

Chapter 24



Science Panel for the Amazon (SPA)

Working Group 8

**CLIMATE CHANGE IN THE AMAZON: TENDENCIES, IMPACTS AND
ECOLOGICAL CONSEQUENCES**

Lead Authors: Paulo Artaxo and José Marengo

**THE RESILIENCE OF THE AMAZON FOREST TO GLOBAL CHANGES:
ASSESSING THE RISK OF TIPPING POINTS**

Lead Authors: Marina Hirota, Bernardo Flores

*Contributing Authors: Richard Betts, Laura S. Borma, Adriane Esquivel-Muelbert,
Catarina Jakovac, David M. Lapola, Encarni Montoya, Rafael S. Oliveira, Boris
Sakschewski*

Chapter 24

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22

THE RESILIENCE OF THE AMAZON FOREST TO GLOBAL CHANGES: ASSESSING THE RISK OF TIPPING POINTS

*Marina Hirota¹, Bernardo M. Flores², Richard Betts³, Laura S. Borma⁴, Adriane Esquivel-
Muelbert⁵, Catarina Jakovac⁶, David M. Lapola⁷, Encarni Montoya⁸, Rafael S. Oliveira⁹,
Boris Sakschewski¹⁰*

AUTHOR AFFILIATION:

¹ Federal University of Santa Catarina, Campus Universitário Reitor João David Ferreira
Lima, s/n. Trindade. 88040-900. Florianópolis, Brazil, marinahirota@gmail.com

² Federal University of Santa Catarina, Campus Universitário Reitor João David Ferreira
Lima, s/n. Trindade. 88040-900. Florianópolis, Brazil

³ MetOffice, Exeter, United Kingdom

⁴ INPE/DIIAV, Av. dos Astronautas, 1758. São José dos Campos, Brazil

⁵ University of Birmingham, United Kingdom

⁶ Wageningen University and Research, Wageningen, the Netherlands

⁷ University of Campinas, Av. André Tosello 209. 13083-886, Campinas, Brazil

⁸ Department of Geography and Planning, School of Environmental Sciences, University of
Liverpool, Roxby Building, L69 7ZT, UK

⁹ University of Campinas, Rua Monteiro Lobato, 255. 13083-862, Campinas, Brazil

¹⁰ Potsdam Institute for Climate Impact Research, Telegrafenberg A62. 14412 Potsdam,
Germany

Chapter 24

1 ACRONYMS AND ABBREVIATIONS

2	AFEX	Amazon Fertilization Experiment
3	DGVMs	Dynamic Global Vegetation Models
4	eCO ₂	CO ₂ fertilization effect
5	ESMs	Earth System Models
6	FACE	Free-air concentration enrichment
7	GHG	Greenhouse gas
8	HadCM3	Hadley Center Coupled Model, version 3
9	IPCC	Intergovernmental Panel on Climate Change
10	LGM	Last Glacial Maximum
11	LSMs	Land Surface Models
12	MHDE	Mid-Holocene Dry Event
13	PFTs	Plant functional types
14	SDTF	Seasonally dry tropical forest
15	SST	Sea surface temperature

16

Chapter 24

INDEX

1		
2	KEY MESSAGES	i
3	ABSTRACT	ii
4	GRAPHICAL ABSTRACT	iii
5	1. INTRODUCTION	1
6	2. POTENTIAL TIPPING POINTS AND NEW CONFIGURATIONS	6
7	2.1 Forest shift to a closed-canopy, seasonally dry tropical forest	9
8	2.2 Forest shift to a native savanna state	9
9	2.3 Forest shift to an open-canopy, degraded state	10
10	2.4 Forest shift to a closed-canopy, secondary forest state	12
11	3. PAST EVIDENCE OF THE DYNAMICS OF AMAZONIAN ECOSYSTEMS SINCE	
12	THE LAST GLACIAL MAXIMUM (20 KA)	15
13	4. DRIVERS OF THE AMAZON FOREST RESILIENCE	18
14	5. UNCERTAINTIES ASSOCIATED WITH TIPPING POINTS WITHIN THE AMAZON	
15	SYSTEM	20
16	5.1 How does forest heterogeneity affect large-scale tipping points?	20
17	5.2 How does forest connectivity affect large-scale tipping points?	22
18	5.3 The interplay between CO ₂ fertilization effect and nutrient availability	23
19	6. MODELING THE RESILIENCE AND THE TIPPING POINTS OF THE AMAZON	
20	FOREST	25
21	7. CONCLUSIONS	31
22	9. RECOMMENDATIONS	32
23	10. REFERENCES	34
24	CORE GLOSSARY	55

Chapter 24

1 BOXES

56

2

3

Chapter 24

1 KEY MESSAGES

- 2 • Five tipping points described in the literature comprise disturbances triggered by
3 changes in climatic conditions and human activities, and associated large-scale
4 feedback mechanisms. Nevertheless, the heterogeneity in forest responses
5 throughout the Amazon basin (i.e., how resistant and recoverable different forests
6 are) seem to be key in determining the systemic resilience of the entire Amazon
7 system, and should be a research priority;
- 8 • Based on empirical evidence, four different ecosystem configurations have been
9 proposed for Amazonian forests: (i) a closed-canopy seasonally dry tropical forest
10 state; (ii) a native savanna state; (iii) an open-canopy degraded state; and (iv) a
11 closed-canopy secondary forest state. Due to the existence of novel feedbacks
12 associated with invasive plants and human-modified landscapes, we consider the
13 open degraded state and the closed-canopy secondary forest state as more likely to
14 occur over broad areas, particularly across the ‘arc of deforestation’;
- 15 • Further studies focusing on how past underlying conditions (e.g., soil fertility and
16 rainfall regimes) selected species that cope differently with the same amount of
17 disturbance will be key to unveil how such response heterogeneity may either
18 increase or dampen the systemic resilience of the Amazon ecosystem;
- 19 • Amazonian tipping point has been best studied so far with the use of models.
20 Despite continuous model improvements that reduce the uncertainties, there is a
21 lack of observational (field and remote sensing) and experimental evidence to
22 improve these models and evaluate their results. As such, there is no
23 reasonable/strong scientific agreement, from a modeling perspective, on the
24 likelihood of crossing such an Amazonian tipping point in the future. Priority areas
25 for model-data integration are CO₂ fertilization effect, soil nutrient limitation,
26 recruitment/mortality dynamics, plant functional diversity, as well as reducing
27 uncertainty in Amazon rainfall projections.

28

Chapter 24

1 **ABSTRACT**

2 Here we review and discuss existing evidence of ongoing changes in the Amazon forest
3 system that may lead to resilience loss and tipping points in which the ecosystem may shift
4 persistently to an alternative state. Grounded on the theory of complex dynamical systems,
5 we analyze the state of the Amazon forest and its potential trajectories in the 21st-century,
6 aiming to provide support for a science-based management scheme for enhancing its
7 systemic resilience. This review is based on five systemic tipping points for which there is
8 evidence, being four climate-related: (1) annual rainfall value below the range between
9 1,000 and 1,500 mm/yr, (2) dry season length above seven months, (3) for Amazon
10 lowlands, maximum cumulative water deficit above 200 mm/yr, (4) a global increase of
11 2°C on the equilibrium temperature of the Earth; and one associated with human-induced
12 changes: (5) the 20-25% accumulated deforestation of the whole basin. Evidence suggests
13 that depending on varying combinations of stressing conditions, disturbances and feedback
14 mechanisms, forests could be replaced at local scales by: (i) a closed-canopy seasonally dry
15 tropical forest; (ii) a savanna state; (iii) an open-canopy degraded state; and (iv) a closed-
16 canopy secondary forest. Local-scale forest collapses could trigger cascading effects on
17 rainfall recycling, intensifying drought seasons, wildfires and leading to massive forest loss
18 at continental scales, particularly at the southwest of the basin. The probability of crossing
19 such tipping points depends largely on heterogeneities across the system including
20 geological, physical, chemical and cultural processes that influence connectivity and the
21 likelihood of contagious disturbances. Biodiversity patterns were historically shaped over
22 the past 60 million years by these processes and still today influence forest adaptive
23 capacity and resilience. Thus, maintaining biodiversity is critical for enhancing resilience
24 and reducing the risk of systemic forest collapse in the near future.

25 *Keywords:* tipping points, resilience, biodiversity, heterogeneity, connectivity, climate
26 change, land use change.

27

Chapter 24

1 **GRAPHICAL ABSTRACT**

2 TBD

3

4

5

Chapter 24

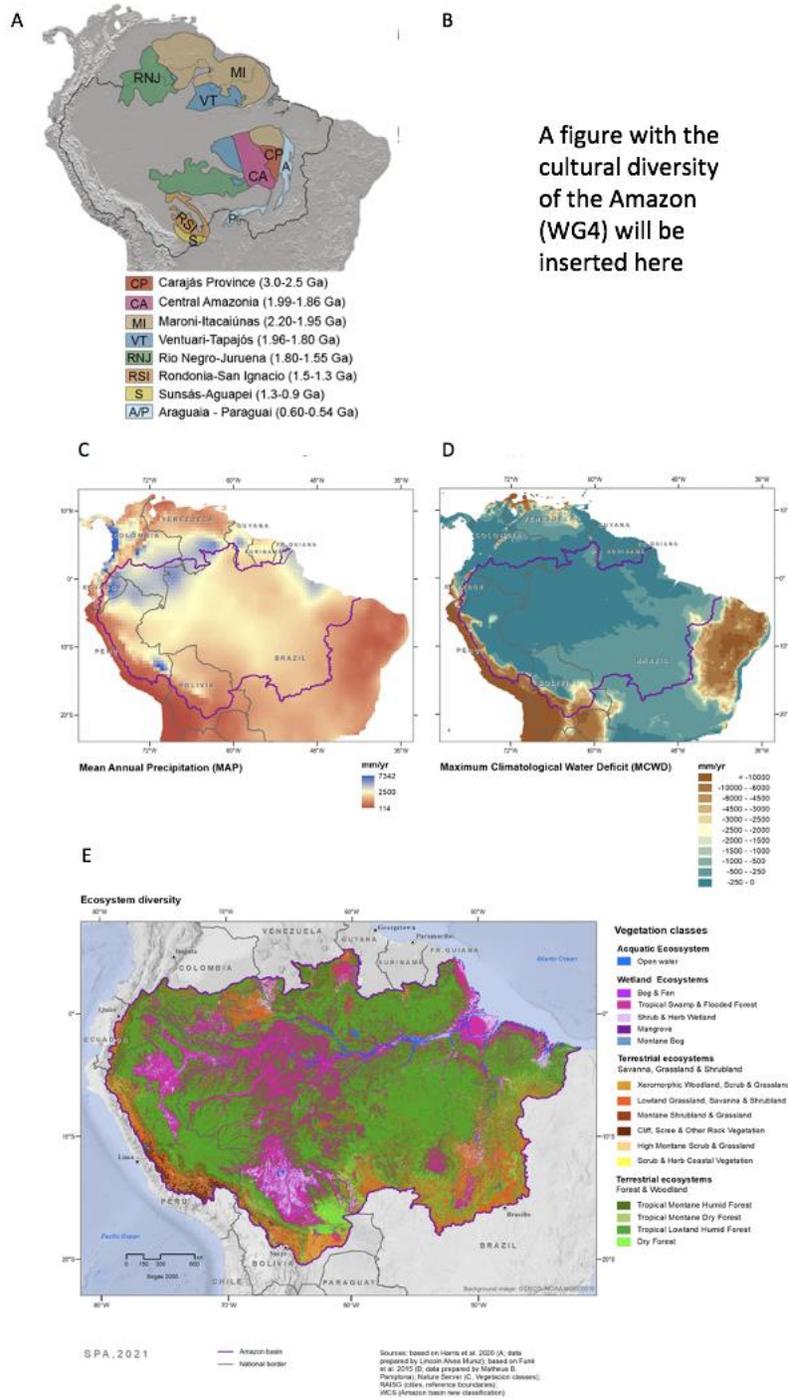
1. INTRODUCTION

2 The Amazon is a complex dynamical system that has been constantly changing for at least
3 60 million years ago (Ma), with geological, hydrological and evolutionary processes
4 shaping the system that we know today (see Chapters 1-7 and Figure 24.1). While the
5 Amazon River was formed around 7 Ma, forests expanded over non-forest habitats, and
6 during the same time, massive wetlands retreated at the western parts of the basin. This
7 process altered the courses of most rivers, causing new geographical barriers to emerge,
8 altering the distribution of species, and creating conditions for diversification and
9 speciation (Hoorn *et al.* 2010, see also Chapters 1 and 2). More recently, during the
10 Holocene, around 13 thousand years ago (ka), humans arrived in the Amazon (Roosevelt
11 2013) and began to contribute to further changes in the landscapes and alter plant species
12 distributions (Levis *et al.* 2017, see also Chapters 8 and 10).

13 As a result of the interplay between these processes (both natural and anthropogenic)
14 operating at different spatial and temporal scales, the Amazon is currently an extremely
15 heterogeneous and biodiverse system (see Chapters 3 and 4, and Figure 24.1b). Forest tree
16 communities across the basin are formed by different sets of species with contrasting
17 functional traits selected by continental to local environmental conditions, with main
18 drivers of this heterogeneity including soil (Quesada *et al.* 2012), climate (Davidson *et al.*
19 2012; ter Steege *et al.* 2013; Esquivel-Muelbert *et al.* 2017), topography (Oliveira *et al.*
20 2019) and microclimate (Barros *et al.* 2019). Savannas also occur along the fringes of the
21 Amazon basin and as “islands” within the dominant forest habitat (Prance 1996). The
22 varying types of forest and non-forest habitats that exist are connected through a rich web
23 of ecological interactions, which have contributed to maintaining the whole system resilient
24 for the past 45 ka. Such resilience has been observed even under the extremely dry
25 conditions of the Last Glacial Maximum (LGM) around 20 ka (Wang *et al.* 2017).

