occurrence of the climate tipping point for Amazon forest dieback projected in the models therefore depends partly on the nature of the regional climate response to global warming and the impact of CO_2 fertilization, wildfires, and deforestation (Figure 24.4). If the regional climate response is relatively small, forest dieback does not occur. However, if the regional climate response is large, forest dieback could in principle occur and magnify itself through local and global climate feedbacks.

Regardless of the feedbacks involved, after correcting for biases (found in climatic projections under climate change conditions) identified using observation data, a basin-wide Amazon dieback would

be unlikely to occur, even under the most pessimist IPCC pathway (Chai *et al.* 2021). Furthermore, there are some ecological processes that can potentially dampen, offset, or prevent Amazon dieback, namely the CO_2-fertilization effect under enhanced atmospheric CO_2 (section 22.5.3) (Hickler *et al.* 2008; Huntingford *et al.* 2013; Kooperman *et al.* 2018), the acclimation of tree physiology to warmer and drier climates (Kumaranthunge *et al.* 2018), as well as the reorganization of forest communities and/or their functional characteristics such that biomass and other broad characteristics that define crucial ecosystem functions are maintained (Sakschewski *et al.* 2016).

Processes related to functional diversity (e.g., Fyllas *et al.* 2014; Fischer *et al.* 2016; Sakschewski *et al.* 2016), including plant hydraulics (e.g., Christoffersen *et al.* 2016; Xu *et al.* 2016; Eller *et al.* 2020) and rooting depth (Langan *et al.* 2017; Sakschewski *et al.* 2020), have already started to be implemented in current vegetation models to improve the representation of local-scale heterogeneity of the Amazon basin and consequently the ability models have to capture resilience increases due to biotic and abiotic heterogeneity (section 22.5.1) (Levine *et al.* 2016; Sakschewski *et al.* 2016; Longo *et al.* 2018). Furthermore, models demand a high amount of observational, field-based, and/or experimental data, which are still scarce. Kooperman *et al.* (2018), for example, point out that stomatal closure under enhanced CO_2 (as part of the CO_2-fertilization effect) can drive significant modeled rainfall reduction in the Amazon through reduced forest transpiration and moisture recycling (Zemp *et al.* 2017), even though ecosystem-scale evidence on the interplay between enhanced CO_2 and stomatal conductance is very scarce. Adding to that complexity, other studies suggest that stomatal closure under enhanced CO_2 might not turn out to be as strong as anticipated by models, since leaves need to increase transpiration cooling under elevated temperatures (Dong *et al*. 2014). Another example is that modeled phosphorus limitation (existent in about 60% of Amazonian soils, Quesada *et al.* 2012; see Chapter 1) might reduce or even eliminate any gains in primary productivity arising

from a supposed CO_2 fertilization effect in the Amazon (Fleischer *et al.* 2019); but, again, there is lack of field data and knowledge on the Amazon phosphorus cycle to corroborate such a result (section 22.5.3).

As such, the way forward for modeling and evaluating the likelihood and mechanisms behind an Amazon tipping point passes first through a closer integration between models, data, and field experiments. Field data show us, for example, that community dynamics – tree recruitment and mortality – play a key role in the impact of climate change and climatic extremes in the Amazon (section 22.4) (Esquivel-Muelbert *et al.* 2019, 2020; Hubau *et al.* 2020). Thus, improving the representation of such recruitment and mortality dynamics and its driving causes is one priority for modeling. Other processes such as the role of plant hydraulics (Eller *et al.* 2018) and increased plant functional diversity (Scheiter *et al.* 2013; Sakschewski *et al.* 2016), as well as large scale heterogeneities related to climate, hydrology, and soil chemistry, for instance, should be explored in more depth by other models. The potential CO_2 fertilization effect on photosynthesis and water use and possible limitation of forest productivity by soil nutrients (section 22.5.3) represent a *quasi*-complete gap in existing models of the Amazon forest vegetation due to the lack of understanding of mechanisms and field data. Last, but not least, narrowing down the uncertainties of rainfall projections for the region would also be very important for better constraining modeling studies on the Amazon tipping point.

24.7 Conclusions

The pressure of intensified anthropogenic activities has promoted the appearance of new stressing factors operating in Amazonian forests, as well as an intensification of some environmental drivers at different spatial and temporal scales. It has been hypothesized that the cumulative effect of disturbances such as deforestation, droughts, and fires may unbalance the natural dynamics of these globally important ecosystems due to the systemic loss of forest resilience. The analysis of the existing lit-

erature performed in this chapter has highlighted five different scenarios of tipping points to which Amazonian forests could be sensitive (Figure 24.2), namely: (1) the annual rainfall between 1,000 mm/yr and 1,500 mm/yr inferred from global climate models, (2) the dry season length of seven months, inferred from satellite observations of tree cover distributions, (3) for the Amazon lowlands, the maximum cumulative water deficit values between 200 mm/yr and 350 mm/yr, inferred from global climate models; (4) an increase of 2°C on the equilibrium temperature of the Earth, inferred from a coupled climate–vegetation model, and (5) the 20-25% accumulated deforestation of the whole basin, inferred from a combination of environmental changes and human-induced degradation via deforestation. Based on empirical evidence, four different ecosystem configurations, some of which could be alternative stable states, have been proposed for Amazonian forests if a tipping point or threshold is crossed, including: (i) a closed-canopy seasonally dry tropical forest state; (ii) a native savanna state; (iii) an open-canopy degraded state; and (iv) a closed-canopy secondary forest state. However, due to the existence of novel feedbacks associated with invasive plants and human-modified landscapes, we consider the open degraded state and the closed-canopy secondary forest state as more likely to occur over broad areas, particularly across the "arc of deforestation". New evidence, however, indicates that in remote parts of the Amazon basin far from the agricultural frontier, the native savanna state could be replacing seasonally inundated forests disturbed by wildfires. Ecological features including differential tree growth, recruitment, and survival among Amazonian species are key to promote forest resistance to, as well recover from, disturbances at local scales. We identify three mechanisms that may affect the risk of a large-scale tipping point due to contagious forest dieback: (a) the environmental heterogeneity and connectivity among forests across the basin; (b) the functional diversity and adaptive capacity of the species present in the different forest types; and (c) the uncertain effect of enhanced CO_2 and nutrient limitation. The lack of this ecological information for many Amazonian

