

# Regional and local determinants of drought resilience in tropical forests

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## Abstract

The increase in severity of droughts associated with greater mortality and reduced vegetation growth is one of the main threats to tropical forests. Drought resilience of tropical forests is affected by multiple biotic and abiotic factors varying at different scales. Identifying those factors can help understanding the resilience to ongoing and future climate change. Altitude leads to high climate variation and to different forest formations, principally moist or dry tropical forests with contrasted vegetation structure. Each tropical forest can show distinct responses to droughts. Locally, topography is also a key factor controlling biotic and abiotic factors related to drought resilience in each forest type. Both dry tropical forests and ridges (steeper and drier habitats) are more sensitive to droughts than moist tropical forest and valleys (flatter and wetter habitats). The most important biotic factors are leaf economic and hydraulic plant traits, and vegetation structure. The most important abiotic factors are soil nutrients, water availability and microclimate. Here we show that topography has key roles controlling biotic and abiotic factors in each forest type. Our synthesis highlights that gradients of altitude and topography are essential to understand tropical forest's resilience to future drought events. We described important factors related to drought resilience, however many important knowledge gaps remain. Filling those gaps will help improve future practices and studies about mitigation capacity, conservation, and restoration of tropical ecosystems.

## Regional and local determinants of drought resilience in tropical forests

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## Abstract

The increase in severity of droughts associated with greater mortality and reduced vegetation growth is one of the main threats to tropical forests. Drought resilience of tropical forests is affected by multiple biotic and abiotic factors varying at different scales. Identifying those factors can help understanding the resilience to ongoing and future climate change. Altitude leads to high climate variation and to different forest formations, principally moist or dry tropical forests with contrasted vegetation structure. Each tropical forest can show distinct responses to droughts. Locally, topography is also a key factor controlling biotic and abiotic factors

related to drought resilience in each forest type. Both dry tropical forests and ridges (steeper and drier habitats) are more sensitive to droughts than moist tropical forest and valleys (flatter and wetter habitats). The most important biotic factors are leaf economic and hydraulic plant traits, and vegetation structure. The most important abiotic factors are soil nutrients, water availability and microclimate. Here we show that topography has key roles controlling biotic and abiotic factors in each forest type. Our synthesis highlights that gradients of altitude and topography are essential to understand tropical forest's resilience to future drought events. We described important factors related to drought resilience, however many important knowledge gaps remain. Filling those gaps will help improve future practices and studies about mitigation capacity, conservation, and restoration of tropical ecosystems.

**Keywords:** Climate change, El Niño, mortality, growth, recovery, resistance

## Introduction

Drought is a natural phenomenon characterized by abnormally low precipitations and high temperatures, which strongly affect plants at different scales, from individuals, to populations and communities, and thus ecosystems worldwide (Dai 2011, Fauset et al. 2012). Drought events are predicted to modify species composition and abundance, as well as ecosystem functioning and dynamics (Boeck et al. 2017), especially in tropical forests (Reichstein et al. 2013) due to high exposure to El Niño events (IPCC, 2018). Nevertheless, resilience to droughts in tropical forests remains poorly understood (Xu et al. 2013, Meir et al. 2015). Identifying biotic and abiotic factors related to mortality and low growth induced by droughts would allow us to better understand and predict forest resilience and dynamics.

The interest in studying drought effects in tropical forests has increased more than four times during the last 20 years (Fig. 1). This is likely because tropical forests are among the most vulnerable ecosystems to climate change (Bellard et al. 2014). Indeed, tropical forests were strongly affected by the two most severe droughts ever recorded, in 2015/2016 (Otto et al. 2015, Kogan and Guo 2017) and 1998/1999 (Slik 2004). The former and most recent one led to a high net carbon loss, even higher than the 2010 drought in the Amazonian forest (Liu et al. 2017). Tropical forests provide key ecosystem services – such as water supply, carbon sequestration, pollination and climate control – to urban and rural areas (Joly et al. 2014, Silva et al. 2021). Although our understanding of drought effects worldwide is growing, the impacts of droughts in tropical forests are still poorly understood, which limits our ability to model forest responses to future climate scenarios.

Repeated occurrences of strong droughts can select for drought-tolerant species due to higher mortality of vulnerable species (Aguirre-Gutiérrez et al. 2020). Thus, it has been predicted that trees of tropical forests will become smaller with denser wood (Phillips et al. 2010), due to high mortality rates of canopy trees and shade-tolerant species (Fauset et al. 2012). There is a field of evidence that tropical forests can change to a drier ecosystem due to the interactions between recurrent fires and climate change. This process drives communities through a savannization (Sansevero et al. 2020) and/or a secundarization process (Barlow and Peres 2008), thus decreasing carbon sequestration and enhancing climate change effects, because dry ecosystems sequester less CO<sub>2</sub> than moist forests (Taylor et al. 2017). Therefore, repeated drought events associated with high deforestation and recovery can drive tropical forests into a different type of forest following the future climate scenarios. This process can lead to changes in forest composition, vegetation structure, traits and ecosystem services (Aguirre-Gutiérrez et al. 2020). Predictions of which plant species are most vulnerable to drought effects, and where they occur, are needed to model consequences of climate change and to determine the best mitigation strategies.