26

Chapter 24



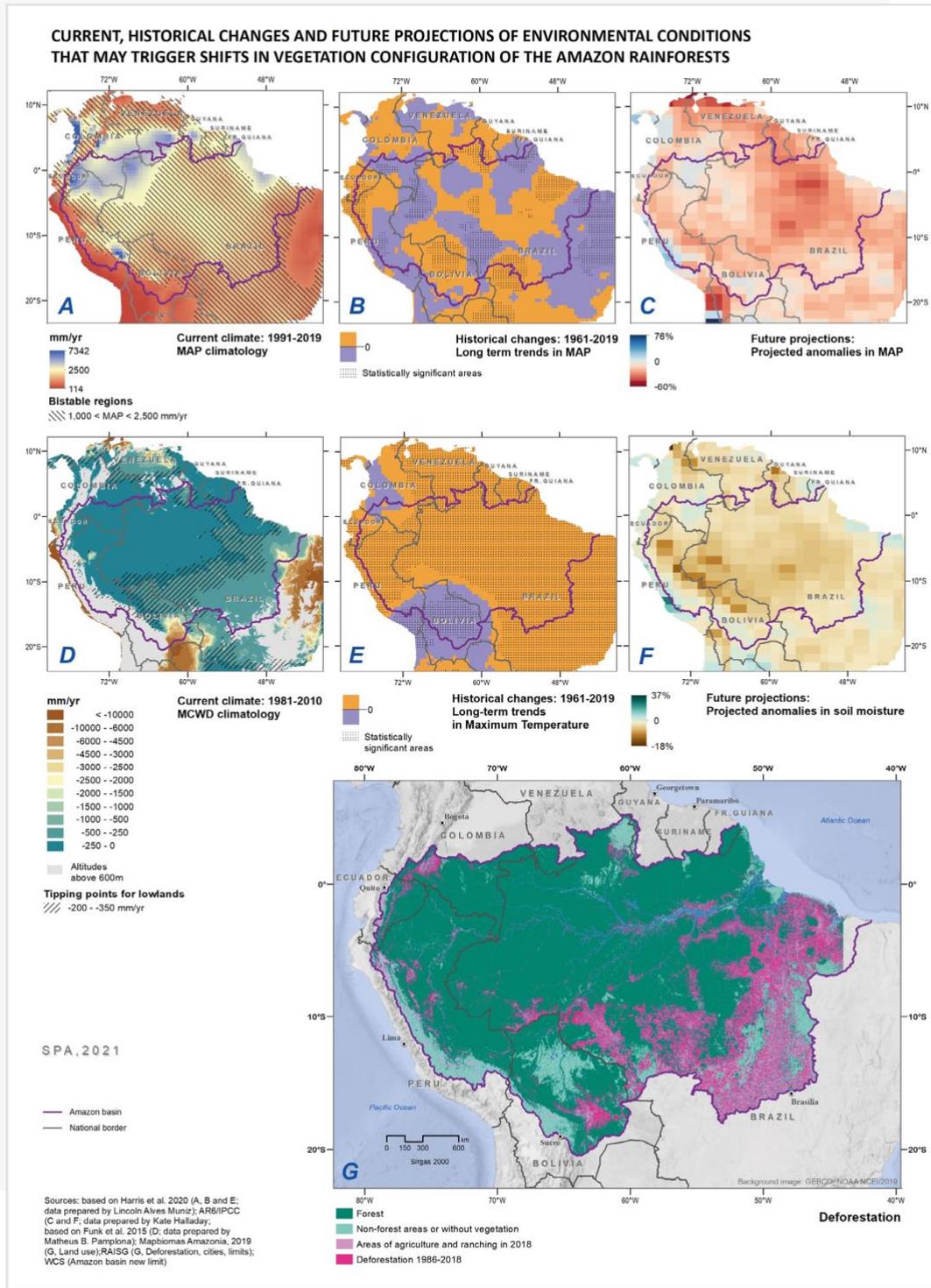
1

2 **Figure 24.1.** Heterogeneity in abiotic and biotic conditions throughout the Amazon system,
 3 which shaped a range of plant community assemblages within different time and spatial
 4 scales. (a) geochronological map of South America with the main provinces of the Amazon

Chapter 24

1 Craton (see Chapter 1); (b) past cultural diversity (to be defined either early ceramics
2 complexes or Holocene ceramic complexes - still to be built by the map team) (see Chapter
3 8); (c) 1981-2010 climatology mean annual precipitation (MAP, mm/yr) from CHIRPS
4 dataset (Funk *et al.* 2015); (d) 1981 - 2010 maximum climatological water deficit (MCWD,
5 mm/yr) from CHIRPS dataset (Funk *et al.* 2015); (e) wetland and terrestrial ecosystems of
6 the Amazon to show the tremendous biodiversity embedded within the system (See Chapter
7 4).

8 In the last century, however, the Amazon system began to change faster, mostly due to
9 local, regional, and global human activities that intensified particularly since the 1970s
10 (See Chapters 14-21, and Figs. 24.2c-e). Within the last two decades, extreme droughts
11 have become more frequent, and extremes in precipitation during the wet and dry seasons
12 have intensified (see Chapter 22; Marengo *et al.* 2011; Gloor *et al.* 2013; Jiménez-Muñoz
13 *et al.* 2016). Mean, maximum and minimum temperatures have also risen (see Chapter 22;
14 Jiménez-Muñoz *et al.* 2013), particularly on fragmented landscapes due to deforestation
15 (Zeppetello *et al.* 2020). As a result, mature Amazonian forests are now losing drought-
16 sensitive species and becoming more dominated by drought-tolerant species (Esquivel-
17 Muelbert *et al.* 2016, 2019; see also Chapter 23), with higher mortality rates of the drought-
18 sensitive ones particularly along the southern fringes of the Amazon boundaries (Esquivel-
19 Muelbert *et al.* 2020). In central Amazon, interactions between extremely wet and dry
20 periods are increasing tree mortality rates and reducing growth (Aleixo *et al.* 2019; Esteban
21 *et al.* 2021).



Chapter 24

1 **Figure 24.2.** Tipping points (section 2) and disturbances/perturbations which may affect
2 the resilience of the Amazon. (A) 1991 - 2019 climatology of mean annual precipitation
3 (MAP, mm/yr) showing bistable areas for tipping point range (tipping point 1) using CRU
4 4.04 dataset (Harris *et al.* 2020); (B) long-term trends (Kendall t) in MAP (hatched areas
5 are statistically significant) using CRU 4.04 (Harris *et al.* 2020); (C) projected relative
6 changes in MAP at 4°C global warming with the UKESM1 climate model (Sellar *et al.*
7 2019); (D) 1981-2010 MCWD climatology showing tipping points (-200 and -350 mm/yr
8 for lowlands) (tipping point 3); (E) long-term trends (Kendall t) in maximum temperatures
9 (hatched areas are statistically significant) using CRU 4.04 dataset; (F) projected relative
10 changes in soil moisture at 4°C global warming with the UKESM1 climate model (Sellar *et*
11 *al.* 2019); (G) deforestation according to MapBiomass.

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

Chapter 24

1 A topic that has raised concern is the potential existence of an ecological tipping point that
2 could affect the stability of the Amazon, causing large scale forest dieback or collapse (Box
3 24.1). Despite increasing evidence of tree mortality caused by extreme rainfall events (both
4 dry and wet), fire, deforestation, and the potential of their combined effects (Cochrane *et al.*
5 1999; Aragão *et al.* 2007, 2008; Phillips *et al.* 2009; Brando *et al.* 2014; Esquivel-Muelbert
6 *et al.* 2020; Staal *et al.* 2020; Esteban *et al.* 2021), the actual behavior of the Amazon
7 system still remains uncertain. For instance, with increasing water deficit levels and aridity,
8 the Amazon forest may not necessarily shift abruptly across the whole basin, but instead,
9 shift gradually as least resilient forests are affected first, followed by the more resilient ones
10 (Levine *et al.* 2016; Figure 24.1). On the other hand, human-induced changes are likely to
11 occur faster than the time forest communities would need to recover. Moreover, a long
12 lasting hypothesis is that the Amazon forests that collapse may undergo a “savannization”
13 process, i.e., forests would turn into a savanna-like vegetation cover (Nobre *et al.* 1991).
14 Nevertheless, evidence suggests that native savannas are unlikely to replace all portions of
15 the Amazon forest, since most stressors are associated with human activities that would
16 introduce invasive alien grasses instead of native savanna species (Veldman and Putz
17 2011), maintaining forests trapped in a degraded and early successional stage (Barlow and
18 Peres 2008).

19 Grounded on the theory of complex dynamical systems, we review and discuss existing
20 evidence of ongoing changes that may reduce forest resilience and potentially lead to
21 tipping points (Box 24.1), in which the Amazon forest may shift into other types of
22 configurations. By analyzing the state of the Amazon forest and its potential trajectories in
23 the 21st-century, we expect to provide critical information that will support a science-based
24 management scheme for enhancing the resilience of this iconic system.

25 **2. POTENTIAL TIPPING POINTS AND NEW CONFIGURATIONS**

26 The tipping points that have been proposed for the Amazon rainforests so far are: (1)
27 annual rainfall totals below 1,000 mm/yr, inferred from satellite observations of tree cover
28 distributions (Hirota *et al.* 2011; Staver *et al.* 2011; Figs. 24.2a-d) or 1,500 mm/yr inferred

Chapter 24

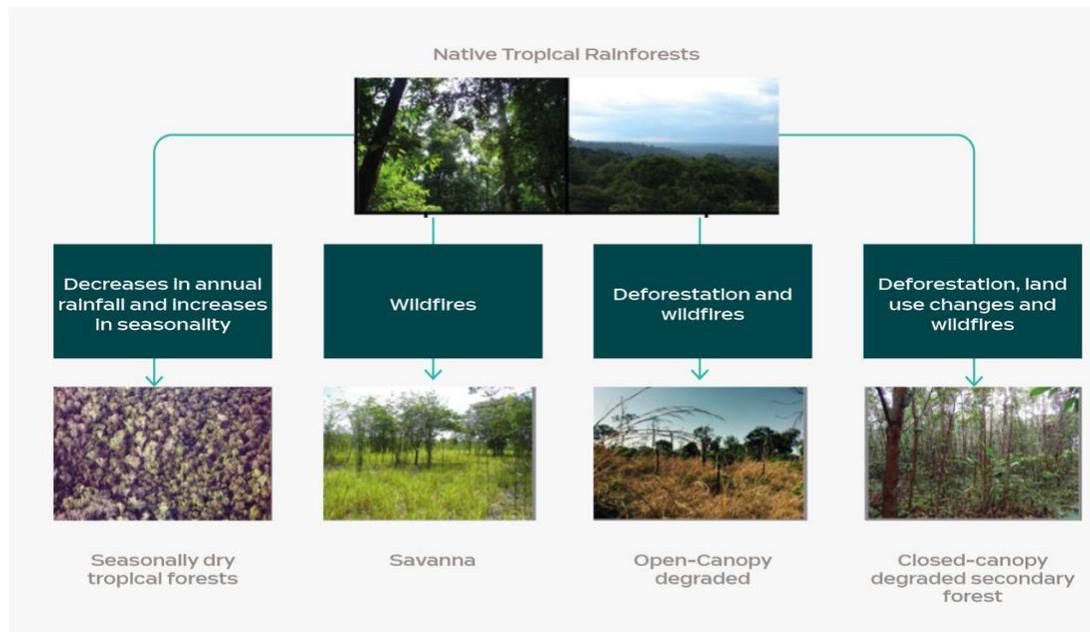
1 from global climate models (Malhi *et al.* 2009), (2) the dry season length longer than seven
2 months, inferred from satellite observations of tree cover distributions (Staver *et al.* 2011),
3 (3) for the Amazon lowlands, larger maximum cumulative water deficit values than 200
4 mm/yr or 350 mm/yr, inferred from different analysis with global climate models
5 (respectively, from Malhi *et al.* 2009; Zelazowski *et al.* 2011; Figure 24.2e); (4) an increase
6 of 2°C on the equilibrium temperature of the Earth, inferred from a coupled climate–
7 vegetation model (Jones *et al.* 2009; for instance, with consequences shown in Figs.
8 24.2d,g), and (5) surpass 20-25% accumulated deforestation, inferred from a combination
9 of environmental changes (i.e., increases in dry season length, see Chapter 22), climate
10 projections for the most pessimistic pathway of the Intergovernmental Panel on Climate
11 Change (IPCC; Figs. 24.2d,g), and human-induced degradation via deforestation (Figure
12 24.2h) (Nobre *et al.* 2016; Lovejoy and Nobre 2019). The main concern is that beyond
13 these possible tipping points, the system would enter a loop of rainfall reduction, fire and
14 forest mortality.

15 Given the constraints to acquire sufficiently long time series to effectively and directly
16 account for temporal changes, their impacts on vegetation cover, and consequent tipping
17 points (Box 24.1), the ones mentioned above have been inferred and proposed by different
18 types of modeling and observational approaches. The first two use a space-for-time
19 substitution method, which replaces temporal information on changing conditions and their
20 impacts (e.g., changes in precipitation intensity leading to changes in vegetation cover) by
21 observational data of vegetation status (canopy closure using tree cover values) along a
22 gradient of precipitation (e.g., 1,000 to 2,500 mm/yr) at a single snapshot in time. Tipping
23 points (3) to (5) are based on coupled climate-vegetation models, which are able to
24 simulate long time series with their integrative structure, but depending on a set of
25 parameterizations that may fail to adequately represent soil-plant-atmosphere interactions.
26 Thus, even having a glimpse of thresholds that may trigger irreversible changes, the
27 trajectories leading to stable and transient configurations of the Amazon basin need to be
28 further explored and studied by a combination of experimental and modeling studies. For
29 instance, a recent study has shown that, after correcting for models' biases identified using

Chapter 24

1 observation data, a basin-wide Amazon dieback is unlikely to occur, even under the most
2 pessimist IPCC pathway (Chai *et al.* 2021).

3 Based on existing evidence, we identify four main configurations Amazonian forests may
4 shift and persist due to self-reinforcing feedbacks (Figure 24.3) to: (i) a closed-canopy
5 seasonally dry tropical forest, with increasing abundance of deciduous tree species; (ii) a
6 savanna state, dominated by native grass and tree species; (iii) an open-canopy degraded
7 state, dominated by invasive alien grasses and native fire-tolerant tree species; and (iv) a
8 closed-canopy secondary forest, dominated by native early successional tree and other
9 plants species. In the following subsections, we explain how current environmental changes
10 in the Amazon system (see Chapters 14-21 and Figure 24.2) may alter forest dynamics, as
11 well as feedback mechanisms (Box 24.1) that could arrest Amazonian ecosystems in the
12 configurations (i) to (iv), and illustrate these trajectories with evidence on past and current
13 changes.



14

15 **Figure 22.3.** Potential alternative configurations and drivers. Photo credits: Native tropical
16 rainforests at ZF2 Station (AM, Brazil) by Marina Hirota; seasonally dry tropical forests at

Chapter 24

1 Maracá Island (RR, Brazil) by Marcelo Trindade Nascimento; savanna at Barcelos (AM,
2 Brazil) by Bernardo M. Flores; open-canopy degraded at Fazenda Tanguro (MT, Brazil) by
3 Paulo Brando; closed-canopy degraded secondary forest at Tefé (AM, Brazil) by Catarina
4 Jakovac.

5

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

7 Considering the observed trends towards a drier climate in some parts of the Amazon (see
8 Chapter 22), there is a possibility that forests over nutrient-rich soils may shift into a
9 closed-canopy state that resembles in terms of structure and functioning a seasonally dry
10 tropical forest (SDTF) (Malhi *et al.* 2009; Dexter *et al.* 2018), dominated by deciduous
11 fast-growing trees, with high tolerance to drought conditions, and a higher demand for
12 nutrients. This type of semi-deciduous forest (i.e., with varying abundances of deciduous
13 species) is very common in transitional zones of the Amazon boundaries, and under drier
14 climatic conditions (Silva de Miranda *et al.* 2018), they may expand over wet Amazonian
15 forests (Dexter *et al.* 2018). For instance, drought tolerant species are widely distributed
16 across the Amazon region (Esquivel-Muelbert *et al.* 2017), which would allow them to
17 dominate in case of a shift of climatic regime (Esquivel-Muelbert *et al.* 2019). However,
18 drought-tolerance is not only expressed in terms of deciduousness and alternative
19 phenotypes may include trees with more resistant water-transporting systems (Barros *et al.*
20 2019) and/or deeper-rooted species. Nonetheless, a shift to semi-deciduous forest would
21 probably not follow a catastrophic non-linear dynamics, with associated *tipping points*
22 (Box 24.1, Figure 24.B1) because rainforests and STDFs occupy separate climatic niches
23 (Silva de Miranda *et al.* 2018), implying that tree species may have to migrate long
24 geographical distances. Hence, such changes might occur smoothly and more gradually
25 with increasing aridity and seasonality (Oliveira *et al.*).

2.2 Forest shift to a native savanna state

26

Chapter 24

1 The Amazon forest is often assumed to shift into a savanna-like state, once it passes tipping
2 points such as the ones mentioned in (1) – (5) (Cox *et al.* 2004; Jones *et al.* 2009; Hirota *et*
3 *al.* 2011; Staver *et al.* 2011; Lovejoy and Nobre 2019). However, evidence for such shifts
4 at the local scale is lacking, mostly because disturbed forests are commonly invaded by
5 alien grasses (see section 2.3) instead of native grass species from South American
6 savannas (Veldman 2016). This happens particularly in landscapes where forest is widely
7 converted into pastures, from where such invasive grasses escape and become dominant in
8 disturbed forests. Nonetheless, far from the agricultural frontier (arc of deforestation), and
9 far from small-scale pastures at the core of the Amazon forest system, black water
10 floodplain forests disturbed by wildfires are being replaced by native savanna vegetation
11 (Flores and Holmgren 2021) (Figure 24.3). In floodplain landscapes of the Rio Negro, fires
12 are highly destructive, killing practically all trees, and allowing the ecosystem to shift to a
13 savanna state within only 40 years. After the first wildfire, soils start to change from clayey
14 to sandy, while tree composition shifts from forest to white-sand savanna species, and the
15 herbaceous community remains dominated by native opportunistic plants (Flores and
16 Holmgren 2021). This local abrupt shift from forest to white-sand savanna seems to be
17 driven by repeated wildfires and a strong flood erosion mechanism that alters plant-soil
18 interactions, favoring savanna species. Previous analyses at the basin scale have shown that
19 these floodplain forests are less resilient than the upland forests (Flores *et al.* 2017),
20 including in the watersheds of large white-water rivers, such as the Madeira and Solimões.
21 Hence, as in other forest-savanna transition zones, evidence suggests that savannas of the
22 Amazon system may expand and persist due to feedback mechanisms involving repeated
23 wildfires and soil erosion processes (Flores *et al.* 2020; Flores and Holmgren 2021).

