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REVIEW ARTICLE

Soil erosion as a resilience drain in disturbed tropical forests

Bernardo M. Flores · Arie Staal · Catarina C. Jakovac · Marina Hirota · Milena Holmgren · Rafael S. Oliveira

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Abstract
Background Tropical forests are threatened by intensifying natural and anthropogenic disturbance regimes. Disturbances reduce tree cover and leave the organic topsoil vulnerable to erosion processes, but when resources are still abundant forests usually recover.
Scope Across the tropics, variation in rainfall erosivity – a measure of potential soil exposure to water erosion – indicates that soils in the wetter regions would experience high erosion rates if they were not protected by tree cover. However, twenty-first-century global land cover data reveal that in wet South America tropical tree cover is decreasing and bare soil area is increasing. Here we address the role of soil erosion in a positive feedback mechanism that may persistently alter the functioning of disturbed tropical forests.
Conclusions Based on an extensive literature review, we propose a conceptual model in which soil erosion reinforces disturbance effects on tropical forests, reducing their resilience with time and increasing their likelihood of being trapped in an alternative vegetation state that is persistently vulnerable to erosion. We present supporting field evidence from two distinct forests in central Amazonia that have been repeatedly disturbed. Overall, the strength of the erosion feedback depends on disturbance types and regimes, as well as on local environmental conditions, such as topography, flooding, and soil fertility. As disturbances intensify in tropical landscapes, we argue that the erosion feedback may help to explain why certain forests persist in a degraded state and often undergo critical functional shifts.

Keywords Dynamics · Ecosystem services · Feedback · Forest restoration · Global change · Secondary forests

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B. M. Flores (✉) · M. Hirota · R. S. Oliveira
Department of Plant Biology, University of Campinas, Campinas, SP 13083-970, Brazil
e-mail: mflores.bernardo@gmail.com

A. Staal
Aquatic Ecology and Water Quality Management Group, Wageningen University, P. O Box 47, 6700 AA Wageningen, The Netherlands

A. Staal
Stockholm Resilience Centre, Stockholm University, Kräftriket 2B, 10691 Stockholm, Sweden

C. C. Jakovac
International Institute for Sustainability - IIS Rio, Rio de Janeiro 22460-320, Brazil

M. Hirota
Department of Physics, Federal University of Santa Catarina, Florianópolis, Brazil

M. Holmgren
Resource Ecology Group, Wageningen University, P.O Box 47, 6700 AA Wageningen, The Netherlands

Introduction

Tropical forests across the world are disappearing due to natural and human-related causes (Barlow et al. 2018; Song et al. 2018). While extreme droughts and wildfires are happening more frequently (Alencar et al. 2015; Brando et al. 2014), agricultural frontiers are expanding, converting forests into croplands, pastures and plantations (Gibbs et al. 2010), and also spreading more subtle disturbances deeper into the forest, such as fragmentation and logging (Barlow et al. 2016; Berenguer et al. 2018). These disturbances reduce biodiversity, alter ecosystem functioning (Hooper et al. 2012; Naeem et al. 2012) and threaten the provision of vital services, such as carbon storage, rainfall recycling, and food supply for local societies (Cardinale et al. 2012; Millennium Ecosystem Assessment 2005). When it comes to tropical landscapes converted to croplands or pasture, one important service provided by trees is soil protection from erosion (Millennium Ecosystem Assessment 2005).

Erosion is the physical process of topsoil removal, which degrades soil quality and reduces ecosystem productivity (Lal 2001). In all ecosystems, common natural erosion agents are wind and water (Pimentel and Kounang 1998). In semi-arid regions for instance, the vegetation is often patchy because plants retain water and avoid erosion, facilitating the establishment of new individuals (Ludwig et al. 2005). Yet, when fires transform plants and soil organic matter into ashes, winds can easily blow them away (Kauffman et al. 1993). In contrast, tropical rainforests are exposed to high rainfall erosivity, an energy unit that reflects how external rainfall conditions can potentially influence erosion (Panagos et al. 2017). In these ecosystems, vegetation and litter cover removal may strongly accelerate erosion (Borrelli et al. 2017; Labrière et al. 2015). Moreover, soil vulnerability to erosion, known as erodibility (Lal and Elliot 1994), is usually lower when the soil has more organic matter, which stabilizes soil aggregates, increases porosity and reduces vulnerability to runoff (Don et al. 2011; Feller and Beare 1997; Pimentel and Kounang 1998). Disturbances that expose the soil organic layer, such as fire or tillage, increase erodibility by making soils more detached and ready to be removed (Certini 2005; Lal 2001; Pimentel and Kounang 1998; Shakesby and Doerr 2006). When topsoils erode, usually most of the organic matter and nutrients present in the soil are also lost (El-Swaify et al. 1982; Feller and Beare 1997; Pimentel and Kounang 1998; Ross et al. 1990), implying that erosion may lead to more erosion, until soils become highly degraded (Anselmetti et al. 2007; Stocking 2003). Also, erosion can directly alter vegetation composition via removal of the soil seed bank (García-Fayos et al. 2010). There are several other important processes that cause soil degradation, such as chemical leaching and volatilization of nutrients, salinization, and soil biodiversity loss. Nonetheless, the physical process of erosion is arguably the degradation process that has caused most drastic and potentially irreversible changes in ecosystems around the world (El-Swaify et al. 1982; Lal 2001; Pimentel and Kounang 1998).

Over geological timescales, erosion-deposition processes have contributed to shape natural landscapes. Humans have accelerated these processes (El-Swaify et al. 1982; Wilkinson and McElroy 2007) with consequences for ecological systems (Ellis 2015). Erosion has been a societal and ecological problem since the start of sedentary agriculture (Lowdermilk 1953; Middleton 1930; Olson 1981). In pre-Classic Maya landscapes, for example, extensive deforestation exposed shallow fertile soils to long-term erosion (Beach et al. 2006; Olson 1981), reducing soil carbon so severely that its effects persist until today (Douglas et al. 2018). Soil degradation by erosion has negative consequences for ecosystem productivity and can lead to economic losses at local, regional and continental scales (García-Ruiz et al. 2017; Lal 1998, 2001). More recently, when humans expanded their industrial agriculture into tropical forests around 1945, a wave of erosion reached places where heavy rain events caused the strongest erosion rates ever recorded, such as on steep slopes in Rwanda and Guatemala (McNeill and Winiwarter 2004).