Climate changes impact forests at multiple spatial scales, and this is the interaction of processes across scales that may determine forest resilience (Reyer et al. 2015). For instance, drought effects are influenced by gradients varying at global, regional and local scales (O'Brien et al. 2017). Thus, looking at multiple spatial scales may offer the best way to predict forest resilience because plant mortality and reduced growth can occur locally with potentially negative effects, but they may smooth out at larger spatial scales (Reyer et al. 2015). The aim of this study was to synthesize biotic and abiotic factors, mostly controlled by topography,

that can be used to predict drought-induced mortality in tropical forests. We expect that this review will help identify knowledge gaps in drought resilience research and provide a framework for future studies.

### **What is drought resilience and how do we quantify it?**

Resilience is the capacity of a biome, an ecosystem or a species to both resist and recover from a disturbance (Oliver et al. 2015). Resistance is the ability of a system to maintain its properties and functions during a disturbance (Mariotte et al. 2013) whereas recovery is the ability of a system to return to initial conditions (Verbesselt et al. 2016). Droughts are associated with vegetation mortality and reduced growth (Adams et al. 2009, Verbesselt et al. 2016, Greenwood et al. 2017, Meir et al. 2018). Thus, quantifying mortality and growth to estimate drought resilience is an important approach to measure vulnerability and drought resilience of plant species (Redmond et al. 2018). Evidences suggest a growth-survival trade-off, showing for example, that survival rates are negatively correlated to growth rates (Wright et al. 2010, O'Brien et al. 2017). Another pattern can be found when recovery rates are measured after a normal condition, for example, after a La Niña event. In this case, a resistance-recovery trade-off is expected, with sites or species showing greater resistance rate during drought but lower recovery rate after a rainy period (Gazol et al. 2017). Furthermore, during the recovery period, new individuals can be recruited, mainly because of the available niches resulting from large tree mortality (Redmond et al. 2018). Tree resistance and recovery to droughts will likely determine the long-term trajectory of tropical forests. Therefore, resilience is an important component to determine community and ecosystem sensitivity to disturbances and to predict shifts in forest carbon stocks caused by climate changes (Sánchez-Salguero et al. 2018).

Drought timing and severity, as well as forest type, are important factors to take into account when estimating the resistance and necessary time for the recovery. For instance, in 2017, savannas and grasslands had already recovered from the 2015/2016 drought but tropical forests did not because tropical trees have slower growth and recruitment rates (Wigneron et al. 2020). Drought legacy, *i.e.*, the time of recovery after a drought, can take longer according to the drought magnitude (Huang et al. 2018, Kannenberg et al. 2020). For instance, tropical forests in Costa Rica recovered from the 1997 drought within two years (Silva et al. 2013) and the Puerto Rican forests recovered from the 2015 drought within 1 year (Schwartz et al. 2019, 2020). Quantifying the local magnitude of droughts can be difficult due to spatial variation in precipitation and temperature. An El Niño event does not mean the same dry condition because some forests can be more exposed to such conditions depending on the latitude and the topography.

### **Drought resilience in different types of forests**

Tropical forests include dry and moist forests (Olson et al. 2001). Dry tropical forests (also called seasonally dry tropical forest) range from tall forest on moister regions to shrublands on the driest regions and the vegetation is mostly deciduous during the dry season (Pennington et al. 2009). Moist tropical forests are characterized by the presence of evergreen plant species in high-altitude moister areas of the tropics but also by the presence of deciduous species in areas with seasonal climatic regime (WCMC 1992). Therefore, this classification (*dry vs. moist tropical forest*) is mainly due to different climatic conditions, which are driven by altitude, latitude and longitude (Fig. 2).

Distinct patterns of drought resilience likely exist among different forest types because each type of forest will impact differently soil nutrients and water availability, vegetation structure and functional traits (Fig. 2). For instance, African tropical forests are more resistant to climatic extremes than Amazonian and Asian forests due to differences in their vegetation structure (Bennett et al. 2021). Furthermore, El Niño impacts vary latitudinally in the Atlantic Forest, with tropical areas being more impacted by El Niño events than subtropical areas (Rodrigues et al. 2011). Eastern and southern regions of the Amazon Forest experienced stronger drought impacts than the north-western region (Van Schaik et al. 2018).

