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The development of agriculture in the Americas: an ecological perspective

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Abstract. Agriculture began independently in both North and South America ~10,000 years before present (YBP), within a few thousand years of the arrival of humans in the Americas. This contrasts with the thousands of years that people were present in the old world before agriculture developed. In this paper, I hypothesize that the drastic extinctions of most large herbivores in the Americas may have accelerated the onset of agriculture in the Americas for three reasons: net primary production (NPP) became available for human utilization, the domestication of wild crop types was more feasible in the absence of megaherbivore competition, and hunting societies became more sedentary as their prey went extinct, the first step towards agriculture. I test these theories by calculating NPP liberated following the megafauna extinctions and find that the availability of NPP and the absence of competitive herbivory were significantly correlated with the timing of the onset of agriculture. The extinction of so many keystone herbivores may have accelerated the development of agriculture in the Americas, with humans essentially filling the empty herbivore niches.

Key words: agriculture; extinctions; herbivores; megafauna; NPP.

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INTRODUCTION

Between about 10,500 and 4,500 BP, agriculture based on domestication of wild plants arose independently in many different geographic areas (Diamond and Bellwood 2003). Recent studies have pushed back the dates in which agriculture developed independently in both North and South America, and pushed forward the dates of onset in the near East so all three are currently thought to have begun ~10,000 years ago (Diamond and Bellwood 2003, Balter 2007, Dillehay et al. 2007, Smith 1997).

Why did agriculture only began ~10,000 years ago instead of ~50,000–100,000 years ago when humans first become cognitively modern? Multiple independent origins of agriculture during a similar period suggest a global environmental driver. The onset of the Holocene ~10,000 years ago is an attractive hypothesis for why agriculture began independently at this time because the warmer, wetter, higher CO_2 conditions of the Holocene generally encourage plant growth (Childe 1951, Sage 1995). The Holocene was also less prone than the Pleistocene to large climatic shifts that would be harmful to agriculture. These environmental changes have led some to theorize that agriculture may have been "mandatory" in the Holocene but "impossible" during the Pleistocene (Richerson et al. 2001).

Others have hypothesized that the warmer, wetter conditions of the Holocene accelerated human population growth, causing a food crisis that forced people to selectively exploit easily storable food, leading to agriculture (Cohen 1977). However, others doubt economic and environmental explanations for the rise of agriculture, instead hypothesizing that changing social structures or increasing social obligations led to the development of agriculture. For instance, it may have arisen through an increase in religious symbolism (Cauvin 2000), or by ambitious hunter gatherer's seeking greater wealth in their communities (Hayden 1990). However, a global driver, such as climate, is also likely because agriculture developed independently in several regions ~10,000 years before present; but climate was not the only potential global driver during this period.

Another such event at this time was the extinction of the Pleistocene megaherbivores. These extinctions are generally explained as driven by human over-hunting, climate change, or a combination of the two (Barnosky et al. 2004). Animals occupying entire ecological roles went extinct, with extinctions of animals greater than 44kg in Australia (88% of megaherbivores genera), South America (84%), North America (72%), Eurasia (36%) and Africa (18%) (Barnosky et al. 2004). The extinctions took place in approximately the following order: Australia (50000 BP), Africa (45000 BP), Eurasia (12000 BP), North America (12000 BP), northern South America (10000 BP) (Barnosky et al. 2004).

An ecological hypothesis explaining the independent onset of agriculture is that humans began to fill open herbivore niches abandoned by the extinct megaherbivores. Much of the NPP once used by these extinct animals was eventually consumed by humans through agriculture (Doughty and Field 2010). There are several ways the absence of keystone herbivores could accelerate the development of agriculture. For instance, the domestication of crops is a slow process, with both corn (Jaenicke-Despres et al. 2003), wheat (Tanno and Willcox 2006), and other crops (Fuller 2007) needing thousands of years to be domesticated, with humans exerting weak, rather than strong domestication pressure (Fuller 2007). Such a long, weak domestication process would have been continually disrupted by the competitive herbivory of megaherbivores before they went extinct. In addition, the development of agriculture was preceded by a period of intensive foraging that would also have been more difficult with megaherbivore competition (Richerson et al. 2001).