Although the impacts of soil erosion on agricultural productivity and sustainability have been well studied globally (Lal 1998; Lawrence et al. 2010; Song et al. 2005), we still do not understand how it affects the resilience of tropical heterogeneous forests under intensifying disturbance regimes. Some tropical forest soils are exposed to very high rainfall, which makes them particularly at risk (Fig. 1a). Most of these soils have remained protected by tropical forest during the Holocene, especially in the Neotropics (Nolan et al. 2018). Current human activities, however, are expanding areas with bare soil and low tree cover (Fig. 1b-i), particularly in South America (Fig. 1b, f). The Millennium Ecosystem Assessment (2005) states that "*Severe depletion of soil fertility results in a spiral of soil degradation that can eventually render the land unsuitable for crop production.*" In this article, we ask: could tropical forests exposed to varying forms of

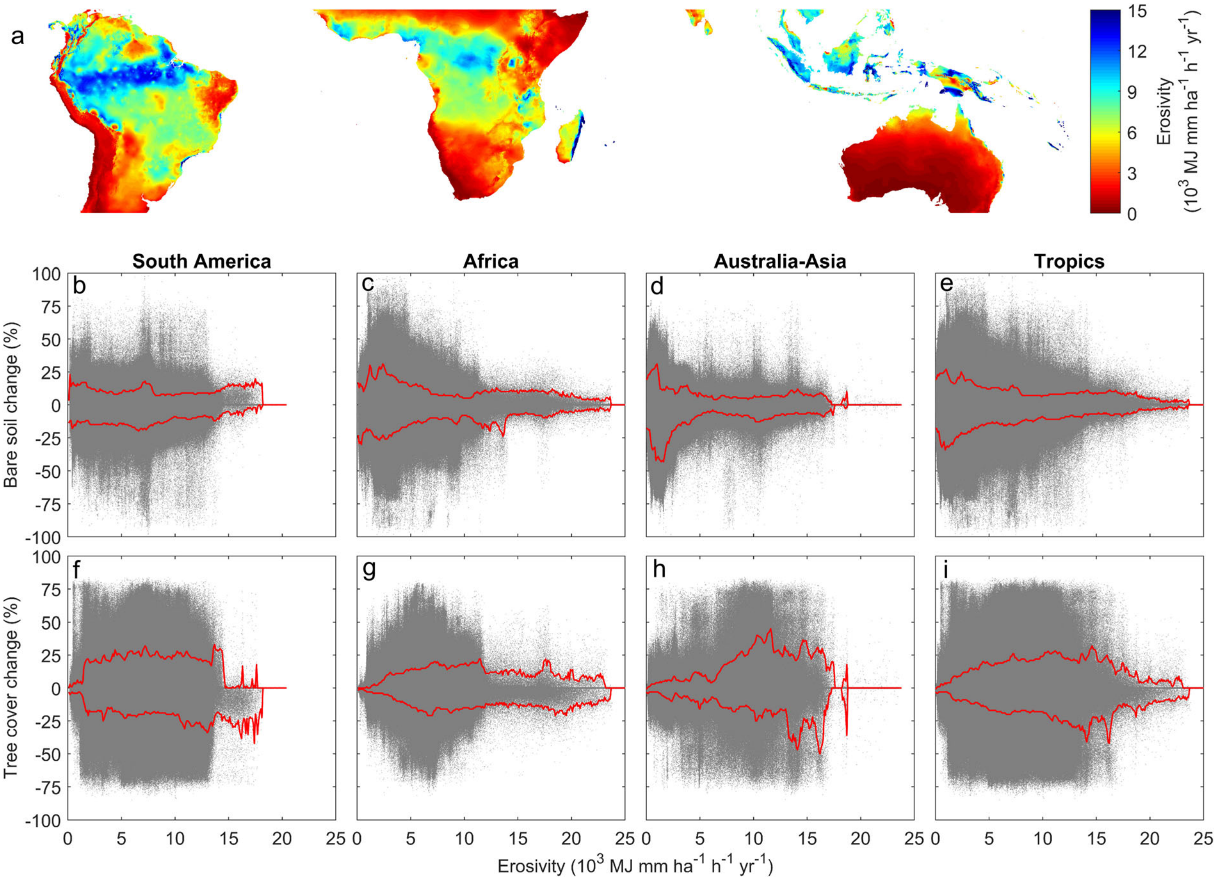

Fig. 1 Rainfall erosivity vs. trends in land-cover change. **a**. Global rainfall erosivity map (MJ mm ha^{-1} h^{-1} yr.$^{-1}$) showing regions with highest erosivity in blue, and with lowest in red. The colour-scale is cut at 15,000 MJ mm ha^{-1} h^{-1} yr.$^{-1}$. Changes in bare soil from 2000 through 2015 for (**b**) South America, (**c**) Africa, (**d**) Australia-Asia and (**e**) the whole tropics (between 15°N and 35°S). Changes in tree cover from 2000 through 2015 for the (**f**) South America, (**g**) Africa, (**h**) Australia-Asia and (**i**) whole tropics. In all plots (**b**-**i**), red curves indicate 5th and 95th percentiles. They show that tropical soils are being increasingly exposed to high rainfall erosion due to deforestation and degradation, especially in South America. Land cover data were resampled to 30 arcsecond resolution to match erosivity data (Panagos et al. 2017). High temporal resolution rainfall data from 3540 stations across the world were calculated for the R-factor (rainfall erosivity) considering spatial variations in rainfall regimes (duration, magnitude and intensity) with the Revised Universal Soil Loss Equation (RUSLE), and erosivity was extrapolated globally based on correlations with climatic data. Land-cover changes were extracted from MODIS VCF 5 (DiMiceli et al. 2011)

disturbance, such as wildfires and logging, also undergo such a downward spiral of soil degradation? What would be the consequences for forest resilience? One possibility is that forests may undergo compositional and functional changes. However, as erosion gradually depletes soil fertility, forest resilience may drop so severely (Fig. 2) that the ecosystem could collapse into an alternative savanna-like state (Hirota et al. 2011) or an open degraded forest state (Ghazoul et al. 2015). Here we define resilience as the ability to maintain current functioning and interactions while facing repeated disturbances, or in other words, the size of the forest basin of attraction relative to the alternative one (Holling

