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# NEW AND REPEATING TIPPING POINTS: THE INTERPLAY OF FIRE, CLIMATE CHANGE, AND DEFORESTATION IN NEOTROPICAL ECOSYSTEMS<sup>1</sup>

Mark B. Bush<sup>2</sup>

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## ABSTRACT

A 370,000-year paleoecological history of fire spanning four glacial cycles provides evidence of plant migration in response to Andean climate change. Charcoal, an indicator of fire, is only occasionally observed in this record, whereas it is ubiquitous in Holocene-aged Andean records. Fire is a transformative agent in Amazonian and Andean vegetation but is shown to be rare in nature. As humans promote fire, fire-free areas become microrefugia for fire-sensitive species. A distinction is drawn between microrefugia resulting from fire-free zones and those caused by unusual climatic conditions. The importance of this distinction lies in the lack of warmer-than-modern microrefugia aiding upslope migration in response to warming, whereas fire-free microrefugia support tree species above modern tree line or in areas of Amazonia least used by humans. The synergy between fire, deforestation, and climate change could promote a state-change in the ecosystem, one where new microrefugia would be needed to maintain biodiversity. Past tipping points are identified to have occurred within ca. 1°C–1.5°C of modern conditions. The recent climatic instability in both Amazonia and the Andes is viewed in the context of ecological flickering, while the drought-induced and fire-induced tree mortality are aspects of critical slowing down; both possibly portending an imminent tipping point.

*Key words:* Amazonia, Andes, climate change, critical slowing down, deforestation, fire, flickering, paleoecology, tipping point, warming.

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Model-based projections of ongoing climate change generally portray linear responses that follow upward trajectories of varying steepness (IPCC, 2013). While these trend lines are worrying enough, they do not reflect the reality that past climate change has been dominated by abrupt shifts and nonlinear responses (Blunier & Brook, 2001; NGRIP, 2004; Lynch-Stieglitz, 2017). For example, the erratic pulse of the meridional overturning circulation in the last ice age induced rapid and unpredictable warm-cold oscillations. This instability is implicated in megafaunal extinctions in western Europe (Cooper et al., 2015) and may have prevented incipient crop cultivation (Richerson et al., 2001). Today, in Amazonia and the Andes, the heart of Neotropical biodiversity, temperatures are rising and there have been three “droughts of the century” (2005, 2010, and 2015–16) in the last 15 years (Silva et al., 2019). Those droughts increased tree mortality, especially among the largest trees, and many areas transitioned from being a carbon sink to a carbon source (Gatti et al., 2014). What we have witnessed over the past several decades is not just a warming trend, but climatic destabilization.

Climate projections showing linear responses of temperature to future conditions are more likely to be true than similarly smooth projections for precipitation. The physics of temperature response operate at larger scales

than those underlying precipitation and are a lot simpler to model (Gulizia & Camilloni, 2015; Miralles et al., 2019). Hence, the uncertainties surrounding future precipitation are far greater than those of temperature. Even projecting the intensity of major atmospheric oscillations, such as El Niño Southern Oscillation (ENSO), is at the limit of modeling capacity, as there are roughly equal numbers of models projecting increased or decreased ENSO frequency in the future (Chen et al., 2017). The meaning for those projections is further complicated by the radically different outcomes on Amazonia and the Andes that result from the different flavors of ENSO (Sulca et al., 2018). Our best models project that many modern climates will disappear and be replaced by novel climates, with these effects being stronger the larger the overall climate change (Jackson & Williams, 2004).

Novel and disappearing climates form one portion of our estimates of future risk to biodiversity. Another huge portion of risk surrounds biotic responses to climate change, the capacity of species to migrate, and rates of migration (Holm et al., 2017). The required rate of migration is a function both of the degree of change for which migration must compensate, and the distance needed to regain climatic equilibrium (Loarie et al., 2009). Increasingly, it is evident that migration is

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<sup>2</sup> Institute for Global Ecology, Florida Institute of Technology, Melbourne, Florida 32901, U.S.A. mbush@fit.edu

facilitated by outlying populations that have survived previous climatic vicissitudes and that form nuclei of expansion as favorable conditions return (McLachlan & Clark, 2005; Cheddadi et al., 2006). These populations that survived in microrefugia are often genetically distinct, allowing researchers to reassemble past migration paths. Hannah et al. (2014) pointed out that ongoing warming offers no near-term prospect of returning to modern conditions, and that implicit in this understanding of microrefugia is the concept that better conditions will return. Hence Hannah et al. (2014) argue that microrefugial populations would be more accurately described as holdouts. I do not disagree with this assessment but would offer a different view of microrefugia in which the unusual environment is of more significance than the modern species composition (below). This thought is developed in both the context of climate and human-induced fire.

Interglacial warming, fire activity, and human actions have already been potent in shaping Neotropical ecology. The interaction of these elements led to the extinction of the Pleistocene Neotropical megafauna (Metcalf et al., 2016; Rozas-Davila et al., 2016; Raczka et al., 2019) within millennia of first human entry to the continent. Humans have continued their exploitation of the Andes and Amazonia for over 12,000 years, i.e., encompassing the entire Holocene period. In the last 3000 years, when climates were relatively stable, many landscapes continued to change (Chepstow-Lusty et al., 1996; Carson et al., 2015; Åkesson et al., 2020). Those changes reflected humans clearing or enriching natural systems to make way for a landscape manufactured to suit their needs (Balée, 1989). Legacies of past disturbance have already shaped the biota, though the scale and intensity of their late-Holocene influence is far from settled (e.g., Levis et al., 2017; McMichael et al., 2017). The use of fire is a linking theme where landscapes were humanized or manufactured.

Trying to capture the coupled effects of climate change and vegetation alteration has proven to be challenging. A prior generation of climate models that projected Amazonian forest dieback and replacement with bare ground or grassland (Cox et al., 2000; Betts et al., 2004) were largely walked back over modeling uncertainties (Malhi et al., 2009; Rammig et al., 2010). Recent papers, however, have again raised the possibility that Amazonian ecosystems could face a tipping point if ca. 20%–40% (according to study) of the area is converted from forest to pasture or bare ground (Marengo et al., 2011; Silvério et al., 2013; Lovejoy & Nobre, 2018).

Here, I will explore paleoclimatic and paleoecological evidence that can inform us of our vulnerability to a tipping point, and how this relates to microrefugia, climate change, and manufactured landscapes. I will draw on fossil pollen, charcoal, and paleolimnological

data to provide information about changing landscapes through time. Through these proxies I will quantify past tipping points and offer thoughts on the risk of approaching a new and fundamentally more catastrophic system change.

#### FIRE AND MICROREFUGIA

After the uplift of the Andes in the Miocene, fire became rare (Rundel et al., 2016), but determining the timing and frequency of past events requires long paleoecological records. The longest fire history published to date from South America is the charcoal record held in the sediments of Lake Titicaca (Fig. 1).

Fossil pollen from the Lake Titicaca sediments reveal the pattern of vegetation change across four glacial cycles (Fig. 2). The landscape varied in productivity from its modern state to being a near alpine desert at the glacial peak, due to strong cooling. During the times that glacials were ramping up or down there were times when the treelet *Polylepis* Ruiz. & Pav. was abundant (Chepstow-Lusty et al., 2005; Hanselman et al., 2005; Gosling et al., 2008, 2009). *Polylepis* often, but not always, declined in abundance as conditions became cooler during glacials, or when the landscape became fire-prone in interglacials (Fig. 2).

At the last glacial maximum and during the deglacial there are more charcoal and *Polylepis* records to establish a pattern of changing abundance across an elevational range from 2920 to 4150 m.s.m. (Valencia et al., 2018). The rarity of fire under full glacial conditions is a consistent feature of these records, with a huge increase in activity sometime between 15.6 and 8 thousand years ago (hereafter, k BP) (Fig. 3). Broadly, there appears to be an uptick in fire activity beginning earlier at lower elevations compared with high elevations. The trend in *Polylepis* throughout this period does not conform to a simple presence or absence according to fire regime. These fires would have been low intensity ground fires and the coexistence of *Polylepis* alongside charcoal suggests a mosaic of burned and unburned areas within the catchment (Valencia et al., 2016). Another way of thinking of this is that pre-human fire only occurred in these settings in the warmest and driest times and was probably constrained to the driest settings, i.e., north-facing sunny slopes. Thus, fire was natural, but probably always local in its effect and temporally rare.

