

An exceptional role for flowering plant physiology in the expansion of tropical rainforests and biodiversity

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Movement of water from soil to atmosphere by plant transpiration can feed precipitation, but is limited by the hydraulic capacities of plants, which have not been uniform through time. The flowering plants that dominate modern vegetation possess transpiration capacities that are dramatically higher than any other plants, living or extinct. Transpiration operates at the level of the leaf, however, and how the impact of this physiological revolution scales up to the landscape and larger environment remains unclear. Here, climate modelling demonstrates that angiosperms help ensure aseasonally high levels of precipitation in the modern tropics. Most strikingly, replacement of angiosperm with non-angiosperm vegetation would result in a hotter, drier and more seasonal Amazon basin, decreasing the overall area of ever-wet rainforest by 80 per cent. Thus, flowering plant ecological dominance has strongly altered climate and the global hydrological cycle. Because tropical biodiversity is closely tied to precipitation and rainforest area, angiosperm climate modification may have promoted diversification of the angiosperms themselves, as well as radiations of diverse vertebrate and invertebrate animal lineages and of epiphytic plants. Their exceptional potential for environmental modification may have contributed to divergent responses to similar climates and global perturbations, like mass extinctions, before and after angiosperm evolution.

Keywords: leaf; transpiration; angiosperm; tropical rainforest; precipitation

1. INTRODUCTION

Recycling of water through evapotranspiration provides an important contribution to precipitation, particularly in the tropics (Salati *et al.* 1979), and the effect of transpiration on the hydrological cycle has been studied in the context of hypothetical deforestation (e.g. Shukla & Mintz 1982; Oyama & Nobre 2004), glacial–interglacial climate change (e.g. Kleidon & Lorenz 2001) and future global warming (e.g. Cramer *et al.* 2001). However, this capacity to move water from soil to atmosphere has not been uniform through time: the flowering plants that now dominate most terrestrial environments recently have been shown to have unparalleled capacities to transpire water (Boyce *et al.* 2009). Because water loss is an inevitable component of leaf gas exchange, photosynthesis is limited by the ability of the plant to replace water lost through transpiration. Since the path length from vein to stomata is an important determinant of leaf hydraulic conductivity, both CO₂ assimilation and water transpirational loss are tightly correlated with the density of veins within the leaf (Brodribb *et al.* 2007; Boyce *et al.* 2009; Brodribb & Feild 2010; McKown *et al.* 2010). Vein density, therefore, provides a physiological proxy measurable in the fossil record and allows assessment of long extinct taxa with physiologies previously unconstrained. A fourfold increase in mean and maximum vein density has been documented with the

evolution of angiosperms over all other fossil and extant plants (Boyce *et al.* 2009), indicating that the flowering plants represent a fundamental physiological shift. Thus, angiosperms represent an unprecedented increase in transpiration capacities at the level of the leaf. However, the scaling-up of this leaf-level effect to the canopy and landscape is complexly dependent on feedbacks between the plant, soil moisture and atmospheric humidity. As a result, the magnitude of this biotic effect on global climate and ecosystems is unclear.

Flowering plants dominate modern terrestrial environments except in alpine and high-latitude regions, and they are the basis of the photosynthetic formulations in global climate models (e.g. Collatz *et al.* 1991). Here, we investigate the potential dependence of terrestrial environments on angiosperm physiology with climate model simulations. Standard global climate models that are widely used by the climate science community are modified only in that non-angiosperm physiology is substituted globally for that of the angiosperms while maintaining modern vegetative biomass. The environmental impact of angiosperms would have been first felt in the Cretaceous, albeit with extensively debated timing, geography and ecology (Morley 2000; Ziegler *et al.* 2003; Burnham & Johnson 2004; Jaramillo *et al.* 2006). Although modelling of the effect of angiosperm evolution on Cretaceous climates is ongoing, the emphasis here is not on the specific climate regime in which they originated but on determining the significance of their elevated transpirational capacities for climate in general. The effect of angiosperms is conflated in the Cretaceous system with several poorly constrained or variable physical parameters, including the timing and geography of

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angiosperm ecological spread, atmospheric composition, sea surface temperatures and palaeogeography. These variables are both complex and inter-related. For example, the elevated CO₂ concentrations of the Cretaceous would both decrease the need to facilitate CO₂ uptake with high maximal stomatal conductance (Gedney *et al.* 2006; Betts *et al.* 2007; Franks & Beerling 2009) and increase average evapotranspirational demand by increasing global temperatures, with the overall effect on transpiration representing the summation of these positive and negative elements. Thus, modern climate is used here as the best-constrained system in which to isolate and investigate angiosperm influence.

