The resilience of Amazon tree cover to past and present drying

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The Amazon forest is increasingly vulnerable to dieback and encroachment of grasslands and agricultural fields. Threats to these forested ecosystems include drying, deforestation, and fire, but feedbacks among these make it difficult to determine their relative importance. Here, we reconstruct the central and western Amazon tree cover response to aridity and fire in the mid-Holocene—a time of less intensive human land use and markedly drier conditions than today—to assess the resilience of tree cover to drying and the strength of vegetation-climate feedbacks. We use pollen, charcoal, and speleothem oxygen isotope proxy data to show that Amazon tree cover in the mid-Holocene was resilient to drying in excess of the driest bias-corrected future precipitation projections. Experiments with a dynamic global vegetation model (LPJ-GUESS) suggest tree cover resilience may be owed to weak feedbacks that act to amplify tree cover loss with drying. We also compare these results to observational data and find that, under limited human interference, modern tree cover is likely similarly resilient to mid-Holocene levels of aridification. Our results suggest human-driven fire and deforestation likely pose a greater threat to the future of Amazon ecosystems than drying alone.

1. Introduction

Ecological resilience is a measure of how much disturbance, or forcing, a system can absorb without changing its state (Holling, 1973; Gunderson, 2000; Kombiadou et al., 2019). The state of the system can be defined in a number of ways, but usually refers to its feedbacks and/or function (Holling, 1973; Gunderson, 2000; Scheffer and Carpenter, 2003). Thus, ecological resilience (hereafter, resilience) is a useful concept for identifying the range of external conditions under which a system's behavior may vary, but its state does not fundamentally change.

As Amazon vegetation faces increasing ecological stress from climate change (Li et al., 2006; Cook and Vizy, 2008; Nobre and Borma, 2009; Le Page et al., 2017; Amigo, 2020) and human development (Neppstad et al., 2008; Nobre and Borma, 2009; Davidson et al., 2012; Le Page et al., 2017; Lovejoy and Nobre, 2018; Lovejoy and Nobre, 2019; Amigo, 2020), the resilience of Amazon vegetation to external forcing becomes a central question surrounding the future of Amazon ecosystems. Amazon resilience can be understood from a wide range of perspectives depending on how the state of the system and its external forcings are defined. For example, some studies explore the resilience of biomass to future climate change, using biomass as the metric defining the state of the system and climate change to define the forcing (Levine et al., 2016; Sakschewski et al., 2016). Other studies isolate the effect of water availability by examining the resilience of tree cover (the state of the system) to precipitation or drying (the forcing) (van Nes and Scheffer, 2005; Malhi et al., 2009; Hirota et al., 2011; Ahlström et al., 2017; Ciemer et al., 2019).

Building on this extensive modern work, this study aims to characterize the resilience of central and western Amazon tree cover to drier, mid-Holocene (~6 ka) conditions (Baker et al., 2001a; Baker et al., 2001b; Fritz et al., 2007; Nace et al., 2014; Mulitza et al., 2017; Smith and Mayle, 2018; Campos et al., 2019; Nascimento et al., 2019), and compare mid-Holocene tree cover resilience to the present. We stress...
that this approach cannot account for other dimensions of rainforest resilience, like species composition or diversity. Instead, we focus specifically on the resilience of tree cover to drying for three reasons. First, tree cover and precipitation can be reasonably inferred from paleo proxy data (Mayle and Power, 2008; Cruz et al., 2009; Cheng et al., 2013; Wang et al., 2017; Smith and Mayle, 2018; Nascimento et al., 2019). Second, tree cover is a useful metric for comparing two alternative, well-defined states of Amazon vegetation—a high-tree cover forest and a low-tree cover savanna/grassland (Hirota et al., 2011; Staver et al., 2011). Third, some modern data indicate that annual precipitation rates are near a “tipping-point” of 2000 mm/yr, below which vegetation water-stress is enhanced along with feedbacks that may favor a forest-to-grassland transition (Lenton et al., 2008; Guan et al., 2015; Zemp et al., 2017). If precipitation is near this tipping-point today, it is possible that the tipping point was crossed during drier times in the past.

The 2000 mm/yr tipping point is ecologically meaningful because, across the tropics, it approximates a transition between a dry-season water surplus (>2,000 mm/yr) and a dry-season water deficit (<2,000 mm/yr) (Guan et al., 2015). Below this threshold forests take more time to recover from a drought (Verbesselt et al., 2016), dry-season photosynthesis declines, favoring deciduous and semi-deciduous vegetation (Enquist and Enquist, 2011; Guan et al., 2015), and the wet season may grow shorter with a delayed onset, amplifying drying (Kleidon and Heimann, 2000; Li and Fu, 2004; Wright et al., 2017; Leite-Filho et al., 2019a; Leite-Filho et al., 2019b). Further, both natural and human fires may increase under a dry-season water deficit. Fire correlates positively with the dry-season water deficit and negatively with relative humidity in Amazonia (Ray et al., 2005; Aragão et al., 2008) and seasonal aridity makes human-driven fire and deforestation easier in the dry season (Aragão et al., 2008; Barlow et al., 2020; Staal et al., 2020). A seasonal water deficit and fire is often thought to favor grasslands in competition against forests because grasses generally recover faster from droughts and fires and they tend to be more flammable, inhibiting some tree growth (Bond et al., 2005; Mouillot and Field, 2005; Aragão et al., 2008; Bond, 2008; Cochrane and Ryan, 2009; Verbesselt et al., 2016). But could future aridity alone drive widespread forest dieback and grassland expansion in Amazonia?

Some models suggest that future climate change can devastate large swathes of Amazon tree cover (Cox et al., 2000; Betts et al., 2004; Cox et al., 2004; Cook and Vizy, 2008), but recent work has brought models and observations into agreement that Amazon tree cover may remain high despite future drying (Malahi et al., 2009; Davidson et al., 2012; Ahlstrom et al., 2017; Zemp et al., 2017). Still, models and observations have their own limitations when unraveling the relationship between precipitation and tree cover. Models can simulate the effect of aridity in the absence of human deforestation (Le Page et al., 2017) but the tree cover response to drying is highly sensitive to parameterizations (Cox et al., 2004; Staal et al., 2015; Lasslop et al., 2016; Zemp et al., 2017). Observational datasets can be filtered to remove deforested sites (Ahlstrom et al., 2017; Ciemer et al., 2019), but this can introduce biases associated with the spatial pattern of deforestation and does not account for non-local consequences of deforestation (Zemp et al., 2014; Zemp et al., 2017; Staal et al., 2018). To circumvent these challenges, paleo-archives from times when human land use was less intensive are useful for exploring the relationship between precipitation and tree cover while limiting confounding factors.