Valencia et al. (2016, 2018) identified landscape rugosity as a critical predictor for whether *Polylepis* could survive the fires associated with the mid-Holocene dry event. Steep slopes provided natural firebreaks and allowed *Polylepis* to exist in fire-free microrefugia. Thus, there are two complementary but different uses of microrefugia. The first deals with the existence of an isolated subpopulation, and is important for the possible

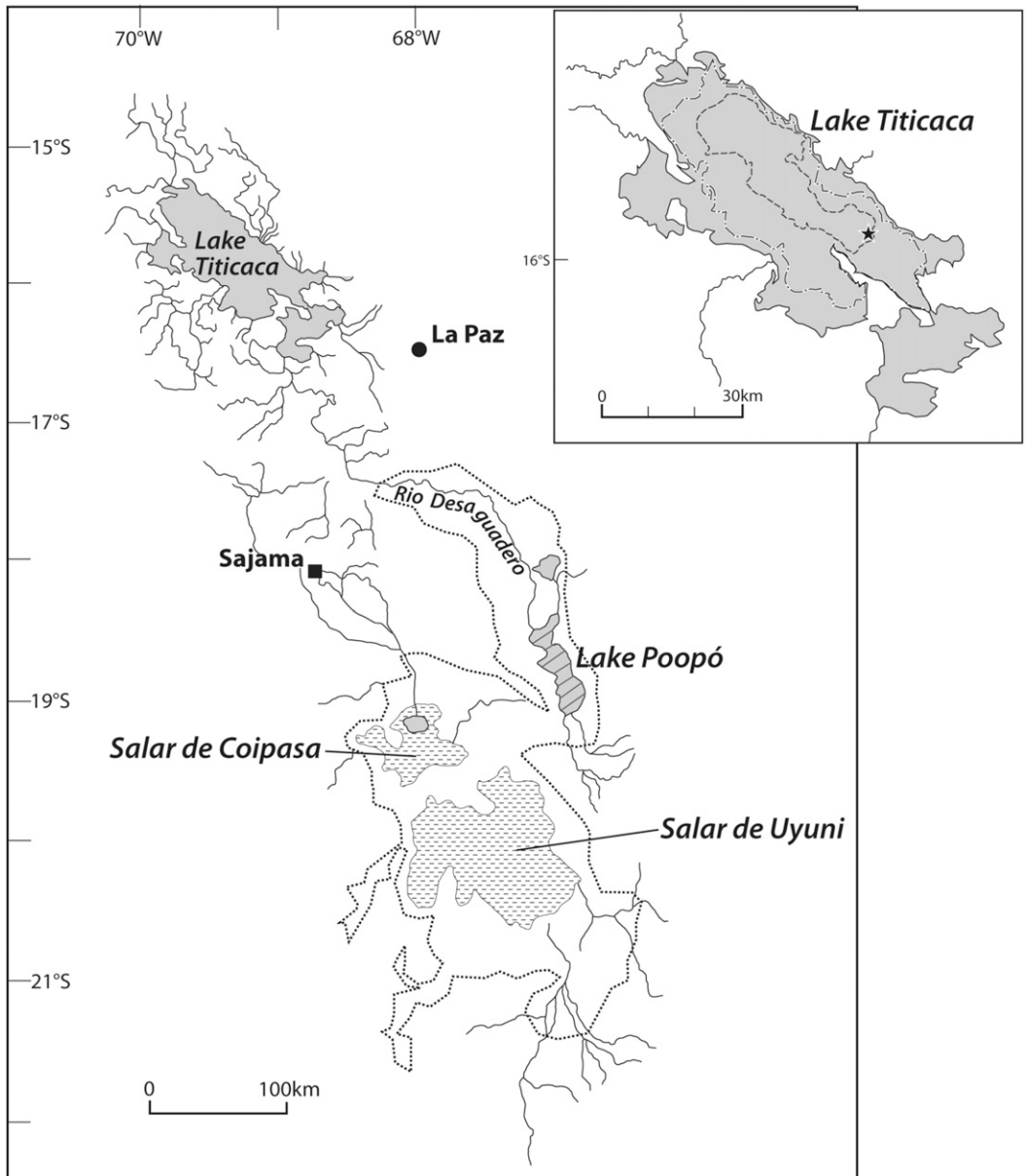


Figure 1. Lake Titicaca shorelines and megalakes of the Altiplano. Main map: modern lakes are filled with gray. Stippled lakes are modern salt pans, and Lake Poopó is hatched to indicate instability. The dotted outline shows the shoreline of Lake Tauca, a megalake that formed in the deglacial period. Inset shows the modern shoreline of Lake Titicaca, the dashed and dotted line is the mid-Holocene lowstand, and the inner dashed line is the last interglacial lowstand. Star marks the location of core LT01-2B (after Bush et al., 2010).

migrational and genetic implications (Rull, 2009; Mosblech et al., 2011; Hannah et al., 2014; Cheddadi et al., 2017). These populations can greatly speed the range expansion of a species and can account for unique genotypes that emerge and win the race into available territory. The second meaning is that there are landscape patches that are distinct from the adjacent matrix, and whose

characteristics supports a disjunct biota. Examples of this type of microrefugium are a cold spring that upwells and provides a cool microclimate, wet, cold microclimates of deep ravines, and the hot dry climates of a sunny slope (Sylvester et al., 2017). This use of microrefugia deals with the environmental anomaly relative to the broader landscape, what I call the delta ( $\Delta$ ) of difference.

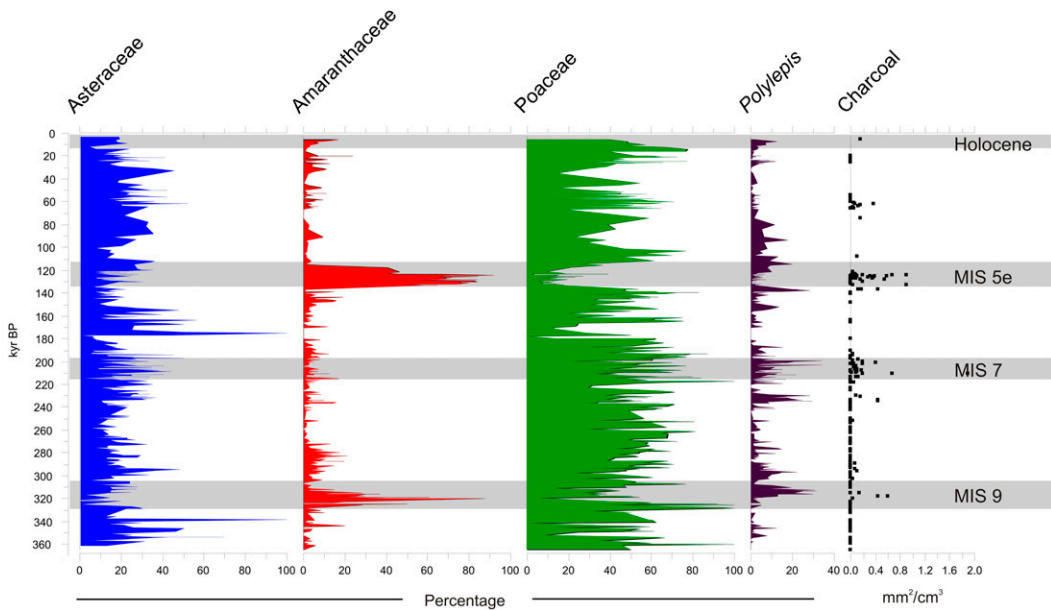


Figure 2. A summary of the fossil pollen and charcoal record from Lake Titicaca core LT01-2B (after Hanselman et al., 2011). MIS stands for Marine Isotope Stage, and MIS 1, 5e, 7, and 9 were the interglacial periods of the last 370,000 years.

The difference could be temperature, wetness, or any other fundamentally microclimatic variable. Alternatively, the difference could be unrelated to climate, such as topographic differentiation offering protection from fire or under extreme scenarios even grazers (Sylvester et al., 2014, 2017; Valencia et al., 2016). The important point to recognize here is that these settings are not “locked” into a set of conditions. For example, under global warming the temperature of the matrix would rise, but so too would the temperature of the spring water that provides a cooled microclimate. Eventually, even the spring water may not provide enough cooling to retain the most stenophilous species, and then there would be species turnover. Thus, no setting will have an unchanging suite of species. Note that no record in Figure 3 retains a stable population of *Polyalepis* throughout the sequence. The replacement species although different, may still reflect a need for cooler conditions than the matrix. Rather than maintaining absolute conditions, the relative difference to the matrix will be maintained in the microrefugium. So that, even though the spring is warming it still provides a microclimate cooler than that of the matrix, thus some  $\Delta$  of difference is maintained.