In both North and South America, there would have been pressure on the megaherbivore hunters to become more sedentary and to find a new stable source of food once their prey had gone extinct. One event, the extinction of the megaherbivores, led to both the closing of a hunting niche while simultaneously opening a larger herbivore niche. Model simulations suggest that following the extinction of the megaherbivores, human population densities would have decreased drastically as their major food source was gone (Alroy 2001). The Pleistocene extinctions would also force the once mobile hunters of the megafauna to become more sedentary because their new, smaller prey would have smaller ranges, and becoming sedentary is a first step towards developing agriculture (Harris 1977).

Did the extinctions of the Pleistocene megaherbivores have any impact on the timing of the development of agriculture? The chief problem with this theory is that in Eurasia and Africa, where most agriculture began independently, extinctions were milder, and they took place long before the development of agriculture. In contrast, in the Americas, the extinctions were severe and agriculture began in two independent regions in the new world within ~3000 years of the arrival of people. Why would agriculture develop more rapidly in the Americas versus Eurasia and Africa? The independent rapid origin of agriculture in North and South America suggests a non-local, non-cultural driver. I hypothesize that people were able to develop agriculture in much less time in the new world versus the old world because of the following potential reasons: (1) Agriculture developed more rapidly in the Americas because there was more NPP that became available for human utilization. (2) Agriculture developed more rapidly in the Americas because the domestication of wild crop types was more feasible in the absence of megaherbivore competition. (3) Agriculture developed more rapidly in the Americas because there was selective pressure on hunting societies to find a new food source and become sedentary as their prey went extinct. (4) An alternative hypothesis is that agriculture developed more rapidly in the Americas because the warmer, wetter, higher CO_2 conditions of the Holocene preferentially increased photosynthesis in the Americas.

I test these theories by calculating the NPP that was potentially liberated following the Pleistocene megafauna extinctions and correlating this to the timing of the onset of agriculture. I test the alternative hypothesis, that climate preferentially increased photosynthesis in the Americas more than the Old World, using the NCAR Community Land Model (CLM) 3.0 climate model.

Methods

NPP usage by extinct Pleistocene megaherbivores

I calculate NPP usage for each individual extinct species using animal biomass data from (Smith et al. 2003) (N = 5731 species) (Doughty and Field 2010). To calculate caloric intake as a function of animal mass, I used the metabolic mass equivalent scaling law where M is the mass of the animal (Owens-Smith 1988):

$$\text{Metabolic rate} = M^{0.75}.$$

I used the following relationship to estimate animal densities (number/km^2) based on average large (>100 kg) mammal herbivore individual mass (Silva and Downing 1995)

$$\text{Log } 10(\text{density}) = -0.44 \times \log 10(M) + 1.01.$$

I used only herbivore species and did not use species in the orders Carnivora or Insectivora for the NPP calculations. Following Barnosky (2008), I assume that each species had a range of ~8% of the continental area (Australia, Africa, Eurasia, North America, and South America, geographic ranges sizes were set to 7.8%, 8.6%, 8.1%, 8.2%, and 7.2% of the respective continental areas) (Smith et al. 1994, Barnosky 2008). I multiplied the caloric needs of an individual of each species by its density and estimated continental range to get total liberated joules of energy per continent, divided this by ~12.55 kJ/g of dry plant mass and assumed a 22.4% assimilation efficiency (Rees 1982), summed for all extinct species to calculate liberated NPP. Discarded plant mass represents a quarter to half of the mass consumed for elephants (Paley 1997), which I estimate at 30% of food NPP for all extinct megaherbivores. To get percent liberated NPP for each continent, I divide total continental liberated NPP by the continent's total potential NPP on grassland (for extinct savanna animals) and forest (for extinct forest animals) for the Holocene (Haberl et al. 2007) and the Pleistocene (Crowley 1995). I use Carnegie Ames Stanford approach (CASA) to calculate present day NPP (Field et al. 1998), results from the Lund–Potsdam–Jena dynamic vegetation model to calculate potential vegetation NPP (Haberl et al. 2007), and results from Crowley (1995) to calculate Pleistocene potential vegetation NPP (Crowley 1995). I assume each species has the same continental range (~7–9%) during the Holocene and the Pleistocene.