species, the uncertainty of the potential feedbacks operating, as well as the need for further improvements in climate change projections hamper the development of robust models for anticipating the potential shifts that Amazonian forests may undergo in the near future. The way forward for modeling and evaluating the likelihood and mechanisms behind an Amazonian tipping point passes first through a closer integration between models, observational data, and/or field experiments. Even with models where a tipping point is not met, and accounting for the uncertainty due to the limited data available, we need to urge the international community within and outside academia to protect, maintain, and sustainably manage the resilience of these complex and dynamic entities that are Amazonian forests.

24.8 Recommendations

- Combining analysis of future environmental change scenarios with past and present dynamics can help improve our understanding of alternative ecosystem configurations.
- A holistic and integrative scientific framework is needed to assess the main heterogeneities, drivers, and ways to manage the resilience of Amazonian forest systems.
- Understanding the heterogeneities of the Amazon is key to assessing the risk of a large-scale tipping point and to design ways to manage the resilience of the system.
- An effective transnational monitoring system is needed to improve our knowledge on the dynamics of different Amazonian ecosystems (embedded in a wider range of environmental conditions), and their potentially heterogeneous response to various types of disturbances (e.g., climatic extremes, wildfires, deforestation).
- Managing Amazonian resilience locally can help reduce the risk of reaching a tipping point. This requires protecting and restoring forest cover, biodiversity, agrobiodiversity, and cultural diversity, as well as controlling the use of fire.

24.9 References

Absy ML and Hammen T van der. 1976. Some palaeoecological data from Rondonia, southern part of the Amazon Basin. *Acta Amaz* **6**: 293–9.

Ainsworth EA and Long SP. 2005. What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. *New Phytol* **165**: 351–72.

Aleixo I, Norris D, Hemerik L, *et al.* 2019. Amazonian rainforest tree mortality driven by climate and functional traits. *Nat Clim Chang* **9**: 384–8.

Alencar AA, Brando PM, Asner GP, and Putz FE. 2015. Landscape fragmentation, severe drought, and the new Amazon forest fire regime. *Ecol Appl* **25**: 1493–505.

Anderegg WRL, Konings AG, Trugman AT, *et al.* 2018. Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature* **561**: 538–41.

Anderson LO, Neto GR, Cunha AP, *et al.* 2018. Vulnerability of Amazonian forests to repeated droughts. *Philos Trans R Soc B Biol Sci* **373**.

Aragão LEOC, Malhi Y, Barbier N, *et al.* 2008. Interactions between rainfall, deforestation and fires during recent years in the Brazilian Amazonia. *Philos Trans R Soc Lond B Biol Sci* **363**: 1779–85.

Aragão LEOC, Malhi Y, Roman-Cuesta RM, *et al.* 2007. Spatial patterns and fire response of recent Amazonian droughts. *Geophys Res Lett* **34**.

Araújo I, Marimon BS, Scalon MC, *et al.* 2021. Trees at the Amazonia-Cerrado transition are approaching high temperature thresholds. *Environ Res Lett* **16**: 034047.

Arroyo-Rodríguez V, Melo FPL, Martínez-Ramos M, *et al.* 2015. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biol Rev* **92**: 326–40.

Bagchi R, Swamy V, Latorre Farfan J, *et al.* 2018. Defaunation increases the spatial clustering of lowland Western Amazonian tree communities (G Durigan, Ed). *J Ecol* **106**: 1470–82.

Balch JK, Nepstad DC, Curran LM, *et al.* 2011. Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon. *For Ecol Manage* **261**: 68–77.

Banks-Leite C, Pardini R, Tambosi LR, *et al.* 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science* **345**: 1041–5.

Barlow J, Lennox GD, Ferreira J, *et al.* 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* **535**: 144–7.

Barlow J and Peres C a. 2008. Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philos Trans R Soc London B* **363**: 1787–94.

Barreto JR, Berenguer E, Ferreira J *et al.* 2021. Assessing invertebrate herbivory in human-modified tropical forest canopies. *Ecol. Evol.* **11**: 4012–4022. doi:10.1002/ece3.7295.

Barros F de V., Bittencourt PRL, Brum M, *et al.* 2019. Hydraulic

traits explain differential responses of Amazonian forests to the 2015 El Niño-induced drought. *New Phytol* **223**: 1253–66.

Berenguer E, Ferreira J, Gardner TA, *et al.* 2014. A large-scale field assessment of carbon stocks in human-modified tropical forests. *Glob. Chang. Biol.* **20**:3713–3726.

Betts RA, Arnell NW, Boorman PM, *et al.* 2012. Climate change impacts and adaptation: an Earth System view. In: Cornell SE, Prentice IC, House JI, Downy CJ (Eds). Understanding the Earth System. Cambridge: Cambridge University Press.

Betts RA, Cox PM, Collins M, *et al.* 2004. The role of ecosystem-atmosphere interactions in simulated AMazonian precipitation decrease and forest dieback under global climate warming. *Theor Appl Climatol* **78**: 157–75.