Humans are the principal cause of fire in the Holocene in both the Andes and Amazonia (Cochrane, 2009; White, 2013). As such, humans have created a class of microrefugia, fire-free areas, that were not previously as distinct from the matrix. In pre-human times, fire was so rare in the humid tropics that plants evolved no adaptations to it (Barlow & Peres, 2008). The vast majority of this flora is

fire-sensitive, and even a single ground fire changes the ecology of a setting, perhaps not irreversibly, but increasing the probability of subsequent fire (Barlow & Peres, 2006). A series of several fires in a decade or so has been shown to drive an intact Amazonian forest toward savanna (Barlow & Peres, 2008; Morton et al., 2013).

It is fortunate that in the lowlands where there are no topographic barriers to fire, natural fires do not readily spread into intact forest (Cochrane, 2003). Lightning strikes have been observed to burn out in a few meters from the point of impact, and experiments show that the forest only becomes flammable after unrealistically long drought intervals (Nepstad et al., 2004). Indeed, paleoecological records reveal that fire in most areas of the Amazon is uniquely associated with people, and that the magnitude of recent fire activity has no historical precedent (Bush et al., 2007; Nascimento et al., 2019). In other settings, where pre-Columbian people practiced slash-and-burn agriculture or set fires to improve hunting, there can be long histories of land use through burning (Bush et al., 2008; Maezumi et al., 2018). Considerable discussion surrounds the spatial scale of such forest modification with some arguing for all of Amazonian forest being heavily modified by human actions (Clement et al., 2015; Ferreira et al., 2019). Another view is that many rivers and lakes were prime occupational settings and were modified by crop cultivation, timber removal, and enrichment with palms (Bush & Silman, 2007). But at more than 10 km from a river, modern hunting had little effect on game

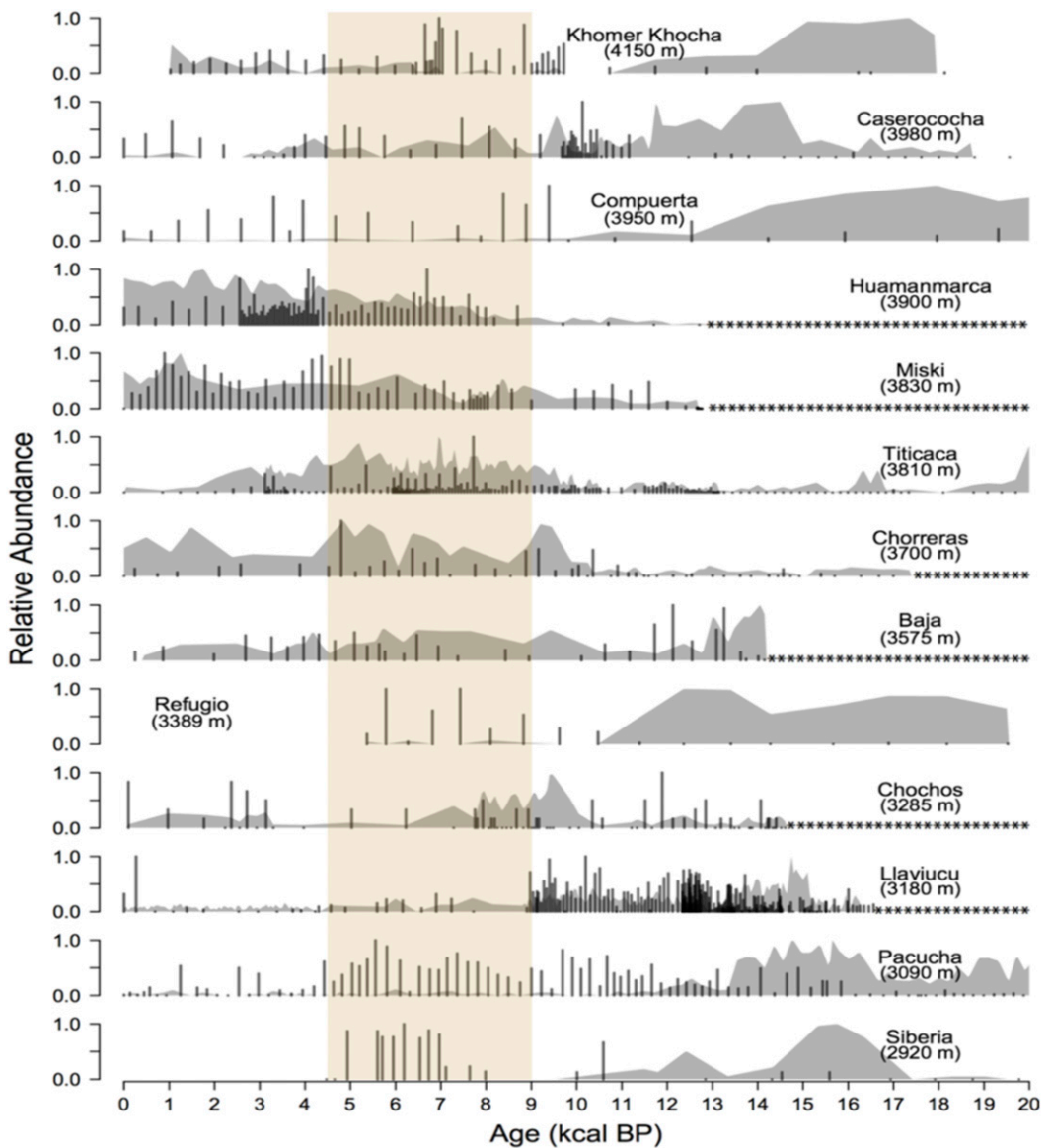


Figure 3. The relative abundance of *Polylepis* Ruiz. & Pav. pollen (gray shapes) in Andean paleoecological records relative to charcoal (black bars) from lake sediments. Values for both *Polylepis* and charcoal are normalized to one being the maximal value in each record. Stars indicate no data. The Mid-Holocene Dry Event is the shaded box (after Valencia et al., 2018).

density (Peres et al., 2016), and there was little pre-historic modification of the forest (McMichael et al., 2012; Piperno et al., 2015). In this sense, these interfluvial forests remote from major human influence were the microrefugia of the lowlands.

We have legacies of this human activity in the lack of Pleistocene megafauna, and empty riverine forests that have simply never had a chance to recover from waves of use beginning in pre-Columbian times, through the Rubber Boom (McMichael & Bush, 2019), and now with defauna-tion to support oil and mineral extraction or dam building

(Antunes et al., 2016). Forest remnants isolated by the advancing wall of cultivation and new roads (Barber et al., 2014) form another class of modern microrefugia.

#### ASYMMETRIES OF DISPERSAL AND MICROREFUGIA

The velocity of climate change requires a compensating migrational velocity if species are to keep pace with climate change. Those migrational velocities are likely to be lower where ecological gradients are steep, such as on mountainsides, but are seen to be wholly unattainable in large flat areas (Loarie et al., 2009;

VanDerWal et al., 2013). Here I argue that the capacity for montane tree species to migrate to keep pace with climate change is inherently easier and quicker during times of cooling than warming. This asymmetry primarily influences the capacity of species to expand upslope or downslope. Lowland species, for the most part, have nowhere to migrate to, and must simply absorb the impacts of climate change, perhaps surviving the worst times only in microrefugia.

Gravity exerts local effects on dispersal through seeds being moved downslope through rolling, landslides, or slope wash. This secondary dispersal would occur after the primary dispersal by wind or animal. Indeed, almost all fallen seeds could increase the effective seed shadow of the parent through such dispersal. Seeds with adaptations, such as wings, air sacs, or that are buoyant, would be readily transported downslope by streams and rivers. Such transport is happening all the time, but the seeds fail to establish in the overly warm downslope conditions. But when the climate cools this flux of seeds may meet with much greater success, allowing rapid downslope range expansion. Traits conferring tolerance to immersion in water and fluvial transport may explain why there is a consistent subset of “cool-tolerant” species that are so characteristic of glacial climates. Trees that today occur primarily in montane forest, e.g., *Podocarpus* L'Hér. ex Pers., *Alnus* Mill., *Myrsine* L., and *Drimys* J. R. Forst. & G. Forst., seem to occur in almost all glacial-aged records (Bush et al., 1990; Colinvaux et al., 1996; Ledru et al., 2007), whether it is in the Atlantic Coastal forest, the cerrado, or Amazonia. This subset is often augmented by *Araucaria* Juss. outside of the Amazonian watershed (Ledru et al., 2009; Niemann & Behling, 2009; de Oliveira et al., 2020). All of these cool-tolerant taxa can be found in modern riparian forests (Junk et al., 2011). Species of riparian forest often survive flooding and show adaptation to fluvial transport. Consequently, species that occur in riparian forest are most likely to have the capacity to be spread by fluvial dispersal (Junk, 1997) and can provide a rapid vegetative response to cooler climates.