Tropical dry forests are less resistant to droughts (Allen et al. 2017). Furthermore, tropical forest communities in West Africa that normally experience higher seasonal water deficit, and that became drier through time, tended to become more homogeneous in functional, taxonomic and phylogenetic diversity (Aguirre-Gutiérrez et al. 2020). Some areas of tropical forest are secondary forest patches recovering from land use, timber

extraction or natural disturbances (Rüger et al. 2020). Pioneer species occurring in those secondary forests present high mortality during drought periods (Rocha et al. 2020), but high recovery rates after a drought event (Poorter et al. 2016, Gazol et al. 2017). Those findings highlight that each forest type of tropical forest can show different patterns of growth and mortality and this regulates how much carbon each forest type will store under the future climate.

## Drought resilience across topographic gradients

Locally, topography is also a source of environmental heterogeneity within each forest type (Jucker, Bongalov, et al. 2018, Nettesheim et al. 2018). Abiotic factors strongly vary across topographic gradients, such as water availability, soil nutrients and microclimate (Fig. 2, Fig. 3, Fyllas et al., 2017). Topographic variation of tropical forests can be distinguished into two main habitats: valleys (flatter and wetter habitats) and ridges (steeper and drier habitats). Biotic factors, such as species traits and vegetation structure, are also driven by topography (Fig. 2, Fig. 3, Jucker et al., 2018a; Rodrigues et al., 2019). Topography is thus an important factor to take into account to understand drought impacts in plant communities due to the role of those factors in survival and growth of plant species (O'Brien et al. 2017, Hollunder et al. 2021).

Species occurring in different topographical habitats can show distinct patterns of mortality and growth rate. Studies in tropical forests have shown that woody plant species occurring in valleys can be more resistant than the ones occurring in ridges (Table 1). Valleys can act as refuges, providing nutrients and water during droughts (Costa et al. 2020, Hollunder et al. 2021). Furthermore, shade availability in valleys can reduce drought impacts and improve the performance of plant species during drought periods (Holmgren et al. 2012). Species occurring in dry habitats are living under their microclimate limits and under water stress, and a small change in precipitation and temperature can be physiologically stressful (Allen et al. 2017, Aguirre-Gutiérrez et al. 2020, Cartwright et al. 2020). In turn, species from dry habitats can show high recovery rates during a post-drought period (Schwartz et al. 2019), following the resistance-recovery trade-off. However, it has been suggested that dry habitats can also show strong drought legacies (Anderegg et al. 2015, Allen et al. 2017).

Other studies have shown that valleys can be less resistant than the ones occurring in ridges (Table 1). Species from valleys do not have traits related to drought tolerance, while species occurring in ridges have traits related to survival during periods of water-stress (Allen et al. 2017, Gessler et al. 2017). Such distinct evidences indicate that there is no general pattern of drought impacts for all tropical forests, though most of the studies found stronger resistance in wetter habitats. Biotic and abiotic factors controlled by topographic gradients are also strong drivers of tree growth and mortality, as well as of forest resilience, and can thus contribute to help elucidating such patterns (Fig. 2).

## Abiotic factors

### 5.1. Water availability and soil nutrients

Climate changes are strongly related to changes in rainfall patterns worldwide, involving reductions in the total amount of annual precipitation and/or increase in the dry season duration (Grossiord et al. 2016). Furthermore, at local scales, soil water availability is highly variable along topographic gradients, with wetter valleys and drier ridges (Fig. 3, Gibbons & Newbery 2002). Both changes in soil moisture and reduced precipitation strongly drive changes in physiological traits (Pezzola et al. 2017). For instance, drought-induced water stress decreases photosynthesis rate, which leads to slow and reduced plant growth (McDowell et al. 2008). In addition, low water availability decreases the physiological mechanisms (secondary metabolites) related to plant defense and favors the reproduction of insects (Mattson and Haack 1987, McDowell et al. 2011), increasing woody species vulnerability to death (Das et al. 2016). Water availability also plays a vital role in forest recovery, increasing the growth rate of plant tissues during post-drought periods (Poorter et al. 2016, Álvarez-Yépez et al. 2018). Due to its strong spatial and temporal variations, water availability is the most important driver of resistance and recovery rates.

Soil nutrients also play an essential role in plant communities distributed across topographic gradients (Fig.