2. METHODS

The National Center for Atmospheric Research Community Atmospheric Model v. 3.0 (Collins *et al.* 2006) was coupled with the Community Land Model 3.5 (CLM 3.5; Oleson *et al.* 2008). Stomatal conductance for the leaves is formulated using canopy temperature, CO₂ concentration, soil moisture availability and sunlight. Gas (CO₂ and H₂O) exchange across the stomata is calculated by the diffusive flux along the gas concentration gradient and stomatal conductance (Bonan 1996). Transpiration capacities, thus, were modified by decreasing the maximum carboxylation rate when intercellular air space is saturated with CO₂ (V_{\max}), which decreases the effective photosynthetic/transpirational capacity. This close link between photosynthetic and hydraulic capacities is well supported throughout land plants (Brodribb *et al.* 2007). The modern world without flowering plants was simulated by lowering V_{\max} by a factor of four (Boyce *et al.* 2009). All runs were integrated for 13 years and results were averaged for the last 10 years. The resolution of the model is approximately 2.8° latitude and approximately 2.8° longitude—with 10 layers in the soil and 26 layers in the atmosphere. Climatological sea surface temperatures and sea ice distributions were specified. The results presented involve the standard convection scheme (Zhang & McFarlane 1995), but are robust to alternative convection schemes (Emanuel 1991).

The decrease in transpiration per unit leaf area with the loss of high angiosperm transpiration capacities could be partially offset if there was an accompanying increase in total leaf area. In such a case, a smaller overall transpiration decrease of approximately one-half might be the most accurate; however, this scenario is unrealistic, particularly in the tropics where transpiration recycling is most important. The increased self-shading that results in plants with highly elevated leaf area index (LAI) requires open, high light environments limited to marginal habitats and areas of recent disturbance, particularly in the wet tropics (e.g. Brodribb & Feild 2008). In practice, the highest LAI values are found in temperate conifers, particularly the Pinaceae, a conifer family that has never had more than limited presence in the lowland tropics. Many of the groups that would have been important before angiosperm evolution actually tend to have either intermediate LAIs, including the often broad-leaved conifers in the Podocarpaceae (LAI near approx. 3.0 in *Dacrydium* (DeLucia *et al.* 2003) and *Podocarpus* (Fetene & Beck 2004)) and Araucariaceae (LAI of 1–3.7 in *Agathis*; Silvester & Orchard 1999) that are important in the modern tropics, or have low LAIs, particularly the cycads, tree ferns and various extinct seed plant lineages with a distal rosette of leaves (LAI of 1.7

in *Cibotium*; Harrington *et al.* 2001). LAI might also be expected to be lower without angiosperms given the relationships of biomass production with transpiration (figure 1a) and precipitation: a loss of transpiration leads to less precipitation, which leads to a reduction in biomass and feeds back to a further reduction in transpiration. Thus, an effect somewhere between one-quarter and one-eighth of modern transpiration levels is deemed the most likely impact of angiosperm replacement, and a reduction to one-quarter of modern levels, as a conservative estimate, is coupled with full maintenance of modern leaf area as the primary point of consideration here. In order to establish the robustness of the results, drops in transpiration rate of one-half and one-eighth were also modelled. Effects are large and are seen across all three modelled stages of transpiration reduction (electronic supplementary material, figure S1).