Ongoing warming in the highlands is resulting in species migrating upslope in response to warming, but the pace of this migration is significantly slower than the rate of warming (Feeley et al., 2011). Upslope seed dispersal can occur on a very local scale as a result of upslope winds and animal movement. While pushing a seed up a hill may not be as arduous as a boulder, it is nevertheless going to be much less common and effective than downslope dispersal.

As Andean forest species disperse upslope in response to warming, they will eventually encounter the upper limit of Andean forest or tree line. The tree line is not a natural boundary set by climate but a “grass

ceiling” (Feeley & Silman, 2010; Sarmiento, 2012; Rehm & Feeley, 2015) set by humans burning the puna grasslands. Paleoecological studies of the tree line in Ecuador showed that burning has created a sharper ecotone between forest and grassland, while at the same time degrading the quality of the uppermost forest (Bush et al., 2015). The net result of species pressing upward due to climate change against the implacable force of people burning to maintain grazing lands creates the “Big Squeeze” as species have their realized niches truncated to the point where they may face extinction (Bush et al., 2008).

A last thought on migration and microrefugia is that we have no climatic microrefugia for future warming, whereas there are fire microrefugia. Because it has been > 100,000 years since there were substantially warmer-than-modern conditions, and because there was an intervening ice age, there are no ancient upslope microrefugia to speed migration. Unusually warm spots, such as sunny slopes, may host assemblages biased toward warmth, but there will not be “holdouts” from a prior warm time. Hence species dispersal upslope will be at the pace of local migration, not from the kind of microrefugial expansions seen during the deglacial warming (McLachlan & Clark, 2005). Contrastingly, fire-free microrefugia, which are not climatically dependent, could offer the potential starting points of rapid range expansions—if fire were controlled.

#### TIPPING POINTS

Ecological tipping points are state changes in a system where a small incremental change in conditions induces a profound shift in vegetation (Scheffer et al., 2001; Marengo et al., 2011), for example, a system transitions from having no fire to having occasional fire, which leads to forest being replaced by grassland. Temperature and precipitation are commonly measured variables applied to thinking about tipping points (Sternberg, 2001), though decreasing relative humidity, dry season lengthening, and increasing drought severity are more deterministic of fire probability (Díaz et al., 2007; Nepstad et al., 2008).

Over the past 50 years the present rate of warming in the Andes is about 1°C–1.5°C per century (Duque et al., 2015; Vuille et al., 2018), but there are concerns that this rate might accelerate. The two interglacials that occurred at ~320 and 125 k BP, corresponding to Marine Isotope Stages (MIS) 9 and 5e, were between 1°C and 1.5°C warmer than modern (Hearty & Tormey, 2017).

The fossil pollen sequence from Lake Titicaca provides an example of what happens when a tipping point is exceeded. Lake Titicaca lies in the Altiplano at 16°S–18°S and is the highest great lake in the world

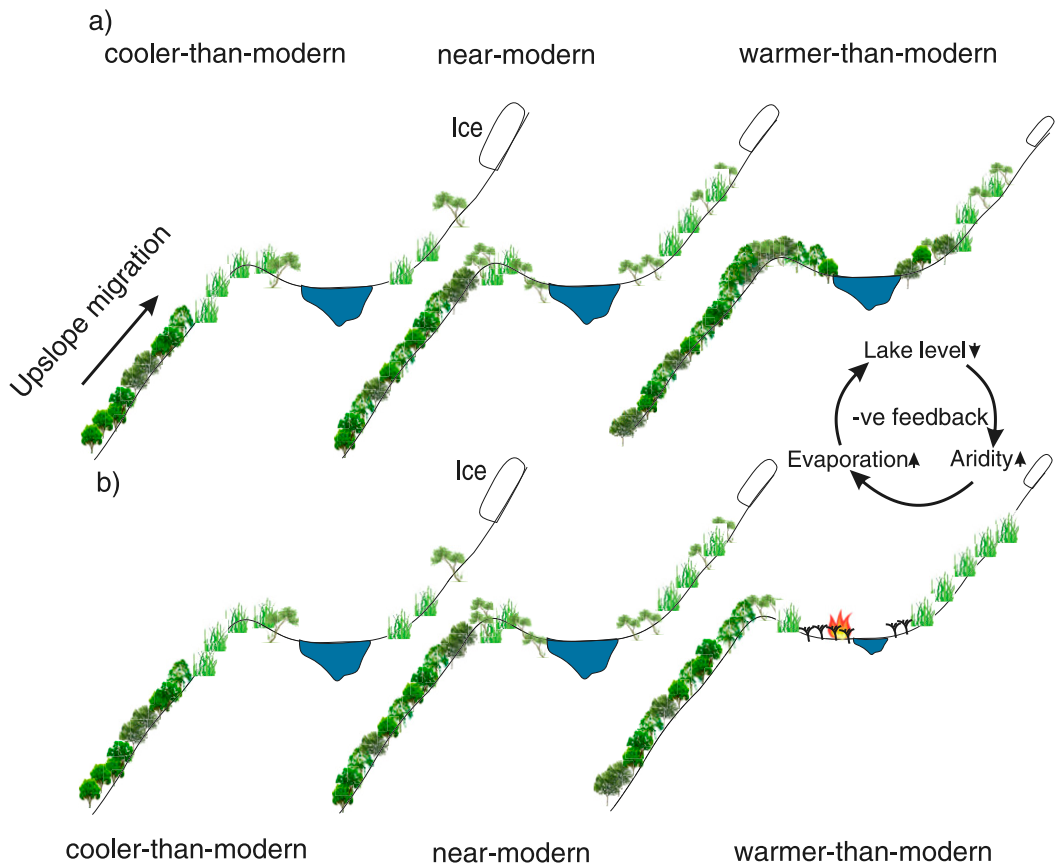


Figure 4. Annotated schematic of Andean forest migration from mid-deglaciation to the peak of Quaternary warming: a) what would be expected from a linear response to a  $1^{\circ}\text{C}$ – $1.5^{\circ}\text{C}$  warming relative to modern, versus b) the tipping point that was manifested in MIS 5e and 9 (after Bush et al., 2010).

(Fig. 1). The modern lake is  $> 280$  m deep, and excess water flows into the Huinamarca sub-basin and then exits to the south down the Rio Desaguadero. The Rio Desaguadero in turn supplies Lake Poopó. During the last 125,000 years the Altiplano has been arid and at other times supported vast paleolakes that were as much as 100 m deep (Baker et al., 2001; Placzek et al., 2006) (Fig. 1).

In the Lake Titicaca pollen sequence, MIS 5e and 9 were clearly different from the other two less extreme interglacials (Hanselman et al., 2011). The onset of all four interglacials had similar characteristics: an overall increase in pollen concentrations indicated higher landscape productivity, with *Polylepis* pollen percentages initially increasing until fire became a regular ecological component. (Fig. 2). As the peak of the interglacial was reached, fire activity increased, negatively impacting *Polylepis*. These signatures were consistent with a linear warming allowing denser growth of Puna vegetation. If that linear response continued until a warming of  $1^{\circ}\text{C}$ – $1.5^{\circ}\text{C}$  above modern was reached, Andean forest

should have invaded the basin (Fig. 4a). In the two stronger interglacials (MIS 9 and MIS 5e) that showed such a warming, instead of forest development, the system flipped to an Amaranthaceae-dominated saltpan (Fig. 4b). Lake level fell by 120 m, causing the lake to lose  $\sim 80\%$  of its surface area (D'Agostino et al., 2002) (Fig. 1), the lake became saline (Baker & Fritz, 2015), and fire intensity increased (Fig. 2). A tipping point had been exceeded (Fig. 4b). Though the chronological accuracy of this record must be recognized as coarse, the new state lasted for what appears to be several thousand years (Fig. 2). While peak warming in these interglacials may have been brief, the feedback mechanisms could have sustained a drive toward aridity even as somewhat cooler conditions returned. Hysteresis, an asymmetry in the tipping points leading into and out of alternative stable states, is predicted by ecological theory (Sternberg, 2001; Scheffer et al., 2003) and our limited practical observations (Schroder et al., 2005; Fauchald, 2010). Thus, once the warming-drying cycle was initiated, the reversal to a wetter system would

require a greater cooling or wetting to reverse the tipping point (Scheffer et al., 2001). It is important to realize that this flip between states occurred not once but twice, with a tipping point within ca.  $\sim 1^{\circ}\text{C}$ – $1.5^{\circ}\text{C}$  of modern temperatures.