24 2.3 Forest shift to an open-canopy, degraded state

25 When forests are repeatedly disturbed and native savanna species are not able to colonize,
26 the ecosystem often becomes trapped in an open vegetation state, dominated by fire-
27 tolerant tree and palm species that usually occur in the forest, together with invasive alien
28 grasses and opportunistic herbaceous plants (Perz and Skole 2003; Veldman and Putz

Chapter 24

1 2011), as well as vines and lianas (Tymen *et al.* 2016; Maia *et al.* 2021; Medina-Vega *et al.*
2 2021) (Figure 24.3). Below, we describe the feedback mechanisms that have been proposed
3 to explain how the ecosystem can be trapped in this state.

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

16 Other feedback mechanisms are also known to contribute to this ecosystem shift at the
17 landscape scale. For instance, the expansion of invasive alien grasses may also directly
18 reduce tree recruitment due to light competition with young seedlings (Hoffmann *et al.*
19 2004), which maintains low tree cover and grass dominance. Forest loss, degradation and
20 fragmentation inhibit the movement of many mobile animal species, particularly the ones
21 that are sensitive to open habitats (Laurance *et al.* 2004), causing many species to disappear
22 from the system (Barlow *et al.* 2016). In the case of frugivore species, by avoiding the use
23 of open disturbed habitats, tree seed dispersal in those sites may become limited, reducing
24 tree recruitment and forest regrowth. This dispersal limitation feedback is expected to be
25 stronger where disturbances are most severe (Turner *et al.* 1998). Evidence from the
26 tropical Atlantic Forest suggests that 30% tree cover could be a threshold in which many
27 forest adapted animal species disappear, and are replaced by disturbance adapted species

Chapter 24

1 (Banks-Leite *et al.* 2014), potentially disrupting plant-animal interactions that are critical
2 for forest recovery.

3 The current expansion of open degraded ecosystems across vast portions of the
4 southeastern Amazon forest is triggering other types of feedback mechanisms at the
5 regional and global scales. Forests play a major role in maintaining the rainfall regime of
6 the Amazon by allowing moisture that originates in the Atlantic Ocean to be transported
7 across the basin; a process that may involve up to seven cycles of rainfall and re-
8 evapotranspiration (Spracklen *et al.* 2012; Zemp *et al.* 2017; Staal *et al.* 2018; see also
9 Chapter 7). Hence, by interrupting this process, deforestation and forest degradation will
10 likely reduce rainfall at the central and western Amazon, with stronger potential impacts
11 particularly during the dry season. This process also involves a feedback between drought
12 and deforestation that is already strengthening with accumulated deforestation, in which the
13 more forest area is lost, the stronger dry seasons will be, further increasing deforestation
14 rates (Staal *et al.* 2020) and forest fires (Xu *et al.* 2020). In addition to its effects on
15 precipitation, deforestation also affects regional temperatures, with fragmented landscapes
16 being considerably hotter than non-fragmented ones (Zeppetello *et al.* 2020). Due to this
17 large-scale feedback, a tipping point (5) has been proposed to cause a major forest dieback
18 within the Amazon basin (Nobre *et al.* 2016; Lovejoy and Nobre 2019). A previous model
19 study had estimated this deforestation tipping point at 40% (Sampaio *et al.* 2007), yet,
20 recent evidence based on a climate-vegetation model that accounts for the combined effects
21 of climate change, deforestation and wildfires (Nobre *et al.* 2016; Lovejoy and Nobre
22 2019), suggests that this threshold might indeed be closer to the 20-25%. In sum,
23 considering these broad-scale interactions, the more Amazonian forests become trapped in
24 an open-canopy degraded state, the more likely that a 20-25% threshold is sufficient to
25 accelerate a critical systemic transition.

26 **2.4 Forest shift to a closed-canopy, secondary forest state**

27 Differently from the previous cases, in which the forest is trapped in a contrasting open-
28 canopy state, here, disturbed forests recover their closed-canopies but do not progress

Chapter 24

1 towards a mature forest state. Instead, they persist in an early successional stage, trapped by
2 different feedback mechanisms (Figure 24.3). Such secondary forests may not be identified
3 through satellite monitoring of canopy conditions, as high levels of greenness and leaf area
4 index may be interpreted as if the ecosystem has recovered its original forest state, when
5 aspects such as biodiversity and carbon storage remain at much lower values (Poorter *et al.*
6 2016; Rozendaal *et al.* 2019). In the Brazilian Amazon, for example, around 21% of the
7 previously deforested land is currently covered by secondary forests (INPE and
8 EMBRAPA 2011), but the ecological state of such regrown vegetation is unknown.

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

20 A combination of socio-economic and biophysical factors defines where and when forests
21 recover back to their previous state in terms of structure and composition. Within
22 traditional shifting cultivation systems that dominate riverine landscapes of the Amazon,
23 forest regrowth constitutes the fallow period that supports repeated crop yields, being an
24 essential element of the rotational system. In contrast, throughout the extensive
25 pasturelands that dominate Amazonian landscapes at the “arc of deforestation”, forest
26 regrowth constitutes an obstacle to pasture productivity and is often managed with
27 prescribed burning. Eventually, regrowth may occur in abandoned areas when landowners
28 do not have the means to continue managing the land or when land productivity is reduced

Chapter 24

1 by soil degradation (Vieira *et al.* 2014; Nanni *et al.* 2019). Therefore, feedback
2 mechanisms between social and ecological elements partly determine whether the
3 ecosystem will become arrested in a closed-canopy secondary forest state.

4 The capacity of secondary forests to fully recover depends on the management practices
5 applied prior to abandonment and on the landscape context where it occurs (Jakovac *et al.*
6 2021). The repeated fire use to clean pastures and fertilize cropping fields reduces soil
7 fertility and consequently the rates of forest recovery, particularly when return-intervals
8 between slash-and-burn events are shortened (Zarin *et al.* 2005; Jakovac *et al.* 2015;
9 Heinrich *et al.* 2020). Under a high disturbance regime, survival strategies are favored over
10 growth strategies and a plant community with conservative traits is more likely to thrive.
11 Survival traits include high sprouting ability and low nutrient demand (Jakovac *et al.*
12 2015), high wood density and high leaf toughness (Fernandes Neto *et al.* 2019), all of
13 which are traits associated with resistance to disturbance and often with slow growth rates
14 (Poorter *et al.* 2010). Lianas and grasses are also favored by disturbances (Roeder *et al.*
15 2010; Veldman and Putz 2011), contributing to arrest succession by competing with trees
16 and leading to reduced growth rates and higher tree mortality (Schnitzer and Bongers
17 2002). Combined, these feedbacks arrest forest succession, maintaining lower basal area,
18 biomass, canopy height and species diversity, as well as higher density of stems, lianas in
19 the canopy and grass cover in the understory.

20 Furthermore, forest fragmentation associated with deforestation causes tree seed dispersal
21 limitations, consequently reducing tree recruitment (Arroyo-Rodríguez *et al.* 2015),
22 representing another amplifying feedback that can hinder secondary forest succession. The
23 seed rain in such landscapes is mainly composed by early successional pioneers dispersed
24 by wind or by generalist bats and birds that are able to cross large extents of pasture or
25 cropping fields (Cubiña and Aide 2001; Wieland *et al.* 2011). Overhunting in degraded
26 forests embedded within human-modified landscapes further contributes to reduce the
27 availability of animal dispersers and increase dispersal limitation (Bagchi *et al.* 2018). The

Chapter 24

1 slow inputs of seeds from mature forests results in consistently slow species accumulation
2 over time and therefore a slow species turnover during regrowth (Mesquita *et al.* 2015).

3 In sum, different combinations of drivers and feedback mechanisms can cause Amazonian
4 forests to be trapped in different configurations, some of which are alternative states (Box
5 24.1). Here, we have identified four of these configurations, based on existing evidence: (i)
6 a closed-canopy semi-deciduous forest state, potentially with a more gradual shift; (ii) a
7 native savanna state; (iii) an open-canopy degraded state; and (iv) a closed-canopy
8 secondary forest state. Shifts to these alternative configurations may occur locally, but
9 depending on the scale of the feedbacks, they may become contagious and spread
10 disturbances across large parts of the basin, increasing the probability of a systemic forest
11 dieback. Moreover, other types of configurations are possible, such as bamboo-dominated
12 (*Guadua sarcocarpa*) forests of the southwestern Amazon that self-perpetuate facilitated
13 by a fire feedback; however, we have focused on four general types that are more likely to
14 expand in the coming future.

15 **3. PAST EVIDENCE OF THE DYNAMICS OF AMAZONIAN ECOSYSTEMS** 16 **SINCE THE LAST GLACIAL MAXIMUM (20 KA)**

17 Studies focusing on past vegetation changes have documented several of the forest change
18 scenarios outlined in section 2 (see also Chapters 1 and 2). For instance, an expansion of
19 savannas in the northeastern portions of the basin during a climatically unstable period
20 with increasing temperatures was registered at the beginning of the Holocene, i.e.,
21 approximately 11 ka (Rull 2015). However, the changes observed in sedimentary archives
22 have not always shown a change towards savannization, but depended on the nature of the
23 environmental driver. For instance, pollen analysis revealed a rainforest expansion during
24 the last 3,000 years in forest-savanna boundaries of the southern Amazon, driven by wetter
25 conditions related to changes in the location of the intertropical convergence zone (Mayle
26 *et al.* 2000). Hence, these forests have likely reached their maximum potential southern
27 limit expansion for the past 50 ka (Mayle *et al.* 2000), with a 22% increase in the CO₂
28 storage budget since the mid-Holocene (6 ka) (Mayle and Beerling 2004). Given the

Chapter 24

1 historical observations registered during the last decades (see Chapter 22), and the climate
2 projections forecasted for this region towards drier conditions (Magrin *et al.* 2014), it is
3 unlikely that this forest expansion and consequent increased carbon sequestration will
4 continue. Instead, combined evidence suggests that these forests are more likely to recede,
5 being replaced by open vegetation types.

6 Empirical data of long-term forest dynamics have shown the differential sensitivity to past
7 climate change across the Amazon basin. Regions like the southern and southeastern
8 Amazon have shifted between forest and open savanna vegetation in relatively recent
9 periods of colder and drier LGM climate (Absy and Hammen 1976), whereas the Andean
10 flank in the western (van der Hammen and Absy 1994) and eastern portions of the Amazon
11 (Wang *et al.* 2017) seem to have persisted as forest. Long-term ecological data from pollen
12 analysis have shown the prevalence of various types of rainforests, both in southwestern
13 cloud forests and northwestern pre-montane forests of Amazonian highlands, showing the
14 importance of the cloud cover in buffering forests when facing climate change (Urrego *et*
15 *al.* 2010; Montoya *et al.* 2018). Presence of forests with distinct composition during LGM
16 has also been observed in northwestern Brazilian Amazon (Bush *et al.* 2004; D’Apolito *et*
17 *al.* 2013). All these regional evidence of a persistently forested Amazon system are
18 consistent with large-scale speleothem analyses showing a remarkable stability of the
19 Amazon rainforest for the past 45 ka, even under a 60% decrease in precipitation totals
20 (Wang *et al.* 2017).

21 The Mid-Holocene Dry Event (MHDE; 9-4 ka) has been proposed as a potential past
22 analog of current and future trends of decreased precipitation, yet there is still limited
23 evidence covering the entire duration of MHDE throughout the basin. Currently available
24 paleo-records, however, suggest a higher vulnerability of tropical forests to extended
25 droughts in peripheral transitional zones (Mayle and Power 2008; Smith and Mayle 2018).
26 In addition, changes in plant functional traits spanning the termination of the MHDE (i.e., a
27 period of increasing rainfall amount) suggest that rainfall increases led to a replacement of
28 slow-growing, drought-tolerant taxa by fast-growing, drought-vulnerable taxa (van der

Chapter 24

1 Sande *et al.* 2019). Indeed, secondary forest species usually differ in their ecological
2 strategies from mature forest species, changing the forest functioning and stability. In
3 southeastern Venezuela, for instance, rainforest taxa were replaced by secondary dry
4 forests around 2.7 ka, a shift that persisted for more than 1,000 years. These secondary
5 forests were finally replaced 1.4 ka under a period of high fire occurrence by the current
6 vegetation consisting of open savanna (Montoya *et al.* 2011).

7 When a forest is disturbed, the rates of ecosystem change observed in sedimentary archives
8 depend on the ecological scale, being abrupt (decadal) at the species level, but gradual
9 (centennial) at the community level (Montoya *et al.* 2018, 2019). In a tropical meta-data
10 analysis of forest recovery rates after disturbances based on pollen records, Cole *et al.*
11 (2014) observed that South American forests required an average of 325 years to recover
12 from disturbances (natural and human-induced). The recovery rate was calculated in terms
13 of attaining a forest cover (expressed in % of tree pollen) similar to that prior to the
14 disturbance, without differentiating changes in the forest composition, structure or function.
15 Forests exposed to natural large infrequent disturbances (i.e., hurricanes or volcanic
16 eruptions) recovered faster compared to those affected by post-climatic and human
17 impacts. However, forests exposed to more frequent disturbances usually recovered faster,
18 suggesting that repeated disturbances may increase forest adaptive capacity and resilience,
19 yet over multi-centennial time scales (Cole *et al.* 2014). In the Andean Amazon region,
20 Loughlin *et al.* (2018) studied lands that were managed by Indigenous populations, but
21 following European conquest, forests recovered structurally (not compositionally) in only
22 130 years, possibly because the higher soil productivity of this region boosted tree growth.
23 Despite differences in these estimates, both studies manifest that the temporal range
24 required for forest to potentially recover is multi centennial (Cole *et al.* 2014; Loughlin *et*
25 *al.* 2018).

26 In summary, paleoecological evidence hints at two main directions. Firstly, the Amazon
27 forests have undergone local to regional shifts to dry secondary forests or savannas
28 (Montoya *et al.* 2011) depending on the disturbances at play (climate- or human-induced

Chapter 24

1 changes), but not a basin-wide abrupt dieback, even during intense drier and warmer
2 periods that could well represent analogs of the hypothesized climate-related *tipping points*
3 (1) – (4). Secondly, the recovery ability of Amazonian forest ecosystems depends on their
4 disturbance histories: the more disturbance-adapted, the faster the recovery rates.
5 Nevertheless, long-term ecological data are still limited in the basin and concentrate
6 primarily along the Amazon margins; more work is still needed for unraveling the
7 dynamics of such heterogeneous ecosystems (Lombardo *et al.* 2018). In addition, some
8 important caveats need to be addressed when using paleo-data as reference for future
9 dynamics: (1) the increased rates and magnitudes of the changes projected for the near
10 future, with combined disturbance events (climatic and human-induced) acting
11 synchronously are unprecedented and may hamper forest recovery due to novel
12 mechanisms; and (2) the baseline conditions we have shown are no-analog of
13 ecophysiological drivers such as the enhanced atmospheric CO₂ concentrations of the 21st
14 century (section 5.3).