I used data from Underhill et al. (2001) to estimate when people arrived at each region (Underhill et al. 2001), and Balter (2007) to estimate when agriculture was first domesticated in each region (Balter 2007).

Percentage continental extinction rate

To determine continental extinction rates of large herbivores (>200kg), I compiled all animals over 200 kg on each continent and the number and percentage of those to go extinct by 10,000 YBP. I chose a threshold of 200 kg based on the results of damage to farms from herbivory in Uganda (Naughton-Treves 1997). Animals weighing more than 200 kg, like elephants, caused much greater percent damage to farms than animals under 200 kg. I do not include New Guinea in this analysis because it does not have any herbivores larger than 200 kg either extant or extinct.

Photosynthesis simulations

I test whether changes in climate between the Pleistocene and the Holocene preferentially increased photosynthetic capacity in the new world leading people to develop agriculture there in less time. I simulate photosynthetic rates of C3 crops in 7 independent sites of the domestication of agriculture including: Mexico, the Amazon, the Near East, India, China, Africa, and New Guinea. I use NCAR's CAM 3.0 (Collins et al. 2006), coupled with the CLM 3.0 and a slab ocean model run with a 20 minute time step and a resolution of 2 by 2.5° at the equator for 60 years, averaging the final 30 years. This model predicts photosynthesis using a Farquhar photosynthesis model and the Ball Berry stomatal conductance model (Farquhar et al. 1980, Collatz et al. 1991). I convert an area to 100% C3 crops based on predictions of where agriculture may have began in each region (Balter 2007). I simulated the cool, dry Pleistocene conditions by reducing the solar constant from 1367 $W \cdot m^{-2}$ to 1345 $W \cdot m^{-2}$ and 1322 $W \cdot m^{-2}$. I simulated the effect of increased atmospheric CO_2 on photosynthesis with simulations at 180, 213, 247, and 280 ppm atmospheric CO_2. I used the results from Paleoclimate Modeling Inter-comparison Project (PMIP2) to estimate changes in temperature and precipitation between the Pleistocene and the Holocene (Braconnot et al. 2007).

Results

North and South America had the most liberated NPP per ice free continental area (25 g $C \cdot m^{-2} \cdot yr^{-1}$ and 30 g $C \cdot m^{-2} \cdot yr^{-1}$ respectively), followed by Australia (13 g $C \cdot m^{-2} \cdot yr^{-1}$), Africa (6.3 g $C \cdot m^{-2} \cdot yr^{-1}$) and Eurasia (5.7 g $C \cdot m^{-2} \cdot yr^{-1}$). These continental averages hide much regional diversity (Fig. 1). The uneven distribution of liberated NPP was driven mainly by differing continental extinction rates, percentage grassland land cover, and regional NPP (Doughty and Field 2010).

I average liberated NPP in each region where agriculture developed independently (Table 1). There was a wide disparity in liberated NPP, ranging from an average of 3 g $C \cdot m^{-2} \cdot yr^{-1}$ in the Near East to 47–48 g $C \cdot m^{-2} \cdot yr^{-1}$ in South America and Mexico (Table 1). There is a significant ($P < 0.05$) linear relationship between liberated NPP and the amount of time people lived at a site before developing agriculture (Fig. 2a). I then compare average liberated NPP per continental area to the number of independent origins of agriculture per ice free continental area (Fig. 2c). For instance, South America had three independent origins of agriculture in ~16,000,000 km^2 ice free area (an average of 5,300,000 km^2 for each independent origin) and 30 g $C \cdot m^{-2} \cdot yr^{-1}$ of NPP liberated. This is compared to Eurasia which had 4 independent origins in 48,000,000 km^2 ice free area, (an average of 12,000,000 km^2 for each independent origin) and 5.7 g $C \cdot m^{-2} \cdot yr^{-1}$ of NPP liberated.