The climatic mechanism that would lead to such interglacial aridity is not entirely clear, but may be the product of positive feedback mechanisms initiated by warming oceans, propagated through a northward displacement of the Inter-tropical Convergence Zone, which in turn reduces moisture inflows from the Atlantic to Amazonia (Bush et al., 2010). It is this river of wet air, known as the South American Low-level Jet (SALLJ), flowing from east to west across Amazonia, that controls moisture in the Amazon Basin and the Andes (Garreaud et al., 2009). At least, it provides the moisture input, but Amazonia is so vast that water falls out as rain and is then evapotranspired back into the atmosphere five to six times as it crosses the basin (Salati, 1985). Consequently, western Amazonia and the Andes are almost wholly reliant on recycled moisture to maintain humidity and rainfall. Evapotranspiration from savanna is ca. 60% of that of rainforest, whereas evaporation from cropland may be as low as 10% of that of rainforest (Miralles et al., 2011). Thus, western Amazonia and the Andes are potentially more sensitive to changes in landcover than if their moisture input came directly from the ocean. Consequently, because potential changes are magnified through the hydrological cycle, western Amazonian and Andean locations are also potentially more sensitive to changes in moisture variability than their eastern Amazonian counterparts.

Amazonian ecosystems have survived prior climatic turbulence, but as we near the upper limit of their evolutionary experience, the capacity to buffer extreme warmth or drought is diminished (Colwell et al., 2008). A decade ago it was argued that a ca. 40% deforestation of Amazonia and  $3^{\circ}\text{C}$ – $4^{\circ}\text{C}$  warming could result in a tipping point (Nobre & Borma, 2009). More recently, a  $4^{\circ}\text{C}$  warming was estimated to cause replacement of forest by savanna across large areas (Sampaio et al., 2019). A critical missing piece in climate-only analyses is the synergy with deforestation and fire. The projected climate change for this century may not be sufficient to cause an Amazonian tipping point (Boulton et al., 2017), but in concert with deforestation it would (Lovejoy & Nobre, 2018). Even a 20% loss of forest cover, which we are already approaching, is likely to reduce precipitation by as much as 20% (Shukla et al., 1990; Boers et al., 2017; Zemp et al., 2017). But these models are all essentially linear extrapolations and none take into consideration extreme events that could provide feedbacks initiating a new system. In the last 15 years, Amazonia has experienced three “droughts of the century” in 2005, 2010, and 2015–2016 (Silva et al.,

2019). All of these events were attributable to extreme sea-surface temperatures that subsided within 18 months. But on land the effects of the droughts may be more protracted, and possibly irreversible (Anderson et al., 2015).

The droughts increase tree mortality, and the largest, emergent canopy species are disproportionately affected (Barlow et al., 2003; Balch et al., 2011; Doughty et al., 2015). These emergents are likely to be among the oldest trees in the forest and, by definition, are slow to replace. But the effects on the forest are more extensive than the initial loss. The tree mortality plays out over several years as weakened trees take time to die (Barlow et al., 2003). This mortality increases the standing deadwood, which becomes treefall over the next few years, and thus increases the fuel on the forest floor. Consequently, when another drought hits, the prospect of fire increases substantially. Local microclimates warm by  $\sim 10^{\circ}\text{C}$  in a deforested landscape while humidity is lowered by  $\sim 30\%$  (Uhl & Kauffman, 1990). From a human perspective, the forest has just become much easier to clear, burn, and exploit. Thus, the effects of the droughts accumulate over the course of the next decade. The droughts encourage the invasion of areas that are easier to burn and thereby promote settlement, which in turn affects regional climates forcing a negative feedback of drought, fire, and deforestation (Sampaio et al., 2007).

If it is the western Amazon and the Andes that are most sensitive to a potential tipping point, is there evidence of that already? The strongest evidence yet is the drying out of Bolivia’s second largest lake, Lake Poopó, in 2016. This large shallow lake that supported a commercial fishery, dried up between January and November 2016 (Farthing, 2017). Perhaps this loss is just a coincidence, but its location is in the area most dependent on Amazonian evapotranspiration (Weng et al., 2018), and its broad, shallow basin made it highly susceptible to hydrological change. I would contend that Lake Poopó should be viewed as our canary for Amazonian hydrological conditions.

Referring again to the ecological theory surrounding tipping points, there are two expectations that warn us of an impending tipping point. The first is increased variance in the system, termed ecological flickering (Wang et al., 2012). The second is that a disturbed system approaching a tipping point cannot recover to the same sized stimulus as rapidly as before, termed critical slowing down (Dakos et al., 2008). The droughts, and intervening floods (2009, 2012, and 2014) in Amazonia, and the drying of Lake Poopó could constitute the flickering, while the loss of ancient trees could constitute the critical slowing down. The  $3^{\circ}\text{C}$ – $4^{\circ}\text{C}$  and 40% deforestation-induced tipping point projected a decade ago for Amazonia probably needs to be revised downward to ca. 20%–25% deforestation (Lovejoy & Nobre,



2018). Given rates of deforestation and “business-as-usual” climate projections the revised tipping point is likely to occur by mid-century or at 1°C–2°C warming. Even more pressing in this regard is any increase in fire activity that would further damage the system. While anthropogenic forcing is underlying the warm sea-surface temperatures of the flickering, it is local land use that can make the difference between the forest recovering and restoring resilience, albeit slowly, or spiraling rapidly into a degraded savanna-like state.

#### CONCLUSIONS

The risk that our generation will preside over the irreversible collapse of Amazonian and Andean biodiversity is huge, literally existential. Past ice ages and peak interglacials did not diminish Neotropical biodiversity, but the destructive power posed by the synergistic triumvirate of anthropogenic climate change, ENSO variability, and human-induced deforestation is unparalleled.

Past responses of species to climate change have relied either on large intact systems moderating their own climate, natural buffering of systems, or survival and migration being facilitated by microrefugia. As the Neotropical lowlands have almost left the historic range of climate variability, and the variance in the system is increasing, the capacity of forests to buffer their inhabitants from ongoing change diminishes. Resilience is threatened, and recent climate extremes may represent the flickering that coincides with a critical slowing down foreshadowing a tipping point.

No single state or federal government can halt anthropogenic warming nor alter the path of ENSO variability, but deforestation and burning can be controlled through policy. The tipping point for the Altiplano may be almost unavoidable, but for Amazonian ecosystems writ large there may well be a path that can avoid the worst effects. Avoiding widespread savannization of lowland Amazonia will take international and national political priorities to be aligned to reduce deforestation and burning, and for those policies to be implemented quickly.

#### Literature Cited

Åkesson, C. M., F. Matthews-Bird, M. Bitting, C. J. Fennell, W. B. Church, L. C. Peterson, B. G. Valencia, et al. 2020. 2100 years of human adaption to climate change in the High Andes. *Nat. Ecol. Evol.* 4: 66–74.

Anderson, L. O., L. E. Aragão, M. Gloor, E. Arai, M. Adami, S. S. Saatchi, Y. Malhi, et al. 2015. Disentangling the contribution of multiple land covers to fire-mediated carbon emissions in Amazonia during the 2010 drought. *Global Biogeochem. Cycles* 29(10): 1739–1753.

Antunes, A. P., R. M. Fewster, E. M. Venticinque, C. A. Peres, T. Levi, F. Rohe & G. H. Shepard. 2016. Empty forest or empty rivers? A century of commercial hunting in Amazonia. *Sci. Advances* 2(10): E1600936.

Baker, P. A. & S. C. Fritz. 2015. Nature and causes of Quaternary climate variation of tropical South America. *Quatern. Sci. Rev.* 124: 31–47.

Baker, P. A., C. A. Rigsby, G. O. Seltzer, S. C. Fritz, T. K. Lowenstein, N. P. Bacher & C. Veliz. 2001. Tropical climate changes at millennial and orbital timescales on the Bolivian Altiplano. *Nature* 409: 698–701.

Balch, J. K., D. C. Nepstad, L. M. Curran, P. M. Brando, O. Portela, P. Guilherme, J. D. Reuning-Scherer, et al. 2011. Size, species, and fire behavior predict tree and liana mortality from experimental burns in the Brazilian Amazon. *Forest Ecol. Managem.* 261(1): 68–77.