15 **4. DRIVERS OF THE AMAZON FOREST RESILIENCE**

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

22 The resilience of the Amazon forest is directly linked to the functional characteristics of
23 individual trees and their capacity to resist adverse conditions and disturbances. Thus,
24 processes that exert pressure on the capacity of trees to maintain their functioning and
25 survival are critical. Water deficit associated with increasing length of the dry season or
26 extreme droughts (i.e., related to *tipping points* (2) and (3), section 2), is likely to be the
27 major climatic threat to Amazonian trees, as suggested by observational and experimental
28 studies, showing that droughts increase tree mortality rates of individual trees (Nepstad *et*

Chapter 24

1 *al.* 2007; DaCosta *et al.* 2010; Phillips *et al.* 2010; Rowland *et al.* 2015; Zuleta *et al.* 2017;
2 Aleixo *et al.* 2019; Janssen *et al.* 2020b). At least 50% of the Amazon forest is exposed to
3 seasonal droughts of three months or more (Nepstad *et al.* 1994), and contrasting rainfall
4 regimes have selected for species with different drought resistance mechanisms (Oliveira *et*
5 *al.*; Barros *et al.* 2019; Brum *et al.* 2019). In many cases, extreme drought events may not
6 necessarily cause the death of trees, but reduce their growth and capacity to maintain
7 transpiration rates. However, a recent meta-analysis of field observations reveals that
8 highly diverse Amazonian tree communities seems to buffer this effect, conferring higher
9 ecosystem resistance in terms of evapotranspiration rates (Janssen *et al.* 2020a).

10 Examples of functional characteristics of Amazonian trees to cope with seasonal water
11 deficit include: (1) investment in deep roots (Nepstad *et al.* 1994; Brum *et al.* 2019); (2)
12 roots that allow hydraulic redistribution during the dry season (i.e., passive movement of
13 water from deep to shallow soil through roots) (Oliveira *et al.* 2005); (3) high embolism
14 resistance, particularly in shallow-rooted understory trees and trees over plateaus far away
15 from the water table (Oliveira *et al.*; Brum *et al.* 2019); (4) strong stomatal control in the
16 dry season resulting in high water use efficiency (Barros *et al.* 2019; Brum *et al.* 2019); (5)
17 leaf shedding capacity by deciduous species (Wolfe *et al.* 2016). Although these traits do
18 not guarantee survival under future increasingly drier and variable climates, in locations
19 where the dry season has been intensified, changes in forest composition dynamics are
20 already underway through the recruitment of more dry-affiliated species and the mortality
21 of more wet-affiliated species (Esquivel-Muelbert *et al.* 2019). Also, life-history strategies
22 (e.g., fast-slow continuum in growth rates) have been shown to determine species-level
23 mortality, i.e., the faster you grow, the higher is the mortality risk (Esquivel-Muelbert *et al.*
24 2020).

25 There is also evidence that temperature changes (see Chapter 22; Figure 2e) could already
26 be changing forest functioning. Warmer temperatures tend to reduce forest productivity
27 rates (Sullivan *et al.* 2020), particularly by intensifying the atmospheric vapor pressure
28 deficit (Smith *et al.* 2020), indicating that rising temperatures may eventually impact forest

Chapter 24

1 functioning and persistence (Araújo *et al.* 2021). Additional CO₂ is expected to buffer the
2 effect of water stress by increasing plant water-use efficiency and accelerating tree growth
3 (section 5.3). Elevated atmospheric CO₂ may be the cause of the increase in woody
4 biomass and productivity observed across Amazonian forests (Brienen *et al.* 2015).
5 However, CO₂ driven accelerations of tree growth have come at the cost of decreasing tree
6 longevity across the basin, further contributing to increase tree mortality rates (Brienen *et*
7 *al.* 2015; Hubau *et al.* 2020).

8 Despite the uncertainties regarding forest responses to climate change, current findings
9 suggest that, in the absence of fire, Amazonian forests may change both compositionally
10 and functionally in response to climatic changes, but still remain as closed-canopy forests.
11 Furthermore, if climate-related *tipping points* (2) – (4) (section 2) are crossed, shifts are
12 likely to be sparse and local because of the high heterogeneity and diversity of forest types.
13 Increased tree mortality caused by human-induced disturbances (e.g., wildfires and
14 deforestation), however, may contribute to destabilize the Amazon forest (Silva *et al.*
15 2018), increasing the likelihood that forests will be trapped in an open-canopy degraded
16 state, and that the system as a whole will cross the *tipping point* (5) (section 2.3).

17 **5. UNCERTAINTIES ASSOCIATED WITH TIPPING POINTS WITHIN THE** 18 **AMAZON SYSTEM**

19 ***5.1 How does forest heterogeneity affect large-scale tipping points?***

20 Amazonian forests are home to ca. 15,000 tree species (Ter-Steege *et al.* 2020). Most of
21 these species are rare, and many remain unknown to science (ter Steege *et al.* 2013),
22 implying that this huge diversity imposes an enormous challenge to the understanding of
23 how the system functions. In particular, dominant species are responsible for most of the
24 ecosystem functions, such as carbon cycling (Fauset *et al.* 2015). Yet, the many non-
25 dominant and rare species that exist in a forest theoretically also play a fundamental role in
26 ecosystem resilience (Walker *et al.* 1999). When stressing conditions and disturbance
27 regimes change, these rare species can offer new possibilities of functioning, thus

Chapter 24

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

19 Rainfall variability (intra- and inter-annual fluctuations) may also add more heterogeneity
20 to the system, as forests that experience more variability seem to be more resilient, likely
21 due to a training-effect after experiencing multiple wet and dry periods (Ciemer *et al.*
22 2019). For instance, tree communities embedded within a more seasonal rainfall regime are
23 more diverse in terms of their tolerance strategies to cope with drought, when compared to
24 communities within a less seasonal rainfall regime (Barros *et al.* 2019). In other words,
25 while higher mean annual precipitation (above 2,500 mm/yr) increases forest resilience
26 (e.g., northwestern Amazon; Hirota *et al.* 2011; Staver *et al.* 2011), forests exposed to
27 higher average seasonality and interannual variability seem to be more drought tolerant,
28 compensating the lower resilience (e.g., eastern x northwestern forests). Valley forests may
29 also be less resistant to droughts than plateau forests due to a similar mechanism, due to a

Chapter 24

1 training-effect related to water table fluctuations selected for tree communities with
2 contrasting hydraulic traits (Zuleta *et al.* 2017; Cosme *et al.* 2017; Oliveira *et al.* 2019).
3 Nonetheless, *tipping points* (2) and (3), related to dry season increases in length and
4 intensity, imply that in forests where climate is already drier, increases in rainfall
5 seasonality could potentially cause forest loss. Also, increases in frequency of extreme
6 drought events may prevent a proper forest recovery (Anderson *et al.* 2018; Longo *et al.*
7 2018).

8 Another heterogeneity that may affect the probability of *tipping point* (1) (1,000 mm/yr;
9 section 2) is related to seasonal flooding. Amazonian floodplains cover 14% of the basin
10 and the forests in these ecosystems were shown to be less resilient than the dominant
11 upland forests, with a potential tipping point of forest collapse at approximately 1,500
12 mm/yr (Flores *et al.* 2017). Therefore, exploring sources of heterogeneities in forest
13 responses to different types of disturbances is key to understand whether the Amazon could
14 shift gradually or abruptly from local to basin-wide scales (e.g., Higgins and Scheiter 2012;
15 Levine *et al.* 2016).

16 **5.2 How does forest connectivity affect large-scale tipping points?**

17 Spatial heterogeneity implies reduced connectivity (less interactions) and may have a huge
18 influence on the systemic resilience of the Amazon, altering how the forest responds to
19 changes in climate change and human pressures (Levine *et al.* 2016; Longo *et al.* 2018).
20 For instance, the climatic, hydrological and biogeochemical connections between the
21 Andes and the low-lying Amazon are undeniably key factors in determining the
22 functioning of the current and future of the entire system on the large scale (see Chapter 22;
23 Builes-Jaramillo and Poveda 2018). Nonetheless, theoretically, connectivity may still be
24 high even in heterogeneous environments, with different processes linking parts of the
25 system (Scheffer *et al.* 2012). Although forests with contrasting geomorphological,
26 climatological, biological and cultural histories have formed the Amazon (see Chapters 1-
27 13; Figure 24.1), these forests can interact. For instance, biogeochemical cycles involve
28 fluxes that transport water vapor from plateau to valley forests on a landscape scale. At

Chapter 24

1 broader scales, large white-water rivers transport huge loads of sediment rich in nutrients
2 from the west to the east of the basin (see Chapter 1), depositing them along floodplains
3 where forests can grow faster. Eastern Amazonian forests are also connected to western
4 forests through rainfall recycling (Zemp *et al.* 2017, see also Chapter 7); a mechanism that
5 enhances the resilience of western forests but may be losing strength due to deforestation
6 (Staal *et al.* 2020). When a forest is disturbed locally, mobile animals may transport tree
7 seeds and propagules from surrounding forests and accelerate its recovery (Lundberg and
8 Moberg 2003). However, mobile animals may also transport seeds of alien invasive grasses
9 from open areas to degraded forested landscapes, increasing their flammability. Local
10 human populations of different Amazonian regions may share ancient knowledge of forest
11 management practices (Levis *et al.* 2018, see also Chapters 8 and 10), potentially changing
12 tree species composition and re-shaping forest resilience.

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

5.3 The interplay between CO₂ fertilization effect and nutrient availability

20 Two of the most pressing uncertainties regarding the resilience of the Amazon forest to
21 climate change and other anthropogenic disturbances are the potential physiological effect
22 of increased atmospheric CO₂ (also known as “CO₂ fertilization effect”, eCO₂) and the
23 hypothetical limitations to forest productivity and biomass accumulation imposed by soil
24 nutrient constraints, notably phosphorus (P; see Chapter 1). The current generation of
25 ecosystem models (namely standard Dynamic Global Vegetation and Earth System
26 Models), are constrained in their ability to provide more trustful projections on the impact
27 of climate change on the forest, due mainly to the acute lack of evidence about the

Chapter 24

1 existence, magnitude and duration of a CO₂ fertilization effect and associated limitations
2 imposed by soil nutrients (Lapola 2018).

3 On the one hand, the CO₂ fertilization effect could, theoretically, increase forest
4 productivity, biomass accumulation rates (Ainsworth and Long 2005) and water use-
5 efficiency (Kauwe *et al.* 2013). On the other hand, the lack of key nutrients for plant
6 metabolism refrains further biomass gains under elevated CO₂ conditions (Norby *et al.*
7 2010). There are preliminary (i.e., short-term) indications from other phosphorus-limited
8 forests (in sub-tropical Australia), subjected to increased atmospheric CO₂ concentrations,
9 that did not significantly increase biomass (Jiang *et al.* 2020) given that phosphorus is
10 needed especially for making the cell membrane, and also for energetic (ATP) and genetic
11 (DNA and RNA) plant molecules. As such, trees might increase their photosynthetic rates
12 under enhanced CO₂ but do not allocate these extra photosynthates in additional plant
13 biomass, possibly simply increasing biomass turnover rates across the forest ecosystem.
14 Nevertheless, this evidence comes from single-species forests and the response of highly
15 diverse forests such as the Amazon to enhanced CO₂ is yet to be unveiled. In this sense,
16 observational data along a P availability gradient in Panamanian tropical forests revealed
17 that, although such P limitation exists, it does not affect different species in the same way
18 (Turner *et al.* 2018). This latter finding is of particular relevance for the Amazon forest
19 given that climate change and other anthropogenic disturbances may imply significant
20 alteration of the forest tree community composition and dominance relations, both in
21 taxonomic and functional terms (Norby *et al.* 2016). Alternatively, it is hypothesized that
22 Amazon forest trees could change symbiotic exchanges of carbohydrates and nutrients with
23 mycorrhizae fungi to access currently unavailable soil P pools.

24 Besides the implications to the Amazon forest carbon budget and functional diversity, the
25 physiological effects of elevated CO₂ have the potential to interfere in the flux of humidity
26 from trees to the atmosphere, which is especially relevant for the region, where from 20%
27 to 80% of the rainfall is recycled locally (Zemp *et al.* 2017). In that sense, free-air
28 concentration enrichment (FACE) experiments in temperate forests in the United States and

Chapter 24

1 in an Eucalyptus-dominated woodland in Australia have found a reduction of stomatal
2 conductance and canopy transpiration in the order of -20% (Kauwe *et al.* 2013; Gimeno *et*
3 *al.* 2016). That is the same magnitude of reduction in transpiration found in recent coupled
4 climate-vegetation modeling studies for the region, which is ultimately related to a basin-
5 wide reduction of 15% to 20% in rainfall (Kooperman *et al.* 2018). Such a rainfall
6 reduction possibly caused by the physiological effect of elevated CO₂ is equivalent to the
7 rainfall reduction in a scenario with complete deforestation of the Amazon (Sampaio *et al.*
8 2020).

9 Without an enhancement of productivity and with a reduction of forest canopy transpiration
10 due to increased atmospheric CO₂, the actual Amazon forest and its current community
11 compositions and functional relations are thought to become less resilient to climatic
12 changes, deforestation, degradation and other anthropogenic disturbances, with pervasive
13 impacts on the regional socio-economy (Lapola 2018). Two ongoing ecosystem-scale
14 experiments - the AmazonFACE experiment and the Amazon Fertilization Experiment
15 (AFEX) - will soon provide valuable information about the CO₂ fertilization effect and the
16 limitation of forest productivity and biomass stocks by soil nutrients in the Amazon forest
17 (Hofhansl *et al.* 2016).

18 **6. MODELING THE RESILIENCE AND THE TIPPING POINTS OF THE** 19 **AMAZON FOREST**

20 Dynamic Global Vegetation Models (DGVMs) and Land Surface Models (LSMs) are the
21 most used tools to mimic the behavior of vegetation dynamics (Sato *et al.* 2015; Fisher and
22 Koven 2020). As those models are capable of simulating long time series of vegetation
23 under global change, they are key to project the future of the Amazon system (e.g., White
24 *et al.* 1999; Cox *et al.* 2004). Often DGVMs and LSMs are the vegetation component in
25 Earth System Models (ESMs), and their success in comprehensively representing processes
26 of vegetation growth and interactions with other Earth System components relies on
27 empirically-derived evidence. This means those models need to make use of the
28 information described in section 4. Given the extreme complexity involved in soil-plant-

Chapter 24

1 atmosphere interactions at different temporal and spatial scales, selecting the most relevant
2 processes and implementing them into models are very challenging tasks (Fisher and
3 Koven 2020), and leads to substantial uncertainties (e.g., Rammig *et al.* 2010).

4 As stated above, model simulations can be performed a) offline, meaning the vegetation
5 model is driven stand-alone by externally generated climate data or b) coupled, meaning
6 that the vegetation model is part of an ESM in which different compartments of the Earth
7 System (e.g. the vegetation and the atmosphere) can interact. Such a coupling increases the
8 amount of accounted feedback mechanisms (Box 24.1) which are theoretically necessary to
9 identify *classical tipping points*, besides the prerequisite that the DGVM/LSM allows for
10 the existence of two or more alternative vegetation cover configurations under the same
11 underlying conditions (e.g., climatic) (Box 24.1). For the Amazon ecosystems, tipping
12 point simulations performed so far rely on both offline and coupled runs (*tipping points* (4)
13 and (5) from section 2). Taking the inherent limitations of simulating alternative stable
14 states into account, below we present a summary of what such models can already tell us
15 about dieback, thresholds (Box 24.1) and resilience within the Amazon basin.