Brando PM, Balch JK, Nepstad DC, *et al.* 2014. Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proc Natl Acad Sci* **111**: 6347–52.

Brando PM, Nepstad DC, Balch JK, *et al.* 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Glob Chang Biol* **18**: 630–41.

Brienen RJW, Phillips OL, Feldpausch TR, *et al.* 2015. Long-term decline of the Amazon carbon sink. *Nature* **519**: 344–8.

Brienen RJW, Caldwell L, Duchesne SV, *et al.* 2020. Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nature Communications* **11** (4241).

Brum M, Vadeboncoeur MA, Ivanov V, *et al.* 2019. Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest (D Barua, Ed). *J Ecol* **107**: 318–33.

Bules-Jaramillo A and Poveda G. 2018. Conjoint Analysis of Surface and Atmospheric Water Balances in the Andes-Amazon System. *Water Resour Res* **54**: 3472–89.

Burton C, Kelley DI, Jones CD, *et al.* South American fires and their impacts on ecosystems increase with continued emissions. *Submitt to Clim Resil Sustain*.

Bush MB, Oliveira PE De, Colinvaux PA, *et al.* 2004. Amazonian paleoecological histories: one hill, three watersheds. *Palaeogeogr Palaeoclimatol Palaeoecol* **214**: 359–93.

Chai Y, Martins G, Nobre C, *et al.* 2021. Constraining Amazonian land surface temperature sensitivity to precipitation and the probability of forest dieback. *npj Clim Atmos Sci* **4**: 6.

Chazdon RL, Broadbent EN, Rozendaal DMA, *et al.* 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Sci Adv* **2**: e1501639.

Christoffersen BO, Gloor M, Fauset S, *et al.* 2016. Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (TFS v.1-Hydro). *Geosci Model Dev* **9**: 4227–55.

Ciemer C, Boers N, Hirota M, *et al.* 2019. Higher resilience to climatic disturbances in tropical vegetation exposed to more variable rainfall. *Nat Geosci* **12**: 174–9.

Cochrane MA. 2003. Fire science for rainforests. *Nature* **421**: 913–9.

Cochrane MA, Alencar A, Schulze MD, *et al.* 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* **284**: 1832–5.

Cochrane MA and Barber CP. 2009. Climate change, human land use and future fires in the Amazon. *Glob Chang Biol* **15**: 601–12.

Cochrane MA and Schulze MD. 1999. Fire as a recurrent event in tropical forests of the Eastern Amazon: effects on forest structure, biomass, and species composition. : 2–16.

Coelho de Souza F, Dexter KG, Phillips OL, *et al.* 2019. Evolutionary diversity is associated with wood productivity in Amazonian forests. *Nat Ecol Evol* **3**: 1754–61.

Cole LES, Bhagwat SA, and Willis KJ. 2014. Recovery and resilience of tropical forests after disturbance. *Nat Commun* **5**: 1–7.

Cosme LHM, Schietti J, Costa FRC, and Oliveira RS. 2017. The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. *New Phytol* **215**: 113–25.

Cox PM, Betts R a., Collins M, *et al.* 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theor Appl Climatol* **78**: 137–56.

Cox PM, Betts RA, Jones CD, *et al.* 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**: 184–7.

Cramer W, Bondeau A, Woodward FI, *et al.* 2001. Global response of terrestrial ecosystem structure and function to CO 2 and climate change: results from six dynamic global vegetation models. *Glob Chang Biol* **7**: 357–73.

Cubiña A and Aide TM. 2001. The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica* **33**: 260–7.

D'Apolito C, Absy ML, and Latrubesse EM. 2013. The Hill of Six Lakes revisited: New data and re-evaluation of a key Pleistocene Amazon site. *Quat Sci Rev* **76**: 140–55.

DaCosta ACL, Galbraith D, Almeida S, *et al.* 2010. Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytol* **187**: 579–91.

Davidson EA, Araújo AC de, Artaxo P, *et al.* 2012. The Amazon basin in transition. *Nature* **481**: 321–8.

DeAngelis DM, Post WM, and Travis CC. 1986. Positive feedback in natural systems. Berlin, Heidelberg: Springer-Verlag.

Dexter KG, Pennington RT, Oliveira-Filho AT, *et al.* 2018. Inserting Tropical Dry Forests Into the Discussion on Biome Transitions in the Tropics. *Front Ecol Evol* **6**: 1–7.

Eller CB, Rowland L, Mencuccini M, *et al.* 2020. Stomatal optimization based on xylem hydraulics (SOX) improves land surface model simulation of vegetation responses to climate. *New Phytol* **226**: 1622–37.

Eller CB, Rowland L, Oliveira RS, *et al.* 2018. Modelling tropical forest responses to drought and El Niño with a stomatal optimization model based on xylem hydraulics. *Philos Trans R Soc B Biol Sci* **373**: 20170315.

Elmqvist T, Folke C, Nyström M, *et al.* 2003. Response diversity, ecosystem change, and resilience. *Front Ecol Environ* **1**: 488–94.

Esquivel-Muelbert A, Baker TR, Dexter KG, *et al.* 2016. Seasonal drought limits tree species across the Neotropics. *Ecography (Cop)* **40**: 618–29.

Esquivel-Muelbert A, Baker TR, Dexter KG, *et al.* 2019. Compositional response of Amazon forests to climate change. *Glob Chang Biol* **25**.

Esquivel-Muelbert A, Galbraith D, Dexter KG, *et al.* 2017. Biogeographic distributions of neotropical trees reflect their directly measured drought tolerances. *Sci Rep* **7**: 8334.

