Historical socioecological transformations in the global tropics as an Anthropocene analogue

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Large, low-density settlements of the tropical world disintegrated during the first and second millennia of the CE. This phenomenon, which occurred in South Asia, Southeast Asia, and Mesoamerica, is strongly associated with climate variability and extensive landscape transformation. These profound social transformations in the tropical world have been popularized as "collapse," yet archaeological evidence suggests a more complex and nuanced story characterized by persistence, adaptation, and resilience at the local and regional scales. The resulting tension between ideas of climate-driven collapse and evidence for diverse social responses challenges our understanding of long-term resilience and vulnerability to environmental change in the global tropics. Here, we compare the archetypal urban collapse of the Maya, in modern Belize, Guatemala, Honduras, and Mexico, during the 8th to 11th centuries CE, and the Khmer in modern Cambodia, Laos, Thailand, and Vietnam during the 14th to 15th centuries CE. We argue that the social response to environmental stress is spatially and temporally heterogenous, reflecting the generation of large-scale landesque capital surrounding the urban cores. Divergences between vulnerable urban elite and apparently resilient dispersed agricultural settlements sit uncomfortably with simplistic notions of social collapse and raise important questions for humanity as we move deeper into the Anthropocene.

paleoanthropocene | tropics | collapse | Maya | Khmer

A persistent narrative connecting the tropical cultures of South Asia, Southeast Asia, and Mesoamerica is that, between the 9th and 15th centuries, their large urban settlements collapsed in response to climatic variability (1). These common responses to climate stress are of critical concern for the modern world as we move deeper into this century of climatic disruption, such that the precise relationships between climate forcing and social outcomes have come under increasing scrutiny. Indeed, Earth-system models for Mesoamerica and Southeast Asia indicate increased heat and moderate to severe drought but much wetter conditions for eastern India (2).

Comparisons between case studies of societal collapse and its contextual socioecological disruption are common (3–6), and specific comparisons between the canonical collapses of the Maya in the 9th century CE (Fig. 1) and Khmer of Angkor in the 15th (Fig. 2) have been made for nearly 70 y (7). There are good reasons for this. Despite the unbridgeable social and cultural differences between the two civilizations, there are clear parallels in urban form, in the tendency toward large and low-density settlements characterized by extensive water management infrastructure, large penumbral territories, and systemic environmental transformation of the landscape (8).

Approaches to water management, in particular, are a common point of comparison (9). The pronounced seasonality of rainfall common to both tropical regions stimulated the parallel evolution of large and elaborate water management systems—both tangible in terms of material infrastructure but also intangible in terms of religiosocial practices and institutions—which sought to flatten the sharp distinction between water scarcity and surplus. These social adaptations to the seasonally dry tropical savanna and even hot steppe climates (Köppen's climate classes Aw and BSh) are most clearly expressed in a common reliance on large and often complex water storage and distribution networks, settlement focused on or near accessible groundwater, and tendency for settlements in both regions to adopt a peculiar low-density form of urbanism (10–14).

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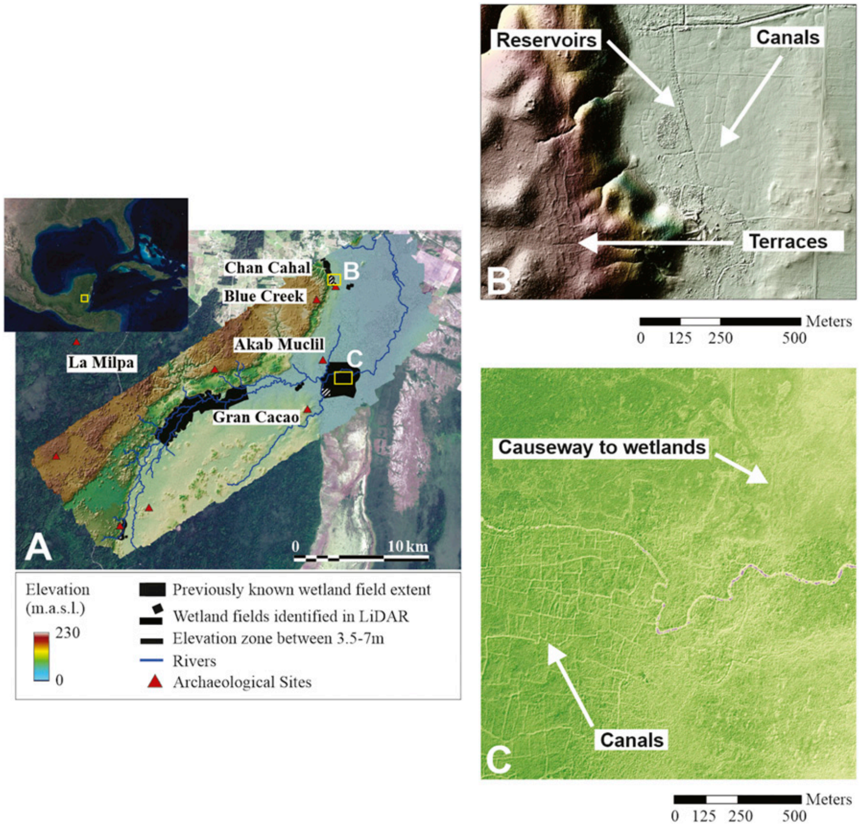