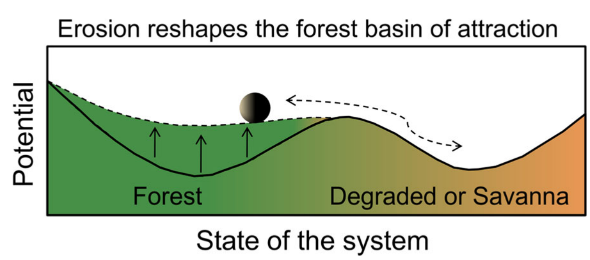

Fig. 2 Soil erosion may reshape the resilience of disturbed tropical forests. Over ecological time-scales, erosion may alter soil fertility and reduce the forest's basin of attraction (vertical arrows), increasing the probability of shifting to an alternative stable state

1973). These questions seem relevant when tropical forests are becoming increasingly trapped by short disturbance return intervals (Barlow and Peres 2008; Berenguer et al. 2018; Flores et al. 2016). Moreover, climate change may alter rainfall erosivity across the tropics (Panagos et al. 2017), as suggested for instance by the recent intensification of the Amazonian hydrological cycle (Gloor et al. 2013), potentially accelerating erosion in disturbed forest sites. In this conceptual article, we explore existing evidence and discuss how future disturbance regimes, involving different types of anthropogenic and natural forest disturbances, may accelerate soil erosion, alter ecosystem functioning and reshape tropical forest resilience.

Disturbance as a window for soil erosion

When disturbances reduce vegetation cover, they open a window of opportunity for soil erosion as geomorphological activities intensify (Prosser and Williams 1998; Shakesby and Doerr 2006). By studying native Australian *eucalyptus* forests, Prosser and Williams (1998) found that the destruction of vegetation and litter cover by fire reduced soil infiltration and increased runoff during strong rain events, making soils vulnerable to erosion. Only when the vegetation started to recover did erosion rates return back to normal. Intense fires, in addition to destroying the vegetation and litter, causing severe nutrient losses through volatilization, may also increase soil hydrophobicity, contributing to make it more vulnerable to water erosion (Certini 2005; DeBano 2000; Kauffman et al. 1995). Similar processes have been observed in temperate ecosystems across the world (Shakesby and Doerr 2006), and reveal that when disturbances expose more than 60% of the soil, sediment yield rates increase abruptly (Johansen et al. 2001; Pimentel and Kounang 1998). Most of our knowledge on how disturbances accelerate erosion processes comes from temperate and semi-arid ecosystems (Lal 2001; Pimentel and Kounang 1998), where wildfires and deforestation for crop production are well-studied disturbances (Pimentel and Kounang 1998; Shakesby and Doerr 2006).

In the tropics, large-scale conversion of forests into croplands and pastures in recent decades has increasingly exposed soils to erosion (Borrelli et al. 2017). When such activities persist over decades, soils become degraded and unproductive (Celentano et al. 2017; Nesper et al. 2015; Pimentel et al. 1995), forcing land owners to expand their activities deeper into the forest (Gibbs et al. 2010). Several studies have also investigated how the intensification of small-scale shifting agriculture may impact forest regrowth capacity (e.g. Chazdon 2014; Jakovac et al. 2015; Lawrence et al. 2010). When the regrowth phase of the cultivation cycle is postponed to enhance short-term profits, nutrient losses from leaching and erosion increase, while atmospheric nutrient inputs via canopy trapping decrease, threatening the system's sustainability (Cunningham 1963; Fearnside 1980; Jakovac et al. 2016a; Jordan and Herrera 1981; Lal 1998, 2001; Lawrence et al. 2007; Pellegrini et al. 2018; Pimentel et al. 1995).

Studies addressing the impacts of land-use on tropical forests commonly consider the process of soil degradation by erosion (e.g. Borrelli et al. 2017; Lawrence et al. 2010). Yet, when it comes to more subtle forest disturbances the elusive temporal changes in the soil are often overlooked (Table 1) (Boardman 2006; Pimentel and Kounang 1998). For instance, severe drought events can cause the death of large trees (Phillips et al. 2009; Rowland et al. 2015), which contribute strongly to soil infiltration (Celentano et al. 2017). Therefore, the loss of these large trees from the system may potentially enhance soil erosion rates. Interestingly, when local people manage their land over generations, they usually realize when soils are degrading (Jakovac et al. 2016a). Soil degradation due to erosion and leaching can be an important legacy of past disturbances, with potentially far-reaching implications for vegetation dynamics (Chazdon 2003). For example, at the core of the Amazon, far from the agricultural frontier, wildfires in intact floodplain forests are resulting in severe topsoil erosion (Flores et al. 2017). In Indonesia, conversion of tropical forest into oil-palm and rubber-tree plantations is resulting in large losses of soil organic carbon due to topsoil erosion (Guillaume et al. 2015). Selective logging in slope forests of Malaysia triggers the formation of gullies along logging roads and trails, which may eventually cause landslides (Douglas et al. 1999). In seasonally dry tropical forests of Mexico and Brazil, studies found that after fire, nutrients converted into ashes were immediately eroded by water (Maass et al. 1988) and wind (Kauffman et al. 1993). Agroforestry practices that involve opening the canopy and cleaning the understory (Levis et al. 2018) may also increase topsoil erosion (Brandt 1988; Guillaume et al. 2015; Labrière et al. 2015).