Here, we test the hypothesis that Amazon tree cover is resilient to drying—specifically near the 2000 mm/yr threshold—using the mid-Holocene as a case study. Existing data suggest that the central and western Amazon Rainforest remained largely intact with high tree cover in the mid-Holocene (Haberle and Maslin, 1999; Mayle and Power, 2008; Smith and Mayle, 2018; Nascimento et al., 2019). However, the vast majority of precipitation proxy records have been interpreted qualitatively, so it is unclear whether high tree cover in the mid-Holocene is owed to high resilience to drying, or whether mid-Holocene proxies record only modest decreases in precipitation. We present a quantitative estimate for mid-Holocene precipitation based on speleothem oxygen isotope gradients and we compile pollen and charcoal proxy data to assess the relationship between precipitation, fire, and tree cover. We then test whether this relationship is supported in a dynamic global vegetation model (LPJ-GUESS v4.0 Smith et al., 2014) and we compare our results to modern precipitation and tree cover data. In doing so, we address two questions: 1) How resilient was mid-Holocene tree cover to drying? And 2) Is Amazon tree cover similarly resilient today?

2. A conceptual model for the tree cover response to external forcing and internal feedbacks

2.1. Conceptual model framework

Following previous work, we consider the state of the system in three groups based on the percent of area covered by trees: 1) a high tree cover state (>70%) to represent forests, 2) a low tree cover state (5–20%) to represent savannas or grasslands and 3) a transitional state at intermediate values (Hirota et al., 2011; Staver et al., 2011; Ciemer et al., 2019). We assess how the state of the system (forest, grass/savanna, or transitional) changes as a function of three forcings (precipitation, deforestation, and anthropogenic fire) and two positive feedbacks that arise from their interactions within the system. The moisture recycling feedback (MRF) connects precipitation, tree cover, and evapotranspiration and illustrates how drying can decrease tree cover which, in turn, decreases evapotranspiration leading to further drying (Zemp et al., 2014; Zemp et al., 2017; Staal et al., 2018). The second feedback includes the MRF loop and adds the effect of fire (MRF + Fire). In this case, a drop in precipitation increases natural fire which decreases tree cover and evapotranspiration, exacerbating the precipitation decline. The system is illustrated in Fig. 1.

2.2. Tree cover response scenarios

The response of tree cover to precipitation depends on the relative contributions of forcings and feedbacks. Deforestation and anthropogenic fire, independent of any feedbacks, decrease tree cover without modifying precipitation (Fig. 2A, pink arrow). Changes in precipitation, independent of feedbacks, change tree cover when water limits primary productivity, following the “maximum potential tree cover” curve in Fig. 2A.

Feedbacks in the system are considered stronger when changes in tree cover are larger for a given change in precipitation (proportional to the area of wedges in Fig. 2A). Thus, the feedback strength can change if the functional form of the precipitation-tree cover relationship changes (moving from one solid line to another in Fig. 2A) or if the initial precipitation rate changes (moving along a solid line in Fig. 2A).

The MRF increases the distance the system moves along a given precipitation-tree cover curve for a given forcing. In this case, precipitation is still the only mechanism limiting tree cover in this feedback loop, so the sensitivity of tree cover to precipitation (the slope of the curve) remains a single function of precipitation. By contrast, increasing the sensitivity of fire to precipitation presents a new limit on tree cover and can push the state of the system to a new curve in precipitation-tree cover space (Fig. 2A, orange arrow). In our conceptual model the MRF + Fire loop is the only mechanism for abruptly “tipping” the state of the system (tree cover) without a proportional change in the forcing (i.e. by moving from one curve to another). The MRF without fire can lead to an abrupt change in tree cover but the forcing—precipitation—will change proportionally so it does not constitute tipping behavior.

The implication of our conceptual framework is that multiple stable states—the condition where more than one ecological regime is stable for a given precipitation rate—can only be driven by fire. This is supported by fire exclusion experiments around the world where closed
forests replace grasslands without a large change in precipitation (Trapnell, 1959; Louppe et al., 1995; Peterson and Reich, 2001; Bond et al., 2003a; Woinarski et al., 2004; Higgins et al., 2007) and by recent modeling work showing multiple stable states are absent from a dynamic global vegetation model unless fire-vegetation feedbacks are included (Lasslop et al., 2016).

Fig. 2B shows how tree cover could change with time (from points 1 to 3) under different feedback scenarios. Beginning at point 1 with high precipitation and high tree cover, drying pushes the state of the system along a defined precipitation-tree cover trajectory from points 1 to 2. If the positive fire feedback is weak, tree cover will remain near the “maximum potential tree cover” line, ending at point 2a. If it is strong, the system moves along a steeper curve to point 2b. In contrast, the MRF increases the magnitude of change along a precipitation-tree cover curve. Thus, with a strong MRF the system will move from points 1 to 3a (3b) with the same forcing otherwise required to move to 2a (2b). If the positive fire feedback strengthens at some precipitation threshold the system can abruptly “tip” from point 2a to 2b. The transition from a forest to grassland thus requires strong, positive feedbacks and/or substantial drying.

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Using this conceptual model with proxy data for fire, vegetation, and precipitation we can infer the strength of the different forcings and feedbacks by reconstructing the history of tree cover and precipitation. To illustrate this, consider a decrease in precipitation from point 1 to points 2a and 2b (Fig. 2B). In order to maintain a forest despite drying, positive feedbacks and anthropogenic forcing must be weak. But a transition to a grassland state indicates that anthropogenic forcing is strong, positive feedbacks are strong, and/or positive feedbacks strengthened within the range of drying causing the system to “tip”. Proxy records can then be used to determine which of these options is most likely by indicating, for example, how sensitive fire is to drying.

3. The Amazon Basin in the mid-Holocene

3.1. Mid-Holocene proxy records

The mid-Holocene (~6 ka) is an ideal period to evaluate the Amazon tree cover response to aridification because it is associated with widespread proxy data indicating one of the driest times of the late Quaternary (de Freitas et al., 2001; Friz et al., 2004; Fritz et al., 2007; Reis et al., 2017; Smith and Mayle, 2018). While the onset of drier conditions varies from the early to mid-Holocene depending on the location, drier conditions generally lasted through, and often peaked at, 6 ka (Abbott, 2000; Baker et al., 2001b; Abbott et al., 2003; Reis et al., 2017; Nascimento et al., 2019; Zular et al., 2019). Drying is especially pronounced in the central, western, and southwestern Amazon and drier conditions are also observed on a continental scale in offshore records of terrestrial runoff (Arz et al., 1998; Behling et al., 2002; Nace et al., 2014; Mulitza et al., 2017; Campos et al., 2019) (Fig. 3A). This coincides with the desiccation of lakes and fluvial systems in the western Andean plateau (Baker et al., 2001a; Baker et al., 2001b; Tapia et al., 2003; Fritz et al., 2007; Morales et al., 2018) and local-to-regional increases in savanna coverage and fire (Mayle and Power, 2008; Smith and Mayle, 2018) (Fig. 3A), particularly in the southwestern Amazon. While patches of savanna expanded within the forested regions of southwestern Amazon at this time (de Freitas et al., 2001; Pessenda et al., 2001), the central and western Amazon domain, or core rainforest region (Fig. 3B, inset), likely remained intact (Haberle and Maslin, 1999; Mayle and Power, 2008; Smith and Mayle, 2018; Nascimento et al., 2019).