Fig. 1. Three maps of intensive ancient farming features or landesque capital: (*A*) Footprint of LiDAR (Light Detection and Ranging) mapping in the Rio Bravo valley of Belize with areas of intensive wetland field complexes in black. (*B*) LiDAR digital elevation model (DEM) of the Chan Cahal polycultural farming complex showing terraces, reservoirs, and canals in close proximity. (*C*) LiDAR DEM of the northeastern corner of the Birds of Paradise wetland field complex with canals and a prominent causeway (derived from refs. 19 and 20). Maps were created by Anais Zimmer, Sam Krause, Sara Eshleman, and Will Pratt.

In both cases, also, systematic transformation of the landscape occurred, particularly the removal of tropical dry or monsoon forests for agriculture and fuel. At Angkor entire forested landscapes were terraformed to create bunded fields for fixed wet tillage of rice (15–18), while the Maya created extensive, polycultural canalized wetland field systems (19, 20) and terraced landscapes (21). In both cases, landscapes were converted into massive and highly conservative traps for sediment, nutrients, and water, and in both cases the initial expenditure of natural environmental capital and the loss of ecosystem services was likely profound. Over time, however, these systems created landesque capital—indigenous improvements in land that persist long after the initial investment—that in some cases enhanced natural capital and services at a variety of scales (22).

Climate Catastrophe

The apparent vulnerability of large and complex socioecological systems to hydroclimate variability in the tropics is a point of contention and fascination (23). This is particularly so given nearly half of the Earth's human population live in the tropics (24), that "mega-urbanism" is a particular characteristic of the tropical "global south" (25), that intensive human modification of tropical forests is both profound and ancient (26), and that urban centers globally are tending toward low-density forms (10). Additionally, climate stressors abound (27), raising the specter of instability in contemporary cities analogous to historical instances of "collapse."

For both the Maya and Khmer, prolonged drought and increased interannual rainfall variability are coincident with apparent decreases in urban populations and, in some cases, the abandonment of major centers. This was particularly so for the Maya, where cities in the hydroclimatically marginal central lowlands suffered population reductions of up to 90% (28), triggering widespread migration out of the interior (1, 29). Even in this case, however, it is widely recognized that the nature and magnitude of climate forcing and the social response to it is more complex than a simplistic rendering of a climate-driven collapse (29). Calls (11, 30) for a greater analytical emphasis on the specific mechanisms by which climate stress becomes social outcome in particular cases require further engagement with "contingent and locally embedded" histories (ref. 31, p. 208) built on careful multidisciplinary work.

At Angkor, climatic variability in the 14th and 15th centuries is coincident with archaeological evidence of damage to the water management network and, it is presumed as a consequence, the water supply and agricultural productivity of the city (32, 33). This physical damage is specifically associated with severe flooding during a late 14th to early 15th century "pluvial" episode and is bracketed by two multidecadal scale drought episodes (1345 to 1374 and 1401 to 1425 CE) that likely disrupted the water management system and increased its vulnerability to the sudden onset of wet monsoon years. Recent modeling of Angkor's water management network (34) demonstrated an unstable domain in the behavior of the network in response to climatic variability,