Table 1 Disturbance types and their influences on tropical forest cover and soil erosion

Disturbance	Impact on forest cover	Duration of impact on forest cover	Frequency	Erosion (t ha^{-1} y^{-1})	References
Undisturbed forest	–	–	–	0–1.2	Borrelli et al. 2017; * Sidle et al. 2006
Agroforestry	low	decades-millennia	persistent	0.2–107	Labrière et al. 2015; * Sidle et al. 2006
Extreme drought	low	months-years	aperiodic	no data	–
Logging w/ roads/trails	medium	years-decades	cyclic	0.03–15.5	Labrière et al. 2015
Wildfire	medium	decades-centuries	stochastic	17.1	Goldammer 1990
Shifting cultivation	high	years-decades	cyclic	1–10	Borrelli et al. 2017
Large-scale croplands	high	decades-centuries	persistent	5–50	Borrelli et al. 2017

* Based on data reported for forests above 0° to 12° slopes

Although some of these disturbances may cause subtle and ephemeral impacts on forest structure, they are also becoming more pervasive in tropical forests (Alencar et al. 2015; Barlow et al. 2016), increasing bare soil area and decreasing forest cover (Fig. 1b-i). Different disturbances (Table 1) also happen in synergy, trapping ecosystems in relatively open vegetation states (Barlow and Peres 2008; Berenguer et al. 2018; Flores et al. 2016) persistently vulnerable to topsoil erosion (Fig. 3). In the wet tropics where rainfall erosivity is high (Panagos et al. 2017), disturbances that expose bare soils, such as logging, can increase erosion rates more than hundredfold (Labrière et al. 2015). Considering that the area of tropical forests exposed to selective logging is comparable or even larger than the area deforested annually (Asner et al. 2005), soil erosion rates in these ecosystems may be much higher than we imagine.

The erosion positive feedback loop

The resilience of tropical forests depends on their ability to deal with disturbances while maintaining similar functioning (Holling 1973; Scheffer et al. 2001). Particularly, feedbacks between vegetation and environment play a crucial role (DeAngelis et al. 1986). A well-known feedback is the interaction between trees and fire, in which dense forest cover suppresses flammability, allowing trees to recruit (Hoffmann et al. 2012). Other examples involve the interaction between trees and rainfall recycling at the regional scale (Staal et al. 2018a; Zemp et al. 2017), and the capture of atmospheric phosphorus at the local scale, which adds external P inputs to the ecosystem increasing forest resilience (Lawrence et al. 2007). However, after disturbances, small changes in ecosystem functioning may suddenly accentuate, often propelled by positive (self-reinforcing) feedbacks, and initiate abrupt transitions in the system (DeAngelis et al. 1986; Scheffer et al. 2001). For example, in the tree-fire feedback case, forests are usually not flammable, but when disturbances reduce forest cover below 60%, flammability increases steeply, allowing fires to trap the ecosystem in an open vegetation state (van Nes et al. 2018).

Normally in undisturbed forests, tree-soil interactions enhance forest resilience (black arrows in Fig. 4) (Paiva et al. 2015; Silva et al. 2013; Staal and Flores 2015). Trees produce litter with high nutrient content, which is quickly recycled back to the soil and re-absorbed by their roots, as shown in forests and woodlands of tropical South America (Bond 2010; de Oliveira et al. 2017; Paiva et al. 2015; Silva et al. 2013; da Silva et al. 2018). Tree litter production may also contribute to soil organic matter accumulation and topsoil formation (Cotrufo et al. 2015). However, when disturbances reduce tree cover, forests becomes vulnerable to changes in important feedbacks. The plant-soil feedback is weakened as young recruiting trees often produce less litter biomass and of lower nutrient quality (da Silva et al. 2018), hence reducing organic soil formation (Cotrufo et al. 2015). In addition, erosion rates are expected to increase (Fig. 3; Table 1) (Allen 2007; Labrière et al. 2015; Reid et al. 1999), removing organic matter and nutrients (Feller and Beare 1997; Lal 2001; Pimentel and Kounang 1998). As soils become gradually less fertile, forest recovery slows-down, until the ecosystem is

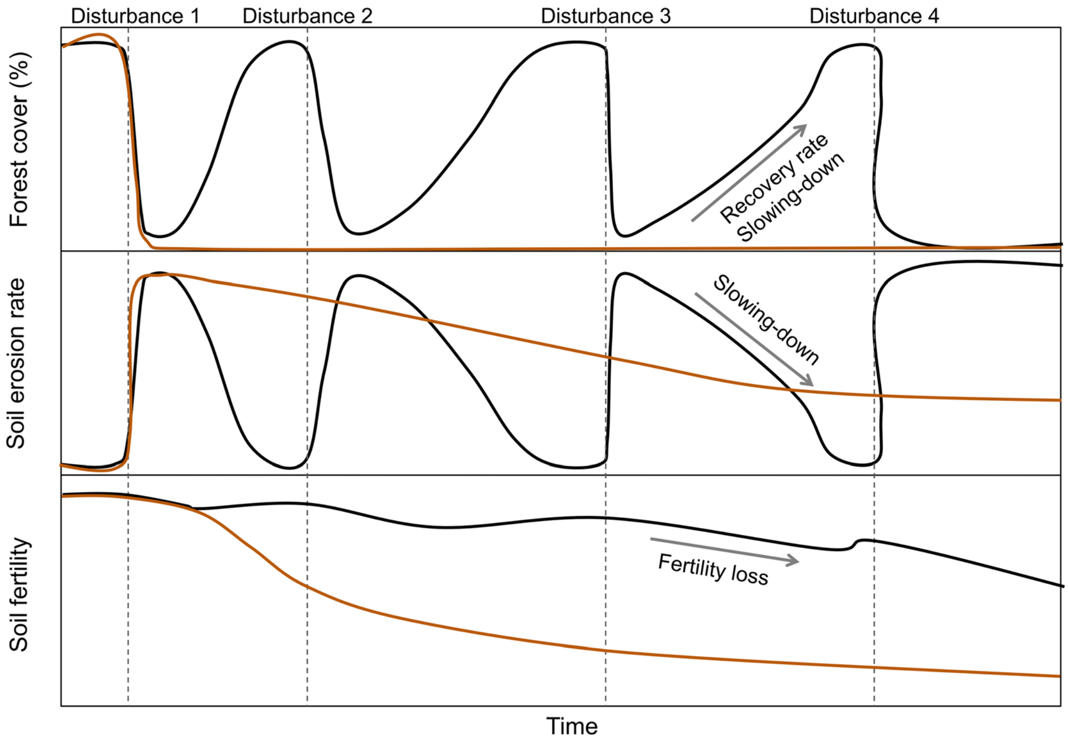

Fig. 3 Hypothetical temporal dynamics of forest tree cover, soil erosion rates, and soil fertility in two tropical forests with different disturbance regimes. Black lines represent a repeatedly disturbed forest, for instance by fire or shifting cultivation. Brown lines represent a persistently disturbed forest, for example by conversion into cropland. Soil erosion rates mirror tree cover; they increase when the forest is disturbed, and decrease as forests recover their crown and litter cover (after Shakesby and Doerr 2006). During the time that forests are open, soils erode and lose fertility cumulatively, making the ecosystem gradually less productive. In the persistently disturbed site (brown lines), while forest cover remains low, erosion rates decrease slowly as mature forest soils lose finer sediments, also causing soil fertility losses to slow-down (Stocking 2003). Nonetheless, soil fertility decreases much faster than in the repeatedly disturbed site (black lines)