3. RESULTS

Model results indicate that the increased hydraulic capacity of angiosperms has a large but variable impact upon terrestrial climates, with the world being both drier and hotter in their absence (figure 1). The largest effects are seen in the tropics, particularly tropical South America. The smaller influence of angiosperm transpiration at extratropical latitudes can still be proportionally large in temperate environments (with a 30–50% reduction in precipitation in eastern North America in the absence of angiosperms: figure 2), but is necessarily limited to the growing season when transpiration occurs and is dwarfed in absolute terms by the impact on tropical climates. The relationship between transpiration and precipitation can be complex: increased angiosperm transpiration can actually result in reduced precipitation in some areas locally owing to changes induced in moisture convergence patterns (figures 1–3). However, the overall effect of angiosperms is still strongly positive. For example, an additional 300 mm of precipitation per year is received averaged over the whole of tropical South America, including drier areas, and with local increases that are much greater (figure 3).

In tropical South America, the impact of angiosperms is particularly strong in the eastern part of the Amazon basin (black box in figure 3), where precipitation is known to be sensitive to local evapotranspiration in austral spring around the time of the onset of the South American monsoon (Fu & Li 2004; Lintner & Neelin 2009). There, the impact of angiosperm presence involves both a generalized increase in rainfall throughout the year—including a wetter dry season with a driest month of 45 mm month⁻¹ of precipitation compared with a driest month of 20 mm month⁻¹ with exclusively non-angiosperm vegetation—and a dramatic decrease in the length of the dry season with the largest changes occurring in austral spring (figure 4). Observations show that the onset of the monsoon in South America is very abrupt (Gan *et al.* 2004), and the timing is governed by the amount of moisture in the boundary layer (Fu & Li 2004). Without the extra boundary layer moistening from high angiosperm transpiration rates, the monsoon would start much later (10 January compared with 26 October; table 1) and end slightly earlier (12 April versus 16 April) for an overall decrease in the wet season duration of about 80 days if this region were covered by plants other than flowering