Esquivel-Muelbert A, Phillips OL, Brienen RJW, *et al.* 2020. Tree mode of death and mortality risk factors across Amazon forests. *Nat Commun* **11**.

Esteban EJL, Castilho C V, Melgaço KL, and Costa FRC. 2021. The other side of droughts: wet extremes and topography as buffers of negative drought effects in an Amazonian forest. *New Phytol* **229**: 1995–2006.

Fauset S, Johnson MO, Gloor M, *et al.* 2015. Hyperdominance in Amazonian forest carbon cycling. *Nat Commun* **6**: 6857.

Feldpausch TR, Phillips OL, Brienen RJW, *et al.* 2016. Amazon forest response to repeated droughts. *Global Biogeochem Cycles* **30**: 964–82.

Fernandes Neto JG, Costa FRC, Williamson GB, and Mesquita RCG. 2019. Alternative functional trajectories along succession after different land uses in central Amazonia. *J Appl Ecol* **56**: 2472–81.

Fischer R, Bohn F, Dantas de Paula M, *et al.* 2016. Lessons learned from applying a forest gap model to understand ecosystem and carbon dynamics of complex tropical forests. *Ecol Modell* **326**: 124–33.

Fisher RA and Koven CD. 2020. Perspectives on the Future of Land Surface Models and the Challenges of Representing Complex Terrestrial Systems. *J Adv Model Earth Syst* **12**.

Fleischer K, Rammig A, Kauwe MG De, *et al.* 2019. Amazon forest response to CO2 fertilization dependent on plant phosphorus acquisition. *Nat Geosci* **12**: 736–41.

Flores BM. 2016. Resilience of Amazonian forests - the role of fire, flooding and climate.

Flores BM, Fagoaga R, Nelson BW, and Holmgren M. 2016. Repeated fires trap Amazonian blackwater floodplains in an open vegetation state. J Appl Ecol 53: 1597–603.

Flores BM and Holmgren M. 2021. White-Sand Savannas Expand at the Core of the Amazon After Forest Wildfires. *Ecosystems*.

Flores BM, Holmgren M, Xu C, *et al.* 2017. Floodplains as an Achilles' heel of Amazonian forest resilience. *Proc Natl Acad Sci* **114**: 4442–6.

Flores BM, Staal A, Jakovac CC, *et al.* 2020. Soil erosion as a resilience drain in disturbed tropical forests. *Plant Soil* **450**: 11–25.

Funk C, Peterson P, Landsfeld M, *et al.* 2015. The climate hazards infrared precipitation with stations—a new environmental record for monitoring extremes. *Sci Data* **2**: 150066.

Fyllas NM, Gloor E, Mercado LM, *et al.* 2014. Analysing Amazonian forest productivity using a new individual and trait-based model (TFS v.1). *Geosci Model Dev* **7**: 1251–69.

Gimeno TE, Crous KY, Cooke J, *et al.* 2016. Conserved stomatal behaviour under elevated CO 2 and varying water availability in a mature woodland (D Whitehead, Ed). *Funct Ecol* **30**: 700–9.

Gloor M, Brienen RJW, Galbraith D, *et al.* 2013. Intensification of

the Amazon hydrological cycle over the last two decades. *Geophys Res Lett* **40**: 1729–33.

Good P, Jones C, Lowe J, *et al.* 2013. Comparing tropical forest projections from two generations of hadley centre earth system models, HadGEM2-ES and HadCM3LC. *J Clim* **26**: 495–511.

Good P, Lowe JA, Collins M, and Moufouma-Okia W. 2008. An objective tropical Atlantic sea surface temperature gradient index for studies of south Amazon dry-season climate variability and change. *Philos Trans R Soc B Biol Sci* **363**: 1761–6.

Gordon C, Cooper C, Senior CA, *et al.* 2000. The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjstments. *Clim Dyn* **16**: 147–68.

Hammen T van der and Absy ML. 1994. Amazonia during the last glacial. *Palaeogeogr Palaeoclimatol Palaeoecol* **109**: 247–61.

Harris PP, Huntingford C, and Cox PM. 2008. Amazon Basin climate under global warming: The role of the sea surface temperature. *Philos Trans R Soc B Biol Sci* **363**: 1753–9.

Harris I, Osborn TJ, Jones P, and Lister D. 2020. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Sci Data* **7**.

Heinrich VHA, Dalagnol R, Cassol HLG, *et al.* 2020. Large carbon sink potential of Amazonian Secondary Forests to mitigate climate change. *Nat Commun.*

Hickler T, Smith B, Prentice IC, *et al.* 2008. CO2 fertilization in temperate FACE experiments not representative of boreal and tropical forests. *Glob Chang Biol* **14**: 1531–42.

Higgins SI and Scheiter S. 2012. Atmospheric CO2 forces abrupt vegetation shifts locally, but not globally. *Nature* **488**: 209–12.

Hirota M, Holmgren M, Nes EH Van, and Scheffer M. 2011. Global resilience of tropical forest and savanna to critical transitions. *Science* **334**: 232–5.

Hoffmann WA, Lucatelli VMPC, Silva FJ, *et al.* 2004. Impact of the invasive alien grass Melinis minutiflora at the savanna-forest ecotone in the Brazilian Cerrado. *Divers Distrib* **10**: 99–103.

Hofhansl F, Andersen KM, Fleischer K, *et al.* 2016. Amazon forest ecosystem responses to elevated atmospheric Co2 and alterations in nutrient availability: Filling the gaps with model-experiment integration. *Front Earth Sci* **4**: 1–9.