eventually trapped in a state of persistently high soil erosion rates and low soil fertility (Fig. 4). This erosion feedback loop is formed by a series of interactions, resulting in a net self-amplifying effect that may potentially push the ecosystem to an alternative state (Fig. 2).

In semiarid and Mediterranean ecosystems, the erosion feedback is a well-known mechanism that determines where plants can establish (Ludwig et al. 2005). Combined with wildfires, this feedback has driven the collapse of cork oak forests and the expansion of shrublands (Acácio et al. 2009). In disturbed tropical forests, the erosion feedback has often been neglected, with only a few examples indicating that it may potentially push the ecosystem to a degraded forest (Jakovac et al. 2016b) or savanna-like state (Flores et al. 2017). Although our simple conceptual model (Fig. 4) does not account for spatial heterogeneity, we expect that variation in disturbance regimes and resource availability might influence how the erosion feedback will affect forest resilience. For instance, in logged forests erosion may be heterogeneous; faster on logging roads and trails, but slower where trees and litter are preserved (Labrière et al. 2015), and resilience will depend on factors such as topography, with slope forests being particularly vulnerable to landslides (Douglas et al. 1999). Natural soil fertility gradients may also affect forest vulnerability to the erosion feedback. On fertile soils, disturbed forests are expected to recover faster, because nutrients remain available even when erosion is intense. In contrast, on highly weathered soils, most nutrients are retained in the forest, litter and soil organic matter, implying that erosion may severely reduce forest resilience (Fig. 2).

Examples from central Amazonian forests

To illustrate how the erosion feedback may reshape the resilience of disturbed tropical forests (Fig. 2), we compare two distinct ecosystems in central Amazonia;

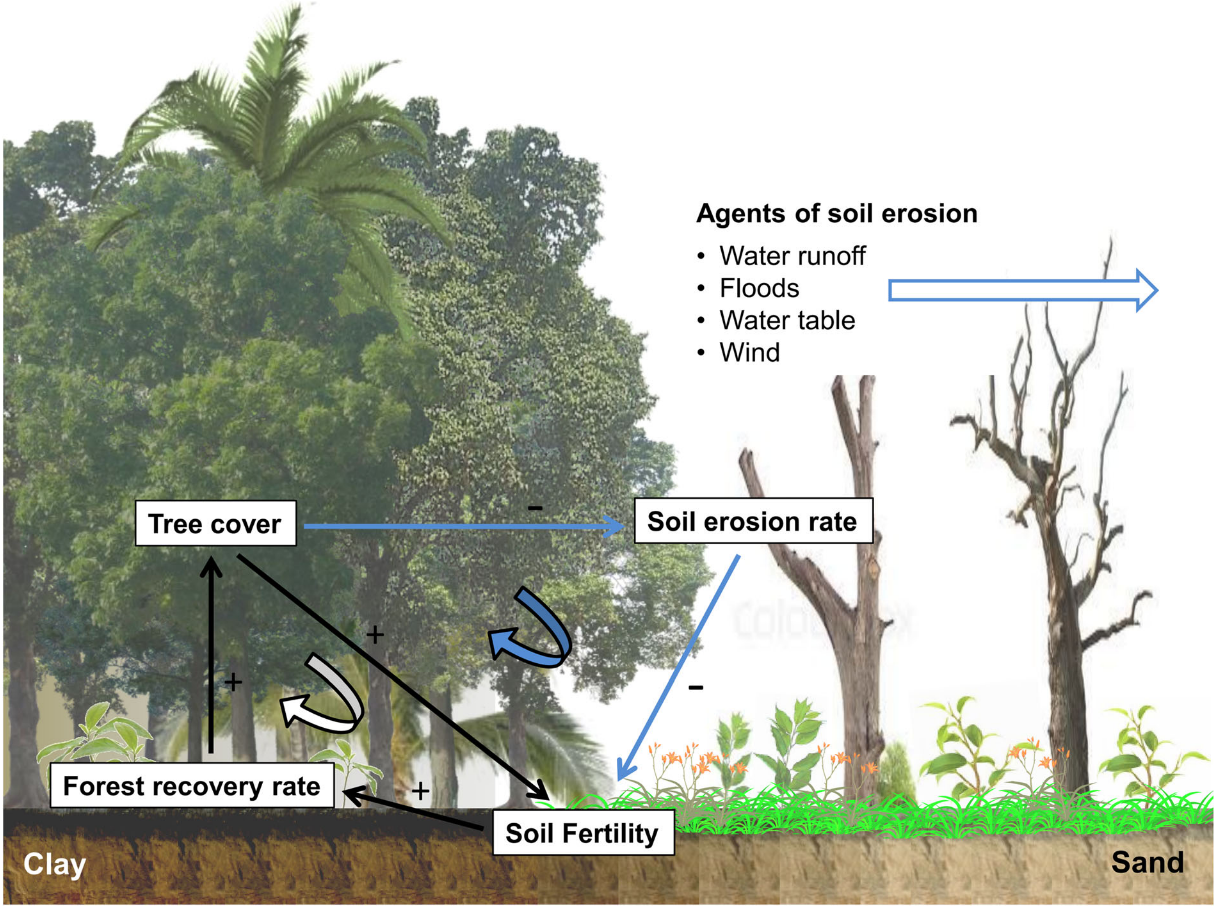

Fig. 4 Diagram of forest-soil interactions, revealing two overlapping feedback loops that may contribute to either stabilize tropical forests, or accelerate the loss of resilience. In black: tree cover enhances soil fertility by supplying nutrient-rich litter that is quickly recycled (de Oliveira et al. 2017; Paiva et al. 2015), and soil fertility accelerates forest recovery after disturbances (Bond 2010; Silva et al. 2013). In blue: high tree cover protects the soil from erosion (Pimentel and Kounang 1998), but when a disturbance reduces tree cover, erosion rates increase, removing the topsoil rich in organic matter and reducing soil fertility (Feller and Beare 1997; Lal 2001; Pimentel and Kounang 1998). Loss of soil productivity slows down forest recovery after disturbances, trapping the ecosystem in a low tree cover state. Illustration adapted from Staal and Flores (2015)