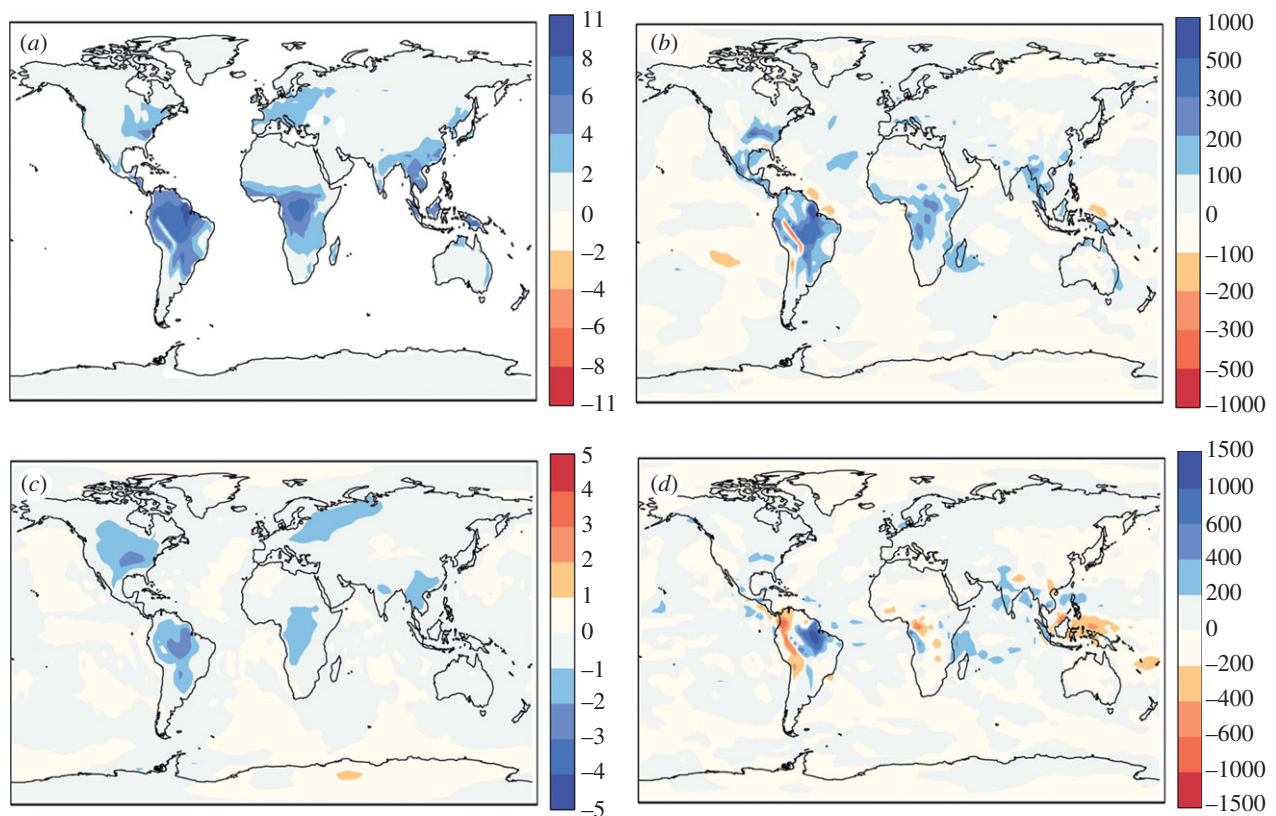


Figure 1. The differences in (a) mean gross primary productivity ($\mu\text{mol m}^{-2} \text{s}^{-1}$), (b) annual evapotranspiration (mm yr^{-1}), (c) mean air temperature ($^{\circ}\text{C}$) 2 m above the surface, and (d) annual precipitation (mm yr^{-1}) between simulations with present day vegetation and with vegetation lacking the high transpiration of angiosperms. Precipitation increases with angiosperms can be larger than local transpiration increases owing to changes induced in atmospheric convection and the redistribution of moisture by prevailing winds.

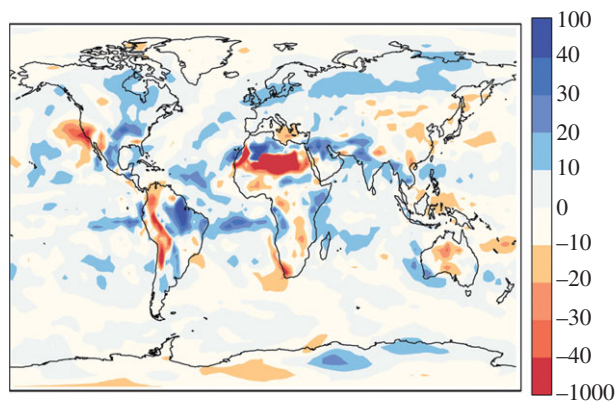


Figure 2. The per cent differences in annual precipitation ($\frac{P_{+A} - P_{-A}}{P_{+A}} \times 100\%$), where P_{+A} and P_{-A} are simulated precipitation with and without angiosperms. Precipitation is higher with angiosperms over most forested regions. The proportional changes in dry regions are exaggerated because there is very little precipitation.

plants. The energy budget and surface temperatures over tropical regions are also tied to evapotranspiration (Lee *et al.* 2005). The increased transpiration in angiosperm ecosystems decreases surface heat loss by sensible heat and results in a large decrease in temperature over tropical/subtropical South America (figure 3a), particularly during the dry-to-wet transition period in September through to November (figure 4b).

The area of tropical South America (10°N – 20°S) subjected to very wet conditions decreases dramatically

if the region is not covered by flowering plants (figure 5). A replacement of angiosperms is calculated to reduce the area of ever-wet conditions (minimum of 100 mm precipitation in each month; Morley 2000) in the central and eastern Amazon (20°S – 10°N ; 70°W – 45°W) from $8.4 \times 10^5 \text{ km}^2$ (observed area $9.8 \times 10^5 \text{ km}^2$) to $1.6 \times 10^5 \text{ km}^2$. Climate changes without angiosperms are also present in other parts of the tropics (figure 1), but the effect is smaller—presumably owing to geographical differences. Maritime proximity and orography help ensure high rainfall in Southeast Asia and Malesia regardless of vegetation type, although angiosperms still influence climate as transpiration over tropical forests shifts convection centres inland and away from over the oceans. African tropical forests are already relatively dry and seasonal owing to the broad tropical extent of continental highlands uplifted in the last 10 Myr (Partridge 1997) and larger latitudinal swings of the intertropical convergence zone (McGregor & Nieuwolt 1998; Ziegler *et al.* 2003). However, South America, where effects are largest, represents more than 50 per cent of global tropical rainforest area (Morley 2000), and our results predict that replacement of angiosperms would reduce the area of ever-wet conditions within the Amazon basin by a factor of five.