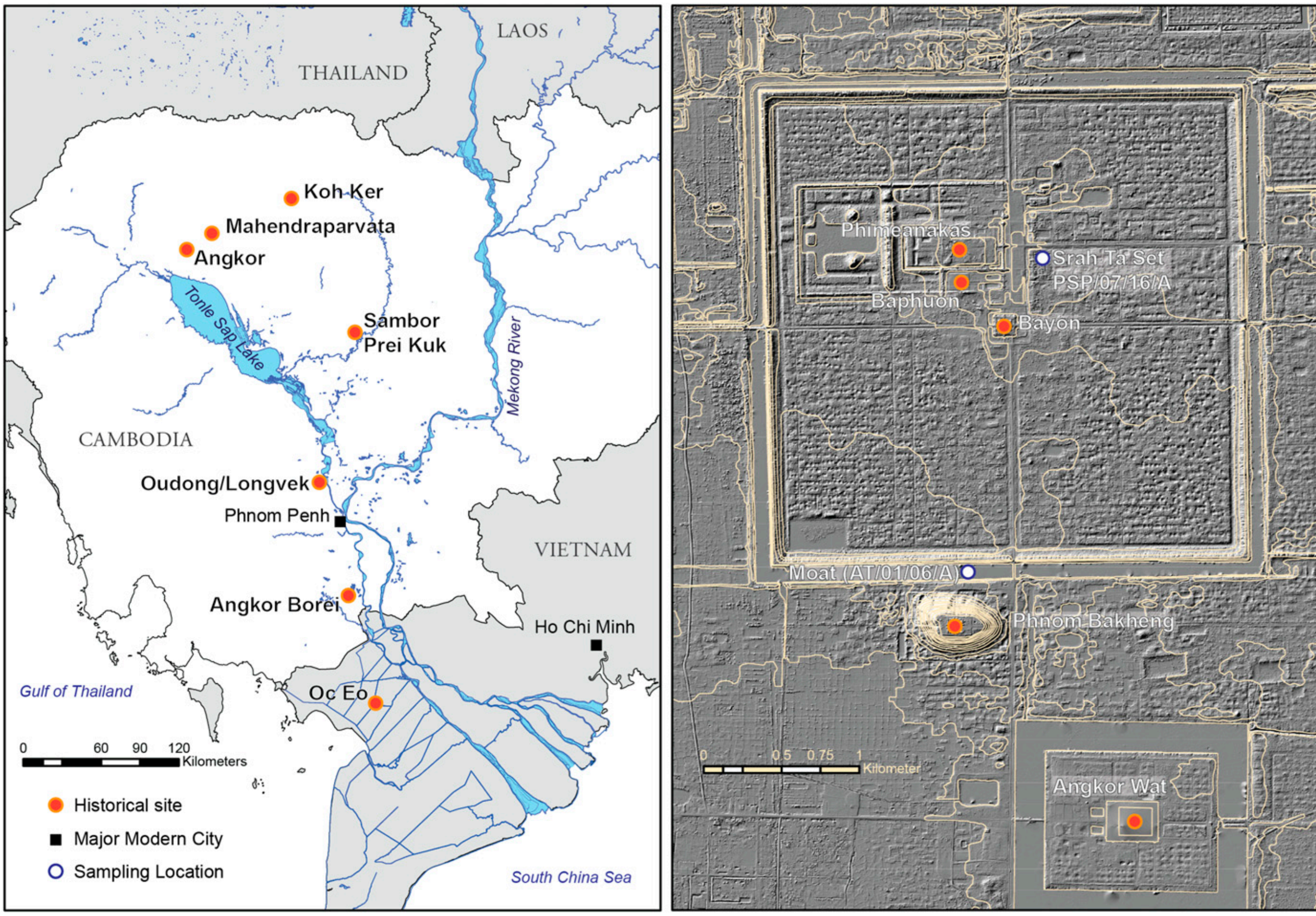

Fig. 2. (*Left*) Map showing the location of major historical centers in Cambodia and Vietnam that reflect the episodic consolidation and dissolution of Khmer political power throughout Southeast Asian history. (*Right*) LiDAR-based topographic map of central Angkor, focused in particular on the major rectilinear enclosures of Angkor Thom and Angkor Wat. This map shows the location of major temple sites mentioned in the text and the location of sampling sites. Data courtesy of Japanese International Cooperation Agency. LiDAR data courtesy of the Khmer Angkor LiDAR Consortium (17).

such that damage can rapidly propagate throughout the network. This information allows us to go beyond mere coincidence in time between climatic events and "collapse" to reveal precisely how these phenomena are articulated.