16 More than 20 years ago, modeling studies pointed out to a potential Amazon dieback under
17 climate change (White *et al.* 1999; Cox *et al.* 2000, 2004; Cramer *et al.* 2001). Up to now a
18 substantial amount of literature has painted a complex picture with key uncertainties
19 regarding the resilience and potential tipping points of the Amazon under global and
20 regional environmental changes. The results span from clear identification of crossing
21 tipping points in time, as represented by levels of tree cover or biomass stock (e.g., Cox *et al.*
22 *et al.* 2004; Sitch *et al.* 2008), up to an overall increase of biomass and forest cover
23 (Schaphoff *et al.* 2006; Lapola *et al.* 2009; Rammig *et al.* 2010; Huntingford *et al.* 2013).
24 Such a large variety of results can be explained by: 1) whether the DGVM/LSM was
25 coupled (e.g., Cox *et al.* 2004); 2) the existing variety of underlying model assumptions
26 and processes; and 3) general uncertainties on future climate changes in the region.
27 Moreover, DGVMs and LSMs represent vegetation using a limited set of plant functional
28 types (PFTs), which are still not capable of comprising the entire range of plant strategies

Chapter 24

1 that confer more or less resilience to the Amazon forests (Oliveira *et al.*). In this sense, a
2 more comprehensive representation of different vegetation ecosystems is needed to
3 improve the simulation of the gradual and abrupt shifts to alternative configurations for the
4 Amazon forests described in section 2. Hence, so far, there is a fairly binary possibility:
5 either the current configuration or a complete replacement of forest by another simulated
6 vegetation type and presented by current models.

7 The main drivers behind this original modeled forest dieback (Cox *et al.* 2004) are the
8 acute reduction in regional rainfall that affects photosynthetic rates and the accompanying
9 increase in temperature that further increases plant respiration, resulting therefore in a
10 considerable reduction of plant productivity and growth. The effects on carbon assimilation
11 also impact the flux of water from the surface vegetation to the atmosphere through
12 transpiration, reinforcing the moisture limitation and ultimately leading to a shift of PFTs,
13 from predominantly tropical broadleaf trees to C₄ grasses with about 30% of broadleaf tree
14 cover, resembling a savanna vegetation (Betts *et al.* 2004; Cox *et al.* 2004). Even without
15 the implementation of such feedbacks through coupling with ESMs, previous offline
16 simulations support such “savannization” processes (section 2.2) under future scenarios of
17 precipitation and temperature changes (Nobre *et al.* 1991; Oyama and Nobre 2003).
18 Importantly, the feedbacks are magnifying the regional climate and vegetation response,
19 and a long-term commitment to Amazon dieback occurs at 2°C global warming,
20 determining an actual *tipping point* (4) from section 2 (Jones *et al.* 2009). Therefore, it is
21 clear that the Amazon dieback is an issue about feedbacks (i.e., interactions within a closed
22 loop) between the regional climate and the forest vegetation functioning. In this sense, a
23 key component is the regional climate response to global warming and the role of non- or
24 dysfunctional forest states in magnifying this process; in other words, whether the regional
25 climate moves from a configuration supporting the rainforest to another, which it does not.
26 This depends on the availability of soil moisture, which itself depends on precipitation and
27 evaporation, both of which change with global warming (see Figure 24.2 for historical and
28 projected changes in some of these variables). If the regional climate reaches a critical

Chapter 24

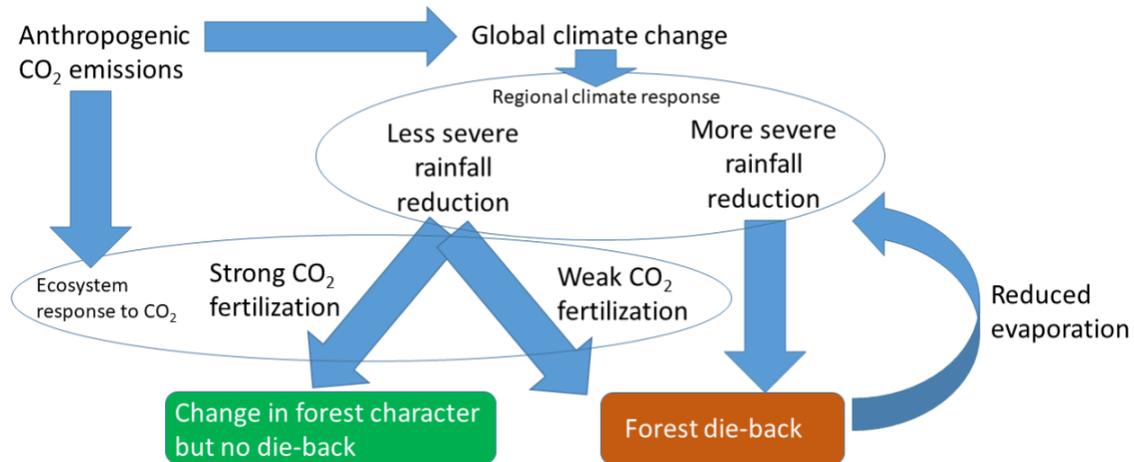
1 state, the resulting forest dieback magnifies the regional climate change and causes further
2 forest dieback.

3 However, as in many regions of the world, the projected changes in precipitation in the
4 Amazon due to anthropogenic climate change are highly uncertain (e.g., Jupp *et al.* 2010).
5 While the majority of the current generation of climate models project a decrease in annual
6 mean precipitation with global warming (see Chapter 22), the rate of the Amazon
7 precipitation decrease in relation to global warming varies widely between the models. A
8 family of climate models notable for their projection of severe Amazon drying, HadCM3
9 (Gordon *et al.* 2000), project the annual precipitation in the eastern Amazon to reduce to
10 below 1,500 mm/yr at approximately 3°C global warming (Betts *et al.* 2012). This
11 precipitation level has been identified as one of the climatic thresholds critical to the
12 support of rainforests (Malhi *et al.* 2009), with empirical evidence suggesting this seems to
13 be the *tipping point* (1) for floodplain forests (Flores *et al.* 2017). The largest decrease in
14 precipitation in the HadCM3 model family was largely a result of atmospheric circulation
15 changes driven by particular patterns of sea surface temperature (SST) (Harris *et al.* 2008).
16 The variation in precipitation change between the models was found to be related to the
17 strength of the SST changes in the equatorial Atlantic (Good *et al.* 2008, 2013). Most other
18 models also project decreased precipitation, but less severely.

19 On the one hand, there are three main underlying drivers to the aforementioned climatic
20 changes that can trigger or reinforce a modeled threshold crossed in the region, even under
21 less severe decreases in precipitation: global climatic changes due to higher atmospheric
22 greenhouse gas (GHG) concentration (Cox *et al.* 2004; Schaphoff *et al.* 2006; Lapola *et al.*
23 2009; Jupp *et al.* 2010; Huntingford *et al.* 2013), deforestation and forest degradation
24 (Sampaio *et al.* 2007; Staal *et al.* 2020), and forest fires (Burton *et al.*; Barlow and Peres
25 2008; Cochrane and Barber 2009; Nobre *et al.* 2016). The occurrence of the climate tipping
26 point for Amazon forest dieback projected in the models therefore depends partly on the
27 nature of the regional climate response to global warming and the impact of CO₂
28 fertilization, wildfires and deforestation (Figure 24.4). If the regional climate response is

Chapter 24

1 relatively small, forest dieback does not occur. However, if the regional climate response is
2 large, forest dieback could in principle occur and magnify itself through local and global
3 climate feedbacks.



4

5

6 **Figure 24.4.** Simplified sketch of processes involved in the potential Amazon dieback
7 tipping point due to climate change.

8 Regardless of the feedbacks involved, after correcting for biases (found in climatic
9 projections under climate change conditions) identified using observation data, a basin-
10 wide Amazon dieback would be unlikely to occur, even under the most pessimist IPCC
11 pathway (Chai *et al.* 2021). Furthermore, there are some ecological processes that can
12 potentially damp, offset or prevent Amazon dieback, namely the CO₂-fertilization effect
13 under enhanced CO₂ (section 1.4.3) (Hickler *et al.* 2008; Huntingford *et al.* 2013;
14 Kooperman *et al.* 2018), the acclimation of tree physiology to warmer and drier climates
15 (Kumaranthunge *et al.* 2018), as well as the reorganization of forest communities and/or
16 their functional characteristics such that biomass and other broad characteristics that define
17 crucial ecosystem functions are maintained (Sakschewski *et al.* 2016).

18 Processes related to functional diversity (e.g., Fyllas *et al.* 2014; Fischer *et al.* 2016;
19 Sakschewski *et al.* 2016), including plant hydraulics (e.g., Christoffersen *et al.* 2016; Xu *et*

Chapter 24

1 *al.* 2016; Eller *et al.* 2020) and rooting depth (Langan *et al.* 2017; Sakschewski *et al.* 2020),
2 have already started to be implemented in current vegetation models to improve the
3 representation of local-scale heterogeneity of the Amazon basin and consequently the
4 ability models have to capture resilience increases due to biotic and abiotic heterogeneity
5 (section 5.1) (Levine *et al.* 2016; Sakschewski *et al.* 2016; Longo *et al.* 2018).
6 Furthermore, models demand a high amount of observational, field-based and/or
7 experimental data, which are still scarce. Kooperman *et al.* (2018), for example, point out
8 that stomatal closure under enhanced CO₂ (as part of the CO₂-fertilization effect) can drive
9 significant modeled rainfall reduction in the Amazon through reduced forest transpiration
10 and moisture recycling (Zemp *et al.* 2017), even though ecosystem-scale evidence on the
11 interplay between enhanced CO₂ and stomatal conductance are very scarce. Adding to that
12 complexity, other studies suggest that stomatal closure under enhanced CO₂ might not turn
13 out as strong as anticipated by models, since leaves need to increase transpiration cooling
14 under elevated temperatures (Dong *et al.* 2014). Another example is that modeled
15 phosphorus limitation (present in about 60% of Amazonian soils (Quesada *et al.* 2012; see
16 Chapter 1) might reduce or even eliminate any gains in primary productivity arising from a
17 supposed CO₂ fertilization effect in the Amazon (Fleischer *et al.* 2019); but, again, there is
18 lack of field data and knowledge on the Amazon phosphorus cycle to corroborate such a
19 result (section 5.3).

20 As such, the way forward for modeling and evaluating the likelihood and mechanisms
21 behind an Amazon tipping point passes first through a closer integration between models,
22 data and field experiments. Field data show us for example that community dynamics – tree
23 recruitment and mortality – plays a key role in the impact of climate change and climatic
24 extremes in the Amazon (section 4) (Esquivel-Muelbert *et al.* 2019, 2020; Hubau *et al.*
25 2020). Thus, improving the representation of such recruitment and mortality dynamics and
26 its driving causes is one priority for modeling. Other processes such as the role of plant
27 hydraulics (Eller *et al.* 2018) and increased plant functional diversity (Scheiter *et al.* 2013;
28 Sakschewski *et al.* 2016), as well as large scale heterogeneities related to climate,
29 hydrology and soil chemistry, for instance, should be explored in more depth by other

Chapter 24

1 models. The potential CO₂ fertilization effect on photosynthesis and water use and possible
2 limitation of forest productivity by soil nutrients (section 5.3) represent a *quasi*-complete
3 gap in existing models of the Amazon forest vegetation due to the lack of mechanisms
4 understanding and field data. Last, but not least, narrowing down the uncertainties of
5 rainfall projections for the region would also be very important for better constraining
6 modeling studies on the Amazon tipping point.

7 **7. CONCLUSIONS**

8 The pressure of intensified anthropogenic activities has promoted the appearance of new
9 stressing factors operating in the Amazon forests, as well as an intensification of some
10 environmental drivers at different spatial and temporal scales. It has been hypothesized that
11 the cumulative effect of disturbances such as deforestation, droughts, and fires may
12 unbalance the natural dynamics of these globally important ecosystems due to the systemic
13 loss of forest resilience. The analysis of the existing literature performed in this chapter has
14 highlighted five different scenarios of tipping points to which the Amazonian forests could
15 be sensitive to (Figure 24.2), namely: (1) the annual rainfall between 1,000 mm/yr and
16 1,500 mm/yr inferred from global climate models, (2) the dry season length of seven
17 months, inferred from satellite observations of tree cover distributions, (3) for the Amazon
18 lowlands, the maximum cumulative water deficit values between 200 mm/yr and 350
19 mm/yr, inferred from global climate models; (4) an increase of 2°C on the equilibrium
20 temperature of the Earth, inferred from a coupled climate–vegetation model, and (5) the 20-
21 25% accumulated deforestation of the whole basin, inferred from a combination of
22 environmental changes and human-induced degradation via deforestation. Based on
23 empirical evidence, four different ecosystem configurations, some of which could be
24 alternative stable states, have been proposed for Amazonian forests if a tipping point or
25 threshold is crossed, including: (i) a closed-canopy seasonally dry tropical forest state; (ii) a
26 native savanna state; (iii) an open-canopy degraded state; and (iv) a closed-canopy
27 secondary forest state. However, due to the existence of novel feedbacks associated with
28 invasive plants and human-modified landscapes, we consider the open degraded state and

Chapter 24

1 the closed-canopy secondary forest state as more likely to occur over broad areas,
2 particularly across the ‘arc of deforestation’. New evidence, however, indicates that in
3 remote parts of the Amazon basin far from the agricultural frontier, the native savanna state
4 could be replacing seasonally inundated forests disturbed by wildfires. Ecological features
5 including differential tree growth, recruitment, and survival among Amazonian species are
6 key to promote forest resistance to, as well recover from, disturbances at local scales. We
7 identify three mechanisms that may affect the risk of a large-scale tipping point due to
8 contagious forest dieback: (a) the environmental heterogeneity and connectivity among
9 forests across the basin; (b) the functional diversity and adaptive capacity of the species
10 present in the different forest types; and (c) the uncertain effect of enhanced CO₂ and
11 nutrient limitation. The lack of this ecological information for many Amazonian species,
12 the uncertainty of the potential feedbacks operating, as well as the need for further
13 improvements in climate change projections hamper the development of robust models for
14 anticipating the potential shifts that Amazonian forests may undergo in the near future. The
15 way forward for modeling and evaluating the likelihood and mechanisms behind an
16 Amazonian tipping point passes first through a closer integration between models,
17 observational data and/or field experiments. Even with models where a tipping point is not
18 met, and accounting for the uncertainty due to the limited data available, we need to urge
19 the international community within and outside academia to protect, maintain and
20 sustainably manage the resilience of these complex and dynamic entities that are the
21 Amazonian forests.

22

23 **9. RECOMMENDATIONS**

- 24 • Combining analysis of future environmental change scenarios with past and present
25 dynamics can help improve our understanding of alternative ecosystem
26 configurations;

Chapter 24

- 1 • Building a holistic and integrative scientific framework with all Working Groups is
2 needed to assess the main heterogeneities, drivers and ways to manage the
3 resilience of the Amazon forest system;
- 4 • Understanding the heterogeneities of the Amazon is key to assess the risk of a
5 large-scale tipping point and manage the resilience of the system;
- 6 • Planning an effective transnational monitoring system to improve our knowledge on
7 the dynamics of different Amazon ecosystems (embedded in a wider range of
8 environmental conditions), and potentially their heterogeneous response to various
9 types of disturbances (e.g., climatic extremes, wildfires, deforestation);
- 10 • Managing Amazonian resilience locally can help reduce the risk of reaching a
11 tipping point. This requires protecting and restoring forest cover, biodiversity,
12 agrobiodiversity, and cultural diversity, as well as improving fire management and
13 fire early-warning systems;
- 14 • Managing Amazonian resilience also requires global action to halt GHG emissions.