3, Guan et al. 2015). Soil nutrients are key factors of photosynthesis, which is an essential mechanism of plant survival and growth (Fatichi et al. 2014). Nutrient stoichiometry can change across topographic gradients due to the unidirectional fluxes from ridges to valleys and of the consequent loss of nutrients in the ridges (Werner and Homeier 2015). Therefore, nutrient limitation can lead to high nutrient competition in ridges (Werner and Homeier 2015). Nitrogen (N), phosphorus (P) and carbon (C) are the main elements required to plant growth and survival, and change in their ratios can have strong consequences for tropical forest communities (Zhang et al., 2012, 2017). For instance, P of tropical forest soil is positively correlated with growth rate and negatively related with mortality rate (Soong et al. 2020). Tropical plants in valleys may require large amounts of leaf N to deal with the intense shading of forest understory (Torres-Leite et al. 2019). Droughts can alter N and P cycles in ecosystems, either directly through changes in N mineralization and P sorption (Mariotte et al. 2017) or indirectly through changes in plant nutrient uptake and growth (Mariotte et al. 2020). Changes in litter N, P and C content alter decomposition rates because decomposers require nutrients from either litter or soil for their functioning (Gartner and Cardon 2004). Deficiency in plant-available nutrients in ridge is enhanced through a positive feedback driven by poor litter decomposability (Werner and Homeier 2015). Furthermore, more frequent droughts slow down litter decomposition and reduce plant-available nutrients (da Silva et al. 2020).

#### *Microclimate variation across topographic gradients*

Vegetation structure (e.g., height, stem density, and canopy biomass) and local topography (e.g., elevation, slope and aspect) strongly influence the microclimate (Hardwick et al. 2015). Understory and canopy species are under different microclimatic conditions due to the vertical structuration in tropical forests. For instance, canopy cover of larger trees regulate the irradiance and light intensity entering the understory layer (Nepstad et al. 2002, Wright et al. 2010). Thus, the light availability is more variable and limiting for understory species than for large trees (Wright et al. 2010). The high drought-induced mortality of large trees can change the microclimate of the understory (Redmond et al. 2018, Zellweger et al. 2020). Small forest fragments have lower abundance of large trees due to high edge effects (Dantas de Paula et al. 2011) and lack suitable microclimatic sites for the persistence of species during drought periods (Hardwick et al. 2015, Laurance et al. 2018). During a water stress period, the low leaf area of large deciduous trees lead to high light availability in the understory (Smith et al. 2019). In turn, the increase in light availability induces high rates of photosynthesis in the understory, thus affecting species adapted to shaded conditions (Guan et al. 2015).

Other microclimate variables, such as air temperature and humidity, are controlled by light availability that reaches the understory stratum. For example, in the valleys with dense forest canopy, air humidity is higher and temperature is lower than ridges with open forest canopy (Fig. 3, Jucker, Hardwick, et al. 2018). The high humidity and low temperature in valley can protect plant species during drought periods. However, the opening of forest canopies during droughts due to leaf loss can affect species adapted to low temperatures and high air humidity (Smith et al. 2019). The high transpiration rates are strongly related to high air moisture in the understory layer (Hardwick et al. 2015). In addition, ridges can show different microclimate conditions depending on the topographic aspect. For example, west facing ridges are warmer due to higher exposure to afternoon sun than east facing ridges that are exposed to morning sun (Stephenson 1990). Therefore, microclimate variables, controlled by topography and vegetation structure, are strongly related to plant growth and mortality, especially for understory species.

#### **Biotic factors**

##### *Drought resilience of dominant and low abundance species*

Plant tropical communities are complex systems due to high diversity and large differences in species abundances. The most basic classification of species in a plant community is based on abundance patterns and it separates species into dominants, subordinates and transients (Whittaker 1965, Grime 1998). In a plant community, few species are classified as dominant species, which are the most abundant, and account for a higher proportion of the overall biomass of the community. On the other hand, low abundance species (subordinates and transients) represent lower amount of biomass, but are the main determinants of plant

diversity (Whittaker 1965, Grime 1998, Mariotte 2014). Dominant and low abundance species differ in their functional traits and play different roles in the ecosystem (Mariotte 2014). In general, dominant species are competitively superior (Mariotte 2014) and respond to environmental filtering, while low abundance species respond to niche differentiation (Maire et al. 2012). Low abundance species can promote the diversity of climbing plants (Garbin et al. 2012) and affect ecosystem functioning (Mariotte et al. 2015). Dominant species play an important role in structuring the species distributions (Wei et al. 2020) due to its homogenous distribution pattern (Mariotte 2014). For example, in a topographic gradient, they can occur in valleys and ridges (Hollunder et al. 2014). On the other hand, as low abundance species have a more aggregated spatial distribution (Mariotte 2014, Garbin et al. 2016), it is expected that they occur in specific habitats and not across a whole topographic gradient (Hollunder et al. 2014). The response to drought depends on species and their spatial distribution and thus, taking into account both habitats (valleys vs. ridges) and species groups (dominant vs. low abundance species) can improve our understanding of the processes that drive the response of tropical forests to severe droughts.