I calculate continental extinction percentages of large herbivores (>200 kg) using data from Smith et al. 2003. South America had an extinction rate of 93% of animals >200 kg (43 species), North America had an extinction rate of 86% (37 species), Eurasia 28% (7 species), Africa 24% (7 species) and Australia 89% (8 species). There is a significant linear relationship between both the percentage and number of large species to go extinct and the amount of time people were in an area before developing agriculture ($P < 0.05$) (Fig. 2b). I then estimate the effect of changing CO_2, temperature, and precipitation on photosynthesis in each independent origin of agriculture. Ice core records indicate that atmospheric CO_2 increased from ~180 ppm in the Pleistocene to ~280 ppm in the early Holocene. Because CO_2 is a well mixed gas, there were no large regional differences in atmospheric CO_2 concentrations. Likewise, PMIP2 studies indicate that temperatures increased relatively uniformly by 2–5°C in all independent domestication sites of agriculture between the last glacial maximum and the Holocene. However, there were large regional differences in precipitation, with no increase in the Near East, increases of 0–1 mm/day in Amazonia and Africa, increases of 0.25–1 mm/day in India and China, and increases of 0.5–1 mm/day in New Guinea and Mexico (Braconnot et al. 2007).

Modeled photosynthetic capacity was most closely related to trends in precipitation with more minor and variable trends with temperature (Fig. 3a and b). The rate of increase of photosynthesis with increased precipitation tends to decrease as a function of total precipitation (Fig. 3 bottom). This means that wetter areas such as Mexico and Amazonia have a smaller increase in photosynthesis for a given change in precipitation than dryer places such as the Near East or Africa.

Discussion

Recent studies estimate that agriculture began independently in two separate regions of the Americas within ~3000 years of the arrival of people, compared to much longer periods of time that people had lived in old world regions before beginning agriculture. Even if the warmer, wetter, higher CO_2 conditions of the Holocene are considered, the onset of agriculture was still rapid in the Americas with 2 of 5 (40%) regions independently developing agriculture near the onset of the Holocene (~10,000 BP) versus 1 of 6 (16%) in the old world. North and South America also had more independent origins of agriculture