15

16

17

18

19

20

21

22

23

24

Chapter 24

10. REFERENCES

- 2 Absy ML and Hammen T van der. 1976. Some palaeoecological data from Rondonia,
3 southern part of the Amazon Basin. *Acta Amaz* **6**: 293–9.
- 4 Ainsworth EA and Long SP. 2005. What have we learned from 15 years of free-air CO₂
5 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis,
6 canopy properties and plant production to rising CO₂. *New Phytol* **165**: 351–72.
- 7 Aleixo I, Norris D, Hemerik L, *et al.* 2019. Amazonian rainforest tree mortality driven by
8 climate and functional traits. *Nat Clim Chang* **9**: 384–8.
- 9 Alencar AA, Brando PM, Asner GP, and Putz FE. 2015. Landscape fragmentation, severe
10 drought, and the new Amazon forest fire regime. *Ecol Appl* **25**: 1493–505.
- 11 Anderegg WRL, Konings AG, Trugman AT, *et al.* 2018. Hydraulic diversity of forests
12 regulates ecosystem resilience during drought. *Nature* **561**: 538–41.
- 13 Anderson LO, Neto GR, Cunha AP, *et al.* 2018. Vulnerability of Amazonian forests to
14 repeated droughts. *Philos Trans R Soc B Biol Sci* **373**.
- 15 Aragão LEOC, Malhi Y, Barbier N, *et al.* 2008. Interactions between rainfall, deforestation
16 and fires during recent years in the Brazilian Amazonia. *Philos Trans R Soc Lond B*
17 *Biol Sci* **363**: 1779–85.
- 18 Aragão LEOC, Malhi Y, Roman-Cuesta RM, *et al.* 2007. Spatial patterns and fire response
19 of recent Amazonian droughts. *Geophys Res Lett* **34**.
- 20 Araújo I, Marimon BS, Scalon MC, *et al.* 2021. Trees at the Amazonia-Cerrado transition
21 are approaching high temperature thresholds. *Environ Res Lett* **16**: 034047.
- 22 Arroyo-Rodríguez V, Melo FPL, Martínez-Ramos M, *et al.* 2015. Multiple successional
23 pathways in human-modified tropical landscapes: new insights from forest succession,
24 forest fragmentation and landscape ecology research. *Biol Rev* **92**: 326–40.

Chapter 24

- 1 Bagchi R, Swamy V, Latorre Farfan J, *et al.* 2018. Defaunation increases the spatial
2 clustering of lowland Western Amazonian tree communities (G Durigan, Ed). *J Ecol*
3 **106**: 1470–82.
- 4 Balch JK, Nepstad DC, Curran LM, *et al.* 2011. Size, species, and fire behavior predict tree
5 and liana mortality from experimental burns in the Brazilian Amazon. *For Ecol*
6 *Manage* **261**: 68–77.
- 7 Banks-Leite C, Pardini R, Tambosi LR, *et al.* 2014. Using ecological thresholds to evaluate
8 the costs and benefits of set-asides in a biodiversity hotspot. *Science* **345**: 1041–5.
- 9 Barlow J, Lennox GD, Ferreira J, *et al.* 2016. Anthropogenic disturbance in tropical forests
10 can double biodiversity loss from deforestation. *Nature* **535**: 144–7.
- 11 Barlow J and Peres C a. 2008. Fire-mediated dieback and compositional cascade in an
12 Amazonian forest. *Philos Trans R Soc London B* **363**: 1787–94.
- 13 Barros F de V., Bittencourt PRL, Brum M, *et al.* 2019. Hydraulic traits explain differential
14 responses of Amazonian forests to the 2015 El Niño-induced drought. *New Phytol*
15 **223**: 1253–66.
- 16 Betts RA, Arnell NW, Boorman PM, *et al.* 2012. Climate change impacts and adaptation:
17 an Earth System view. In: Cornell SE, Prentice IC, House JI, Downy CJ (Eds).
18 Understanding the Earth System. Cambridge: Cambridge University Press.
- 19 Betts RA, Cox PM, Collins M, *et al.* 2004. The role of ecosystem-atmosphere interactions
20 in simulated Amazonian precipitation decrease and forest dieback under global
21 climate warming. *Theor Appl Climatol* **78**: 157–75.
- 22 Brando PM, Balch JK, Nepstad DC, *et al.* 2014. Abrupt increases in Amazonian tree
23 mortality due to drought-fire interactions. *Proc Natl Acad Sci* **111**: 6347–52.
- 24 Brando PM, Nepstad DC, Balch JK, *et al.* 2012. Fire-induced tree mortality in a neotropical

Chapter 24

- 1 forest: the roles of bark traits, tree size, wood density and fire behavior. *Glob Chang*
2 *Biol* **18**: 630–41.
- 3 Brienen RJW, Phillips OL, Feldpausch TR, *et al.* 2015. Long-term decline of the Amazon
4 carbon sink. *Nature* **519**: 344–8.
- 5 Brum M, Vadeboncoeur MA, Ivanov V, *et al.* 2019. Hydrological niche segregation defines
6 forest structure and drought tolerance strategies in a seasonal Amazon forest (D Barua,
7 Ed). *J Ecol* **107**: 318–33.
- 8 Builes-Jaramillo A and Poveda G. 2018. Conjoint Analysis of Surface and Atmospheric
9 Water Balances in the Andes-Amazon System. *Water Resour Res* **54**: 3472–89.
- 10 Burton C, Kelley DI, Jones CD, *et al.* South American fires and their impacts on
11 ecosystems increase with continued emissions. *Submitt to Clim Resil Sustain*.
- 12 Bush MB, Oliveira PE De, Colinvaux PA, *et al.* 2004. Amazonian paleoecological
13 histories: one hill, three watersheds. *Palaeogeogr Palaeoclimatol Palaeoecol* **214**:
14 359–93.
- 15 Chai Y, Martins G, Nobre C, *et al.* 2021. Constraining Amazonian land surface temperature
16 sensitivity to precipitation and the probability of forest dieback. *npj Clim Atmos Sci* **4**:
17 6.
- 18 Chazdon RL, Broadbent EN, Rozendaal DMA, *et al.* 2016. Carbon sequestration potential
19 of second-growth forest regeneration in the Latin American tropics. *Sci Adv* **2**:
20 e1501639.
- 21 Christoffersen BO, Gloor M, Fauset S, *et al.* 2016. Linking hydraulic traits to tropical forest
22 function in a size-structured and trait-driven model (TFS v.1-Hydro). *Geosci Model*
23 *Dev* **9**: 4227–55.
- 24 Ciemer C, Boers N, Hirota M, *et al.* 2019. Higher resilience to climatic disturbances in

Chapter 24

- 1 tropical vegetation exposed to more variable rainfall. *Nat Geosci* **12**: 174–9.
- 2 Cochrane MA. 2003. Fire science for rainforests. *Nature* **421**: 913–9.
- 3 Cochrane MA, Alencar A, Schulze MD, *et al.* 1999. Positive feedbacks in the fire dynamic
4 of closed canopy tropical forests. *Science* **284**: 1832–5.
- 5 Cochrane MA and Barber CP. 2009. Climate change, human land use and future fires in the
6 Amazon. *Glob Chang Biol* **15**: 601–12.
- 7 Cochrane MA and Schulze MD. 1999. Fire as a recurrent event in tropical forests of the
8 Eastern Amazon: effects on forest structure, biomass, and species composition. : 2–16.
- 9 Coelho de Souza F, Dexter KG, Phillips OL, *et al.* 2019. Evolutionary diversity is
10 associated with wood productivity in Amazonian forests. *Nat Ecol Evol* **3**: 1754–61.
- 11 Cole LES, Bhagwat SA, and Willis KJ. 2014. Recovery and resilience of tropical forests
12 after disturbance. *Nat Commun* **5**: 1–7.
- 13 Cosme LHM, Schiatti J, Costa FRC, and Oliveira RS. 2017. The importance of hydraulic
14 architecture to the distribution patterns of trees in a central Amazonian forest. *New*
15 *Phytol* **215**: 113–25.
- 16 Cox PM, Betts R a., Collins M, *et al.* 2004. Amazonian forest dieback under climate-carbon
17 cycle projections for the 21st century. *Theor Appl Climatol* **78**: 137–56.
- 18 Cox PM, Betts RA, Jones CD, *et al.* 2000. Acceleration of global warming due to carbon-
19 cycle feedbacks in a coupled climate model. *Nature* **408**: 184–7.
- 20 Cramer W, Bondeau A, Woodward FI, *et al.* 2001. Global response of terrestrial ecosystem
21 structure and function to CO₂ and climate change: results from six dynamic global
22 vegetation models. *Glob Chang Biol* **7**: 357–73.
- 23 Cubiña A and Aide TM. 2001. The effect of distance from forest edge on seed rain and soil

Chapter 24

- 1 seed bank in a tropical pasture. *Biotropica* **33**: 260–7.
- 2 D’Apolito C, Absy ML, and Latrubesse EM. 2013. The Hill of Six Lakes revisited: New
3 data and re-evaluation of a key Pleistocene Amazon site. *Quat Sci Rev* **76**: 140–55.
- 4 DaCosta ACL, Galbraith D, Almeida S, *et al.* 2010. Effect of 7 yr of experimental drought
5 on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New*
6 *Phytol* **187**: 579–91.
- 7 Davidson EA, Araújo AC de, Artaxo P, *et al.* 2012. The Amazon basin in transition. *Nature*
8 **481**: 321–8.
- 9 DeAngelis DM, Post WM, and Travis CC. 1986. Positive feedback in natural systems.
10 Berlin, Heidelberg: Springer-Verlag.
- 11 Dexter KG, Pennington RT, Oliveira-Filho AT, *et al.* 2018. Inserting Tropical Dry Forests
12 Into the Discussion on Biome Transitions in the Tropics. *Front Ecol Evol* **6**: 1–7.
- 13 Eller CB, Rowland L, Mencuccini M, *et al.* 2020. Stomatal optimization based on xylem
14 hydraulics (SOX) improves land surface model simulation of vegetation responses to
15 climate. *New Phytol* **226**: 1622–37.
- 16 Eller CB, Rowland L, Oliveira RS, *et al.* 2018. Modelling tropical forest responses to
17 drought and El Niño with a stomatal optimization model based on xylem hydraulics.
18 *Philos Trans R Soc B Biol Sci* **373**: 20170315.
- 19 Elmqvist T, Folke C, Nyström M, *et al.* 2003. Response diversity, ecosystem change, and
20 resilience. *Front Ecol Environ* **1**: 488–94.
- 21 Esquivel-Muelbert A, Baker TR, Dexter KG, *et al.* 2016. Seasonal drought limits tree
22 species across the Neotropics. *Ecography (Cop)* **40**: 618–29.
- 23 Esquivel-Muelbert A, Baker TR, Dexter KG, *et al.* 2019. Compositional response of
24 Amazon forests to climate change. *Glob Chang Biol* **25**.

Chapter 24

- 1 Esquivel-Muelbert A, Galbraith D, Dexter KG, *et al.* 2017. Biogeographic distributions of
2 neotropical trees reflect their directly measured drought tolerances. *Sci Rep* **7**: 8334.
- 3 Esquivel-Muelbert A, Phillips OL, Brienen RJW, *et al.* 2020. Tree mode of death and
4 mortality risk factors across Amazon forests. *Nat Commun* **11**.
- 5 Esteban E JL, Castilho C V, Melgaço KL, and Costa FRC. 2021. The other side of droughts:
6 wet extremes and topography as buffers of negative drought effects in an Amazonian
7 forest. *New Phytol* **229**: 1995–2006.
- 8 Fauset S, Johnson MO, Gloor M, *et al.* 2015. Hyperdominance in Amazonian forest carbon
9 cycling. *Nat Commun* **6**: 6857.
- 10 Feldpausch TR, Phillips OL, Brienen RJW, *et al.* 2016. Amazon forest response to repeated
11 droughts. *Global Biogeochem Cycles* **30**: 964–82.
- 12 Fernandes Neto JG, Costa FRC, Williamson GB, and Mesquita RCG. 2019. Alternative
13 functional trajectories along succession after different land uses in central Amazonia. *J*
14 *Appl Ecol* **56**: 2472–81.
- 15 Fischer R, Bohn F, Dantas de Paula M, *et al.* 2016. Lessons learned from applying a forest
16 gap model to understand ecosystem and carbon dynamics of complex tropical forests.
17 *Ecol Modell* **326**: 124–33.
- 18 Fisher RA and Koven CD. 2020. Perspectives on the Future of Land Surface Models and
19 the Challenges of Representing Complex Terrestrial Systems. *J Adv Model Earth Syst*
20 **12**.
- 21 Fleischer K, Rammig A, Kauwe MG De, *et al.* 2019. Amazon forest response to CO₂
22 fertilization dependent on plant phosphorus acquisition. *Nat Geosci* **12**: 736–41.
- 23 Flores BM. 2016. Resilience of Amazonian forests - the role of fire, flooding and climate.
- 24 Flores BM, Fagoaga R, Nelson BW, and Holmgren M. 2016. Repeated fires trap

Chapter 24

- 1 Amazonian blackwater floodplains in an open vegetation state. *J Appl Ecol* 53: 1597–
2 603.
- 3 Flores BM and Holmgren M. 2021. White-Sand Savannas Expand at the Core of the
4 Amazon After Forest Wildfires. *Ecosystems*.
- 5 Flores BM, Holmgren M, Xu C, *et al.* 2017. Floodplains as an Achilles' heel of Amazonian
6 forest resilience. *Proc Natl Acad Sci* **114**: 4442–6.
- 7 Flores BM, Staal A, Jakovac CC, *et al.* 2020. Soil erosion as a resilience drain in disturbed
8 tropical forests. *Plant Soil* **450**: 11–25.
- 9 Funk C, Peterson P, Landsfeld M, *et al.* 2015. The climate hazards infrared precipitation
10 with stations—a new environmental record for monitoring extremes. *Sci Data* **2**:
11 150066.
- 12 Fyllas NM, Gloor E, Mercado LM, *et al.* 2014. Analysing Amazonian forest productivity
13 using a new individual and trait-based model (TFS v.1). *Geosci Model Dev* **7**: 1251–
14 69.
- 15 Gimeno TE, Crous KY, Cooke J, *et al.* 2016. Conserved stomatal behaviour under elevated
16 CO₂ and varying water availability in a mature woodland (D Whitehead, Ed). *Funct*
17 *Ecol* **30**: 700–9.
- 18 Gloor M, Brienen RJW, Galbraith D, *et al.* 2013. Intensification of the Amazon
19 hydrological cycle over the last two decades. *Geophys Res Lett* **40**: 1729–33.
- 20 Good P, Jones C, Lowe J, *et al.* 2013. Comparing tropical forest projections from two
21 generations of hadley centre earth system models, HadGEM2-ES and HadCM3LC. *J*
22 *Clim* **26**: 495–511.
- 23 Good P, Lowe JA, Collins M, and Moufouma-Okia W. 2008. An objective tropical Atlantic
24 sea surface temperature gradient index for studies of south Amazon dry-season climate

Chapter 24

- 1 variability and change. *Philos Trans R Soc B Biol Sci* **363**: 1761–6.
- 2 Gordon C, Cooper C, Senior CA, *et al.* 2000. The simulation of SST, sea ice extents and
3 ocean heat transports in a version of the Hadley Centre coupled model without flux
4 adjustments. *Clim Dyn* **16**: 147–68.
- 5 Hammen T van der and Absy ML. 1994. Amazonia during the last glacial. *Palaeogeogr*
6 *Palaeoclimatol Palaeoecol* **109**: 247–61.
- 7 Harris PP, Huntingford C, and Cox PM. 2008. Amazon Basin climate under global
8 warming: The role of the sea surface temperature. *Philos Trans R Soc B Biol Sci* **363**:
9 1753–9.
- 10 Harris I, Osborn TJ, Jones P, and Lister D. 2020. Version 4 of the CRU TS monthly high-
11 resolution gridded multivariate climate dataset. *Sci Data* **7**.
- 12 Heinrich VHA, Dalagnol R, Cassol HLG, *et al.* 2020. Large carbon sink potential of
13 Amazonian Secondary Forests to mitigate climate change. *Nat Commun*.
- 14 Hickler T, Smith B, Prentice IC, *et al.* 2008. CO2 fertilization in temperate FACE
15 experiments not representative of boreal and tropical forests. *Glob Chang Biol* **14**:
16 1531–42.
- 17 Higgins SI and Scheiter S. 2012. Atmospheric CO2 forces abrupt vegetation shifts locally,
18 but not globally. *Nature* **488**: 209–12.
- 19 Hirota M, Holmgren M, Nes EH Van, and Scheffer M. 2011. Global resilience of tropical
20 forest and savanna to critical transitions. *Science* **334**: 232–5.
- 21 Hoffmann WA, Lucatelli VMPC, Silva FJ, *et al.* 2004. Impact of the invasive alien grass
22 *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. *Divers*
23 *Distrib* **10**: 99–103.
- 24 Hofhansl F, Andersen KM, Fleischer K, *et al.* 2016. Amazon forest ecosystem responses to