In the Maya lowlands climatic variability during the Terminal Classic is unequivocally associated with widespread demographic change and social/economic disruption (29). An early focus on climate-induced collapse of the Maya emerged from an era of simplistic climate determinism (35). Since that time a growing paleoclimate record using climate-sensitive proxy data from lakes, speleothems, and more distant ocean cores has revealed a more complex climatic history (36, 37). Episodes of drought are clear in the paleoenvironment record and were made famous by lake core studies from northern Yucatan that revealed the Late Classic Maya drought (38) that, in some records, persisted to the Early Postclassic (*ca.* 800 to 1100 CE). Maya history is punctuated by periods of severe drought, such as during the Late Preclassic to Early Classic (*ca.* 200 to 300 CE) and during the historical period within the Little Ice Age. Evidence for wetter periods also comes from the Late Preclassic and the Early to Late Classic. There is also some evidence for climate disruption in the Middle Classic, perhaps caused by massive volcanic eruptions in the 530 to 540s CE with their far-reaching global impacts (39). These climate dynamics had environmental and human impacts but, to date, no studies have successfully linked these with environmental impacts on a scale commensurate with anthropogenically induced changes. We note, too, that the impact of drought across the Maya territories is highly variable, both in terms of its magnitude and duration but also in terms of the environmental and social resilience of the regions it impacted (40, 41). The fact of Maya cultural persistence after the Terminal Classic and the emerging archaeological evidence of resilience at sites like Lamanai—which has an uninterrupted history of occupation that spans more than 3,000 y (42, 43) and certainly felt the effects of the outward migration of people fleeing the Terminal Classic collapse on the central lowlands—suggests two overlapping possibilities. First, some Maya centers were located in regions with deep aquifers that were more vulnerable to drought than others, irrespective of the water management infrastructure created to manage surface water resources. Second, some Maya communities had better access to resources or managed resources more sustainably than others and had developed resilient communities that were able to tolerate large climatic shifts (44). Even in these cases, however, sociopolitical factors (including conflict between groups) that may not have been directly related to climatic stress may have triggered abandonment.

Collapse and Landscape Transformation

Maya Lowlands. The Maya world has a rich literature that considers the Anthropocene and "paleoanthropocene" in terms of sustainability, and particularly the sustainability of the soil and water resources (29, 45). Beach et al. (46) coined the term "Mayacene" and developed seven criteria or "golden spikes" that demarcate the Maya Anthropocene, further employed to understand the timing and nature of ancient Maya wetland farming (19, 20) and its possible global impacts (47). These criteria included a range of evidence for human-induced environmental changes spanning from local to global scales.

The idea of the Maya Anthropocene has its roots in the scholarship of the 1920s, when scientists began connecting the region's thin soils to ancient erosion and notions of collapse (48). The earliest human impacts on the Maya tropical lowlands certainly go back to at least the early to middle Holocene, with cultivars like maize (brought from highland Mexico) revealed in pollen cores by *ca*. 5500 to 4600 B.P. (49, 50). By 4000 B.P. paleoecology studies record significant human impacts, such as the expansion of grasslands at the expense of forest (51), or changes in fire regime associated with the appearance of maize pollen around 5000 B.P. (52). A recent study indicates that maize likely made a significant contribution to human diets by the middle Holocene (53). Maize cultivation and fire may indeed be related, as early farmers burnt forest to establish fields or milpas. Other studies have also reported more frequent burning, indicated by the highest sedimentary charcoal abundance, associated with the formation of ancient Maya wetland field systems (20, 46).

Empirical evidence for eroded soils first came from "Maya clay" (54)—a silicate clay layer that occurs in many lakes and other topographic sinks. This material is widely considered to have derived from rapid erosion during the Maya era that began in the Preclassic and which intensified with the emergence of Maya states and monumental centers (55). This clay unit is bracketed by more slowly accumulating organic facies, deposited before invasive landscape transformation and after the adoption of widespread soil conservation practices, respectively. Anselmetti et al. (56) presented a clear example of this typical anthropogenic facies, which revealed that erosion rates in the catchment of Lake Salpetén rose by 60 times following the introduction of agriculture in the mid-Holocene, and remained high to the Late Preclassic at about 1700 B.P. Specifically, at around 5000 B.P. erosion was 16.3 $t{\cdot}km^{-2}{\cdot}y^{-1}$, accelerated to 134 $t{\cdot}km^{-2}{\cdot}y^{-1}$ from 4000 B.P. to 2700 B.P., and peaked to 988 $t{\cdot}km^{-2}{\cdot}y^{-1}$ in the Late Preclassic until 1700 B.P. At the height of Maya population and land use in the Maya Classic period, however, erosion rates fell to 457 $t{\cdot}km^{-2}{\cdot}y^{-1}$ and to 49 $t{\cdot}km^{-2}{\cdot}y^{-1}$ after 1000 B.P. This pattern of accelerated early erosion and declining erosion during the peak of Maya civilization is also apparent in other locations (46). Similarly, declining rates of erosion after the Terminal Classic are apparent in most studies, reflecting a sharp decline in land use from that time, but some studies report that elevated rates of erosion persisted until more recent times (54). More broadly, the early rise of erosion and sedimentation in the Maya Lowlands parallels a recent study of erosion in 632 lakes globally (57), which shows that human-driven soil erosion, mainly from land-use changes, was already underway by 4000 B.P.