Low abundance species are less numerous, making populations of these species more vulnerable to local extinction induced by climate change (Greenwood et al. 2017). Furthermore, populations of low abundance species that occur with few individuals and with an aggregated spatial pattern (Mariotte 2014) can be even more reduced due to habitat loss. On the other hand, dominant species are expected to be more resistant to local extinction due to their higher number of individuals (Greenwood et al. 2017). Therefore, locally, and perhaps even globally, species diversity can decrease under the future climate scenarios due to the role of low abundance species as main determinants of plant diversity. Dominant species play important roles on ecosystem functioning because of their large amount of biomass (Grime 1998) and thus, they can act as a biotic filter in the establishment and survival of low abundance species (Khalil et al. 2019). The mortality of dominant species during droughts can also affect the performance of low abundance species. Therefore, understanding how dominant and low abundance species respond to drought events will highlight their roles in promoting resilience of tropical plant communities.

#### *Use of traits to unravel drought resilience mechanisms*

A functional trait is any feature which impacts fitness indirectly via effects on growth, reproduction and survival at individual and species level (Diaz and Cabido 2001, Violle et al. 2007). Traits are classified based on responses to the environment and/or common effects on ecosystem processes (Lavorel and Garnier 2002). There are traits related to responses to environmental variables, such as resources and disturbances (*i.e.*, response traits), and traits that determine the effects of plants on ecosystem functions (*i.e.*, effect traits), such as biogeochemical cycling and disturbance resistance (Lavorel and Garnier 2002). Furthermore, species may exhibit intraspecific variation in functional traits, which can represent an important strategy to resist and recover from drought impacts (Hof et al. 2011). For instance, small forest fragments sustain smaller populations with low phenotypic variability in traits, making them more sensitive to climate change effects (Hof et al. 2011). Trait-based approaches can help to understand the physiological mechanisms of drought tolerance in different species, as well as how forests will respond to future climate scenarios. Thus, ecologists have to include key traits directly and mechanistically relevant to plant survival and growth. For instance, carbon sequestration, water use efficiency and photosynthesis rate are mechanisms related to plant growth and mortality that can be assessed by measuring plant traits.

Traits can be measured at different levels, from tissue (e.g. stomatal and vein density), organ (*e.g.*, specific leaf area [SLA], leaf dry matter content [LDMC], woody density [WD]) to whole-plant level (*e.g.*, height, root to shoot ratio) (Pérez-Harguindeguy et al. 2013). Plant ecologists have been using trait-based approaches in order to understand mechanisms that explain resilience mechanisms. On one hand, at the community level, functional diversity can enhance resource use and increase the potential for facilitative interactions, which decrease the negative impacts of droughts (Gazol and Camarero 2016). On the other hand, at smaller levels, individual and species are able to change their traits to tolerate droughts. For example, trees can increase chlorophyll concentration in their leaves during El Niño periods (Nunes et al. 2019).

Trait combinations have the potential to explain the growth-mortality and resistance-recovery trade-offs.

Traits that are linked to resource capture (*e.g.*, leaf area), photosynthetic capacity (*e.g.*, specific leaf area and leaf nitrogen content) and nutrient and water uptake (*e.g.*, root length and diameter) generally have positive relationships with growth and negative relationships with mortality (Pérez-Harguindeguy et al. 2013). In turn, traits that are related to structural safety (*e.g.*, wood density) or longevity (*e.g.*, leaf dry-matter content and leaf thickness) have negative relationships with growth, but are often positively related to survival (Poorter and Bongers 2006). However, the growth–trait relationships can exhibit inconsistencies among species group, biomes, and spatial scales. For instance, although WD is widely used to predict drought impacts, it has been suggested that this trait does not provide a mechanistic understanding of drought-induced mortality (O’Brien et al. 2017). Recently, it was found that low wood density is a strong predictor of mortality for angiosperms, but not for gymnosperms (Anderegg et al. 2016). Furthermore, high wood density can be associated to high mortality rate caused by hydraulic failure (Hoffmann et al. 2011). Therefore, the use of specific key traits directly related to growth and mortality is essential to investigate physiological mechanisms of resilience.

### *The importance of tree size*

Tree size is one of the most used traits to understand drought effects on plants (Meakem et al., 2017; Prado-Junior et al., 2017; Shenkin et al., 2018). Tree size is an effect trait, due to its key role in controlling light availability and heterogeneity, and in influencing the structure of understory species communities (Sercu et al. 2017). Tree size is also a response trait related to light competition due to the greater access to light that larger trees can have when compared to understory plants (Laughlin 2014). Plant size can be negatively related to stand density across topographic gradients, from valleys with low stem density and bigger trees (in height and diameter) to ridges with high stem density and smaller trees (Werner and Homeier 2015). This trait can be helpful to understand which trees are more vulnerable to mortality, but its use in drought studies is still limited in tropical forest.