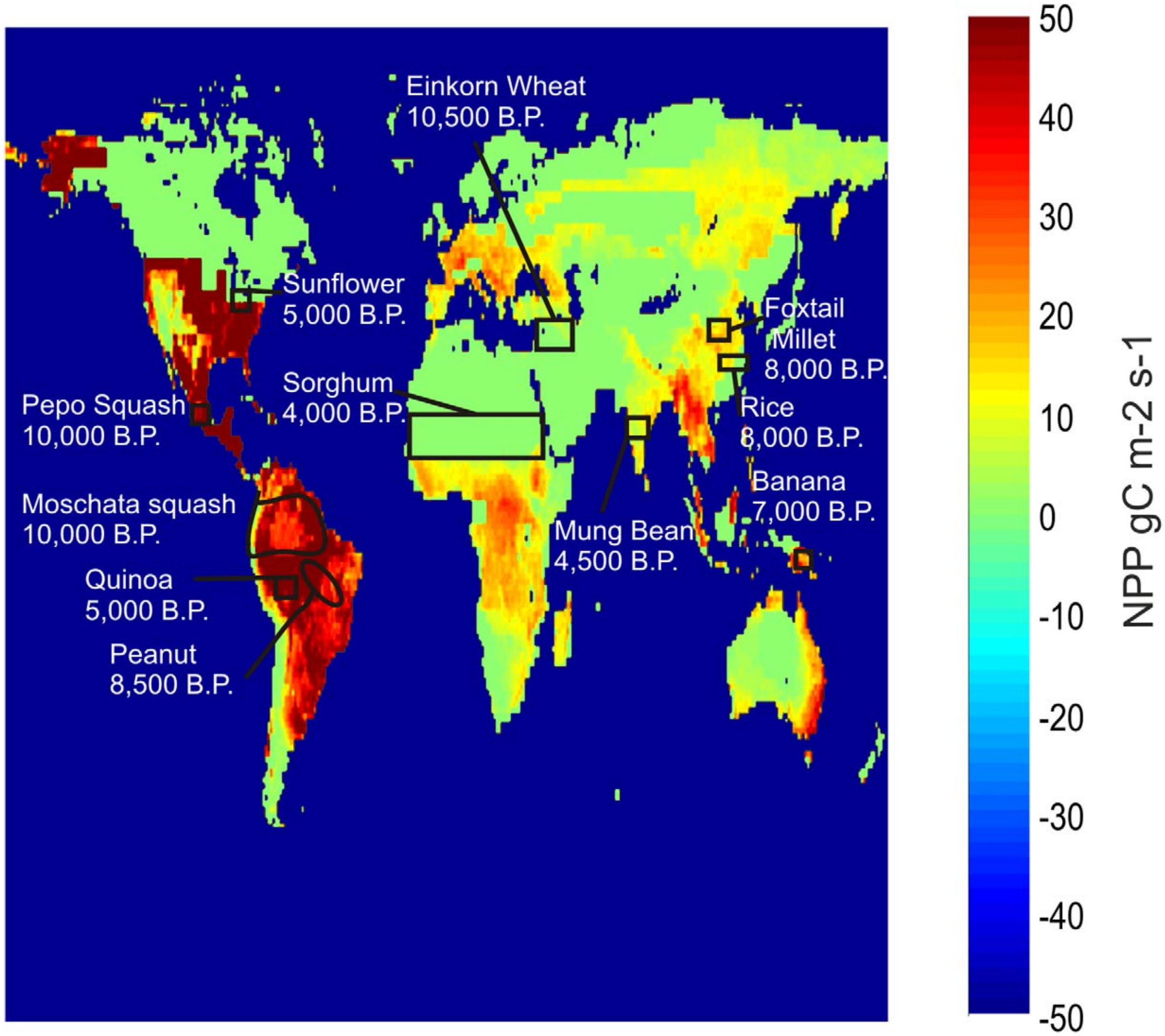

Fig. 1. NPP liberated following the extinction of the megaherbivores. Black lines enclose regions where agriculture developed independently (Balter 2007). The text lists the first crop in each region and the estimated date when that crop was first domesticated.

per area of ice free land than Eurasia or Africa (Fig. 2c). The Americas appear anomalous both with the number of independent origins of agriculture and the speed at which they developed. Was there a relationship between the more drastic extinctions of the Pleistocene megafauna in the Americas and the development of agriculture in the Americas?

To understand the role that liberated NPP plays, it is first important to understand whether available NPP actually increased following the extinction of the megafauna or whether it was simply consumed by the surviving herbivores. Small herbivores have different ecological niches than large herbivores and would be unlikely to consume all the available NPP. For example, in Kruger National Park in South Africa, herbivores over 5kg were excluded from two plots (220 and 230 ha) for 36 and 40 years. There was a large increase in plant biomass in the enclosures with no large herbivores, suggesting that the additional NPP went into plant matter instead of more small herbivores (Asner et al. 2009). In North America, Bison did eventually consume some of the liberated NPP, but only later (Meagher 1986), following extensive physiologi-

Table 1. Estimates of when people arrive in each region of the globe, when agriculture first developed, how long people were at each site before the origin of agriculture, percent of animals over 200 kg to go extinct, and average liberated NPP at each origin of agriculture. Estimates of when people arrived in each region of the globe are highly controversial, and the dates listed in the table are, therefore, rough estimates.

Site of an independent origin of agriculture	People arrive (YBP) (Underhill et al. 2001)	Independent origin of agriculture (YBP) (Balter 2007)	Years to develop agriculture (years)	% extinction (Smith et al. 2003)	NPP (g C·m^{-2} ·yr^{-1})
Mexico	~13,000	10,000	3,000	86	47
N. America	~13,000	5,000	8,000	86	41
Amazon	~13,000	10,000	3,000	93	42
S. America 1	~13,000	5,000	8,000	93	34
S. America 2	~13,000	8,500	4,500	93	48
Near East	~50,000	10,500	39,500	28	3
India	~50,000	4,500	45,500	28	10
N. China	~50,000	8,000	41,000	28	16
S. China	~50,000	8,000	41,000	28	10
Africa	~100,000	4,000	96,000	24	4

cal changes (Guthrie 1990). Therefore, much of the NPP following the extinctions may have been initially available in the Americas.