Angkor. Soil erosion is also closely associated with landscape transformation at Angkor, though there is no equivalent of the Maya Clay or the Amazonian *terra preta* in the Cambodian landscape—no *dei Khmer* (kh. ដីខ្មែរ)—to provide a stratigraphic golden spike indicative of paleoanthropocene landscape transformation. This relates, partly, to the nearly flat alluvial plain on which Angkor was sited, which does not facilitate mass movement. It is only in the higher-relief sandstone uplands of the Kulen hills to the north of Angkor that the deposition of thick beds of pure sand can be observed between the mid 9th and late 11th centuries CE (58), likely related to the development of the massive urban center there (59). Within the lowland cities of Khmer, the flux of mineral sediment from disturbed catchments to temple moats and reservoirs has been used to track land use and land abandonment (e.g., refs. 60 and 61). A recent focus of this type of work is the city-enclosure of Angkor Thom (Fig. 2). Angkor Thom was the locus of elite power for, arguably, the most significant of the Khmer kings of the premodern period, and the focus of elite occupation and urban life from the 12th century (62). In terms of urban form, it was also the "settlement epicenter" of Angkor (63)—a city-enclosure enfolding a dense orthogonal, cardinally oriented city-grid of roads, embankments, occupation mounds, and excavated ponds (17, 64, 65). Angkor Thom becomes, therefore, the decisive case in tracking the occupation and abandonment of Angkor by the urban elite. The fact that only this settlement epicenter was "abandoned to the forest" while the sprawling suburban landscape around it persisted as a functional urban/rural mosaic (62) points to the close association between the royal occupation of Angkor Thom and its continuity as an occupied space.

Stacked mineral accumulation rate data from the moat of Angkor Thom and a small reservoir in the center of the enclosure (Fig. 3; see *SI Appendix, Materials and Methods*) indicate that sedimentation rates are relatively high and stable from the start of the record in the 1st century CE to the early decades of the 9th century, reflecting a clear baseline value ($0.14 + 0.01\ g{\cdot}cm^{-2}{\cdot}y^{-1}$) for the accumulation of the natural alluvial soil into which the depositional basins are excavated. The data become more variable after this time, reflecting disturbance of the soil associated, initially, with the establishment of King Yashovarman I's capital cantered on Phnom Bakheng in the late 9th century and, later, with the progressive excavation and modification of the moat that was, in the 12th century, to be widened and formalized to enclose Angkor Thom (65). Soil erosion increased progressively from that time to reach peak values in the 12th/13th centuries (the highest value in the entire record is recorded at *ca*. 1140 CE, about 40 y before Jayavarman VII's reign), reflecting both the creation of accommodation space for mobilized sediment and an increasing intensity of proximal land use as Angkor Thom became the focus of urban life. Thereafter, there is a consistent and quite precipitous decline in mineral accumulation rates from the midlate 13th century until the midlate 16th century (Fig. 3*B*), which we suggest reflects a decline in land use intensity in and around the urban epicenter of Angkor. This decline precedes the two episodes of drought that have been associated with the demise of the city (32, 33) by at least one century. We note a sharp increase in mineral accumulation rate in our data at *ca*. 1384 CE and coincident strong positive Palmer Drought Severity Index values in 1375, 1376, 1382, and 1393 CE (32). Recent excavation (66) of a small pond adjacent to the royal palace in Angkor Thom—only a few hundred meters from Srah Ta Set—indicates rapid filling of the pond by sediment, most probably in the final decades of the 14th century. Taken together, this suggests significant flooding and damaging overland flow with the enclosure of Angkor Thom. This is also coincident with dated flood deposits (32) from southern Angkor that indicate one or more high-energy flood events in the latter half of the 14th century. Within Angkor Thom, soil erosion appears to stabilize after *ca*. 1665 CE at a rate lower than the baseline value for natural soils.