Most studies showed that larger trees are more sensitive to drought effects due to their higher demands for water comparing to smaller trees, which are expected to be more resistant (Phillips et al. 2010, Moser et al. 2014). Nevertheless, small trees can face more water limitation due to their shallower roots (Gibbons and Newbery 2002) and thus they also show higher mortality rates (Rocha et al. 2020) and a more accentuated growth-mortality trade-off pattern than larger trees (Zhu et al. 2017). Trees with a single stem may be more vulnerable to drought effects than shrubs with multiple stems, which can leave one or more viable as an insurance to survive (Tanentzap et al. 2012). In addition, older and taller trees can show high resistance to precipitation variations (Giardina et al. 2018). These findings suggest that small and big trees are more vulnerable to droughts and trees with intermediate sizes (*e.g.* understory individuals) are more resistant to drought events. Indeed, tree mortality may increase, decrease, or show a U-shaped curve with increasing tree size (Zhu et al. 2017). Although tree size is a common trait used in drought studies, we do not know clearly if there is a size-dependency in mortality.

### *The importance of hydraulic traits*

Traits can be classified according to their responses to different factors (Li et al. 2015): leaf economic traits (*e.g.*, SLA and WD) and hydraulic traits (*e.g.*, stomata density and water-use efficiency). Leaf economic traits are related to light use and carbon sequestration while hydraulic traits are related to gas exchange and water transport capacity (Li et al. 2015). Variation in hydraulic traits is independent of variation in economic traits in tropical forests (Powell et al. 2017), but hydraulic traits are strongly influenced by plant size and water availability (Liu et al. 2019). Plants can reduce water loss by shedding their leaves or closing their stomata to maintain plant water potential and avoid or reduce the risk of xylem cavitation (Vitória et al. 2019). The sensitivity of trees to drought is best predicted by hydraulic traits (Anderegg et al. 2016, Li et al. 2020) and forests with higher diversity in hydraulic traits are more resistant to drought impacts (Anderegg et al. 2018). Hydraulic failure was the main mechanism explaining tree mortality during the 2015/2016 drought, while wood density, SLA, tree size and foliar nutrients were poorly correlated with drought vulnerability in a seasonally dry tropical forest in Costa Rica (Powers et al. 2020). Hydraulic failure occurs when the water transport to the canopy is decreased, resulting in desiccation and death of plant tissues (Hoffmann et al.

2011). In addition, tropical rainforests showed high water use efficiency to deal with the negative impacts of 2015/2016 drought (Nunes et al. 2019). Therefore, the use of hydraulic traits and leaf economic traits, as well as their relationships, can help to understand the cause of mortality and reduced growth.

Deciduousness is a phenological but also a hydraulic trait related to drought avoidance strategy for trees from dry tropical trees (Wolfe et al. 2016), but it is rarely used in drought studies. Deciduous species lose their leaves during drought periods to reduce transpiration and maintain water balance (Wolfe et al. 2016). When the water is available again, these species show high stomatal conductance and photosynthesis, both important mechanisms to grow and increase canopy cover (Lambers et al. 2008). The duration of the deciduousness strongly affect carbon sequestration by tropical deciduous and it has the potential to indicate the magnitude of the drought (Singh and Kushwaha 2016). Deciduousness can explain why the recovery is faster in ridges and in dry forests. However, most of the studies investigating drought response mechanism focused on leaf economic traits, and not on hydraulic traits. Repeated droughts can act as filter selecting tolerant species (Aguirre-Gutiérrez et al. 2020) and increasing the abundance of drought-tolerant deciduous species (Fauset et al. 2012). Focusing on traits related to water use and balance is a way to fill most of the remaining mechanistic gaps regarding drought effects (Martinez-Vilalta et al. 2019).

## Conclusion

This literature review summarizes the role of abiotic and biotic factors mediating drought resilience in tropical forests. Our synthesis highlights that the regional climate conditions shape the forest types, and the topography controls biotic and abiotic factors at a local scale in different forest types. Both dry tropical forests and ridges are more sensitive to droughts than moist tropical forest and valleys but the mechanisms explaining these patterns remain unknown. Field studies are essential to identify local and regional differences in drought resilience and to predict the future of tropical forests. This literature review also highlights the main gaps in drought resilience research, which are: 1) to identify mechanisms explaining both the growth-mortality and resistance-recovery trade-offs; 2) to understand how different functional groups (dominant vs. subordinate species, shade-species vs. sun-species, trees vs. shrubs) deal with droughts; 3) to describe the physiological mechanisms explaining the forest resilience of different habitats (valley *versus* ridge), forest types (moist *versus* dry forests) and successional stages (secondary *versus* primary forests); 4) to understand how droughts change the microclimate in different habitats.