In addition to climate, humans may have also played a role in modifying Amazon vegetation in the mid-Holocene. Human settlements were extensive in the mid-Holocene, spanning much of southwestern Amazonia with evidence for cultivation and food production (Dillehay et al., 2007; Carson et al., 2014; Bush et al., 2016; Watling et al., 2017; Watling et al., 2018). Some evidence suggests human populations declined in the mid-Holocene (Riris and Arroyo-Kalin, 2019), but this signal may be related to geomorphic or sampling biases (Iriarte et al., 2020). Despite the broad spatial coverage of human settlement in the mid-Holocene, land use and human-driven vegetation change was more localized and less intensive than today. Many human settlements took advantage of naturally open vegetation rather than creating space through widespread clear-cutting (Carson et al., 2014; Iriarte et al., 2020). Further, at least in the late Holocene the climate-driven expansion of rainforest around human settlements provides evidence for sustainable land management practices that did not interfere with regionscale climate-vegetation relationships (Carson et al., 2014; Maezumi et al., 2018). Thus, while human occupation was extensively distributed across some parts of the basin during the mid-Holocene, climate most likely remained the primary control on regional tree cover with human land use occurring on a smaller scale than today.

Our compiled proxy data includes charcoal and pollen records, along with speleothem oxygen isotope data from sites spanning the central and western Amazon (Fig. 3B). We also compare to a variety of proxy types used to reconstruct mid-Holocene vegetation in Smith and Mayle (2018). We align our proxy data with the isotope gradient in order to directly compare precipitation, tree cover, and fire, but most available pollen and charcoal records are in the western Amazon and we lack uniform coverage across the central basin. Here, the assorted proxy

Fig. 3. (A) Proxy compilation for the mid-Holocene (defined here as 5–7 ka). See Supplementary data for full reference list. Blue points represent a proxy indicating wet or wetter conditions and red points are drier. Diamonds are local/regional proxies and open squares are marine core records of continental runoff. (B) Map of the pollen (magenta triangles), charcoal (yellow squares) and speleothem δ¹⁸O (purple diamonds) records used in this study. Teal circles show proxy records of assorted type from Smith and Mayle (2018) that fall within our domain. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
records of Smith and Mayle (Smith and Mayle, 2018) help compensate for a paucity of pollen and charcoal data. Some records to the north approach regions where previous studies have interpreted wet mid-Holocene conditions (3A), and this may also bias our results. However, we repeat our analysis with southwestern Amazon pollen and charcoal records, where proxy data reveal more uniform drying, and find that this sampling bias does not affect our conclusions (Supplemental Fig. S1).

3.2. Mid-Holocene climate

Amazon precipitation in the late Quaternary is thought to follow a zonal dipole pattern, with anomalous precipitation shifts between the eastern and western/southwestern basin on precessional and glacial-interglacial timescales (Martin et al., 1997; Abouchami and Zabel, 2003; Cruz et al., 2009; Cheng et al., 2013; Baker and Fritz, 2015; Mason et al., 2019). During the mid-Holocene, data suggest the dipole was likely in its “eastern phase” with positive anomalous precipitation over eastern Amazonia and NE Brazil (Martin et al., 1997; Cruz et al., 2009). The mechanism for precipitation dipole transitions remains debated, but it is usually linked to the strength of the South American Monsoon with the eastern phase occurring during a weaker monsoon (Cruz et al., 2009; Cheng et al., 2013; Liu and Battisti, 2015; Shimizu et al., 2020).

In addition to dynamic changes in the spatial pattern of moisture convergence, Amazon precipitation is also sensitive to how moisture is recycled across the basin. Today and in the mid-Holocene the central and western Amazon sits inland from the primary moisture source—the easterly trade winds that cross the Atlantic Ocean (Zhou and Lau, 1998; Silva and Kousky, 2012)—so precipitation is strongly dependent on upstream moisture recycling. About one-third to half of all precipitation in this region is derived from evapotranspiration within the basin today (Eltahir and Bras, 1994; Zemp et al., 2014; Staal et al., 2018; Yang and Dominguez, 2019), making it particularly sensitive to feedbacks like the MRF that can promote forest-grassland transitions (Zeng et al., 1996; Kleidon and Heimann, 2000; Zemp et al., 2014; Zemp et al., 2017; Levy et al., 2018; Staal et al., 2018; Staal et al., 2020). If feedbacks like the MRF can promote forest-grassland transitions, the western Amazon is an ideal place to detect this signal.

4. Methods

4.1. Oxygen isotope gradient and precipitation reconstruction

4.1.1. Isotope gradient reconstruction and the importance of the “hydrostat”

Oxygen isotopes in calcite cave deposits, or speleothems, can reflect the isotopic compositions of past rainfall and provide useful information for reconstructing monsoon dynamics (Cruz et al., 2007; van Breukelen et al., 2008; Cruz et al., 2009; Strikis et al., 2011; Cheng et al., 2013; Novello et al., 2017; Wang et al., 2017). We use the change in Amazon speleothem $\delta^{18}O$ over space—the isotope gradient ($\Delta \delta^{18}O$; ‰/1000 km)—with a reactive transport model (Hendricks et al., 2000; Chamberlain et al., 2014; Winnick et al., 2014; Kukla et al., 2019) to solve for precipitation rates. This is done by reconstructing past isotope gradients along the South American Monsoon moisture trajectory with $\delta^{18}O$ records from three sites—one in east-central Amazon (Wang et al., 2017) and two that form a composite record in the western Amazon (van Breukelen et al., 2008; Cheng et al., 2013) (Fig. 4). We also adopt the $\delta^{18}O$ correction that accounts for differential cave temperatures at the sites previously used in references (Wang et al., 2017; Ampuero et al., 2020).

The isotope gradient is useful because it reflects changes in the regional water balance while limiting the influence of confounding factors. The balance of precipitation (P) and evapotranspiration (ET) across a moisture trajectory sets the isotope gradient because P tends to decrease $\delta^{18}O$ by removing moisture from an air mass while ET increases $\delta^{18}O$ by replenishing the air mass (Salati et al., 1979). Thus, $\Delta \delta^{18}O$ decreases as P increases relative to ET. Additional effects unrelated to the water balance, like upstream effects and temperature, can influence $\delta^{18}O$ at a single site, but isotope gradients are insensitive to these factors because they do not modify the rainout-recycling balance (Hu et al., 2008; Winnick et al., 2014; Kukla et al., 2019). As a result, the isotope gradient across Amazonia has long been used as a metric for the balance of P and ET (Salati et al., 1979).