A decline in elite occupation within the civic–ceremonial core of Angkor that began in the midlate 13th century does not fit

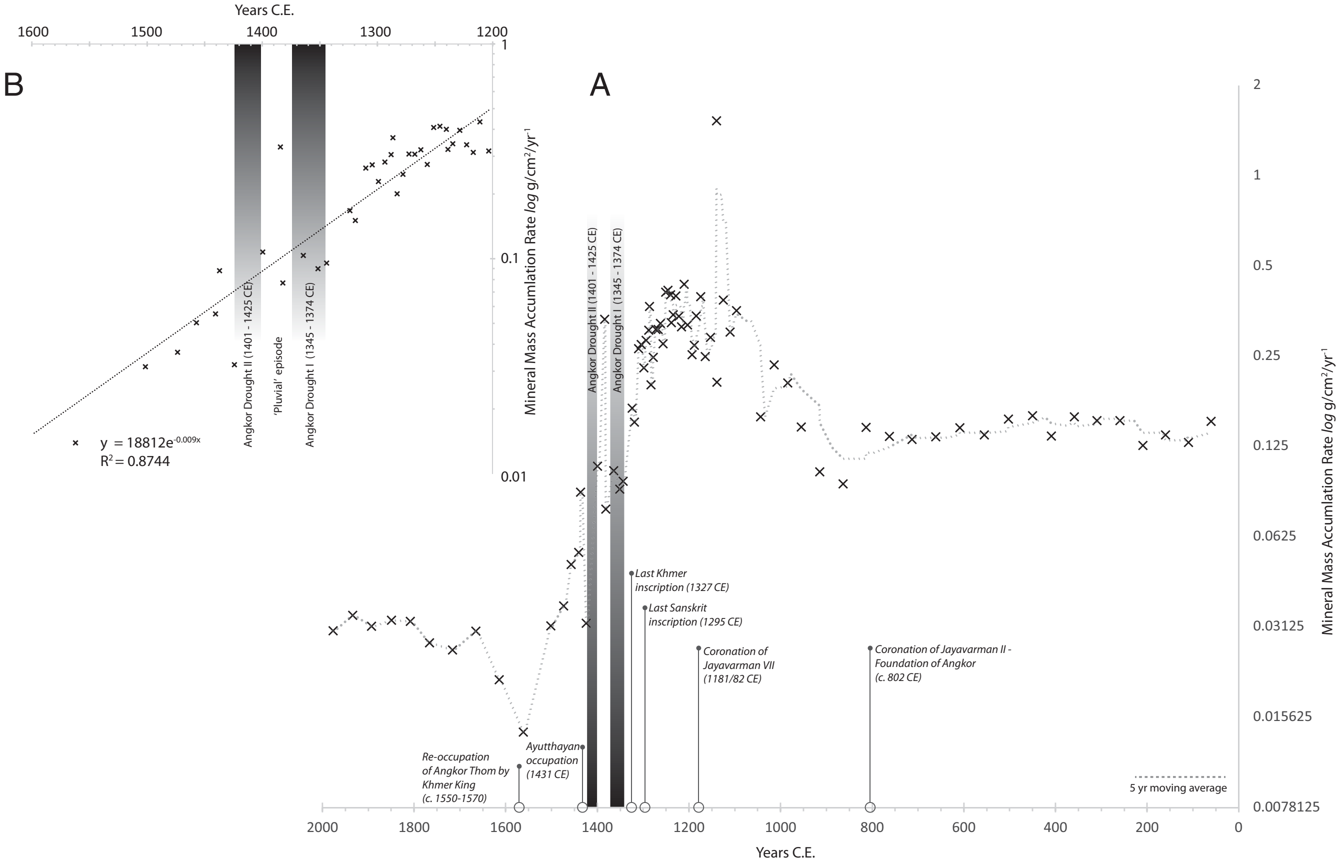

Fig. 3. (*A*) Plot of "stacked" siliciclastic mineral accumulation rate from two locations at Angkor Thom against time, which we argue represents the intensity of land use within the settlement epicenter of Angkor. (*B*) Detail of mineral accumulation rates for the 13th to 17th centuries of the CE, with the trend highlighted by an exponential trendline. These stacked data imply that land use was attenuating as much as a century before the onset of disruptive hydroclimatic variability in the 14th and 15th century.