uplands (*terra firme*) and blackwater floodplains (*igapó*). In both cases, the forest has experienced decades of repeated disturbance events. We analysed changes in tree basal area recovery rates and in the topsoil clay fraction. Because clay fraction often correlates with organic matter, it is a good indicator of soil fertility (Feller and Beare 1997). For floodplain ecosystems, data were collected from the middle Negro river region, where in extremely dry years wildfires spread from campfires and swiddens to undisturbed floodplain forests (Flores et al. 2014). We obtained data for 15 forest sites burnt once or twice in the past 40 years. For upland forests, data were collected from the lower Tefé river region, where most disturbances are associated with small-scale shifting agriculture (Jakovac et al. 2015). We obtained data for 33 forest sites disturbed multiple times (1–7) by slash-and-burn practices for manioc plantation. In this system, each cycle lasts on average seven years; two for cultivation, and five for secondary forest regrowth. For all study sites, we obtained data from all trees >1 cm of diameter at breast height (DBH) and superficial soil. We produced chronosequences (space-for-time substitution) to analyse temporal changes in tree basal area based on the time after the latest disturbance, and for clay fraction based on the time after the first disturbance event. In this way, we could observe how forest recovery rates changed after each disturbance event, and how this related to soil changes that accumulated since the start of the disturbance regime (as shown in Fig. 3).

In Fig. 5 (left panels), we show how recovery rates of tree basal area in floodplain and upland forests change after each disturbance event. Floodplain forests already recover more slowly than upland forests after the first fire event, yet after a second fire, recovery slows-down even more. Upland forests recover faster than floodplain forests, but with each disturbance event, recovery slows-down as well. In both cases, loss of forest recovery capacity seems to be linked with a reduction in soil fertility. Figure 5 (right panels) shows that clay is lost from the soil, suggesting that both ecosystems are also losing organic matter (Feller and Beare 1997). Such gradual loss of soil fertility is expected to reduce forest recovery capacity, as shown in the left panels (Fig. 5). Because clay fraction seems to erode faster in floodplains than in uplands, floodplain forests should be more vulnerable to the erosion feedback. The slowing-down of forest recovery by itself can be interpreted as an indicator of approaching collapse (van de Leemput et al. 2018), and the soil erosion feedback loop may be an important underlying mechanism (Fig. 4).