Importantly, the oxygen isotope gradient (along with $\delta^{18}O$ at a given point) is not always sensitive to precipitation rates (Chamberlain et al., 2014; Caves et al., 2015; Kukla et al., 2019). As P decreases, the isotope gradient shallows until it asymptotes at the theoretical maximum value of zero (meaning there is no change in $\delta^{18}O$ between the upstream and downstream sites). The point where the isotope gradient reaches zero is...
called the “hydrostat”—the condition where further aridification will have no affect on $\Delta^18O$ values (Chamberlain et al., 2014; Caves et al., 2015; Kukla et al., 2019). The hydrostat is reached because the net distillation of moisture is near zero as climatological rates of P and ET are nearly equal. This can occur when P rates are similar to or below potential evapotranspiration (ET) rates. Since ET is an upper limit on ET, P must exceed ET when P > ET, leading to a decrease in $\delta^18O$ and a negative P-$\delta^18O$ relationship known as the “amount effect” (Dansgaard, 1964; Lee et al., 2007; Lee et al., 2009; Moore et al., 2014; Bailey et al., 2018; Kukla et al., 2019). Therefore, when $\Delta^18O$ is near zero it is possible to constrain the upper bound of precipitation rates—the point where P exceeds potential ET—but not the lower bound.

4.1.2. Reconstructing past mean annual rainfall

We use the reactive transport model (RTM) (Kukla et al., 2019), which simulates atmospheric vapor transport (w), rainout (P), and evapotranspiration (ET), to inversely solve for mid-Holocene rainfall rates from speleothem $\Delta^18O$ data. We initialize the model with distributions of the source moisture content (similar to specific humidity), potential evapotranspiration, surface temperature, the wind speed profile, evapotranspiration partitioning, a moisture recycling efficiency parameter, and a vapor condensation rate constant. Sampling from these input distributions >50,000 times, the model solves for the spatial pattern of precipitation and evapotranspiration as well as the oxygen isotope ratios of these fluxes (Kukla et al., 2019). See Supplemental Text S1 for further information on model initialization.

Using the results of our Monte Carlo routine we calculate the mean rainfall consistent with the observed $\Delta^18O$ to produce a mean annual rainfall distribution. During the mid-Holocene, $\Delta^18O$ values fall along the hydrostat and the RTM loses sensitivity to the lower bound of rainfall (while the upper bound is still constrained). In order to extract a rainfall distribution in this case we impose a lower bound, thus assuming that any rainfall value below the imposed threshold is unreasonable. To develop a conservative estimate of mid-Holocene aridification we exclude any iteration where mean annual rainfall drops below half the potential evapotranspiration rate, a point at which modern tree cover is mostly below 50% (e.g. Guan et al., 2015; Ahlström et al., 2017). We test the sensitivity of our results to this assumption with a range of thresholds (Supplemental Fig. S2) and find that this decision influences the mean rainfall value but does not affect our conclusions.

Our analysis implicitly assumes that moisture is transported directly from the eastern (upstream) speleothem site to the western sites. While this trajectory aligns well with the direction of the easterly trade winds (especially during the wet season) it is reasonable to expect that the effective moisture transport distance between these sites may have differed in the mid-Holocene due to changes in atmospheric circulation patterns. However, because $\Delta^18O$ is near zero at the mid-Holocene the isotope gradient (and, thus, our results) are not sensitive to changes in assumptions about the effective moisture transport distance (Supplemental Fig. S3).

4.2. Pollen compilation

Twenty-three terrestrial pollen records were extracted from the Neotoma Paleoecology Database (Williams et al., 2018) and the ACER pollen and charcoal database (Goni et al., 2017) in March 2020 across our study area (with data spanning 55° - 80° W and 8° S - 0° N; see Fig. 2B). Pollen percentages for all records were calculated based on the sum of terrestrial pollen taxa only (the pollen taxa classified as ‘Tree/ Shrub’, ‘Succulent’, ‘Upland herbs’ and ‘Palms’ in Neotoma). Pollen samples were subsequently grouped into 200-year bins, which corresponds with the average resolution of the selected records (197 years between consecutive samples, on average), to extract a regional signal. The average bin size is 22.4 pollen samples with a range of 2–86 samples. For each bin, we calculate the ratio of arboreal (Tree and Shrubs, Palms) to non-arboreal (Herbs and Succulents) pollen taxa. While the classification of pollen taxa into unique vegetation forms contains some inaccuracies (i.e. all the species producing a pollen morphotype may not all belong to the same vegetation form), the associated uncertainties are expected to only have a negligible impact and/or compensate each other in our broad-scale, multi-site reconstruction.

4.3. Charcoal compilation

Charcoal records are compiled from the Global Charcoal Database (GCD version 2.0) and other published datasets. Charcoal data were analyzed using the paleofire R package software (version 1.1.8) (Blarquez et al., 2014). Eleven charcoal records spanning 53° - 80° W and 8° S - 0° N are included in this analysis to create a regional charcoal curve (Supplemental Data, Fig. 4C). These sites provide an average of regional biomass burning during the Holocene. To facilitate inter-site comparison, the eleven records are pre-treated using a standard protocol (Marlon et al., 2008; Power et al., 2008) for transforming and standardizing individual records that includes: (1) transforming non-infux data (e.g. concentration particles cm$^{-3}$) to influx values (particle cm$^{-2}$/yr), (2) homogenizing the variance using the Box-Cox transformation, (3) rescaling the values using a minimax transformation to allow comparisons among sites, and (4) rescaling the values to z-scores using a base period of 200 years. Sites are smoothed with a 500-year half width smoothing window and a bootstrap of 200 years (Blarquez et al., 2014).

4.4. Dynamic global vegetation modeling

To evaluate the mid-Holocene precipitation-tree cover relationship inferred from proxies while accounting for changes in other climate variables we conducted simulations with the second generation dynamic global vegetation model (DGVM) LPJ-GUESS (Smith and Prentice, 2001; Smith et al., 2014). The simulated vegetation states emerge as an outcome of simulated vegetation structure, demography, resource competition for light, water and nutrients, and wild fires. Vegetation is represented as a mixture of plant functional types (PFTs) (11 in this study) (Ahlström et al., 2012), distinguished by photosynthetic pathway (C3 or C4), life history strategy (shade tolerance), phenology (evergreen, summergreen or raingreen), growth form (trees or herbaceous plants) and bioclimatic distributional limits.

LPJ-GUESS incorporates a fire model to link the fire regime and its effects on vegetation dynamics and biogeochemical cycling (Thonicke et al., 2001). Fires are modeled prognostically based on temperature, current fuel load, and moisture. Daily litter moisture is used to estimate the fire season length which, in turn, determines the fraction of a grid cell that is burnt in a year. The relationships between litter moisture, fire season length, and burnt area are calibrated with modern data (Thonicke et al., 2001). Fire return intervals are simulated by the model based on the yearly burnt area fraction. When driven by 20th century climate data, the simulated fire return intervals are in good agreement with observations in the Amazon and globally (Thonicke et al., 2001). Since observational data for model calibration are assumed to be the most representative for natural conditions, human-changed fire regimes and other land use impacts are not explicitly considered, but could still have an effect on the final model processes (Thonicke et al., 2001).