If early humans were able to access this NPP, it would likely represent a significant resource. I graphed available NPP in each region versus the speed of the onset of agriculture and found a significant correlation ($P < 0.05$). Intensification of foraging generally precedes the onset of agriculture (Richerson et al. 2001). This period of intensive foraging involves using an increased range of stone tools to more efficiently forage large seeded grasses. It also allows people to become familiar with future potential domesticable crop types. Would fewer large herbivores mean less competitive herbivory to disrupt the domestication of plants? Large herbivores such as elephants can cause much damage to farms. For instance, in Uganda, mean damage inflicted by elephants per event was 874 m^2 (~21% of the farm area) compared to 136 m^2 from the next most damaging herbivore (Naughton-Treves 1997). Another study found that the only successful deterrent to elephant damage was electric fences (O'Connell-Rodwell et al. 2000), an option obviously not available to early farmers. There was a significant correlation between the extinction rate of large herbivores (>200 kg) and the speed of the onset of agriculture (Fig. 2b). The domestication of crops is a slow process, with both corn (Jaenicke-Despres et al. 2003), wheat (Tanno and Willcox 2006), and other crops (Fuller 2007) needing thousands of years to be domesticated with humans exerting weak, rather than strong domestication pressure (Fuller 2007). Such a long, weak domestication process would have been continually disrupted by the competitive herbivory of megaherbivores before they went extinct.

The third hypothesis examined whether the development of agriculture was accelerated because formerly mobile hunting societies became more sedentary following the extinction of their prey (Harris 1977), a precondition for the adaptation of agriculture. This argument was initially discounted due to the many millennia thought to separate the extinctions and the onset of agriculture. However, agriculture in the Americas is now thought to have begun much sooner and is generally preceded by several thousand years of intensive foraging. So the timing appears less problematic than when Harris (1977) first developed the hypothesis. Simulations indicate that these early hunters would have been under intense food pressure as their populations were drastically reduced following the extinction of the megafauna prey (Alroy 2001). The extinction of the prey and the sedentary lifestyle would be a "push" towards agriculture, while more NPP and less competitive herbivory would be a "pull" (Stark 1986) As an alternate explanation to the megafauna hypothesis, I questioned whether differences in climate between the Pleistocene and the Holocene would preferentially increase photosynthesis in the Americas, leading to increased plant growth and greater likelihood of agriculture. Neither temperature nor atmospheric CO_2 concentrations