Balée, W. 1989. The culture of Amazonian forests. Pp. 1–21 in D. A. Posey & W. Balée (editors), *Resource Management in Amazonia: Indigenous and Folk Strategies*. New York Botanical Garden, New York.

Barber, C. P., M. A. Cochrane, C. M. Souza Jr. & W. F. Laurance. 2014. Roads, deforestation, and the mitigating effect of protected areas in the Amazon. *Biol. Conservation* 177: 203–209.

Barlow, J. & C. Peres. 2006. Effects of single and recurrent wildfires on fruit production and large vertebrate abundance in a central Amazonian forest. *Biodivers. & Conservation* 15(3): 985–1012. doi:10.1007/s10531-004-3952-1.

Barlow, J. & C. A. Peres. 2008. Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philos. Trans., Ser. B* 363(1498): 1787–1794. doi:10.1098/rstb.2007.0013.

Barlow, J., C. A. Peres, B. O. Lagan & T. Haugaasen. 2003. Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecol. Lett.* 6(1): 6–8. doi: 10.1046/j.1461-0248.2003.00394.x.

Betts, R. A., P. M. Cox, M. Collins, P. P. Harris, C. Huntingford & C. D. Jones. 2004. The role of ecosystem–atmosphere interactions in simulated Amazonian precipitation decrease and forest dieback under global climate warming. *Theor. Appl. Climatol.* 78: 157–175.

Blunier, T. & E. J. Brook. 2001. Timing of millennial-scale climate change in Antarctica and Greenland during the last glacial period. *Science* 291: 109–112.

Boers, N., N. Marwan, H. M. Barbosa & J. Kurths. 2017. A deforestation-induced tipping point for the South American monsoon system. *Sci. Rep.* 7: 41489.

Boulton, C. A., B. B. Booth & P. Good. 2017. Exploring uncertainty of Amazon dieback in a perturbed parameter Earth system ensemble. *Global Change Biol.* 23(12): 5032–5044.

Bush, M. B. & M. R. Silman. 2007. Amazonian exploitation revisited: Ecological asymmetry and the policy pendulum. *Frontiers Ecol. Environm.* 5: 457–465.

Bush, M. B., M. Weimann, D. R. Piperno, K.-b. Liu & P. A. Colinvaux. 1990. Pleistocene temperature depression and vegetation change in Ecuadorean Amazonia. *Quatern. Res.* 34: 330–345.

Bush, M. B., M. R. Silman, M. B. de Toledo, C. R. S. Listopad, W. D. Gosling, C. Williams, P. E. de Oliveira, et al. 2007. Holocene fire and occupation in Amazonia: Records from two lake districts. *Philos. Trans., Ser. B* 362: 209–218.

Bush, M. B., M. R. Silman, C. McMichael & S. Saatchi. 2008. Fire, climate change and biodiversity in Amazonia: A Late-Holocene perspective. *Philos. Trans., Ser. B* 363(1498): 1795–1802.

Bush, M. B., J. A. Hanselman & W. D. Gosling. 2010. Non-linear climate change and Andean feedbacks: An imminent turning point? *Global Change Biol.* 16: 3223–3232.

Bush, M. B., A. M. Alfonso-Reynolds, D. H. Urrego, B. G. Valencia, Y. A. Correa-Metrio, M. Zimmermann & M. R.

- Silman. 2015. Fire and climate: Contrasting pressures on tropical Andean timberline species. *J. Biogeogr.* 42(5): 938–950.
- Carson, J. F., J. Watling, F. E. Mayle, B. S. Whitney, J. Iriarte, H. Prímers & J. D. Soto. 2015. Pre-Columbian land use in the ring-ditch region of the Bolivian Amazon. *Holocene* 25: 1285–1300.
- Cheddadi, R., G. G. Vendramin, T. Litt, L. François, M. Kageyama, S. Lorentz, J. M. Laurent, et al. 2006. Imprints of glacial refugia in the modern genetic diversity of *Pinus sylvestris*. *Global Ecol. Biogeogr.* 15(3): 271–282.
- Cheddadi, R., A.-J. Henrot, L. François, F. Boyer, M. Bush, M. Carré, E. Coissac, et al. 2017. Microrefugia, climate change, and conservation of *Cedrus atlantica* in the Rif Mountains, Morocco. *Frontiers Ecol. Evol.* 5: 114.
- Chen, L., T. Li, Y. Yu & S. K. Behera. 2017. A possible explanation for the divergent projection of ENSO amplitude change under global warming. *Clim. Dynam.* 49(11–12): 3799–3811.
- Chepstow-Lusty, A. J., K. D. Bennett, V. R. Switsur & A. Kendall. 1996. 4000 years of human impact and vegetation change in the central Peruvian Andes—with events paralleling the Maya record? *Antiquity* 70: 824–833.
- Chepstow-Lusty, A. J., M. B. Bush, M. R. Frogley, P. A. Baker, S. C. Fritz & J. Aronson. 2005. Vegetation and climate change on the Bolivian Altiplano between 108,000 and 18,000 yr ago. *Quatern. Res.* 63: 90–98.
- Clement, C. R., W. M. Denevan, M. J. Heckenberger, A. Braga Junqueira, E. G. Neves, W. G. Teixeira & W. I. Woods. 2015. The domestication of Amazonia before European conquest. *Proc. Trans., Ser. B* 282. doi:10.1098/rspb.2015.0813.
- Cochrane, M. A. 2003. Fire science for rainforests. *Nature* 421(6926): 913.
- Cochrane, M. A. 2009. Fire in the tropics. Pp. 1–23 in M. A. Cochrane (editor), *Tropical Fire Ecology*. Springer Berlin, Heidelberg.
- Colinvaux, P. A., P. E. De Oliveira, J. E. Moreno, M. C. Miller & M. B. Bush. 1996. A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science* 274: 85–88.
- Colwell, R. K., G. Brehm, C. L. Cardelus, A. C. Gilman & J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322(5899): 258–261. doi:10.1126/science.1162547.
- Cooper, A., C. Turney, K. A. Huguen, B. W. Brook, H. G. McDonald & C. J. A. Bradshaw. 2015. Abrupt warming events drove Late Pleistocene Holarctic megafaunal turnover. *Science* 349: 602–606.
- Cox, P. M., R. A. Betts, C. D. Jones, S. A. Spall & I. J. Totterdell. 2000. Acceleration of global warming due to carbon-cycling feedbacks in a coupled climate model. *Nature* 408: 184–187.
- D'Agostino, K., G. O. Seltzer, P. A. Baker, S. C. Fritz & R. B. Dunbar. 2002. Late-Quaternary lowstands of Lake Titicaca: Evidence from high-resolution seismic data. *Palaeogeogr. Paleoclimatol. Palaeoecol.* 179(1): 97–111.
- Dakos, V., M. Scheffer, E. H. van Nes, V. Brovkin, V. Petoukhov & H. Held. 2008. Slowing down as an early warning signal for abrupt climate change. *Proc. Natl. Acad. Sci. U.S.A.* 105(38): 14308–14312. doi:10.1073/pnas.0802430105.
- de Oliveira, P. E., M. Raczka, J. L. D. Pinaya, C. N. H. McMichael & M. B. Bush. 2020. Climate change and biogeographic connectivity across the Brazilian cerrado. *J. Biogeogr.* 47: 396–407.
- Díaz, M. F., S. Bigelow & J. J. Armesto. 2007. Alteration of the hydrologic cycle due to forest clearing and its consequences for rainforest succession. *Forest Ecol. Managem.* 244(1–3): 32–40.
- Doughty, C. E., D. Metcalfe, C. Girardin, F. F. Amézquita, D. G. Cabrera, W. H. Huasco, J. Silva-Espejo, et al. 2015. Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature* 519(7541): 78.
- Duque, A., P. R. Stevenson & K. J. Feeley. 2015. Thermophilization of adult and juvenile tree communities in the northern tropical Andes. *Proc. Natl. Acad. Sci. U.S.A.* 112(34): 10744–10749.
- Farthing, L. 2017. Bolivia's disappearing lake. *Earth Island J.* 1. <[https://www.earthisland.org/journal/index.php/articles/entry/bolivia\\_disappearing\\_lake/](https://www.earthisland.org/journal/index.php/articles/entry/bolivia_disappearing_lake/)>.
- Fauchald, P. 2010. Predator–prey reversal: A possible mechanism for ecosystem hysteresis in the North Sea? *Ecology* 91(8): 2191–2197.
- Feeley, K. J. & M. R. Silman. 2010. Land-use and climate change effects on population size and extinction risk of Andean plants. *Global Change Biol.* 16(12): 3215–3222.
- Feeley, K. J., M. R. Silman, M. B. Bush, W. Farfan, K. G. Cabrera, Y. Malhi, P. Meir, et al. 2011. Upslope migration of Andean trees. *J. Biogeogr.* 38: 783–791.
- Ferreira, M. J., C. Levis, J. Iriarte & C. R. Clement. 2019. Legacies of intensive management in forests around pre-Columbian and modern settlements in the Madeira-Tapajós interfluvium, Amazonia. *Acta Bot. Bras.* 33: 212–220. <http://dx.doi.org/10.1590/0102-33062018abb0339>.
- Garreaud, R., M. Vuille, R. Compagnucci & J. Marengo. 2009. Present-day South American climate. *Palaeogeogr. Paleoclimatol. Palaeoecol.* 281: 180–195.
- Gatti, L., M. Gloor, J. Miller, C. Doughty, Y. Malhi, L. Domingues, L. Basso, et al. 2014. Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* 506(7486): 76.
- Gosling, W. D., M. B. Bush, J. A. Hanselman & A. Chepstow-Lusty. 2008. Glacial-interglacial changes in moisture balance and the impact on vegetation in the Southern Hemisphere tropical Andes (Bolivia/Peru). *Palaeogeogr. Paleoclimatol. Palaeoecol.* 259(1): 35–50. doi:10.1016/j.palaeo.2007.02.050.
- Gosling, W. D., J. A. Hanselman, C. Knox, B. G. Valencia & M. B. Bush. 2009. Long-term drivers of change in *Polylepis* woodland distribution in the central Andes. *J. Veg. Sci.* 20: 1041–1052.
- Gulizia, C. & I. Camilloni. 2015. Comparative analysis of the ability of a set of CMIP3 and CMIP5 global climate models to represent precipitation in South America. *Int. J. Climatol.* 35(4): 583–595.
- Hannah, L., L. Flint, A. D. Syphard, M. A. Moritz, L. B. Buckley & I. M. McCullough. 2014. Fine-grain modeling of species' response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends Ecol. Evol.* 29(7): 390–397.
- Hanselman, J. A., W. D. Gosling, G. M. Paduano & M. B. Bush. 2005. Contrasting pollen histories of MIS 5e and the Holocene from Lake Titicaca (Bolivia/Peru). *J. Quatern. Sci.* 20: 663–670.
- Hanselman, J. A., M. B. Bush, W. D. Gosling, A. Collins, C. Knox, P. A. Baker & S. C. Fritz. 2011. A 370,000-year record of vegetation and fire history around Lake Titicaca (Bolivia/Peru). *Palaeogeogr. Paleoclimatol. Palaeoecol.* 305: 201–214.
- Hearty, P. & B. Torrey. 2017. Sea-level change and superstorms; geologic evidence from the last interglacial (MIS 5e)