4. DISCUSSION

The increased transpiration capacity of angiosperms results in large increases in moisture recycling, and an overall increase in precipitation. The largest impact is

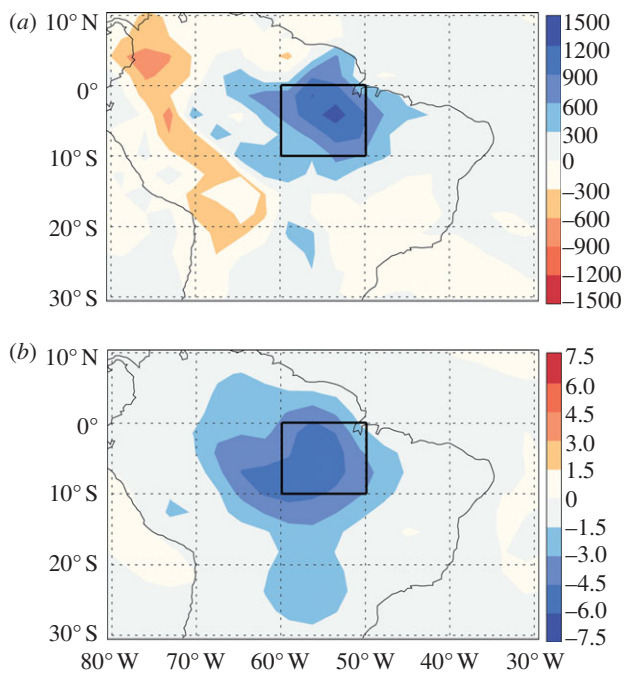


Figure 3. (a) The differences in annual precipitation (mm yr^{-1}) and (b) September–October–November temperature ($^{\circ}\text{C}$) for tropical South America between simulations with the present day angiosperm-dominated vegetation and with vegetation lacking the high transpiration of angiosperms.

seen in areas with a year-round growing season, thus the tropics in the current cool global climate. At higher latitudes, the effects can still be proportionally large, but are necessarily curtailed by leafless winters. However, during the global warm period of the Early Cenozoic, tropical-aspect rainforests spread extensively to temperate latitudes in both hemispheres (Morley 2000), and the year-round growth of angiosperms may have been essential for maintaining the high rainfall of these ‘Boreotropical’ rainforests.

Seasonal limits on photosynthesis can also be imposed by drought, but angiosperm effects on precipitation can limit the duration and severity of dry seasons in areas where rainfall is at least seasonally available (figures 4 and 5). Wet conditions can thereby be propagated out from areas that would already have high precipitation: ever-wet rainforest would exist in tropical South America with or without the angiosperms, but the area of ever-wet conditions is dramatically increased with their presence (figure 5). Angiosperms first appeared in the Mid-Cretaceous, which was followed by a more protracted rise to ecological dominance (Tiffney 1984; Wing *et al.* 1993; Wing & Boucher 1998). Global temperatures were warm before and after their ecological spread, but climates differed dramatically. Direct modeling of the impact of angiosperms under Cretaceous conditions is needed, but it is notable that the fossil record indicates at least seasonal aridity was widespread in the Cretaceous at both tropical and temperate latitudes, while vegetation consistent with ever-wet conditions was well established at similar temperatures at both tropical and temperate latitudes after the rise of angiosperm ecological dominance (Upchurch & Wolfe 1987; Morley 2000; Johnson & Ellis 2002; Burnham & Johnson 2004; Jaramillo *et al.* 2006; Wing *et al.* 2009).