Holling CS. 1973. Resilience and stability of ecological systems. *Annu Rev Ecol Evol Syst* **4**: 1–23.

Hoorn C, Wesselingh FP, Steege H ter, *et al.* 2010. Amazonia Through Time: Andean Uplift, Climate Change, Landscape Evolution, and Biodiversity. *Science* **330**: 927–31.

Hubau W, Lewis SL, Phillips OL, *et al.* 2020. Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature* **579**: 80–7.

Huntingford C, Zelazowski P, Galbraith D, *et al.* 2013. Simulated resilience of tropical rainforests to CO2 -induced climate change. *Nat Geosci* **6**: 268–73.

INPE & EMBRAPA. Avaliação da dinâmica do uso e cobertura da terra no período de 10 anos nas áreas desflorestadas da Amazônia legal Brasileira. Report TerraClass 2016

Jakovac CC, Dutrieux LP, Siti L, *et al.* 2017. Spatial and temporal dynamics of shifting cultivation in the middle-Amazonas river: Expansion and intensification. *PLoS One* **12**: 1–15.

Jakovac CC, Junqueira AB, Crouzeilles R, *et al.* 2021. The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests. *Biol Rev*: brv.12694.

Jakovac CC, Peña-Claros M, Kuyper TW, and Bongers F. 2015. Loss of secondary-forest resilience by land-use intensification in the Amazon. *J Ecol* **103**: 67–77.

Janssen T, Fleischer K, Luyssaert S, *et al.* 2020a. Drought resistance increases from the individual to the ecosystem level in highly diverse Neotropical rainforest: A meta-analysis of leaf, tree and ecosystem responses to drought. *Biogeosciences* **17**: 2621–45.

Janssen TAJ, Hölttä T, Fleischer K, *et al.* 2020b. Wood allocation trade-offs between fiber wall, fiber lumen, and axial parenchyma drive drought resistance in neotropical trees. *Plant Cell Environ* **43**: 965–80.

Jiang M, Medlyn BE, Drake JE, *et al.* 2020. The fate of carbon in a mature forest under carbon dioxide enrichment. *Nature* **580**: 227–31.

Jiménez-Muñoz JC, Mattar C, Barichivich J, *et al.* 2016. Record-breaking warming and extreme drought in the Amazon rainforest during the course of El Niño 2015–2016. *Sci Rep* **6**: 33130.

Jiménez-Muñoz JC, Sobrino JA, Mattar C, and Malhi Y. 2013. Spatial and temporal patterns of the recent warming of the Amazon forest. *J Geophys Res Atmos.*

Jones C, Lowe J, Liddicoat S, and Betts R. 2009. Committed terrestrial ecosystem changes due to climate change. *Nat Geosci* **2**: 484–7.

Jupp TE, Cox PM, Rammig A, *et al.* 2010. Development of probability density functions for future South American rainfall. *New Phytol* **187**: 682–93.

Kauwe MG, Medlyn BE, Zaehle S, *et al.* 2013. Forest water use and water use efficiency at elevated CO2: A model-data intercomparison at two contrasting temperate forest FACE sites. *Glob Chang Biol* **19**: 1759–79.

Kooperman GJ, Chen Y, Hoffman FM, *et al.* 2018. Forest response to rising CO2 drives zonally asymmetric rainfall change over tropical land. *Nat Clim Chang* **8**: 434–40.

Langan L, Higgins SI, and Scheiter S. 2017. Climate-biomes, pedo-biomes or pyro-biomes: which world view explains the tropical forest–savanna boundary in South America? *J Biogeogr* **44**: 2319–30.

Lapola DM. 2018. Bytes and boots to understand the future of the Amazon forest. *New Phytol* **219**: 845–7.

Lapola DM, Oyama MD, and Nobre CA. 2009. Exploring the range of climate biome projections for tropical South America: The role of CO2 fertilization and seasonality. *Global Biogeochem Cycles* **23**: 1–16.

Laurance SGW, Stouffer PC, and Laurance WF. 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conserv Biol* **18**: 1099–109.

Levine NM, Zhang K, Longo M, *et al.* 2016. Ecosystem heterogeneity determines the ecological resilience of the Amazon

to climate change. *Proc Natl Acad Sci* **113**: 793–7.

Levis C, Costa FRC, Bongers F, *et al.* 2017. Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* **355**: 925–31.

Levis C, Flores BM, Mazzochini GG, *et al.* 2020. Help restore Brazil's governance of globally important ecosystem services. *Nat Ecol Evol* **4**: 172–3.

Levis C, Flores BM, Moreira PA, *et al.* 2018. How People Domesticated Amazonian Forests. *Front Ecol Evol* **5**.

Lombardo U, McMichael C, and Kazuo Tamanaha E. 2018. Mapping pre-Columbian land use in Amazonia. *Past Glob Chang Mag* **26**: 14–5.

Longo M, Knox RG, Levine NM, *et al.* 2018. Ecosystem heterogeneity and diversity mitigate Amazon forest resilience to frequent extreme droughts. *New Phytol* **219**: 914–31.

Longo M, Saatchi S, Keller M, *et al.* 2020. Impacts of Degradation on Water, Energy, and Carbon Cycling of the Amazon Tropical Forests. *J Geophys Res Biogeosciences* **125**.

Loughlin NJD, Gosling WD, Mothes P, and Montoya E. 2018. Ecological consequences of post-Columbian indigenous depopulation in the Andean–Amazonian corridor. *Nat Ecol Evol* **2**: 1233–6.

Lovejoy TE and Nobre C. 2019. Amazon tipping point: Last chance for action. *Sci Adv* **5**: eaba2949.