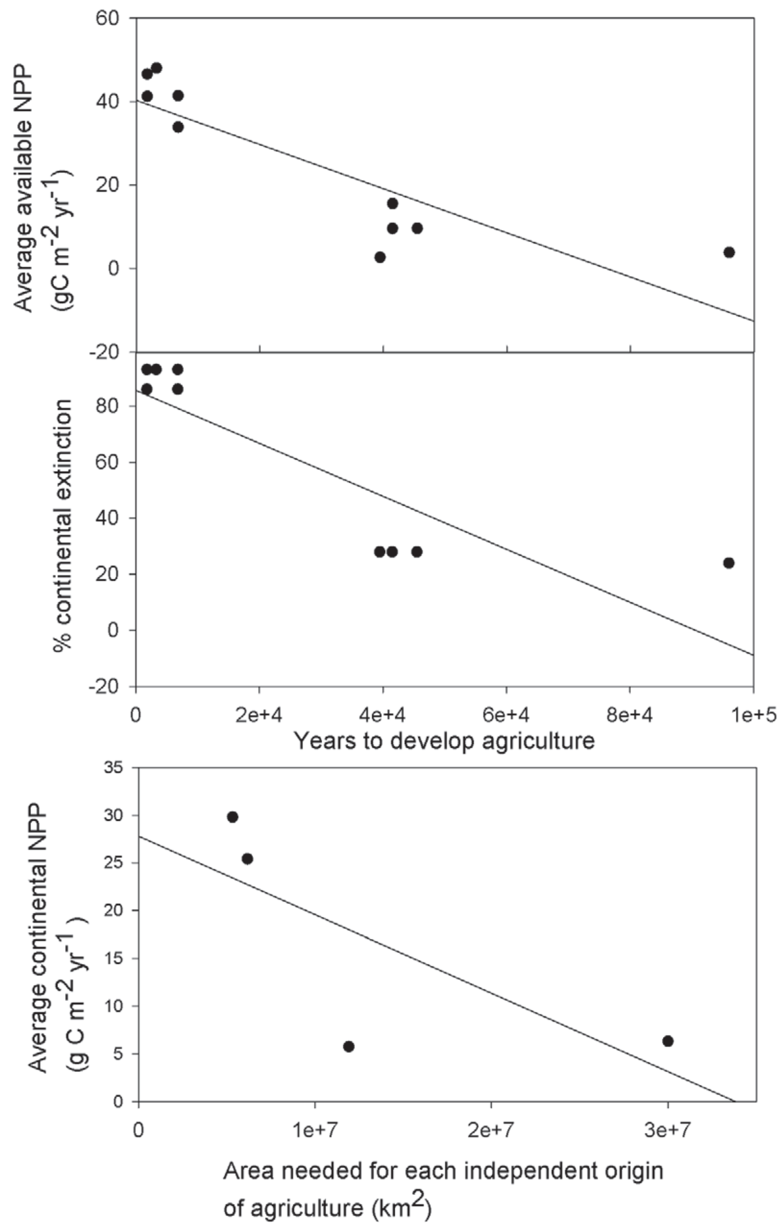

Fig. 2. (Top) Average liberated NPP ($gC \cdot m^{-2} \cdot yr^{-1}$) and (middle) continental extinction rate for animals >200 kg versus time needed to develop agriculture in each region of an independent origin of agriculture. (Bottom) Continental averaged liberated NPP for N. America, S. America, Eurasia, and Africa versus the average area needed for each independent origin of agriculture (a ratio of the number of independent origins of agriculture per continent versus total continental ice free area).

showed regional diversity that could explain variations in the timing of the start of agriculture. Changes in precipitation, however, were highly variable (Braconnot et al. 2007).

There was a significant linear trend between increasing photosynthesis and increasing precipitation. However, the rate of increase of photosynthesis with precipitation was negatively correlated with absolute rainfall, meaning that sites with less rainfall increased photosynthesis