Chapter 24

- 1 elevated atmospheric Co₂ and alterations in nutrient availability: Filling the gaps with
2 model-experiment integration. *Front Earth Sci* **4**: 1–9.
- 3 Holling CS. 1973. Resilience and stability of ecological systems. *Annu Rev Ecol Evol Syst*
4 **4**: 1–23.
- 5 Hoorn C, Wesselingh FP, Steege H ter, *et al.* 2010. Amazonia Through Time: Andean
6 Uplift, Climate Change, Landscape Evolution, and Biodiversity. *Science* **330**: 927–31.
- 7 Hubau W, Lewis SL, Phillips OL, *et al.* 2020. Asynchronous carbon sink saturation in
8 African and Amazonian tropical forests. *Nature* **579**: 80–7.
- 9 Huntingford C, Zelazowski P, Galbraith D, *et al.* 2013. Simulated resilience of tropical
10 rainforests to CO₂ -induced climate change. *Nat Geosci* **6**: 268–73.
- 11 INPE and EMBRAPA. 2011. Levantamento de informações de uso e cobertura da terra na
12 Amazônia: sumário executivo. Belém.
- 13 Jakovac CC, Dutrieux LP, Siti L, *et al.* 2017. Spatial and temporal dynamics of shifting
14 cultivation in the middle-Amazonas river: Expansion and intensification. *PLoS One*
15 **12**: 1–15.
- 16 Jakovac CC, Junqueira AB, Crouzeilles R, *et al.* 2021. The role of land-use history in
17 driving successional pathways and its implications for the restoration of tropical
18 forests. *Biol Rev*: brv.12694.
- 19 Jakovac CC, Peña-Claros M, Kuyper TW, and Bongers F. 2015. Loss of secondary-forest
20 resilience by land-use intensification in the Amazon. *J Ecol* **103**: 67–77.
- 21 Janssen T, Fleischer K, Luysaert S, *et al.* 2020a. Drought resistance increases from the
22 individual to the ecosystem level in highly diverse Neotropical rainforest: A meta-
23 analysis of leaf, tree and ecosystem responses to drought. *Biogeosciences* **17**: 2621–
24 45.

Chapter 24

- 1 Janssen TAJ, Hölttä T, Fleischer K, *et al.* 2020b. Wood allocation trade-offs between fiber
2 wall, fiber lumen, and axial parenchyma drive drought resistance in neotropical trees.
3 *Plant Cell Environ* **43**: 965–80.
- 4 Jiang M, Medlyn BE, Drake JE, *et al.* 2020. The fate of carbon in a mature forest under
5 carbon dioxide enrichment. *Nature* **580**: 227–31.
- 6 Jiménez-Muñoz JC, Mattar C, Barichivich J, *et al.* 2016. Record-breaking warming and
7 extreme drought in the Amazon rainforest during the course of El Niño 2015–2016.
8 *Sci Rep* **6**: 33130.
- 9 Jiménez-Muñoz JC, Sobrino JA, Mattar C, and Malhi Y. 2013. Spatial and temporal
10 patterns of the recent warming of the Amazon forest. *J Geophys Res Atmos*.
- 11 Jones C, Lowe J, Liddicoat S, and Betts R. 2009. Committed terrestrial ecosystem changes
12 due to climate change. *Nat Geosci* **2**: 484–7.
- 13 Jupp TE, Cox PM, Rammig A, *et al.* 2010. Development of probability density functions
14 for future South American rainfall. *New Phytol* **187**: 682–93.
- 15 Kauwe MG, Medlyn BE, Zaehle S, *et al.* 2013. Forest water use and water use efficiency at
16 elevated CO₂: A model-data intercomparison at two contrasting temperate forest
17 FACE sites. *Glob Chang Biol* **19**: 1759–79.
- 18 Kooperman GJ, Chen Y, Hoffman FM, *et al.* 2018. Forest response to rising CO₂ drives
19 zonally asymmetric rainfall change over tropical land. *Nat Clim Chang* **8**: 434–40.
- 20 Langan L, Higgins SI, and Scheiter S. 2017. Climate-biomes, pedo-biomes or pyro-biomes:
21 which world view explains the tropical forest–savanna boundary in South America? *J*
22 *Biogeogr* **44**: 2319–30.
- 23 Lapola DM. 2018. Bytes and boots to understand the future of the Amazon forest. *New*
24 *Phytol* **219**: 845–7.

Chapter 24

- 1 Lapola DM, Oyama MD, and Nobre CA. 2009. Exploring the range of climate biome
2 projections for tropical South America: The role of CO₂ fertilization and seasonality.
3 *Global Biogeochem Cycles* **23**: 1–16.
- 4 Laurance SGW, Stouffer PC, and Laurance WF. 2004. Effects of road clearings on
5 movement patterns of understory rainforest birds in central Amazonia. *Conserv Biol*
6 **18**: 1099–109.
- 7 Levine NM, Zhang K, Longo M, *et al.* 2016. Ecosystem heterogeneity determines the
8 ecological resilience of the Amazon to climate change. *Proc Natl Acad Sci* **113**: 793–
9 7.
- 10 Levis C, Costa FRC, Bongers F, *et al.* 2017. Persistent effects of pre-Columbian plant
11 domestication on Amazonian forest composition. *Science* **355**: 925–31.
- 12 Levis C, Flores BM, Mazzochini GG, *et al.* 2020. Help restore Brazil’s governance of
13 globally important ecosystem services. *Nat Ecol Evol* **4**: 172–3.
- 14 Levis C, Flores BM, Moreira PA, *et al.* 2018. How People Domesticated Amazonian
15 Forests. *Front Ecol Evol* **5**.
- 16 Lombardo U, McMichael C, and Kazuo Tamanaha E. 2018. Mapping pre-Columbian land
17 use in Amazonia. *Past Glob Chang Mag* **26**: 14–5.
- 18 Longo M, Knox RG, Levine NM, *et al.* 2018. Ecosystem heterogeneity and diversity
19 mitigate Amazon forest resilience to frequent extreme droughts. *New Phytol* **219**: 914–
20 31.
- 21 Longo M, Saatchi S, Keller M, *et al.* 2020. Impacts of Degradation on Water, Energy, and
22 Carbon Cycling of the Amazon Tropical Forests. *J Geophys Res Biogeosciences* **125**.
- 23 Loughlin NJD, Gosling WD, Mothes P, and Montoya E. 2018. Ecological consequences of
24 post-Columbian indigenous depopulation in the Andean–Amazonian corridor. *Nat*

Chapter 24

- 1 *Ecol Evol* **2**: 1233–6.
- 2 Lovejoy TE and Nobre C. 2019. Amazon tipping point: Last chance for action. *Sci Adv* **5**:
3 eaba2949.
- 4 Lundberg J and Moberg F. 2003. Mobile link organisms and ecosystem functioning:
5 Implications for ecosystem resilience and management. *Ecosystems* **6**: 87–98.
- 6 Magrin G, Marengo J, Boulanger J-P, *et al.* 2014. Central and South America. In: Barros V,
7 Field C, Dokken D, *et al.* (Eds). *Climate Change 2014: Impacts, Adaptation, and*
8 *Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth*
9 *Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge,
10 NY, USA: Cambridge University Press.
- 11 Maia V, Santos A, Aguiar-Campos N de, *et al.* 2021. Climate and soil mediate the effects
12 of liana density on forest dynamics. *Biotropica* **53**: 509–5019.
- 13 Malhi Y, Aragão LEOC, Galbraith D, *et al.* 2009. Exploring the likelihood and mechanism
14 of a climate-change-induced dieback of the Amazon rainforest. *Proc Natl Acad Sci U*
15 *S A* **106**: 20610–5.
- 16 MAPBIOMAS. 2020. Mapbiomas Amazonia. <https://amazonia.mapbiomas.org/en>. Viewed
17 28 Apr 2021.
- 18 Marengo JA, Tomasella J, Soares WR, *et al.* 2011. Extreme climatic events in the Amazon
19 basin. *Theor Appl Climatol* **107**: 73–85.
- 20 Mayle FE and Beerling DJ. 2004. Late Quaternary changes in Amazonian ecosystems and
21 their implications for global carbon cycling. *Palaeogeogr Palaeoclimatol Palaeoecol*
22 **214**: 11–25.
- 23 Mayle FE, Burbridge R, and Killeen TJ. 2000. Millennial-scale dynamics of southern
24 Amazonian rain forests. *Science* **290**: 2291–4.

Chapter 24

- 1 Mayle FE and Power MJ. 2008. Impact of a drier Early-Mid-Holocene climate upon
2 Amazonian forests. *Philos Trans R Soc B Biol Sci* **363**: 1829–38.
- 3 Medina-Vega JA, Bongers F, Poorter L, *et al.* 2021. Lianas have more acquisitive traits
4 than trees in a dry but not in a wet forest. *J Ecol*: 1–18.
- 5 Mesquita RDCG, Massoca PEDS, Jakovac CC, *et al.* 2015. Amazon Rain Forest
6 Succession: Stochasticity or Land-Use Legacy? *Bioscience* **65**: 849–61.
- 7 Montoya E, Keen HF, Luzuriaga CX, and Gosling WD. 2018. Long-term vegetation
8 dynamics in a megadiverse hotspot: The ice-age record of a pre-montane forest of
9 central Ecuador. *Front Plant Sci* **9**: 1–14.
- 10 Montoya E, Pedra-Méndez J, García-Falcó E, *et al.* 2019. Long-term vegetation dynamics
11 of a tropical megadelta: Mid-Holocene palaeoecology of the Orinoco Delta (NE
12 Venezuela). *Quat Sci Rev* **221**.
- 13 Montoya E, Rull V, and Nogué S. 2011. Early human occupation and land use changes near
14 the boundary of the Orinoco and the Amazon basins (SE Venezuela): Palynological
15 evidence from El Paují record. *Palaeogeogr Palaeoclimatol Palaeoecol* **310**: 413–26.
- 16 Nanni AS, Sloan S, Aide TM, *et al.* 2019. The neotropical reforestation hotspots: A
17 biophysical and socioeconomic typology of contemporary forest expansion. *Glob
18 Environ Chang* **54**: 148–59.
- 19 Nepstad DC, Carvalho CR de, Davidson EA, *et al.* 1994. The role of deep roots in the
20 hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **372**: 666–
21 9.
- 22 Nepstad DC, Tohver IM, Ray D, *et al.* 2007. Mortality of large trees and lianas following
23 experimental drought in an Amazon forest. *Ecology* **88**: 2259–69.
- 24 Nobre CA, Sampaio G, Borma LS, *et al.* 2016. Land-use and climate change risks in the

Chapter 24

- 1 amazon and the need of a novel sustainable development paradigm. *Proc Natl Acad*
2 *Sci U S A* **113**.
- 3 Nobre CA, Sellers PJ, and Shukla J. 1991. Amazonian Deforestation and Regional Climate
4 Change. *J Clim* **4**: 957–88.
- 5 Norby RJ, Kauwe MG De, Domingues TF, *et al.* 2016. Model – data synthesis for the next
6 generation of forest free-air CO₂ enrichment (FACE) experiments. *New Phytol* **209**:
7 17–28.
- 8 Norby RJ, Warren JM, Iversen CM, *et al.* 2010. CO₂ enhancement of forest productivity
9 constrained by limited nitrogen availability. *Proc Natl Acad Sci U S A* **107**: 19368–73.
- 10 Oliveira RS, Costa FRC, Baalen E van, *et al.* 2019. Embolism resistance drives the
11 distribution of Amazonian rainforest tree species along hydro-topographic gradients.
12 *New Phytol* **221**: 1457–65.
- 13 Oliveira RS, Dawson TE, Burgess SSO, and Nepstad DC. 2005. Hydraulic redistribution in
14 three Amazonian trees. *Oecologia* **145**: 354–63.
- 15 Oliveira RS, Eller CB, Barros F de V., *et al.* Linking plant hydraulics and the fast-slow
16 continuum to understand resilience to drought in tropical ecosystems. *New Phytol*.
- 17 Oyama MD and Nobre CA. 2003. A new climate-vegetation equilibrium state for tropical
18 South America. *Geophys Res Lett* **30**.
- 19 Perz SG and Skole DL. 2003. Secondary forest expansion in the brazilian amazon and the
20 refinement of forest transition theory. *Soc Nat Resour* **16**: 277–94.
- 21 Phillips OL, Aragão LEOCOC, Lewis SL, *et al.* 2009. Drought sensitivity of the Amazon
22 rainforest. *Science* **323**: 1344–7.
- 23 Phillips OL, Heijden G Van der, Lewis SL, *et al.* 2010. Drought-mortality relationships for
24 tropical forests. *New Phytol* **187**: 631–46.

Chapter 24

- 1 Poorter L, Bongers F, Aide TM, *et al.* 2016. Biomass resilience of Neotropical secondary
2 forests. *Nature* **530**: 211–4.
- 3 Poorter L, McDonald I, Alarcón A, *et al.* 2010. The importance of wood traits and
4 hydraulic conductance for the performance and life history strategies of 42 rainforest
5 tree species. *New Phytol* **185**: 481–92.
- 6 Poorter L, Sande MT van der, Thompson J, *et al.* 2015. Diversity enhances carbon storage
7 in tropical forests. *Glob Ecol Biogeogr* **24**: 1314–28.
- 8 Prance GT. 1996. The islands in Amazonia. *Philos Trans R Soc London B* **351**: 823–33.
- 9 Quesada CA, Phillips OL, Schwarz M, *et al.* 2012. Basin-wide variations in Amazon forest
10 structure and function are mediated by both soils and climate. *Biogeosciences* **9**:
11 2203–46.
- 12 RAISG. 2020. Amazonian Network of Georeferenced Socio-Environmental
13 Information <https://www.amazoniasocioambiental.org/en/>. Viewed
- 14 Rajão R, Soares-Filho B, Nunes F, *et al.* 2020. The rotten apples of Brazil’s agribusiness.
15 *Science* **369**: 246–8.
- 16 Rammig A, Jupp T, Thonicke K, *et al.* 2010. Estimating the risk of Amazonian forest
17 dieback. *New Phytol* **187**: 694–706.
- 18 Roeder M, Hölscher D, and Ferraz IDK. 2010. Liana regeneration in secondary and
19 primary forests of central Amazonia. *Plant Ecol Divers* **3**: 165–74.
- 20 Roosevelt AC. 2013. The Amazon and the Anthropocene: 13,000 years of human influence
21 in a tropical rainforest. *Anthropocene* **4**: 69–87.
- 22 Rowland L, Costa ACL da, Galbraith DR, *et al.* 2015. Death from drought in tropical
23 forests is triggered by hydraulics not carbon starvation. *Nature* **528**: 119–22.