- in the Bahamas and Bermuda offers ominous prospects for a warming Earth. *Mar. Geol.* 390: 347–365.
- Holm, J. A., L. M. Kueppers & J. Q. Chambers. 2017. Novel tropical forests: Response to global change. *New Phytol.* 213: 988–992. doi:10.1111/nph.14407.
- IPCC (Intergovernmental Panel on Climate Change). 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge.
- Jackson, S. T. & J. W. Williams. 2004. Modern analogs in Quaternary palaeoecology: Here today, gone yesterday, gone tomorrow? *Annual Rev. Earth Planet. Sci.* 32: 495–537.
- Junk, W. J. 1997. *The Central Amazon Floodplain: Ecology of a Pulsing System.* Vol. 126. Springer Verlag, Berlin.
- Junk, W. J., M. T. F. Piedade, J. Schöngart, M. Cohn-Haft, J. M. Adeney & F. Wittmann. 2011. A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands* 31(4): 623–640.
- Ledru, M.-P., P. Mourguiart & C. Riccomini. 2009. Related changes in biodiversity, insolation and climate in the Atlantic rainforest since the last interglacial. *Palaeogeogr. Paleoclimatol. Palaeoecol.* 271(1): 140–152.
- Ledru, M.-P., M. L. F. Salatino, G. Ceccantini, A. Salatino, F. Pinheiro & J.-C. Pintaud. 2007. Regional assessment of the impact of climatic change on the distribution of a tropical conifer in the lowlands of South America. *Diversity Distrib.* 13(6): 761–771. doi:10.1111/j.1472-4642.2007.00389.x.
- Levis, C., F. R. Costa, F. Bongers, M. Peña-Claros, C. R. Clement, A. B. Junqueira, E. G. Neves, et al. 2017. Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* 355(6328): 925–931.
- Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field & D. D. Ackerly. 2009. The velocity of climate change. *Nature* 462(7276): 1052–1055.
- Lovejoy, T. E. & C. Nobre. 2018. Amazon tipping point. *Sci. Advances* 4: Ea2340.
- Lynch-Stieglitz, J. 2017. The Atlantic meridional overturning circulation and abrupt climate change. *Annual Rev. Mar. Sci.* 9: 83–104.
- Maezumi, Y., M. Robinson, J. de Souza, D. H. Urrego, D. Shaan, J. Iriarte & D. Alves. 2018. New insights from pre-Columbian land use and fire management in Amazonian Dark Earth forests. *Frontiers Ecol. Evol.* https://doi.org/10.3389/fevo.2018.00111.
- Malhi, Y., L. Aragão, D. Galbraith, C. Huntingford, R. Fisher, P. Zelazowski, S. Sitch, et al. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proc. Natl. Acad. Sci* 106: 20610–5. doi:10.1073/pnas.0804619106.
- Marengo, J. A., C. A. Nobre, G. Sampaio, L. F. Salazar & L. S. Borma. 2011. Climate change in the Amazon Basin: Tipping points, changes in extremes, and impacts on natural and human systems. Pp. 259–283 in M. Bush, J. Flenley & W. Gosling (editors), *Tropical Rainforest Responses to Climatic Change.* Springer, Berlin, Heidelberg.
- McLachlan, J. S. & J. S. Clark. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86: 2088–2098.
- McMichael, C. N. H. & M. B. Bush. 2019. Spatiotemporal patterns of pre-Columbian people in Amazonia. *Quatern. Res.* 92: 53–69.
- McMichael, C. N. H., D. R. Piperno, M. B. Bush, M. R. Silman, A. R. Zimmerman, M. F. Raczka & L. C. Lobato. 2012. Sparse pre-Columbian human habitation in western Amazonia. *Science* 336: 1429–1431.
- McMichael, C. N. H., K. J. Feeley, C. W. Dick, D. R. Piperno & M. B. Bush. 2017. Comment on “Persistent effects of pre-Columbian plant domestication on Amazonian forest composition.” *Science* 358(6361). <http://science.sciencemag.org/content/358/6361/ean8347>.
- Metcalf, J. L., C. Turney, R. Barnett, F. Martin, S. C. Bray, J. T. Vilstrup, L. Orlando, et al. 2016. Synergistic roles of climate warming and human occupation in Patagonian megafaunal extinctions during the Last Deglaciation. *Sci. Advances* 2(6): E1501682. doi:10.1126/sciadv.1501682.
- Miralles, D. G., P. Gentile, S. I. Seneviratne & A. J. Teuling. 2019. Land–atmospheric feedbacks during droughts and heatwaves: State of the science and current challenges. *Ann. New York Acad. Sci.* 1436(1): 19.
- Miralles, D. G., R. A. M. De Jeu, J. H. Gash, T. R. H. Holmes & A. J. Dolman. 2011. Magnitude and variability of land evaporation and its components at the global scale. *Hydrol. Earth Syst. Sci.* 15: 967–981. https://doi.org/10.5194/hess-15-967-2011.
- Morton, D., Y. Le Page, R. DeFries, G. Collatz & G. Hurtt. 2013. Understorey fire frequency and the fate of burned forests in southern Amazonia. *Philos. Trans., Ser. B* 368(1619): 20120163.
- Mosblech, N. A., M. B. Bush & R. Van Woesik. 2011. On metapopulations and microrefugia: Palaeoecological insights. *J. Biogeogr.* 38: 419–429.
- Nascimento, M. N., G. S. Martins, R. C. Cordeiro, B. Turcq, L. S. Moreira & M. B. Bush. 2019. Vegetation response to climatic changes in western Amazonia over the last 7,600 years. *J. Biogeogr.* 46: 2389–2406. https://doi.org/10.1111/jbi.13704.
- Nepstad, D., P. Lefebvre, U. L. D. Silva, J. Tomasella, P. Schlesinger, L. Solorzano, P. Moutinho, et al. 2004. Amazon drought and its implications for forest flammability and tree growth: A basin-wide analysis. *Global Change Biol.* 10: 704–717.
- Nepstad, D. C., C. M. Stickler, B. Soares-Filho & F. Merry. 2008. Interactions among Amazon land use, forests and climate: Prospects for a near-term forest tipping point. *Philos. Trans., Ser. B* 363(1498): 1737–1746. https://doi.org/10.1098/rstb.2007.0036.
- NGRIP (North Greenland Ice Core Project members). 2004. High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature* 431: 147–151. https://doi.org/10.1038/nature02805.
- Niemann, H. & H. Behling. 2009. Late Pleistocene and Holocene environmental change inferred from the Cocha Caranga sediment and soil records in the southeastern Ecuadorian Andes. *Palaeogeogr. Paleoclimatol. Palaeoecol.* 276(1–4): 1–14.
- Nobre, C. A. & L. D. S. Borma. 2009. ‘Tipping points’ for the Amazon forest. *Curr. Opin. Environ. Sustain.* 1(1): 28–36.
- Peres, C. A., T. Emilio, J. Schietti, S. J. Desmoulière & T. Levi. 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl. Acad. Sci. U.S.A.* 113(4): 892–897.
- Piperno, D. R., C. McMichael & M. B. Bush. 2015. Amazonia and the Anthropocene: What was the spatial extent and intensity of human landscape modification in the Amazon Basin at the end of prehistory? *Holocene* 25(10): 1588–1597.
- Placzek, C., J. Quade & P. J. Patchett. 2006. Geochronology and stratigraphy of late Pleistocene lake cycles on the southern Bolivian Altiplano: Implications for causes of tropical climate change. *Geol. Soc. Amer. Bull.* 118(5–6): 515–532.
- Raczka, M. F., N. A. Mosblech, L. Giosan, A. M. Folcik, B. G. Valencia, M. Kingston, S. Baskin, et al. 2019. A human role