Climate forcing (temperature, precipitation and radiation) of the offline LPJ-GUESS simulations comes from output of the coupled global climate model, EC-Earth (Hazeleger et al., 2010). The mid-Holocene orbital parameters and greenhouse gas concentration were prescribed for the standard mid-Holocene EC-Earth simulation (MH), while boundary conditions such as a vegetated Sahara and reduced dust aerosol (MHSrd) were further added to a sensitivity simulation to reproduce a climate regime more consistent with proxy reconstructions (Pausata et al., 2016). The vegetation response in North Africa in these simulations was investigated in detail in a previous study (Lu et al., 2018). In total, we performed six simulations. Three simulations—one pre-industrial (PI) and two mid-Holocene (MH, MHSrd)—were forced...
with unperturbed climate forcing from EC-Earth and three simulations included further precipitation reductions. Amazon annual precipitation in the unperturbed simulations is 2175, 2002, and 1776 mm/year for Pl, MH, and MHgsrd. The precipitation reduction experiments use MHgsrd boundary conditions with annual precipitation reduced to 1520, 1420 and 1260 mm/year. We compare our precipitation reduction experiments to MHgsrd in Fig. 6, but all results can be found in Supplemental Fig. S4 and S5.

Precipitation reductions were applied with a multiplier to scale average precipitation in the proxy region of Fig. 3B to the desired level. All grid cells (inside or outside the proxy domain) were multiplied by the same factor. Therefore, we restrict our analysis to the vegetation patterns within the proxy domain to avoid regions where precipitation scaling is unrealistic and outside the domain of \( \Delta^{18}O \) constraints. We also exclude the Andes to avoid a confounding, Andean taxa signal. To understand the role of fire disturbance, the 1520 and 1260 mm/year simulations were repeated with the fire module disabled (purple squares in Fig. 7). All LPJ-GUESS simulations were spun-up from bareground and run for 500-years to reach an equilibrium state. We use the last 10 years of output for analysis. Further information about our LPJ-GUESS simulations can be found in the Supplementary Text (S2).

4.5. Modern tree cover and precipitation data

We compile modern data for tree cover, precipitation, and human land use in order to compare past and DGVM-simulated estimates of tree cover and precipitation to modern conditions. Tree cover, precipitation, and land use data were compiled in Ahlström et al. (2017). Tree cover was collected from Landsat remote sensing data at 30 m spatial resolution (Hansen et al., 2013) with trees defined as being greater than 5 m tall. Mean annual precipitation rates were calculated from the Global Precipitation Climatology Centre (GPCCv7) (Schneider et al., 2016) using the correction of Fuchs et al. (2001) for the years 1993–2012. Land use data are derived from Hurtt et al. (2011).

5. Results

5.1. Oxygen isotope gradient reconstruction

The kernel smoothed oxygen isotope gradient values range from –1.3 to 0.1‰/1000 km through the Holocene. The record plateaus and hovers around the hydrostat, the theoretical maximum isotope gradient (Chamberlain et al., 2014; Kukla et al., 2019), from –11 to 5 ka, before decreasing toward its lowest values in the present (Fig. 4A). The oxygen isotope gradient in modern precipitation across the Amazon is \(-1\%o/1000 \text{ km}\) (Salati et al., 1979; Kukla et al., 2019), similar to the gradient from the most recent speleothem \( \delta^{18}O \) data.

While \( \Delta^{18}O \) values are stable near zero for much of the early-to-middle Holocene, independent proxy evidence from western Amazonia indicates precipitation was decreasing during this time (Baker et al., 2001a; Baker et al., 2001b; Tapia et al., 2003; Fritz et al., 2004; de Toledo and Bush, 2008; Fornace et al., 2014; Morales et al., 2018). Thus, the \( \Delta^{18}O \) record may not fully reflect the trends in precipitation through the Holocene due to \( \Delta^{18}O \) being insensitive to precipitation at the hydrostat.

5.2. Vegetation in the mid-Holocene

In western Amazonia the arboreal to non-arboreal pollen ratio ranges from 0.8 to 5.9 throughout the Holocene. Kernel smoothing of the data shows gradual increase in this ratio from –5 ka to present, mirroring a shift to lower \( \Delta^{18}O \) values. There is a weak, negative correlation between the ratio of arboreal to non-arboreal pollen and the oxygen isotope gradient (Supplemental Fig. S6). Some of the lowest arboreal/ non-arboreal pollen ratios occur in the mid-Holocene, suggesting the possibility of some savanna expansion. We note that the arboreal/non-arboreal pollen ratio is not necessarily a reliable indicator of tree cover (Zanon et al., 2018) and therefore we use it only to infer relative trends. Data from Smith and Mayle (2018) show that, from 6 ka to present, between 69 and 76% of sites in our proxy domain record humid evergreen tropical forest conditions, consistent with the rainforest remaining intact (Haberle and Maslin, 1999; Mayle and Power, 2008; Smith and Mayle, 2018) (Fig. 4D).

5.3. Fire in the mid-Holocene

Our composite charcoal record shows a progressive increase of the charcoal index from –1 to 0.6 between 12 ka and 10 ka (Fig. 4C). Fire activity declines to a local minimum with a charcoal index of 0 around 6 ka, followed by a sharp increase to 0.7 around 5 ka. Another local minimum occurs around 3.5 ka, after which charcoal index values remain just above zero until present (Fig. 4C). The charcoal index is not significantly correlated with \( \Delta^{18}O \) nor the arboreal/non-arboreal pollen ratio (Supplemental Fig. S6). Despite the lack of correlation, fire may still be responsive to vegetation if it tracks changes in species composition, which may not vary with the arboreal/non-arboreal pollen ratio. Further, in contrast to our charcoal index curve, tropical glacier proxy records from the southwest, outside of our domain, indicate increased fire activity during the mid-Holocene (Brugger et al., 2019; Osment et al., 2019). However, it is unclear whether this discrepancy with our composite record is owed to greater aridity in the southwest, a difference in vegetation composition, or something else.

5.4. RTM modeling and rainfall reconstruction

Our RTM results for the pre-industrial show modeled rainfall rates that are consistent with distributions from GPCC data (Schneider et al., 2016) (Fig. 5). Inverting the isotope gradient from the most recent speleothem \( \delta^{18}O \) yields a domain-mean rainfall estimate of 2300 \(+/-500 \text{ mm/yr, comparable to modern} \) (2480 \(+/-470 \text{ mm/yr)} (Fig. 5). This builds on previous work indicating that spatial isotope gradients record information about climatological moisture fluxes (Salati et al., 1979; Hu et al., 2008; Chamberlain et al., 2014; Winnick et al., 2014; Kukla et al., 2019).