comfortably with preconceived notions of societal collapse in response to climate stress. Yet, throughout Angkor evidence is emerging that confirms an early and protracted decline in elite occupation. Excavations at Angkor Wat (67) indicate a marked change in residential occupation within the temple enclosure beginning in the late 12th or early 13th century, reflecting reduced occupation or abandonment of residential sites (68). This precedes the evidence presented here for the start of a gradual decline in land-use intensity in and around Angkor Thom by half a century or more and implies that the shift in elite occupation throughout the core of the city may be even longer and more profound than our data indicate. Heterogeneity is apparent across the city, with occupation within the temple enclosure of Ta Prohm throughout this period and up to the 15th century (68). Angkor Wat was reoccupied sometime in the late 14th or early 15th centuries, presumably by the *saṅghar*, and remained a site of worship and pilgrimage. Angkor Thom was also briefly reoccupied by the Khmer elite in the 15th century (62), but this seems to have been unsuccessful. Nonelite occupation continued within the enclosure of Angkor Thom into the 15th century (66) and, at the same time, major architectural renovations occurred within the city-enclosure (69). These recent data add to a disparate constellation of architectural, art-historical, epigraphic, and archaeological information that point to continuity, reuse, and reoccupation of urban spaces after the events of the 15th century.

An "early" and protracted decline in elite occupation at Angkor supports the interpretation that burgeoning international maritime trade stimulated the gradual migration of the ruling elite from Angkor to smaller *entrepôt* at the margins of the ancient agrarian kingdom (1), a process that probably took place over more than a century. Anthony Reid suggests that international commerce "subverted that extraordinary autocracy which had directed surplus resources to royal religious monuments" (ref. 70, p. 67) at Angkor and elsewhere in Southeast Asia. Equally, international trade corroded the reliance on sprawling agrarian hinterlands, prodigious civil engineering works, and infrastructure that was both intricate and rigidly interdependent.

Such dramatic political and social transformations have precedents in Khmer history. Indeed, Miriam Stark (71) has highlighted a distinct cyclical pattern of political disruption, reorganization and, frequently, movement over space; what Damian Evans calls "rupture and mobility" (72). From Funan to Chenla to Angkor and to the premodern Khmer state there is a clear trajectory of episodic and cyclical consolidation and dissolution of political power that circumscribes a loop beginning on the Mekong Delta in the 5th century BCE and ending on the Mekong Delta in the 16th century CE. Even within the region of Angkor, power and its location have shifted dramatically (73), from the 8th century CE capital of Mahendraparvata (58, 59, 74) to Hariharalaya (75, 76), to Yashodharapura in the 9th century and, briefly, to Koh Ker in the 10th century (60, 74, 77). The demise of Angkor and the transition to pre-Modern Cambodia—the last great premodern transformation in the Khmer state—should be seen not as a catastrophic episode of collapse but as part of a millennium-long tradition of transformation

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and adaptation characterized by the resilience and durability of Khmer society.

Landesque Capital. The "terraforming" nature of large, low-density settlements in the global tropics is now well-established (78), and both the Khmer (79, 80) and Maya (41, 46, 47, 81) civilizations have been used explicitly as examples of "early Anthropocene" environmental transformation. Despite the fact that the spatial imprint of intensive agriculture on the planet is observable from *ca*. 3,000 y ago (82), the scale of environmental transformation associated with the growth of these civilizations resonates strongly with contemporary tropical urbanism and its attendant environmental challenges and earth system feedbacks. The perceived "collapse" of historic settlements has, therefore, attracted considerable interest and scholars from diverse disciplines who have sought to distill lessons that might assist contemporary societies navigate the sustainability challenges of the Anthropocene. Very often this is conflated with environmental "overreach" (83)—a state paupered by unchecked expenditure of environmental capital and thus made vulnerable to the impact of climatic variability, particularly drought. However, the messy detail of transformation in historic tropical societies implies complex and heterogenous social responses that can be characterized equally by adaptation, continuity, and, as we argue here, by building landscape resilience.

In the Khmer and Maya lowlands, large-scale conversion of tropical forest to agriculture—bunded field systems, reservoirs, and canal networks in the case of the Khmer, and an admixture of agricultural terraces, reservoirs, and wetland field systems in the Maya lowlands—represent profound transformations at the landscape scale (Fig. 1). Maya terrace systems, which have been dated to as early as the Preclassic, represent an intensification of agricultural land use in areas with relatively poor soils and high relief. They appear to have expanded coincident with peak population densities in some areas of the interior lowlands during the Classic and had declined by the Postclassic. The terraces thus correlate in time with abating soil erosion and some even have more direct evidence of Maya terrace construction as an adaptation to erosion and sedimentation (46). In parallel, reservoirs (84) and wetland field systems have similar chronologies of development and expansion from the Preclassic to the Late Classic (19, 20). Such systems lie in depressions and floodplains particularly along the western flank of the interior lowlands where groundwater was more accessible. While their suitability for agriculture was highly variable over space, their development would have induced minimal erosion due to their position within the landscape. Thus, as agriculture shifted to terraces and wetland fields, erosion into lakes and depressions that created the golden spike of the "Maya clay" declined, even as farming became more intensive and widespread.