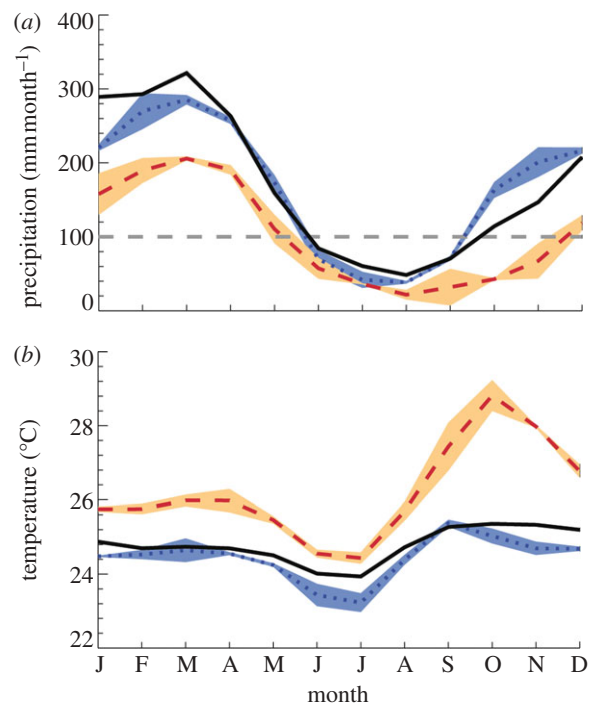


Figure 4. (a) Monthly mean precipitation and (b) temperature over the eastern part of the Amazon basin (figure 3, inset) from observations (solid black line) and in simulations with either present day vegetation (blue dotted line) or vegetation lacking the high transpiration of angiosperms (red dotted line). Shaded areas show one standard deviation. $100 \text{ mm month}^{-1}$ represents minimum precipitation for rainy season (Morley 2000).

Although patterns within subgroups can be complex (Punyasena *et al.* 2008), the diversities of tropical plants, invertebrates and vertebrates are fostered by abundance of rainfall, evenness of rainfall and the broad geographical extent of rainforests (Reed & Fleagle 1995; Kleidon & Mooney 2000; Hawkins *et al.* 2003; Leigh *et al.* 2004; Jaramillo *et al.* 2006; Kreft & Jetz 2007)—all shown here to be bolstered by the high transpiration rates of the angiosperms. For example, if the particularly strong correlation between tropical plant diversity and number of wet days (Kreft & Jetz 2007) is taken at face value—not including other important factors such as regional history, geography and nutrient dynamics in determining plant diversity—then 50 per cent reductions in local plant diversities would be expected to accompany the average loss of 86 wet days per year in the eastern part of the Amazon when angiosperm vegetation is replaced (figure 5). Thus, in no small part, angiosperm tropical diversity is the result of the ecosystem modifications initiated by the hydraulic physiology of angiosperms themselves.

The increases in animal diversity with increasing precipitation are probably an indirect consequence of the impact of precipitation on plant diversity and productivity, upon which animal diversity depends more directly (Kay *et al.* 1997; Novotny *et al.* 2006). Since plant epiphytes require frequent and aseasonal rainfall, they would have benefited more directly from the increased precipitation that angiosperms initiated (Boyce 2008), and epiphytic angiosperms, ferns, lycophytes and bryophytes all radiated only after angiosperms came to dominate tropical ecosystems (Boyce *et al.*

Table 1. Mean onset, demise and duration of the rainy season, as well as minimum and maximum values of any individual year in runs with and without angiosperm transpiration capacities. (Following Gan *et al.* (2004), the onset and demise of the rainy season are defined as the pentad with rainfall greater (onset) or less (demise) than 4 mm d^{-1} for at least 75% of the following eight pentads. Dates represent the centre of the relevant pentad. The ranges of onset and demise of the monsoon in the run with angiosperms are close to the observed ranges (Gan *et al.* 2004; Li & Fu 2004).)

	with angiosperms			without angiosperms		
	onset	demise	duration (days)	onset	demise	duration (days)
min	14 Nov	3 Apr	185	23 Jan	3 Apr	100
mean	26 Oct	16 Apr	202	10 Jan	12 Apr	122
max	15 Oct	28 Apr	220	29 Dec	18 Apr	140