Our mid-Holocene results indicate substantially drier conditions compared to the pre-industrial. In the mid-Holocene we estimate a rainfall rate of \(~1300 \text{ mm/yr} \) (Fig. 5), about 45% lower than present. This estimate is based on the wettest 25% of RTM iterations above the imposed lower-bound. We find no possible solutions exceeding 2000 mm/yr and the maximum simulated precipitation rate is
~1900 mm/yr. Despite the loss of model leverage at low precipitation rates, the exercise provides a valuable upper-bound on mean annual precipitation.

Our results demonstrate that mid-Holocene precipitation rates are likely substantially lower than most end-of-century precipitation estimates from simulations of unabated carbon emissions (RCP 8.5; Fig. 5). On average, models predict precipitation by the year 2100 will be ~400 mm/yr less than today with over half the models predicting future rainfall below the 2000 mm/yr threshold. However, when accounting for model precipitation bias (usually a dry-bias in Amazonia) the mean change in future precipitation is much smaller—~26 mm/yr—with no models falling below 2000 mm/yr. Since our mid-Holocene precipitation distribution does not exceed ~1900 mm/yr, the lowest bias-corrected future estimate is greater than our highest estimates of mid-

Fig. 6. Dynamic global vegetation model results and comparison with comprehensive proxy compilation of Smith and Mayle (2018). (A) Proxy-derived biomes from the 6–5.5 ka timeslice of Smith and Mayle (2018). Sites with two major biomes are given two, jittered data points. Southwestern proxy region (Smith and Mayle, 2018) is included for comparison with DGVM. (B–F) Results of DGVM simulations when precipitation is set to the simulations of Lu et al. (2018) (pre-Industrial and mid-Holocene in B, C) or scaled to 1520, 1420, or 1260 mm/yr within the proxy domain (black boxes) (D–F). Extensive savanna expansion in northeastern Brazil in panels D–F is likely unrealistic because it is outside the proxy domain and does not account for possible wetter conditions in this region in the mid-Holocene (Martin et al., 1997; Cruz et al., 2009; Prado et al., 2013; Liu and Battisti, 2015).
Holocene precipitation (Supplemental Fig. S7).

5.5. Dynamic global vegetation model response to mid-Holocene rainfall

Tree cover in the core rainforest region (central and western Amazonia) remains intact in our DGVM simulations in a wide range of mean annual precipitation conditions (Fig. 6B-F) (Lu et al., 2018). Turning off fire in our simulations leads to substantial increases in tree cover outside of the proxy domain (Supplemental Fig. S4) but has little effect within the domain (Fig. 7; Supplemental Fig. S8). This suggests that fire is effective at promoting grassland and savanna expansion near the forest fringes (ecotones) in the model, but may not lead to vast tree cover loss in the core forest regions. Most of the savanna and grassland expansion in the southwestern Amazon is inhibited in simulations where fire is turned off, suggesting that drying alone is not sufficient to drive large changes in tree cover within the range of precipitation rates simulated here.

Within the proxy domain tree cover remains at forested levels (>70%) at all precipitation rates whether fire is enabled or not (Fig. 7). Tree cover decreases from ~92% when precipitation is ~2200 mm/yr to ~80% when precipitation drops to ~1300 mm/yr. Disabling fire leads to an increase in tree cover of ~4–5% in the range of precipitation rates we tested. While our precipitation estimates span the range where forests and savanna are thought to reflect alternative stable states (the "bistability range" of 1300–2100 mm/yr; Clmer et al., 2019) we do not observe any marked shift to a savanna vegetation state in our simulations.

6. Discussion

6.1. Strength of mid-Holocene forcings and feedbacks

High tree cover in the mid-Holocene supports the hypothesis that central and western Amazon tree cover is resilient to crossing below the 2000 mm/yr precipitation threshold, at least down to ~1300 mm/yr. Here, we explore why tree cover might be so resilient. We compare the mid-Holocene estimates to the modern precipitation-tree cover relationship to construct an aridification trajectory that defines a tree cover response to drying. Using the proxy records in our conceptual model framework (Section 2), we infer the contributions of forcings and feedbacks from the trajectory. We note that precipitation-tree cover relationships have been theorized to follow a “hysteresis” pattern where the direction of change (wetting or drying) can determine the tree cover response (van Nes and Scheffer, 2005). This does not invalidate our approach of looking back in time to infer a forward aridification trajectory for two reasons. First, forests prevail in the core of Amazonia in the mid-Holocene through today (Haberle and Maslin, 1999; Mayle and Power, 2008; Smith and Mayle, 2018) and hysteresis should only arise when the state of the system changes (i.e. forest to savanna or grassland). Second tree cover and precipitation were both higher prior to the Holocene (Baker et al., 2001a; Baker et al., 2001b; Tapi et al., 2003; Mayle and Power, 2008; Fornace et al., 2014; Nace et al., 2014; Mulitza et al., 2017; Venancio et al., 2018), so the modern conditions can also approximate an initial state for Holocene aridification.

Our precipitation constraints and existing vegetation reconstructions (Haberle and Maslin, 1999; Mayle and Power, 2008; Smith and Mayle, 2018; Nascimento et al., 2019) are supported by our DGVM simulations showing forest tree cover is maintained as precipitation reaches mid-Holocene levels (Fig. 7). This result is consistent with the forest scenario of Fig. 2B. In this scenario, tree cover is near the maximum potential tree cover curve (gray line of Fig. 7) and precipitation is the dominant forcing on the system. High tree cover is maintained in this scenario as human forcing and the feedbacks that amplify tree cover loss (like the MRF and MRF + Fire) are not strong enough to change the state of the system.

Indeed, proxy estimates support, at most, a minor role for human forcing (deforestation) and fire in determining the state of Amazon tree cover in the central and western basin (Mayle and Power, 2008; Maslin et al., 2012; Carson et al., 2014; Watling et al., 2017; Maezumi et al., 2018; Iriarte et al., 2020). Our charcoal index composite (which integrates anthropogenic and natural fire) does not show consistent trends with arboreal pollen or precipitation in the Holocene (Fig. 4; Supplemental Fig. S6). While this suggests fire is not strongly responsive to climate, we note the possibility that a long-term link between precipitation (Fig. 4A) and natural fire (Fig. 4C) might be overprinted by opposing trends in anthropogenic fire (Mayle and Power, 2008; Riris and Arroyo-Kalin, 2019; Montoya et al., 2020). In either case, these proxy data suggest that human-driven fire forcing, natural fire feedbacks, or both, are too weak to drive grassland expansion in our proxy domain in the mid-Holocene.