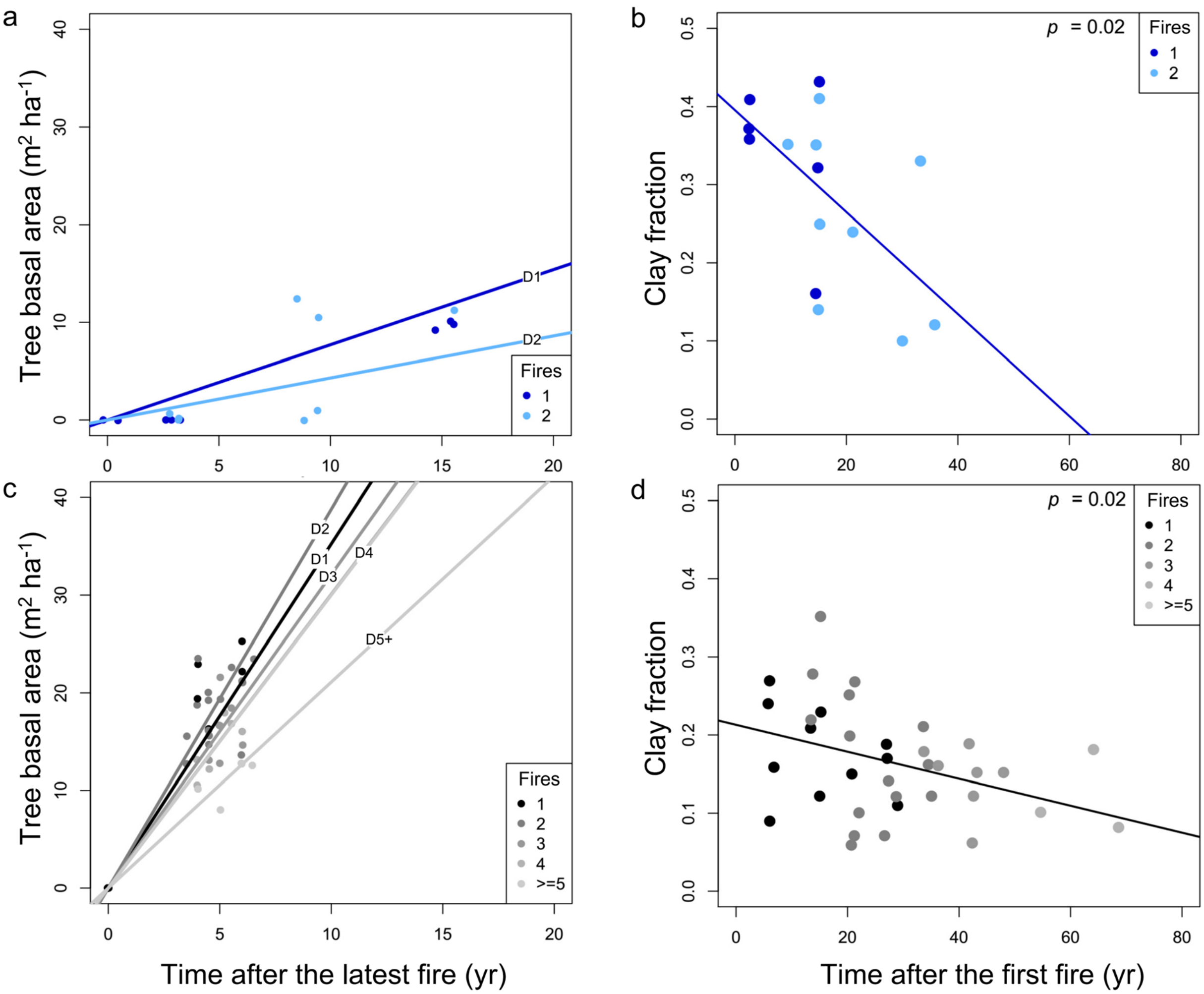

Fig. 5 Field evidence from central Amazonian forests of how ecosystem dynamics changes when it is disturbed repeatedly. (**a**, **b** in blue-scale) Floodplain forests were disturbed by wildfires, and (**c**, **d** in gray-scale) upland forests by slash-and-burn shifting agriculture. Left panels show how recovery rates of tree basal area change after each fire event. Because in both cases, disturbances caused near 100% tree mortality (Flores et al. 2016; Jakovac et al. 2015), we forced the intercept at time = 0. Letters D indicate the sequence of disturbances: from one to two in floodplain forests, and from one to more than five in upland forests. Right panels show how clay fraction changes after the first disturbance event. Note how forest recovery rate decreases faster in floodplains than on uplands, suggesting that erosion is more intense on these ecosystems

Spatial heterogeneity in soil erosion risk

As our study cases illustrate, following disturbances, changes in forest dynamics will depend on environmental conditions that affect erosion. At continental scales, soil erosion risk varies in response to rainfall, with soils in wetter regions being more exposed to storms (Panagos et al. 2017) (Fig. 1). At the landscape scale, it varies with other environmental factors that interfere with how water and wind will act upon the soil (Lal 2001; Pimentel and Kounang 1998). Arguably the most striking factors are topography and flooding, which may enhance particularly water erosion (Pettit and Naiman 2007). Spatial differences in these landscape features may not be so important when forest cover is intact, but may become relevant after disturbances. We illustrate this in Fig. 6, for which we have selected three classical tropical forest ecosystems that represent well how some of these factors may influence soil erosion risk: (1) upland (non-flooded) forests, (2) floodplain forests, and (3) white-sand forests. We also show some variations among them that may be relevant for erosion risk.

In disturbed upland forests (Fig. 6a), soils erode by water runoff during heavy rain events, by trade winds and also by wind storms such as blowdowns (Certini 2005; Lal 2001; Pimentel and Kounang 1998). Runoff impact is more severe on steep slopes, where it can lead to rill and gully erosion, and in extreme cases causing landslides (Fig. 6b). This has been shown in forests that were damaged for instance by logging roads and trails (Douglas et al. 1999; Pettit and Naiman 2007). On windward slopes, wind erosion removes light sediments, such as clay and silt, as well as nutrients (Tao 2004). This process is well-known in dune ecosystems (Moeslund et al. 2013), yet it may also affect other forest landscapes with marked topography. In addition to removing clay and nutrients, winds may transport heavier sand particles (Moeslund et al. 2013; Tao 2004), contributing to reduce soil fertility in the places where sand is deposited (Anderson 1981; Martinelli et al. 1999). Sand deposition by wind has been shown as a mechanism for the expansion of deserts in drylands (Shi et al. 2004; Tao 2004; Tomasella et al. 2018), and of white-sand ecosystems in the Amazon (Anderson 1981; Carneiro Filho et al. 2002).

Close to streams, in disturbed valley and gallery forests (Fig. 6c), soils are eroded not only by runoff and wind, but also by flood events that occur in aperiodic pulses (Junk et al. 2011), carrying sediments and nutrients to stream channels (Luizão et al. 2004; Pettit and Naiman 2007). Flooding can be a strong erosion agent, as we have shown in our study case (Fig. 5), implying that floodable forests may be particularly vulnerable to the erosion feedback loop. Forests that are seasonally flooded by nutrient-poor blackwater or clearwater rivers (Fig. 6d) are perhaps among the most

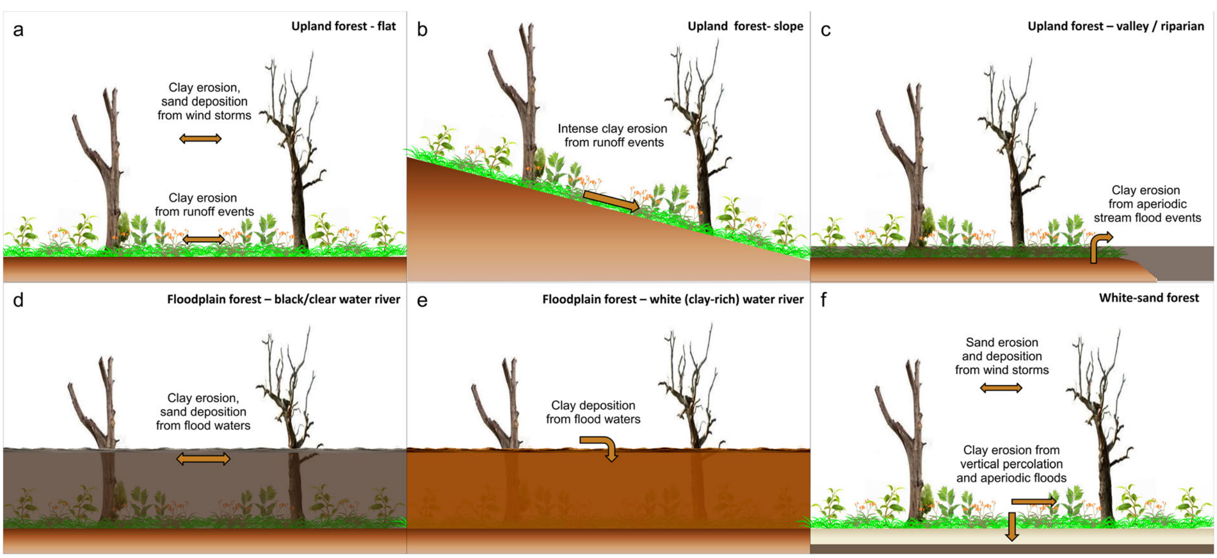

Fig. 6 Tropical forests in different environmental conditions that may determine erosion risk after disturbances. The main erosion-deposition processes are: (**a**) and (**b**) sheet and rill erosion from runoff, (**c**) and (**d**) flood erosion, (**e**) high clay deposition, (**f**) vertical water erosion, flood erosion and wind erosion/deposition