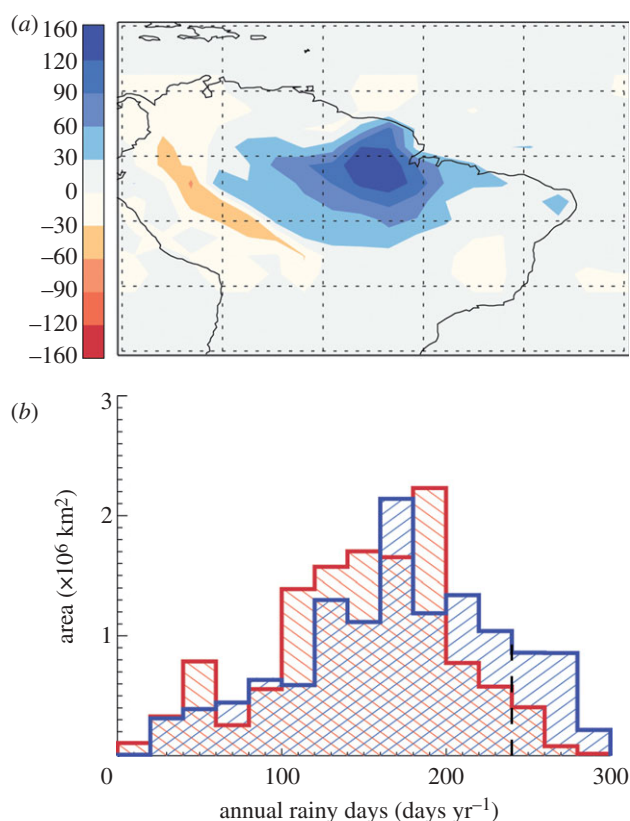


Figure 5. (a) Differences in number of rainy days per year between simulations with present day vegetation and with vegetation lacking the high transpiration of angiosperms. (b) Histogram of the area in tropical/subtropical South America ($30^\circ \text{ S} - 10^\circ \text{ N}$) for each 20-day bin of the number of rainy days per year for simulations with present day vegetation (blue, back crosshatch) or with vegetation lacking the high transpiration of angiosperms (red, forward crosshatch). A wet day is defined as one with more than 3 mm of rain. Number of rainy days greater than 240 days (dashed black line) roughly coincides with ever-wet rainforest.

2009; Schuettpelz & Pryer 2009). Indeed, numerous lineages of vertebrate and invertebrate animals are also now thought to have radiated shortly after angiosperm diversification (Wang *et al.* 2009), and the propagation of high rainfall conditions by angiosperms provides a potential causal mechanism explaining this phenomenon.

Because angiosperms can so strongly modify their climates, any environmental perturbation severe enough to degrade that vegetation would be exacerbated by its loss. Tropical South America would be both hotter and drier without angiosperm forests—in line with the climate

change expected to accompany the current anthropogenic degradation of rainforest vegetation (Shukla *et al.* 1990; Lawton *et al.* 2001; Pielke *et al.* 2007). Along with the various other climate effects that have been hypothesized for the End-Cretaceous bolide impact (O’Keefe & Ahrens 1989; Gupta *et al.* 2001), the destruction of forest canopies in its immediate aftermath may be expected to have resulted in substantially less precipitation until the vegetation recovered, as well as a temperature increase owing to the loss of transpirational cooling—an effect that is seasonally as large as 5° C in the Amazon basin today (figures 1, 3 and 4). Alternatively, the degradation of non-angiosperm vegetation during earlier events, such as the End-Permian (Looy *et al.* 1999) or Triassic/Jurassic extinctions (McElwain *et al.* 2009), would have had a much smaller feedback with climate. Thus, angiosperm evolution should be a consideration in future studies of mass extinctions and other environmental perturbations like the Palaeocene/Eocene Thermal Maximum (Wing *et al.* 2005) because the same angiosperm-initiated climate modifications that contribute to the high diversity of angiosperm ecosystems may also make those ecosystems prone to more exaggerated responses to environmentally destructive events.

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