Grassland and fire expansion, however, may have occurred near forest-savanna boundaries (or ecotones) in the mid-Holocene. Consistent with our DGVM results, most proxy evidence for grassland and fire expansion is restricted to ecotones (Mayle and Power, 2008) while central and western Amazon records (Smith and Mayle, 2018; Nascimento et al., 2019) and basin-integrated records (Haberle and Maslin, 1999; Maslin et al., 2012) show little-to-no change through the mid-Holocene. This distinction between ecotonal and basin-integrated records suggests that fire and savanna expansion in ecotonal regions is a small portion of the basin mean, or their expansion is balanced by decreases in fire and grass coverage elsewhere. Fire plays an important role in ecotone migration in our DGVM simulations but this effect occurs mostly outside our proxy domain where our precipitation scaling is not constrained by proxy data (Supplemental Fig. S4). Within our proxy domain, however, the fire feedback in our DGVM simulations is weak and the tree cover response to drying is similar whether the fire module is enabled or disabled (Fig. 7). Overall, DGVM results are consistent with the finding that mid-Holocene fires were limited to forest-grassland ecotones and did not cause the system to tip to a savanna state. The fire feedback may have been strong in ecotonal regions, but it was weak in the core forested region where high tree cover persisted.

Fig. 7. Modeled and proxy-based estimates for fire, precipitation, and tree cover dynamics in the mid-Holocene. Gray circles show the top decile of tree cover observations for each precipitation bin as an estimate of maximum potential tree cover. Black circles show tree cover and precipitation in the proxy domain (see Fig. 6A). Squares show DGVM output with fire (yellow) and without (purple) within the proxy domain. Proxy-based precipitation and tree cover estimates are shown in teal and red rectangles (region of overlap is boxed in black). Overall, observations, models, and proxy data agree that tree cover remains high at ~1300 mm/yr of precipitation with no tipping to a grassland state. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
6.2. A seasonal water deficit in the mid-Holocene

The survival of Amazon forests and the passive nature of feedbacks that promote tree cover loss in our analysis is remarkable when we consider the consequences of mid-Holocene water stress. Today, regions of tropical South America that receive less precipitation than 2000 mm/yr are vulnerable to seasonal water deficits (Guan et al., 2015). Below this threshold more water is lost to evapotranspiration and runoff in the dry season than can be replenished by wet season water storage. The 2000 mm/yr threshold should also apply in the mid-Holocene because it is set by the balance of potential evapotranspiration and water storage (Guan et al., 2015) and potential evapotranspiration scales weakly with temperature in the tropics (~1.5%/K) (Scheff and Frierson, 2014). Based on our precipitation estimates, it is likely that the central and western Amazon was affected by a seasonal water deficit in the mid-Holocene. Such a deficit would probably have an outsized effect on evergreen taxa that rely on stored water for dry season photosynthesis, while favoring seasonally dry forest taxa and grasses (Enquist and Enquist, 2011; Guan et al., 2015; Verbesselt et al., 2016).

A seasonal water deficit can also amplify fire occurrence and lengthen the dry season in Amazonia. Fires have have been shown to increase exponentially with drying (Ray et al., 2005; Aragão et al., 2008) but the lack of a correlation between Δ¹⁸O and fire across the mid-Holocene suggests that dry season aridity does not increase fire sufficiently to drive widespread forest dieback. Meanwhile, under a water surplus in the dry season, transpiration of stored water acts as a “moisture pump” that prompts the onset of deep wet season convection 2–3 months before the peak shift in wind patterns associated with southward ITCZ migration (Wright et al., 2017). If seasonal drying made it difficult for deep-rooted trees to access water and transpire, the onset of the wet season may have been substantially delayed in the mid-Holocene (Kleidon and Heimann, 2000; Li and Fu, 2004; Wright et al., 2017; Leite-Filho et al., 2019a; Leite-Filho et al., 2019b).

The consequences of seasonality characterize the 2000 mm/yr threshold as a possible “tipping” point where Amazon forests can be abruptly replaced by grasslands (Hirota et al., 2011; Verbesselt et al., 2016; Ciemer et al., 2019). We cannot confirm whether the Amazon experienced a delayed onset of the wet season in the mid-Holocene, or whether climate-driven fire occurrence increased. But our results suggest that either (1) Amazon tree cover is resilient to the consequences of a seasonal water deficit or (2) the seasonal water deficit did not increase fire nor dry season length enough to tip the central/western Amazon to a grassland/savanna state.

6.3. Modern tree cover resilience compared to the mid-Holocene

Modern spatial data indicate that when mean annual precipitation falls between 2100 mm/yr and 1300 mm/yr forests and savannas are both stable ecological states (Hirota et al., 2011; Staver et al., 2011; Ciemer et al., 2019). This is referred to as the region of “bistability” within which a forest ecosystem can abruptly tip to a savanna state. Our mid-Holocene precipitation estimates suggest that even at the lower bound of this bistability region tree cover did not tip to a savanna state. Does forest survival in this range indicate drying alone is unlikely to lead to tipping today? Or is modern Amazon tree cover less resilient to drying than it was in the mid-Holocene?

Fire is the only mechanism capable of driving bistability in our conceptual model and is required for bistability in some dynamic global vegetation model simulations (Laslo et al., 2016). But spatial data can appear bistable due to human-driven forcing that decreases tree cover independent from precipitation (Ahlström et al., 2017). Bistability in a system is driven by feedbacks, not forcings, so if human-driven forcing (i.e. deforestation and anthropogenic fire) leads to apparent bistability we cannot characterize the system as bistable. Alternatively, it is possible that fire-aridity feedbacks are stronger today than in the mid-Holocene, characterizing the system as bistable and suggesting Amazon tree cover is less resilient to drying today regardless of human interference.

We test whether Amazon tree cover is as resilient to drying today as in the mid-Holocene by comparing our mid-Holocene reconstructions to modern data with and without accounting for land use (human-driven forcing). Fig. 8A shows precipitation and tree cover across tropical South America today with data points colored by the land use fraction in each pixel (data from Ahlström et al., 2017). Using these data, we can construct potential diagrams to identify the stable states of the system under different precipitation conditions. Potential diagrams are normalized, inverted PDFs (probability density function) of tree cover data for a given range of precipitation. The wells in a potential diagram reflect stable attractors, or stable states, and the ball represents the actual state of the system. For the modern precipitation range—defined by the RTM inversion of modern Δ¹³C data (Fig. 5)—the potential diagram shows a deep potential well at high tree cover, the stable state of the system (Fig. 5B).

Under mid-Holocene precipitation the high tree cover well shallows, tipping the ball to the new, low tree cover stable state (Fig. 8C). While this conflicts with evidence for high tree cover in the mid-Holocene (Haberle and Maslin, 1999; Mayle and Power, 2008; Maslin et al., 2012;Smith and Mayle, 2018; Nascimento et al., 2019), suggesting tree cover is less resilient to drying today, it is mostly an artifact of the intensification of modern human land use. When all pixels where the land use fraction exceeds 15% are removed, high tree cover forests remain the stable state for modern vegetation at low, mid-Holocene precipitation rates (Fig. 8E). This brings the modern precipitation-tree cover data in agreement with our mid-Holocene reconstructions, suggesting that in the absence of human disturbance, Amazon tree cover today is probably as resilient to drying as in the mid-Holocene.