- in Andean megafaunal extinction? *Quatern. Sci. Rev.* 205: 154–165.
- Rammig, A., T. E. Jupp, K. Thonicke, B. Tietjen, J. Heinke, S. Ostberg, W. Lucht, et al. 2010. Estimating the risk of Amazonian forest dieback. *New Phytol.* 187: 694–706.
- Rehm, E. M. & K. J. Feeley. 2015. The inability of tropical cloud forest species to invade grasslands above treeline during climate change: Potential explanations and consequences. *Ecography* 38: 1167–1175. <https://doi.org/10.1111/ecog.01050>.
- Richerson, P. J., R. Boyd & R. L. Bettinger. 2001. Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis. *Amer. Antiq.* 66(3): 387–411.
- Rozas-Davila, A., B. G. Valencia & M. B. Bush. 2016. The functional extinction of Andean megafauna. *Ecology* 97(10): 2533–2539.
- Rull, V. 2009. Microrefugia. *J. Biogeogr.* 36(3): 481–484.
- Rundel, P. W., M. T. Arroyo, R. M. Cowling, J. E. Keeley, B. B. Lamont & P. Vargas. 2016. Mediterranean biomes: Evolution of their vegetation, floras, and climate. *Annual Rev. Ecol. Evol. Syst.* 47: 383–407.
- Salati, E. 1985. The climatology and hydrology of Amazonia. Pp. 18–48 in G. T. Prance & T. E. Lovejoy (editors), *Amazonia*. Pergamon, New York.
- Sampaio, G., C. Nobre, M. H. Costa, P. Satyamurty, B. S. Soares-Filho & M. Cardoso. 2007. Regional climate change over eastern Amazonia caused by pasture and soybean cropland expansion. *Geophys. Res. Lett.* 34(17). <https://doi.org/10.1029/2007GL030612>.
- Sampaio, G., L. S. Borma, M. Cardoso, L. M. Alves, C. von Randow, D. A. Rodriguez, C. A. Nobre, et al. 2019. Assessing the possible impacts of a 4°C or higher warming in Amazonia. Pp. 201–218 in C. A. Nobre, J. A. Marengo & W. R. Soares (editors), *Climate Change Risks in Brazil*. Springer, Cham, Switzerland.
- Sarmiento, F. 2012. Contesting Páramo: Critical Biogeography of the Northern Andean Highlands. Kona Publishers, Charlotte.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke & B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591–596.
- Scheffer, M., F. Westley & W. Brock. 2003. Slow response of societies to new problems: Causes and costs. *Ecosystems* 6(5): 493–502.
- Schröder, A., L. Persson & A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: A review. *Oikos* 110(1): 3–19. doi:10.1111/j.0030-1299.2005.13962.x.
- Shukla, J., C. Nobre & P. Sellers. 1990. Amazon deforestation and climate change. *Science* 247: 1322–1326.
- Silva, C. H. L. J., L. O. Anderson, A. L. Silva, C. T. Almeida, R. Dalagnol, M. A. Pletsch, T. V. Penha, et al. 2019. Fire responses to the 2010 and 2015/2016 Amazonian droughts. *Frontiers Earth Sci.* 7: 97.
- Silvério, D. V., P. M. Brando, J. K. Balch, F. E. Putz, D. C. Nepstad, C. Oliveira-Santos & M. M. Bustamante. 2013. Testing the Amazon savannization hypothesis: Fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. *Philos. Trans., Ser. B* 368(1619): 20120427.
- Sternberg, L. S. L. 2001. Savanna-forest hysteresis in the tropics. *Global Ecol. Biogeogr.* 10: 369–378.
- Sulca, J., K. Takahashi, J. C. Espinoza, M. Vuille & W. Lavado-Casimiro. 2018. Impacts of different ENSO flavors and tropical Pacific convection variability (ITCZ, SPCZ) on austral summer rainfall in South America, with a focus on Peru. *Int. J. Climatol.* 38(1): 420–435.
- Sylvester, S. P., M. D. Sylvester & M. Kessler. 2014. Inaccessible ledges as refuges for the natural vegetation of the high Andes. *J. Veg. Sci.* 25(5): 1225–1234.
- Sylvester, S. P., F. Heitkamp, M. D. Sylvester, H. F. Jungkunst, H. J. Sipman, J. M. Toivonen, C. A. G. Inca, et al. 2017. Relict high-Andean ecosystems challenge our concepts of naturalness and human impact. *Sci. Rep.* 7: 3334. doi:10.1038/s41598-017-03500-7.
- Uhl, C. & J. B. Kauffman. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* 71(2): 437–449.
- Valencia, B. G., F. Matthews-Bird, D. H. Urrego, J. J. Williams, W. D. Gosling & M. Bush. 2016. Andean microrefugia: Testing the Holocene to predict the Anthropocene. *New Phytol.* 212(2): 510–522.
- Valencia, B. G., M. B. Bush, A. L. Coe, E. Orren & W. D. Gosling. 2018. *Polylepis* woodland dynamics during the last 20,000 years. *J. Biogeogr.* 45: 1019–1030. <https://doi.org/10.1111/jbi.13209>.
- VanDerWal, J., H. T. Murphy, A. S. Kutt, G. C. Perkins, B. L. Bateman, J. J. Perry & A. E. Reside. 2013. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nat. Clim. Change* 3(3): 239–243.
- Vuille, M., M. Carey, C. Huggel, W. Buytaert, A. Rabatel, D. Jacobsen, A. Soruco, et al. 2018. Rapid decline of snow and ice in the tropical Andes—Impacts, uncertainties and challenges ahead. *Earth-Sci. Rev.* 176: 195–213.
- Wang, R., J. A. Dearing, P. G. Langdon, E. Zhang, X. Yang, V. Dakos & M. Scheffer. 2012. Flickering gives early warning signals of a critical transition to a eutrophic lake state. *Nature* 492(7429): 419.
- Weng, W., M. K. Luedeke, D. C. Zemp, T. Lakes & J. P. Kropp. 2018. Aerial and surface rivers: Downwind impacts on water availability from land use changes in Amazonia. *Hydrol. Earth Syst. Sci.* 22(1): 911–927.
- White, S. 2013. Grass páramo as hunter-gatherer landscape. *Holocene* 23: 898–915.
- Zemp, D. C., C.-F. Schleussner, H. M. Barbosa, M. Hirota, V. Montade, G. Sampaio, A. Staal, et al. 2017. Self-amplified Amazon forest loss due to vegetation-atmosphere feedbacks. *Nat. Commun.* 8: 14681.