vulnerable, because flooding waters provide few nutrient inputs for tree growth (Schöngart et al. 2005). In contrast, forests that are flooded by white water rivers rich in nutrients and fine sediments (Fig. 6e), such as those along the Amazon river, are expected to be more resilient to disturbances, because they periodically receive new deposits of fertile soil from the Andes (Aalto et al. 2003; Wittmann et al. 2004).

In landscapes where the water-table moves vertically with the seasons, water may carry clay and nutrients deep, far from tree roots (Anderson 1981; Heyligers 1963; Janzen 1974). In the long-term, this process creates white-sand soils known as podzols (Klinge 1965; Richards 1941), which are also vulnerable to erosion (Heyligers 1963; Sauer et al. 2007) (Fig. 6f). A large fraction of these white-sand forests is seasonally flooded by blackwater rivers and streams (Klinge 1965; Junk et al. 2011), which may enhance erosion rates. Trees in these ecosystems are known to form thick (10–30 cm) root mats that retain hummus and nutrients dissolved in the water (Stark and Jordan 1978). These root mats are also common in blackwater floodplains (dos Santos and Nelson 2013), suggesting that both ecosystems share this functional characteristic as a way maximise nutrient acquisition. Yet, when disturbances destroy the root mat, sediments become vulnerable to be transported to other areas (Carneiro Filho et al. 2002; Sauer et al. 2007).

Conclusions and implications

In this conceptual article, we argue that when tropical forests are disturbed repeatedly, low vegetation cover and high soil erosion rates interact in a self-reinforcing feedback loop that reduces forest resilience (Fig. 4) and increases the risk of ecological transitions (Fig. 2). We provide empirical evidence from two distinct forest types in Central Amazonia, supporting the idea that erosion may be a key underlying mechanism for resilience loss (Fig. 5). Therefore, analyses of the erosion feedback in disturbed ecosystems may help us understand, for instance, why certain forests persist degraded, and how biomes expand and retract. Although the erosion feedback is a process that involves interactions between soils and plants at the local scale, its implications may extend to landscapes and broader regions. For instance, Amazonian forests along the deforestation frontier may have been losing resilience due to this feedback, which may cascade further west into the basin through reduced rainfall recycling (Staal et al. 2018a). Also, in other tropical regions exposed to disturbances over centuries, entire forest biomes may have lost resilience, for example due to limited arrival of propagules, and recovery now depends on active restoration (e.g. Cavelier et al. 1998; Mendes et al. 2018).

One important change caused by erosion in disturbed forests is that new environmental filters start to emerge, reshaping plant species composition (e.g. Jakovac et al. 2016b) and altering ecosystem functioning (Hoffmann et al. 2012). Erosion reduces not only soil fertility, but also soil infiltration and storage capacity (Pimentel and Kounang 1998), thus altering fine scale water availability. Nutrient and water availability are factors that may determine variations in tree composition and functioning across tropical landscapes (Baldeck et al. 2013; Cosme et al. 2017; Ter-Steege et al. 2006). Usually, trees adapted to low nutrient and water availability have a conservative physiological strategy (Diaz et al. 2004; Wright et al. 2010), involving small and tough leaves (Wright et al. 2004), as well as other adaptations that provide high hydraulic safety (Anderegg et al. 2016; Oliveira et al. 2019; Santiago et al. 2018). Thus, when nutrient and water availability are reduced due to erosion, slow-growing trees are expected to dominate, potentially altering forest dynamics (Diaz et al. 2004; Quesada et al. 2012; Wright et al. 2010). With reduced soil water availability, small trees are more likely to survive and recruit because they tend to be more drought-resistant than tall trees, which could result in the development of shorter forests (Rowland et al. 2015). Reduced soil water storage capacity in eroded sites may also indirectly increase ecosystem flammability (Chen et al. 2013), which is already high in most landscapes with low tree cover (van Nes et al. 2018). As a result, fires may add another filter to the system, selecting for plants with thick barks and high resprouting ability (Bond and Midgley 2001; Jakovac et al. 2016b). Another indirect mechanism associated with erosion that can determine changes in vegetation composition is the removal of soil seed banks, which excludes seed-dependent tree species and favours resprouters (García-Fayos et al. 2010).

Changes in environmental filters associated with erosion may not only alter forest functioning, but also trigger more drastic shifts in ecosystems. It is now well accepted that across the tropics, forests and savannas can be alternative vegetation states in regions with intermediate levels of mean annual rainfall (Hirota et al. 2011; Staver et al. 2011; Staal et al. 2018b). In these bistable landscapes, forests are commonly found on soils with higher resource availability, whereas savannas tend to occur where soil conditions are more limiting (Hoffmann et al. 2012; Lehmann et al. 2014; Veenendaal et al. 2015). This spatial pattern suggests that shifts between both states might involve changes in soil conditions, and the erosion feedback loop that we describe seems to be a potential underlying mechanism. There is some evidence suggesting that soil erosion can indeed facilitate the expansion of savanna vegetation (Cavelier et al. 1998; Flores et al. 2017), although in most cases, repeatedly disturbed tropical forests tend to persist in a degraded state dominated by forest trees that tolerate fire, low nutrient and water availability, as well as exotic invasive grasses (Barlow and Peres 2008; Berenguer et al. 2018; Devisscher et al. 2016; Jakovac et al. 2016a; Silvério et al. 2013; Veldman and Putz 2011). Considering that tropical forests are increasingly exposed to disturbances, understanding how erosion may act as a resilience drain in these systems may help societies to manage the risk of ecological transitions (Scheffer et al. 2015), for instance by promoting fast recovery and restoration.

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