Chapter 24

- 1 Rozendaal DMA, Bongers F, Aide TM, *et al.* 2019. Biodiversity recovery of Neotropical
2 secondary forests. *Sci Adv* **5**: eaau3114.
- 3 Rull V. 2015. Pleistocene speciation is not refuge speciation. *J Biogeogr* **42**: 602–4.
- 4 Sakschewski B, Bloh W Von, Boit A, *et al.* 2016. Resilience of Amazon forests emerges
5 from plant trait diversity. *Nat Clim Chang* **6**: 1032–6.
- 6 Sakschewski B, Bloh W von, Drüke M, *et al.* 2020. Variable tree rooting strategies improve
7 tropical productivity and evapotranspiration in a dynamic global vegetation model.
8 *Biogeosciences*.
- 9 Sampaio G, Nobre C, Costa MH, *et al.* 2007. Regional climate change over eastern
10 Amazonia caused by pasture and soybean cropland expansion. *Geophys Res Lett* **34**:
11 1–7.
- 12 Sampaio G, Shimizu M, Guimarães-Júnior C, *et al.* 2020. CO₂
13 fertilization effect can cause rainfall decrease as strong as large-scale deforestation in
14 the Amazon. *Biogeosciences Discuss*: 1–21.
- 15 Sande MT van der, Gosling W, Correa-Metrio A, *et al.* 2019. A 7000-year history of
16 changing plant trait composition in an Amazonian landscape; the role of humans and
17 climate. *Ecol Lett* **22**: 925–35.
- 18 Sato H, Ito A, Ito A, *et al.* 2015. Current status and future of land surface models. *Soil Sci*
19 *Plant Nutr* **61**: 34–47.
- 20 Schaphoff S, Lucht W, Gerten D, *et al.* 2006. Terrestrial biosphere carbon storage under
21 alternative climate projections. *Clim Change* **74**: 97–122.
- 22 Scheffer M, Carpenter S, Foley JA, *et al.* 2001. Catastrophic shifts in ecosystems. *Nature*
23 **413**: 591–6.
- 24 Scheffer M, Carpenter SR, Lenton TM, *et al.* 2012. Anticipating critical transitions. *Science*

Chapter 24

- 1 **338**: 344–8.
- 2 Scheiter S, Langan L, and Higgins SI. 2013. Next-generation dynamic global vegetation
3 models: Learning from community ecology. *New Phytol* **198**: 957–69.
- 4 Schnitzer SA and Bongers F. 2002. The ecology of lianas and their role in forests. *Trends*
5 *Ecol Evol* **17**: 223–30.
- 6 Schwartz NB, Aide TM, Graesser J, *et al.* 2020. Reversals of Reforestation Across Latin
7 America Limit Climate Mitigation Potential of Tropical Forests. *Front For Glob*
8 *Chang* **3**: 1–10.
- 9 Sellar AA, Jones CG, Mulcahy JP, *et al.* 2019. UKESM1: Description and Evaluation of
10 the U.K. Earth System Model. *J Adv Model Earth Syst* **11**.
- 11 Silva CVJ, Aragão LEOC, Barlow J, *et al.* 2018. Drought-induced Amazonian wildfires
12 instigate a decadal-scale disruption of forest carbon dynamics. *Philos Trans R Soc B*
13 *Biol Sci* **373**: 20180043.
- 14 Silva de Miranda PL, Oliveira-Filho AT, Pennington RT, *et al.* 2018. Using tree species
15 inventories to map biomes and assess their climatic overlaps in lowland tropical South
16 America. *Glob Ecol Biogeogr* **27**: 899–912.
- 17 Silvério D V, Brando PM, Balch JK, *et al.* 2013. Testing the Amazon savannization
18 hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic
19 pasture grasses. *Philos Trans R Soc B Biol Sci* **368**: 20120427.
- 20 Sitch S, Huntingford C, Gedney N, *et al.* 2008. Evaluation of the terrestrial carbon cycle,
21 future plant geography and climate-carbon cycle feedbacks using five Dynamic Global
22 Vegetation Models (DGVMs). *Glob Chang Biol* **14**: 2015–39.
- 23 Smith R and Mayle FE. 2018. Impact of mid- to late Holocene precipitation changes on
24 vegetation across lowland tropical South America: A paleo-data synthesis.

Chapter 24

- 1 *Quaternary Res* **89**: 1–22.
- 2 Smith MN, Taylor TC, Haren J van, *et al.* 2020. Empirical evidence for resilience of
3 tropical forest photosynthesis in a warmer world. *Nat Plants* **6**: 1225–30.
- 4 Spracklen D V., Arnold SR, and Taylor CM. 2012. Observations of increased tropical
5 rainfall preceded by air passage over forests. *Nature* **489**: 282–5.
- 6 Staal A, Flores BM, Aguiar APD, *et al.* 2020. Feedback between drought and deforestation
7 in the Amazon. *Environ Res Lett* **15**: 44024.
- 8 Staal A, Tuinenburg OA, Bosmans JHC, *et al.* 2018. Forest-rainfall cascades buffer against
9 drought across the Amazon. *Nat Clim Chang* **8**: 539–43.
- 10 Staver AC, Archibald S, and Levin SA. 2011. The global extent and determinants of
11 savanna and forest as alternative biome states. *Science* **334**: 230–2.
- 12 Staver AC, Brando PM, Barlow J, *et al.* 2020. Thinner bark increases sensitivity of wetter
13 Amazonian tropical forests to fire. *Ecol Lett* **23**: 99–106.
- 14 Steege H Ter, Pitman NCA, Killeen TJ, *et al.* 2015. Estimating the global conservation
15 status of more than 15,000 Amazonian tree species. *Sci Adv* **1**: 9–11.
- 16 Steege H ter, Pitman NCA, Sabatier D, *et al.* 2013. Hyperdominance in the Amazonian
17 Tree Flora. *Science* **342**: 1243092–1243092.
- 18 Strogatz SH. 2015. Nonlinear dynamics and chaos with applications to physics, biology,
19 chemistry and engineering. Boulder: Westview Press.
- 20 Sullivan MJP, Lewis SL, Affum-Baffoe K, *et al.* 2020. Long-term thermal sensitivity of
21 earth’s tropical forests. *Science* **368**: 869–74.
- 22 Ter-Steege H, Prado PI, Lima RAF de, *et al.* 2020. Biased-corrected richness estimates for
23 the Amazonian tree flora. *Sci Rep* **10**: 10130.

Chapter 24

- 1 Turner MG, Baker WL, Peterson CJ, and Peet RK. 1998. Factors influencing succession:
2 Lessons from large, infrequent natural disturbances. *Ecosystems* **1**: 511–23.
- 3 Turner BL, Brenes-Arguedas T, and Condit R. 2018. Pervasive phosphorus limitation of
4 tree species but not communities in tropical forests. *Nature* **555**: 367–70.
- 5 Tymen B, Réjou-Méchain M, Dalling JW, *et al.* 2016. Evidence for arrested succession in a
6 liana-infested Amazonian forest. *J Ecol* **104**: 149–59.
- 7 Urrego DH, Bush MB, and Silman MR. 2010. A long history of cloud and forest migration
8 from Lake Consuelo, Peru. *Quat Res* **73**: 364–73.
- 9 Van-Nes EH, Arani BMS, Staal A, *et al.* 2016. What do you mean, tipping point? *Trends*
10 *Ecol Evol* **31**: 902–4.
- 11 Van-Nes EH, Staal A, Hantson S, *et al.* 2018. Fire forbids fifty-fifty forest. *PLoS One* **13**:
12 12–7.
- 13 Veldman JW. 2016. Clarifying the confusion: old-growth savannahs and tropical ecosystem
14 degradation. *Philos Trans R Soc B Biol Sci* **371**: 20150306.
- 15 Veldman JW and Putz FE. 2011. Grass-dominated vegetation, not species-diverse natural
16 savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin.
17 *Biol Conserv* **144**: 1419–29.
- 18 Venticinque E, Forsberg B, Barthem R, *et al.* 2016. An explicit GIS-based river basin
19 framework for aquatic ecosystem conservation in the
20 Amazon [https://knbn.org/view/doi%3A10.5063%2FF1BG2KX8#snapp_](https://knbn.org/view/doi%3A10.5063%2FF1BG2KX8#snapp_computing.6.1)
21 [computing.6.1](https://knbn.org/view/doi%3A10.5063%2FF1BG2KX8#snapp_computing.6.1). Viewed
- 22 Vieira ICG, Gardner T, Ferreira J, *et al.* 2014. Challenges of governing second-growth
23 forests: A case study from the Brazilian Amazonian state of Pará. *Forests* **5**: 1737–52.
- 24 Walker B, Kinzig A, and Langridge J. 1999. Plant attribute diversity, resilience, and

Chapter 24

- 1 ecosystem function: The nature and significance of dominant and minor species.
2 *Ecosystems* **2**: 95–113.
- 3 Wang X, Edwards RL, Auler AS, *et al.* 2017. Hydroclimate changes across the Amazon
4 lowlands over the past 45,000 years. *Nature* **541**: 204–7.
- 5 Wang Y, Ziv G, Adami M, *et al.* 2020. Upturn in secondary forest clearing buffers primary
6 forest loss in the Brazilian Amazon. *Nat Sustain* **3**: 290–5.
- 7 White A, Cannell MGR, and Friend AD. 1999. Climate change impacts on ecosystems and
8 the terrestrial carbon sink: A new assessment. *Glob Environ Chang* **9**.
- 9 Wieland LM, Mesquita RCG, Bobrowiec PED, *et al.* 2011. Seed rain and advance
10 regeneration in secondary succession in the Brazilian Amazon. *Trop Conserv Sci* **4**:
11 300–16.
- 12 Wolfe BT, Sperry JS, and Kursar TA. 2016. Does leaf shedding protect stems from
13 cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis. *New*
14 *Phytol* **212**: 1007–18.
- 15 Xu X, Jia G, Zhang X, *et al.* 2020. Climate regime shift and forest loss amplify fire in
16 Amazonian forests. *Glob Chang Biol* **26**: 5874–85.
- 17 Xu X, Medvigy D, Powers JS, *et al.* 2016. Diversity in plant hydraulic traits explains
18 seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical
19 forests. *New Phytol* **212**.
- 20 Zarin DJ, Davidson EA, Brondizio E, *et al.* 2005. Legacy of fire slows carbon
21 accumulation in Amazonian forest regrowth. *Front Ecol Environ* **3**: 365–9.
- 22 Zelazowski P, Malhi Y, Huntingford C, *et al.* 2011. Changes in the potential distribution of
23 humid tropical forests on a warmer planet. In: Philosophical Transactions of the Royal
24 Society A: Mathematical, Physical and Engineering Sciences.

Chapter 24

- 1 Zemp DC, Schleussner C-F, Barbosa HMJ, *et al.* 2017. Self-amplified Amazon forest loss
2 due to vegetation-atmosphere feedbacks. *Nat Commun* **8**: 1–10.
- 3 Zeppetello LRV, Luke’s LA, Spector JT, *et al.* 2020. Large scale tropical deforestation
4 drives extreme warming. *Environ Res Lett* **15**.
- 5 Zuleta D, Duque A, Cardenas D, *et al.* 2017. Drought-induced mortality patterns and rapid
6 biomass recovery in a terra firme forest in the Colombian Amazon. *Ecology*.

7

8

9

10

11

12

13

14

15

16

17

18

19

20

Chapter 24

1 **CORE GLOSSARY**

2 **Disturbances:** Changes in conditions of a system.

3 **Hysteresis:** Path-dependent behavior of a system.

4 **Perturbations:** Changes in the state of a system.

5 **Positive feedback mechanisms:** Determined by the internal dynamics of the system in a
6 closed loop, i.e., the initial perturbation is self-reinforced and amplified.

7 **Stabilizing (negative) feedback mechanisms:** Occur when system dynamics dampen the
8 initial disturbance/perturbation.

9 **Tipping points:** A critical threshold from which accelerating change caused by positive
10 feedback drives the system to a new state.

11

12

13

14

15

16

17

18

19

20

Chapter 24

1 BOXES

2 BOX 24.1 – Main concepts and definitions based on the theory of dynamical systems.

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

20 [Figure 24.B1 is being developed and will be inserted here]

21 **Figure 24.B1** - (Left panels) Linear and nonlinear responses of ecosystem state (y-axis)
22 depending on underlying conditions (x-axis). (Right panels) Illustration of how catastrophic
23 shifts can occur under changes in conditions (e.g., climate changes) and in the state variable
24 (e.g., human activities). Modified from Scheffer *et al.* (2001).

25 The two black open circles (*F1* and *F2*) are named *bifurcation points*, *tipping points* or
26 *critical thresholds*. In this sense, such *tipping points* exist only when two or more
27 *alternative stable states* occur (Scheffer *et al.* 2001). *Tipping points* can be reached if either

Chapter 24

1 *disturbances* (changes in conditions) or *perturbations* (changes in the state), or both occur
2 (Fig. 24.B1, right panels) (Van-Nes *et al.* 2016). First, **if conditions change** and $F2$ is
3 crossed (Fig. 24.B1, right panel a), a sudden drop (downwards) can occur towards a
4 different state. Interestingly, to return to the original state, the system would need to
5 undergo a much stronger change in conditions, in this case, to reach the other bifurcation
6 point $F1$, which could lead the system upwards again. This *path-dependence* behavior is
7 called *hysteresis*. Such a feature defines the likelihood of irreversibility after crossing a
8 *tipping point*. Eventually, it is so challenging to return conditions to $F1$ levels, and thus
9 return to the original state, that reaching a *tipping point* can indeed cause irreversible
10 changes. In the case of the Amazon rainforests, climate change translated into extreme
11 drought events or increases in dry season length could represent changes in one of
12 underlying conditions that maintain Amazon ecosystems in the current configuration.
13 Secondly, **if changes occur in the ecosystem state**, e.g., decreases in tree cover after
14 deforestation and/or wildfire events, the system could reach the instability region (blue
15 dashed line), causing either a return to the original state or a (irreversible) change in the
16 system configuration. In either case what drives the accelerated shift to a new state are
17 **positive feedback mechanisms** (DeAngelis *et al.* 1986), determined by the internal
18 dynamics of the system in a closed loop, i.e., the initial perturbation is **self-reinforced and**
19 **amplified**. For instance, deforestation leads to less tree cover, which, in turn, leads to less
20 evapotranspiration, less precipitation and thus less tree cover, i.e., in this case, the initial
21 perturbation is reinforced and amplified. On the other hand, **(negative) stabilizing feedback**
22 *mechanisms* occur when they dampen the initial disturbance/perturbation (DeAngelis *et al.*
23 1986). Therefore, in broader context, *tipping points* can refer "to any situation where
24 accelerating change caused by a positive feedback drives the system to a new state" (Van-
25 Nes *et al.* 2016).

26 The connection between *tipping points* and *resilience* is more easily observed when
27 building *stability landscapes* (or ball-in-a-cup diagram) using the concept of *basins of*
28 *attraction* (Fig. 24.B2a, b) (Scheffer *et al.* 2001; Strogatz 2015). In this sense, theoretically
29 *resilience* can be qualitatively understood as the **size** of the *basin of attraction* (valleys on

Chapter 24

1 Fig. 24.B2a). Each cross-section of the ecosystem state vs. conditions graph corresponds to
2 a different *stability landscape*, showing potential *alternative stable states* and the **size** of the
3 *basin of attraction* separating them. Particularly, for tropical forests, Fig. 24.B2b shows
4 five condition cross-sections (for increasing precipitation): 1) only a treeless state, i.e., only
5 one *basin of attraction* representing one state possible; 2) two *alternative stable states*,
6 namely treeless and savanna, with a higher resilience (deeper valley) associated with the
7 treeless state; 3) and 4) forests and savannas as *alternative states* with higher forest
8 resilience related to higher levels of precipitation; 5) only forests as a stable state with the
9 highest levels of precipitation. Note that this diagram shows only precipitation as a driving
10 condition. We can go further and think about changes in the conditions or in the ecosystem
11 state (Fig. 24.B1) using this type of diagram (Figs. 24.B2c-e). For instance, increases in the
12 frequency of extreme droughts and/or in dry season length could **erode** the *basin of*
13 *attraction* of the forest state, i.e., forests lose resilience up to a point that a relatively lower-
14 intensity drought could trigger a shift towards another *basin of attraction* easier than if
15 climate change impacts would not occur (Fig. 24.B2d). Human-induced changes affecting
16 the ecosystem state directly (e.g., wildfires or deforestation) would provoke a state flip
17 independently on whether forests had lost resilience or not (Fig. 24.B2e).

18 [Figure 24.B2 is being developed and will be inserted here]

19 **Figure 24.B2** - The connection between *tipping points* and *resilience* using *stability*
20 *landscapes*. Modified from Scheffer *et al.* (2001); Hirota *et al.* (2011); van Nes *et al.*
21 (2016).

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