6.4. Implications for the future of Amazon tree cover

Despite the vast uncertainty associated with model predictions and modern observations, some agreement surrounding the future of Amazon vegetation is emerging (Malhi et al., 2009; Ahlström et al., 2017). Malhi et al., (2009) show that correcting for precipitation biases in models is crucial for predicting future vegetation assuming the modern spatial distribution of vegetation holds over time. When doing so, grasslands are an unlikely future state of Amazon vegetation (Malhi et al., 2009). More recently, Ahlström et al., (2017) demonstrate that additional corrections for land use, along with precipitation bias-corrections, bring models and observations into agreement that Amazon tree cover is resilient to drying. While our analysis cannot inform how biodiversity or vegetation species composition responds to drying, our results confirm that tree cover can remain high even when precipitation appears to fall well below future projections (e.g. Fig. 5). In the absence of human interference, our analysis could not identify feedbacks that invalidate this conclusion.

Drying alone, at least within the precipitation range studied here, does not pose a major threat to Amazon tree cover within our study region, but land use does. For example, impacts of modern human deforestation on Amazon water cycling are already measurable. Deforested watersheds show increased runoff, balancing the loss of evapotranspiration (Costa et al., 2003; Coe et al., 2011; Hayhoe et al., 2011; Panday et al., 2015; Souza-Filho et al., 2016; Levy et al., 2018). While deforestation reduces tree cover without directly influencing precipitation (Fig. 1) the loss in moisture recycling may lead to a decrease in precipitation, especially in the western Amazon (Zemp et al., 2014; Staal et al., 2018). Drying can also allow for more deforestation by increasing the effectiveness of methods that use fire (Aragão et al., 2008; Barlow et al., 2020), setting the stage for a positive feedback between deforestation and aridity (Staal et al., 2020).

Temperature increases may also threaten Amazon vegetation. While we do not address the vegetation response to temperature (mid-Holocene temperatures were similar to pre-Industrial; Supplemental
Fig. S10), some modeling work suggests the modern Amazon is near a "thermal threshold" where warming has a much larger effect on vegetation than cooling (Cowling and Shin, 2006). Future work reconstructing precipitation and vegetation in warmer and colder paleoclimate states will help account for the role of temperature in climate-vegetation relationships.

The geometry of savanna expansion and fire is another key difference that separates the mid-Holocene from modern forest loss. In the mid-Holocene most grassland expansion and fire was limited to forest-grassland interfaces (Mayle and Power, 2008; Smith and Mayle, 2018). The core forested region of the Amazon Basin remained intact and not fragmented. By contrast, deforestation today extends far into the Amazon Basin, allowing human-driven activity to fragment forested regions and exert ecological stress from the inside-out. This is especially dangerous because human activity deep in the basin interior brings fires closer to core, annually inundated floodplain regions, which may be particularly vulnerable to forest loss and grassland expansion due to their low local tree cover and longer ecological recovery times (Flores et al., 2017). Taken together, this suggests human activity can strengthen the fire feedback, perhaps making tree cover more sensitive to drying than it has been in the past.

7. Conclusion

We attribute the persistence of high central and western Amazon tree cover in the mid-Holocene to resilience to drying rather than to nominal aridification (Smith and Mayle, 2018; Nascimento et al., 2019). Our results suggest Amazon tree cover is highly resilient to the magnitude of drying predicted in the worst-case-scenario, bias-corrected future climate projections (RCP8.5), although forest species composition may likely change. When human land use is locally, but not regionally intensive, mid-Holocene climate-vegetation patterns reveal that Amazon forests are not strongly sensitive to precipitation change (Fig. 4) and high tree cover persists likely because natural fires and the MRF were not strong enough feedbacks to drive widespread dieback. An important implication of this finding is, without human interference, feedbacks that amplify forest loss (particularly fire feedbacks) are too weak to tip Amazon forests to a grassland state, at least under mid-Holocene conditions. This resilience likely holds in seasonally dry conditions, inferred for the mid-Holocene, when fires are more common (Ray et al., 2005; Aragao et al., 2008), evergreen trees are water-stressed (Guan et al., 2015), and forests take longer to recover from drought (Verbesselt et al., 2016).

The bulk of modern data indicate mid-Holocene levels of drying should yield a savanna-state, but accounting for land use brings observations, models (Ahlström et al., 2017), and paleoclimate reconstructions into agreement that Amazon tree cover is resilient to crossing below the 2000 mm/yr precipitation threshold. We argue that, in the absence of extensive anthropogenic deforestation and fire, modern tree cover is just as resilient to drying as it was in the mid-Holocene. Even under the most drastic projections of future aridification, human-driven deforestation, not drying, will play the larger role in the evolution of Amazon tree cover.

Our proxy-model approach allows for a direct comparison between past and modern conditions and leaves room for future work to investigate other forms of resilience. For example, it is unclear how mid-Holocene biodiversity, ecosystem heterogeneity, and rainfall variability affected past resilience (van Nes and Scheffer, 2005; Galbraith et al., 2010; Levine et al., 2016; Sakschewski et al., 2016). Did these factors act to maintain Amazon forests despite growing water stress? Additionally, the Amazon’s resilience to mid-Holocene drying fundamentally depends on our definition of the forest’s function. We use tree cover as a proxy for the system’s function because it is easier to compare past and present states. But ecosystem function may be defined by other characteristics like biodiversity or species composition and the resilience of these to mid-Holocene drying remains unknown. Future mid-Holocene paleoecological work will provide a more comprehensive perspective to the Amazon ecosystem resilience to drying.

We agree that ongoing anthropogenic fire and deforestation pose a serious threat to the survival of the rainforest (Lovejoy and Nobre, 2018;
Strengthen the feedbacks capable of causing widespread forest loss far into the interior of forested regions and providing mechanisms to defend the feedbacks capable of causing widespread forest loss. The resilience of Amazon vegetation to drying when human interference is minimal implies that, despite global climate change, curbing fire and deforestation will have the most immediate and long-lasting effect on the preservation of Amazon tree cover.

Data availability

All proxy and DGVM data are available in the supplemental material of this manuscript. The following data can also be downloaded from their original sources. Charcoal data can be downloaded from the Global Charcoal Database (GCD version 2.0) using the paleofire package in R (https://github.com/paleofire). Pollen data can be downloaded from the Neotoma database (https://neotoma.org) and the ACER pollen and charcoal database (see supplement of ref. (Goni et al., 2017)). The Tigre Perdido isotope record (van Breukelen et al., 2008) (part of the western composite site) can be downloaded from the SISAL database (siteID: 25). The Diamante record (Cheng et al., 2013) (also part of the western composite) was provided by H. Cheng. The Paraíso record can be found in the supplement of ref. (Wang et al., 2017). The time-interpolated and temperature-corrected δ18O and Δδ18O data are in the supplement of this text. The reactive transport model code can be found in the supplement of ref. (Kukla et al., 2019) or at https://github.com/tykukla/Vapor_Transport_Model_KuklaEtAl2019.

Declaration of Competing Interest

The authors declare no competing interests.

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Appendix A. Supplementary data

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