Lundberg J and Moberg F. 2003. Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems* **6**: 87–98.

Magrin G, Marengo J, Boulanger J-P, *et al.* 2014. Central and South America. In: Barros V, Field C, Dokken D, *et al.* (Eds). Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, NY, USA: Cambridge University Press.

Maia V, Santos A, Aguiar-Campos N de, *et al.* 2021. Climate and soil mediate the effects of liana density on forest dynamics. *Biotropica* **53**: 509–5019.

Malhi Y, Aragão LEOC, Galbraith D, *et al.* 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proc Natl Acad Sci U S A* **106**: 20610–5.

MAPBIOMAS. 2020. Mapbiomas Amazonia. https://amazonia.mapbiomas.org/en. Viewed 28 Apr 2021.

Marengo JA, Tomasella J, Soares WR, *et al.* 2011. Extreme climatic events in the Amazon basin. *Theor Appl Climatol* **107**: 73–85.

Mayle FE and Beerling DJ. 2004. Late Quaternary changes in Amazonian ecosystems and their implications for global carbon cycling. *Palaeogeogr Palaeoclimatol Palaeoecol* **214**: 11–25.

Mayle FE, Burbridge R, and Killeen TJ. 2000. Millennial-scale dynamics of southern Amazonian rain forests. *Science* **290**: 2291–4.

Mayle FE and Power MJ. 2008. Impact of a drier Early-Mid-Holocene climate upon Amazonian forests. *Philos Trans R Soc B Biol Sci* **363**: 1829–38.

Medina-Vega JA, Bongers F, Poorter L, *et al.* 2021. Lianas have more acquisitive traits than trees in a dry but not in a wet forest. *J Ecol*: 1–18.

Mesquita RDCG, Massoca PEDS, Jakovac CC, *et al.* 2015. Amazon Rain Forest Succession: Stochasticity or Land-Use Legacy? *Bioscience* **65**: 849–61.

Montoya E, Keen HF, Luzuriaga CX, and Gosling WD. 2018. Long-term vegetation dynamics in a megadiverse hotspot: The ice-age record of a pre-montane forest of central Ecuador. *Front Plant Sci* **9**: 1–14.

Montoya E, Pedra-Méndez J, García-Falcó E, *et al.* 2019. Long-term vegetation dynamics of a tropical megadelta: Mid-Holocene palaeoecology of the Orinoco Delta (NE Venezuela). *Quat Sci Rev* **221**.

Montoya E, Rull V, and Nogué S. 2011. Early human occupation and land use changes near the boundary of the Orinoco and the Amazon basins (SE Venezuela): Palynological evidence from El Paují record. *Palaeogeogr Palaeoclimatol Palaeoecol* **310**: 413–26.

Nanni AS, Sloan S, Aide TM, *et al.* 2019. The neotropical reforestation hotspots: A biophysical and socioeconomic typology of contemporary forest expansion. *Glob Environ Chang* **54**: 148–59.

Nepstad DC, Carvalho CR de, Davidson EA, *et al.* 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **372**: 666–9.

Nepstad DC, Tohver IM, Ray D, *et al.* 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* **88**: 2259–69.

Nobre CA, Sampaio G, Borma LS, *et al.* 2016. Land-use and climate change risks in the amazon and the need of a novel sustainable development paradigm. *Proc Natl Acad Sci U S A* **113**.

Nobre CA, Sellers PJ, and Shukla J. 1991. Amazonian Deforestation and Regional Climate Change. *J Clim* **4**: 957–88.

Norby RJ, Kauwe MG De, Domingues TF, *et al.* 2016. Model – data synthesis for the next generation of forest free-air CO 2 enrichment (FACE) experiments. *New Phytol* **209**: 17–28.

Norby RJ, Warren JM, Iversen CM, *et al.* 2010. CO2 enhancement of forest productivity constrained by limited nitrogen availability. *Proc Natl Acad Sci U S A* **107**: 19368–73.

Oliveira RS, Costa FRC, Baalen E van, *et al.* 2019. Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients. *New Phytol* **221**: 1457–65.

Oliveira RS, Dawson TE, Burgess SSO, and Nepstad DC. 2005. Hydraulic redistribution in three Amazonian trees. *Oecologia* **145**: 354–63.

Oliveira RS, Eller CB, Barros F de V., *et al.* 2021. Linking plant hydraulics and the fast-slow continuum to understand resilience to drought in tropical ecosystems. *New Phytol*.

Oyama MD and Nobre CA. 2003. A new climate-vegetation equilibrium state for tropical South America. *Geophys Res Lett* **30**.

Parrotta JA, Wildburger C and Mansourian S. 2012. Understanding Relationships between Biodiversity, Carbon, Forests and People: The Key to Achieving REDD + Objectives. A Global Assessment Report. Vienna, Austria: International Union of Forest Research Organizations (IUFRO) doi:1016-3263.

Perz SG and Skole DL. 2003. Secondary forest expansion in the brazilian amazon and the refinement of forest transition theory. *Soc Nat Resour* **16**: 277–94.

Phillips OL, Aragão LEOCOC, Lewis SL, *et al.* 2009. Drought sensitivity of the Amazon rainforest. *Science* **323**: 1344–7.

Phillips OL, Heijden G Van der, Lewis SL, *et al.* 2010. Drought-mortality relationships for tropical forests. *New Phytol* **187**: 631–46.

Poorter L, Bongers F, Aide TM, *et al.* 2016. Biomass resilience of Neotropical secondary forests. *Nature* **530**: 211–4.

Poorter L, McDonald I, Alarcón A, *et al.* 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.