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## Declaration of competing interest

The authors declare that they have no conflict of interest.

## Author Contributions

RKH performed the literature review and wrote a draft of the manuscript. Then, all authors revised and contributed critically to the manuscript before giving final approval for publication.

## Data Accessibility Statement

There are no data available for this literature review.

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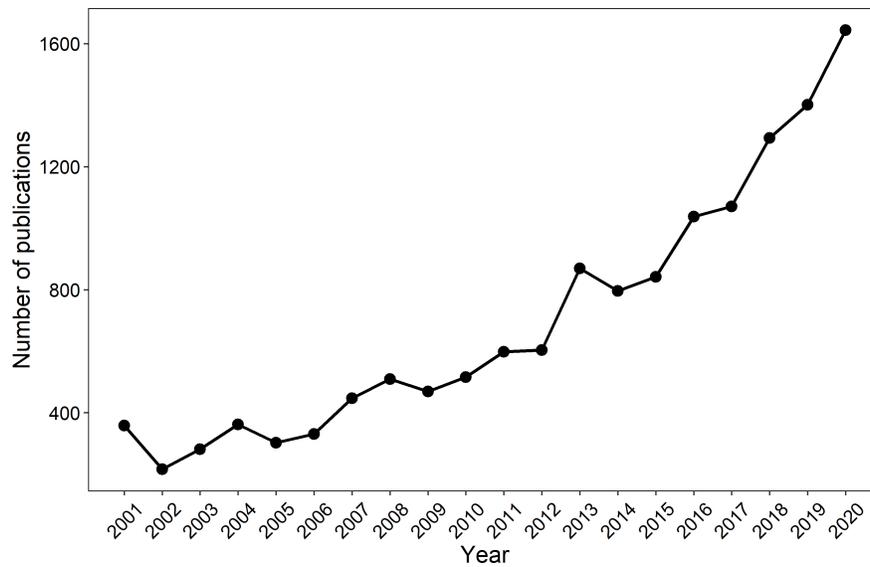
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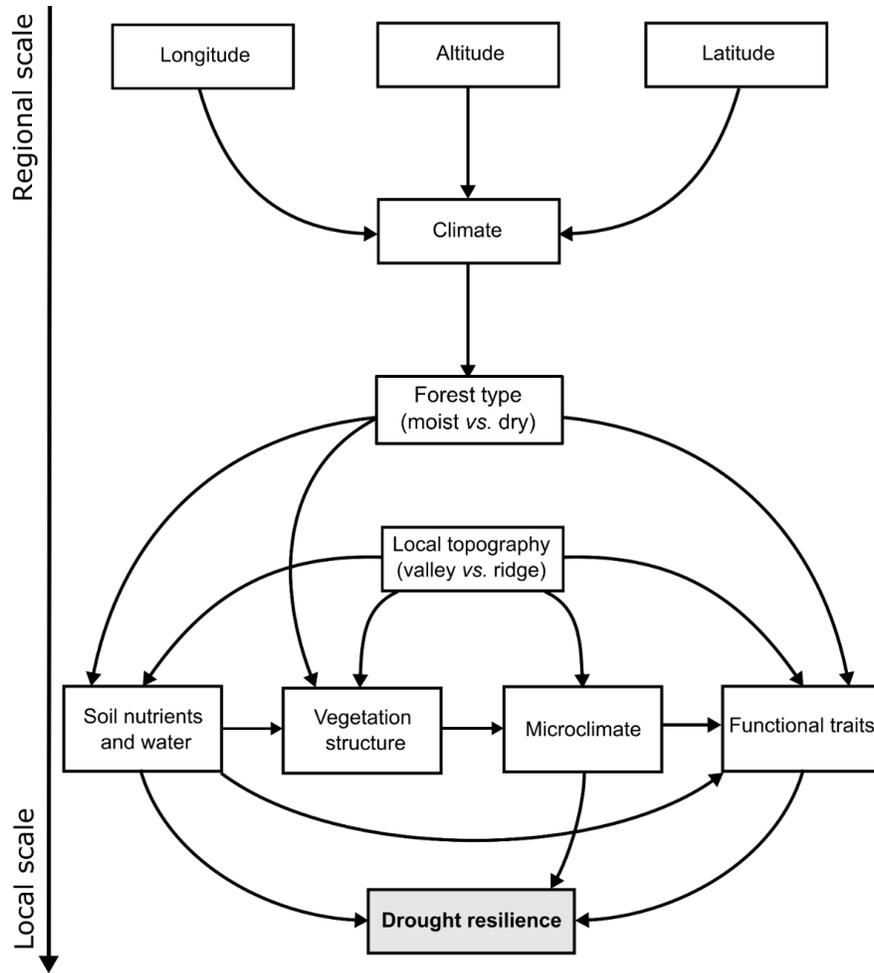
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**Table 1** . Studies that identified differences in drought resistance between valley and ridge of woody plants in tropical forests. Most of the studies have found that woody plants occurring in valleys are more resistant than those from the ridges.