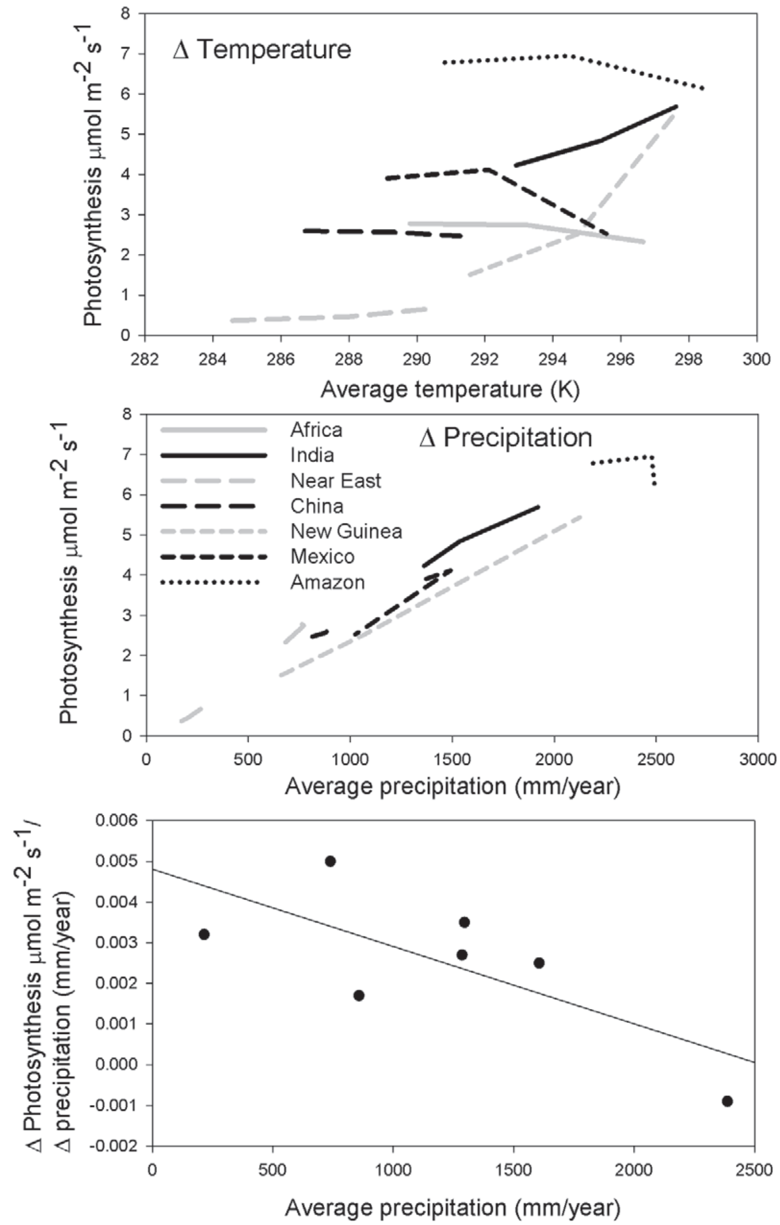

Fig. 3. Results of global climate simulations showing the effects of changing temperature (top) and precipitation (middle) on average daily photosynthesis ($\mu mol \cdot m^{-2} \cdot s^{-1}$) at seven independent origins of agriculture. (bottom) The rate of increase in photosynthesis with precipitation (the slope of the change in photosynthesis with precipitation from the middle figure) versus average precipitation at seven independent origins of agriculture.

by more than sites with more rainfall. Overall, the change in precipitation was not a good predictor for when agriculture would develop. For instance, the Near East, which would have benefitted from an increase in precipitation due to its low rainfall, did not show increased precipitation according to the PMIP2 studies (Braconnot et al. 2007). Precipitation in the Amazon may have increased, but because of its already high rainfall, photosynthesis, both absolute and as a percentage, may benefit less than other sites. Precipitation likely did increase in Mexico, and with its moderate rainfall, photosynthesis would have benefitted from an increase in precipitation. Overall there was no clear trend in timing of the onset of agriculture with changes in precipitation.

There is evidence that agriculture moved rapidly from its origins in warmer, wetter climates to cooler, dryer climates, which further negates the importance of climate in the Americas. For instance, a house in the mountains of the Andes was found to contain squash from ~10,000 years ago and peanuts from ~8,500 years ago. Genetic studies and the location of the wild ancestors indicate the crops were likely first domesticated in the warm, wet, lowland tropical forests. Therefore, these crops quickly spread from their warm, wet origin to the cold, dry region where they were discovered (Dillehay et al. 2007). This change in temperature and precipitation between the lowland Amazon and the highland regions of Peru is larger than the change in the Amazon between the Holocene and Pleistocene (~5°C change in temperature and 40% change in precipitation) (Stute et al. 1995, Maslin and Burns 2000).

The dating of when people first arrived in the Americas is still highly controversial. The most accepted "pre Clovis" settlement is the Monte Verde site in Chile which has been dated to ~12,500 years BP. Some genetic evidence even suggests that people could have arrived in the Americas as early as 30,000 years ago (Torroni et al. 1994). However, such evidence is still slim compared to the thousands of sites where Clovis artifacts have been recovered, the oldest being 11,800 years BP. Therefore, in this paper, I assume a "Clovis first" approach, meaning that people arrived in the Americas by ~11,800 BP. However, if evidence for significant peopling of the Americas prior to these dates were to emerge, then the results of this paper would, of course, change.

The speed of the development of agriculture may have been accelerated in the Americas due to the drastic ecological restructuring following the extinction of most of the continents large herbivores. I argue from an ecological standpoint that humans were filling an open herbivory niche in the Americas through agriculture. Agriculture is considered by many to be one of humanities first great milestones, however, this milestone may have been accelerated in the Americas due to a large, tragic, loss of mammal biodiversity.

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