Poorter L, Sande MT van der, Thompson J, *et al.* 2015. Diversity enhances carbon storage in tropical forests. *Glob Ecol Biogeogr* **24**: 1314–28.

Posth, C. et al. Reconstructing the Deep Population History of Central and South America. Cell 175, 1185-1197.e22 (2018).

Prance GT. 1996. The islands in Amazonia. *Philos Trans R Soc London B* **351**: 823–33.

Putz FE and Redfor KH. 2010. The Importance of Defining 'Forest': Tropical Forest Degradation, Deforestation, Long-term Phase Shifts, and Further Transitions. *Biotropica* **42**(13): 10–20. doi:10.1111/j.1744-7429.2009.00567.x.

Quesada CA, Phillips OL, Schwarz M, *et al.* 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* **9**: 2203–46.

RAISG. 2020. Amazonian Network of Georeferenced Socio-Environmental Informationhttps://www.amazoniasocioambiental.org/en/. Viewed

Rajão R, Soares-Filho B, Nunes F, *et al.* 2020. The rotten apples of Brazil's agribusiness. *Science* **369**: 246–8.

Rammig A, Jupp T, Thonicke K, *et al.* 2010. Estimating the risk of Amazonian forest dieback. *New Phytol* **187**: 694–706.

Roeder M, Hölscher D, and Ferraz IDK. 2010. Liana regeneration in secondary and primary forests of central Amazonia. *Plant Ecol Divers* **3**: 165–74.

Rowland L, Costa ACL da, Galbraith DR, *et al.* 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* **528**: 119–22.

Rozendaal DMA, Bongers F, Aide TM, *et al.* 2019. Biodiversity recovery of Neotropical secondary forests. *Sci Adv* **5**: eaau3114.

Rull V, Montoya E, Vegas-Vilarrúbia T, and Ballesteros T. 2015. New insights on palaeofires and savannisation in northern South America. *Quat Sci Rev* **122**: 158-65.

Sakschewski B, Bloh W Von, Boit A, *et al.* 2016. Resilience of Amazon forests emerges from plant trait diversity. *Nat Clim Chang* **6**: 1032–6.

Sakschewski B, Bloh W von, Drüke M, *et al.* 2020. Variable tree rooting strategies improve tropical productivity and evapotranspiration in a dynamic global vegetation model. *Biogeosciences*.

Sampaio G, Nobre C, Costa MH, *et al.* 2007. Regional climate change over eastern Amazonia caused by pasture and soybean cropland expansion. *Geophys Res Lett* **34**: 1–7.

Sampaio G, Shimizu M, Guimarães-Júnior C, *et al.* 2020. CO<sub>2</sub> fertilization effect can cause rainfall decrease as strong as large-scale deforestation in the Amazon. *Biogeosciences Discuss*: 1–21.

Sande MT van der, Gosling W, Correa-Metrio A, *et al.* 2019. A 7000-year history of changing plant trait composition in an Amazonian landscape; the role of humans and climate. *Ecol Lett* **22**: 925–35.

Sato H, Ito A, Ito A, *et al.* 2015. Current status and future of land surface models. *Soil Sci Plant Nutr* **61**: 34–47.

Schaphoff S, Lucht W, Gerten D, *et al.* 2006. Terrestrial biosphere carbon storage under alternative climate projections. *Clim Change* **74**: 97–122.

Scheffer M, Carpenter S, Foley JA, *et al.* 2001. Catastrophic shifts in ecosystems. *Nature* **413**: 591–6.

Scheffer M, Carpenter SR, Lenton TM, *et al.* 2012. Anticipating critical transitions. *Science* **338**: 344–8.

Scheiter S, Langan L, and Higgins SI. 2013. Next-generation dynamic global vegetation models: Learning from community ecology. *New Phytol* **198**: 957–69.

Schnitzer SA and Bongers F. 2002. The ecology of lianas and their role in forests. *Trends Ecol Evol* **17**: 223–30.

Schwartz NB, Aide TM, Graesser J, *et al.* 2020. Reversals of Reforestation Across Latin America Limit Climate Mitigation Potential of Tropical Forests. *Front For Glob Chang* **3**: 1–10.

Sellar AA, Jones CG, Mulcahy JP, *et al.* 2019. UKESM1: Description and Evaluation of the U.K. Earth System Model. *J Adv Model Earth Syst* **11**.

Silva CVJ, Aragão LEOC, Barlow J, *et al.* 2018. Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics. *Philos Trans R Soc B Biol Sci* **373**: 20180043.

Silva de Miranda PL, Oliveira-Filho AT, Pennington RT, *et al.* 2018. Using tree species inventories to map biomes and assess their climatic overlaps in lowland tropical South America. *Glob Ecol Biogeogr* **27**: 899–912.

Silvério D V, Brando PM, Balch JK, *et al.* 2013. Testing the Amazon savannization hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. *Philos Trans R Soc B Biol Sci* **368**: 20120427.

Sitch S, Huntingford C, Gedney N, *et al.* 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Glob Chang Biol* **14**: 2015–39.

Smith R and Mayle FE. 2018. Impact of mid- to late Holocene precipitation changes on vegetation across lowland tropical South America: A paleo-data synthesis. *Quarternary Res* **89**: 1–22.

Smith MN, Taylor TC, Haren J van, *et al.* 2020. Empirical evidence for resilience of tropical forest photosynthesis in a warmer world. *Nat Plants* **6**: 1225–30.

Spracklen D V., Arnold SR, and Taylor CM. 2012. Observations of increased tropical rainfall preceded by air passage over forests. *Nature* **489**: 282–5.

Staal A, Flores BM, Aguiar APD, *et al.* 2020. Feedback between drought and deforestation in the Amazon. *Environ Res Lett* **15**: 44024.