Maya landesque capital also includes anthropogenic forests and soils, which were adaptations that arose over time to provide more resources. Some examples are Maya anthropogenic soils akin to black earths developed in a few places, but nowhere to the extent of the Amazonian *terra preta* (85). Ethnographic and historical studies provide evidence of forest gardening and soil manipulation (86), but we still are uncertain if forestry evidence and soil enrichment were intentional. It is clear, however, that ancient Maya infrastructure altered soil fertility and thus altered aspects of ecosystems. Studies indicate higher trees and multiple canopies on ancient terraces, where soils are deeper and thus provide firmer rooting foundations and hold more water and nutrients (87). Moreover, wetland fields expanded the floodplain forest extent with ancient canals that still run onto seasonally dry soils (20). It is important to note that these instances of returns on investments in "gray" and "brown" landesque capital are spatially disjunct across the Maya lowlands and strongly dependent on the local environmental context and sociopolitical structures and practices.

The spatially extensive bunded rice fields of the Khmer are the direct equivalent of the Maya terraces but do not present themselves as a distinguishable stratigraphic marker. Arguably, the clay pans associated with prolonged tillage might represent such a stratigraphic marker, but these are often difficult to distinguish stratigraphically, problematic to date using radiometric techniques, and best understood as a spatial phenomenon exposed through remote sensing and open-area excavations that reveal field margins and earthen dykes (ref. 15 and *SI Appendix*, *Supplementary Information Text*). Regardless, the historic extensification of rice fields represents the creation of a landscape-scale sink for water, sediment, nutrients, carbon, and other biogeochemically important materials. This agricultural landscape is an effective sediment trap, decreasing the volume of soil transported into and deposited within the water management network (88). This is most clearly demonstrated by the lack of sedimentation apparent in the massive central reservoirs of Angkor, which have accumulated as little as 30 cm of overburden since the Neolithic (89, 90), and on the bed of which pre-Angkorian-period structures and material culture lay unburied. Indeed, Groslier (91) argued that Angkor's vast agricultural landscape and the elaborate water management infrastructure that supported it were so effective at trapping sediment and other materials that it effectively "starved" downslope field systems of the nutrients sorbed to suspended sediment.

In both the Khmer and Maya worlds the extensification/intensification of agricultural field systems during their respective historical apogees represent the creation of a conservative land-use practice that resulted in a net enrichment of previously marginal soils with sediment, nutrients, carbon, and other materials. The creation of landesque capital should, in theory, have engendered greater resilience to hydroclimate variability in these areas. In the Khmer lowlands it has long been argued that dispersed, low-density settlements, supported by stable bunded rice systems and high and accessible groundwater resources (Groslier's "hydraulic suburbs"), persisted long after the elite had abandoned the urban core (62, 92), perhaps reflecting deep landscape resilience. Certainly, there is no evidence that the *ca*. 700,000 to 900,000 people (93) of Angkor left en masse, and no evidence that they arrived anywhere else, either (72). Widespread abandonment of and migration from settlements was much more pronounced in the Maya lowlands, yet similar pattern of elite abandonment of ceremonial centers while the occupation of surrounding agricultural spaces persisted is also apparent in some parts of the Maya world (94).

This, we propose, reflects the generation of incipient landesque capital in the dispersed, low-density settlements that surround the ceremonial centers. This capital is created through the development of conservative productive landscape-scale systems that turn previously marginal soils into vast sinks for water, sediment, nutrients, and carbon. In the Maya world, the abandonment of ceremonial urban centers was in many cases forced by prolonged drought, while elite mobility at Angkor long preceded periods of hydroclimate stress. What might be seen as a loss of power or social complexity might also be seen as a sensible adaptive response to changed or changing circumstances, and the pejorative "dark age" label as a subjective fascination with "high culture" and its materialities (69).

Data Availability. All study data are included in the article and/or *SI Appendix*.

Acknowledgments

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