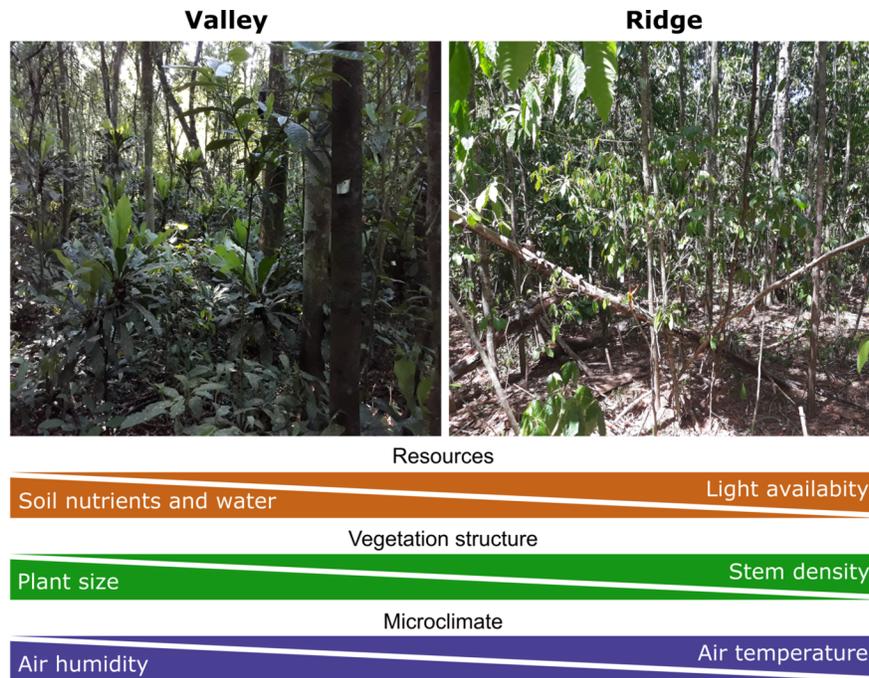
	Local topography	Local topography	Local topography		
References	References	Valley	Ridge	Ridge	Location
Costa et al., 2020	Costa et al., 2020	More resistant	Less resistant	Less resistant	Brazilian
Hollunder et al., 2021	Hollunder et al., 2021	More resistant	Less resistant	Less resistant	Atlantic
Nakagawa et al., 2000	Nakagawa et al., 2000	More resistant	Less resistant	Less resistant	Malaysia
Nishimua et al. 2007	Nishimua et al. 2007	More resistant	Less resistant	Less resistant	Borneo,
Potts, 2003	Potts, 2003	More Resistant	Less resistant	Less resistant	East Ma
Schwartz et al., 2019	Schwartz et al., 2019	More resistant	Less resistant	Less resistant	Puerto R
Schwartz et al. 2020	Schwartz et al. 2020	More resistant	Less resistant	Less resistant	Puerto R
Silva et al., 2013	Silva et al., 2013	More resistant	Less resistant	Less resistant	Costa R.
Engelbrecht et al., 2007	Engelbrecht et al., 2007	Less resistant	More resistant	More resistant	Isthmus
Itoh et al., 2012	Itoh et al., 2012	Less resistant	More resistant	More resistant	Malaysia
Oliveira et al., 2019	Oliveira et al., 2019	Less resistant	More resistant	More resistant	Brazilian
Zuleta et al., 2017	Zuleta et al., 2017	Less resistant	More resistant	More resistant	Colombi



**Figure 1.** Number of publications related to drought effects in tropical forests during the last 20 years (search results in sciencedirect.com for keywords ‘drought’ and ‘tropical forest’).



**Figure 2.** Conceptual model of biotic and abiotic factors mediating drought resilience in tropical forests. Topography is an important factor controlling abiotic and biotic factors related to drought resilience. Altitude, latitude and longitude lead to high climate variation and to different forest types: moist and dry forests. Locally, topography is a key factor controlling biotic and abiotic factors related to drought resilience within each type of forest.



**Figure 3.** Schematic overview of the biotic (vegetation structure) and abiotic (resources and microclimate under the canopy) factors controlled by local topography in tropical forests. Valleys have higher soil nutrients and water availability, air humidity and bigger trees in terms of DBH, height and canopy cover. In turn, ridges have higher light availability, stem density, and air temperature. The photos were taken in Mata das Flores State Park, Southeast Brazil.