Staal A, Tuinenburg OA, Bosmans JHC, *et al.* 2018. Forest-rainfall cascades buffer against drought across the Amazon. *Nat Clim Chang* **8**: 539–43.

Staver AC, Archibald S, and Levin SA. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* **334**: 230–2.

Staver AC, Brando PM, Barlow J, *et al.* 2020. Thinner bark increases sensitivity of wetter Amazonian tropical forests to fire. *Ecol Lett* **23**: 99–106.

Steege H Ter, Pitman NCA, Killeen TJ, *et al.* 2015. Estimating the global conservation status of more than 15,000 Amazonian tree species. *Sci Adv* **1**: 9–11.

Steege H ter, Pitman NCA, Sabatier D, *et al.* 2013. Hyperdominance in the Amazonian Tree Flora. *Science* **342**: 1243092–1243092.

Strogatz SH. 2015. Nonlinear dynamics and chaos with applications to physics, biology, chemistry and enginnering. Boulder: Westview Press.

Sullivan MJP, Lewis SL, Affum-Baffoe K, *et al.* 2020. Long-term thermal sensitivity of earth's tropical forests. *Science* **368**: 869–74.

Ter-Steege H, Prado PI, Lima RAF de, *et al.* 2020. Biased-corrected richness estimates for the Amazonian tree flora. *Sci Rep* **10**: 10130.

Turner MG, Baker WL, Peterson CJ, and Peet RK. 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. *Ecosystems* **1**: 511–23.

Turner BL, Brenes-Arguedas T, and Condit R. 2018. Pervasive phosphorus limitation of tree species but not communities in tropical forests. *Nature* **555**: 367–70.

Tymen B, Réjou-Méchain M, Dalling JW, *et al.* 2016. Evidence for arrested succession in a liana-infested Amazonian forest. *J Ecol* **104**: 149–59.

Urrego DH, Bush MB, and Silman MR. 2010. A long history of cloud and forest migration from Lake Consuelo, Peru. *Quat Res* **73**: 364–73.

Van-Nes EH, Arani BMS, Staal A, *et al.* 2016. What do you mean, tipping point? *Trends Ecol Evol* **31**: 902–4.

Van-Nes EH, Staal A, Hantson S, *et al.* 2018. Fire forbids fifty-fifty forest. *PLoS One* **13**: 12–7.

Veldman JW. 2016. Clarifying the confusion: old-growth savannahs and tropical ecosystem degradation. *Philos Trans R Soc B Biol Sci* **371**: 20150306.

Veldman JW and Putz FE. 2011. Grass-dominated vegetation, not species-diverse natural savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin. *Biol Conserv* **144**: 1419–29.

Venticinque E, Forsberg B, Barthem R, *et al.* 2016. An explicit GIS-based river basin framework for aquatic ecosystem conservation in the Amazonhttps://knb.ecoinformatics.org/view/doi%3A10.5063%2FF1BG2KX8#snapp_computing.6.1. Viewed

Vieira ICG, Gardner T, Ferreira J, *et al.* 2014. Challenges of governing second-growth forests: A case study from the Brazilian Amazonian state of Pará. *Forests* **5**: 1737–52.

Walker B, Kinzig A, and Langridge J. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. *Ecosystems* **2**: 95–113.

Wang X, Edwards RL, Auler AS, *et al.* 2017. Hydroclimate changes across the Amazon lowlands over the past 45,000 years. *Nature* **541**: 204–7.

Wang Y, Ziv G, Adami M, *et al.* 2020. Upturn in secondary forest clearing buffers primary forest loss in the Brazilian Amazon. *Nat Sustain* **3**: 290–5.

White A, Cannell MGR, and Friend AD. 1999. Climate change impacts on ecosystems and the terrestrial carbon sink: A new assessment. *Glob Environ Chang* **9**.

Wieland LM, Mesquita RCG, Bobrowiec PED, *et al.* 2011. Seed rain and advance regeneration in secondary succession in the Brazilian Amazon. *Trop Conserv Sci* **4**: 300–16.

Wolfe BT, Sperry JS, and Kursar TA. 2016. Does leaf shedding protect stems from cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis. *New Phytol* **212**: 1007–18.

Xu X, Jia G, Zhang X, *et al.* 2020. Climate regime shift and forest loss amplify fire in Amazonian forests. *Glob Chang Biol* **26**: 5874–85.

Xu X, Medvigy D, Powers JS, *et al.* 2016. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytol* **212**.

Zarin DJ, Davidson EA, Brondizio E, *et al.* 2005. Legacy of fire slows carbon accumulation in Amazonian forest regrowth. *Front Ecol Environ* **3**: 365–9.

Zelazowski P, Malhi Y, Huntingford C, *et al.* 2011. Changes in the potential distribution of humid tropical forests on a warmer planet. In: Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences.

Zemp DC, Schleussner C-F, Barbosa HMJ, et al. 2014. On the importance of cascading moisture recycling in South America. Atmos Chem Phys 14: 13337–59.

Zemp DC, Schleussner C-F, Barbosa HMJ, *et al.* 2017. Self-amplified Amazon forest loss due to vegetation-atmosphere feedbacks. *Nat Commun* **8**: 1–10.

Zeppetello LRV, Luke's LA, Spector JT, *et al.* 2020. Large scale tropical deforestation drives extreme warming. *Environ Res Lett* **15**.

Zuleta D, Duque A, Cardenas D, *et al.* 2017. Drought-induced mortality patterns and rapid biomass recovery in a terra firme forest in the Colombian Amazon. *Ecology*.

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