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Modeling the rise and demise of Classic Maya cities: Climate, conflict, and economies of scale

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Urbanization was one of the most significant transitions in human history, yet explanations for the rise and expansion of early cities remain contentious. Here, we propose that simple models from population ecology can integrate existing theories for the development of early cities. Using newly synthesized paleoclimatological, paleoecological, demographic, and historical data from across the Classic Period Maya Lowlands (250–1000 CE) integrated with piece-wise structural equation models, we show that climate downturns, intergroup conflict, and strong economies of scale interact to promote the coevolution of urbanism and patron–client relationships, fueling city expansion, urban institutions, and systemic inequality. In addition, we elucidate how these nonlinear pathways structure the persistence or dissolution of cities. This study underscores the importance of robust economies of scale in the development of early cities and provides a comprehensive framework for understanding the conditions that promote or hinder urbanization, offering insights applicable to both ancient and contemporary urban dynamics.

urbanization | population ecology | inequality | agglomeration | collapse

Significance

Over half of people on earth today live in cities, yet the origins of urban living remains a topic of intense debate. To understand why individuals decided to come together in cities, we leverage population ecology theory and quantify the drivers of urbanism across the Classic Maya Lowlands. Results suggest that individuals sought to mitigate climatic downturns and increasing conflict by joining together to construct agricultural infrastructure and institutions of shared defense, at the cost of reduced autonomy. Conversely, improved conditions in rural areas and sustained socioecological disruption around urban centers in-part led to the abandonment of cities. These findings not only illuminate the specific case but provide a framework for understanding processes of urbanization in the past and future.

Today over 55% of the global population live in cities (1), while less than 6,000 y ago the world's populace was almost entirely rural. Urbanization is one of the most significant transitions in human history (2), yet explanations for the emergence of early cities remain contentious (3–5). This is partly because the rise of early cities presents a paradox: Modern and historic cities gain residents through highly efficient manufacturing, technology, and service sectors (6). Early cities, however, lacked these sectors and were instead comprised largely of subsistence-level agrarian populations whose land-extensive economy incentivized population dispersal to minimize travel and transportation costs between residences and farm plots (7). In addition, a city's farming populace is susceptible to crowd diseases (8), increased levels of systemic inequality (9–11), and competition for land and resources (12). Thus, there are high costs for farmers to aggregate into cities. It is no surprise then that the independent emergence of cities is rare in human history (13), and many early cities were short-lived (14, 15).

To help resolve this paradox, we draw on simple models from population ecology to propose a unified theory of why agrarian populations would aggregate into cities. These models describe three nonlinear pathways to urbanization: 1) climate shocks in heterogenous environments, 2) protection from intergroup conflict, and 3) the realization of latent economies of scale through capital investments. These models also suggest mechanisms that establish systemic inequality during the urbanization process, conditions under which population aggregation passes a tipping point to reach urbanization, and factors that may trigger the reverse process of deurbanization. Our aim is not to define rigid demographic trajectories, but to underscore the flexibility of these models in capturing diverse forms and scales of population aggregation.

Our population ecology framework also parallels foundational models in economic and urban geography, which emphasize similar dynamics of agglomeration and increasing returns to scale (e.g., refs. 6 and 7). In this sense, our approach offers an economic explanation that is grounded in evolutionary principles and environmental and demographic dynamics, bridging insights from ecology, economics, history, and geography into a unified conceptual framework.

We test model predictions using piece-wise structural equation models (pSEM) and newly synthesized paleoclimatological, paleoecological, demographic, and historic data from the Classic Period Maya Lowlands (CPML) (250–1000 CE) (Fig. 1*A*). While Maya Lowland urbanization first emerged during the late Middle Preclassic and Late Preclassic periods (700 BCE–250 CE), and debate continues over the degree to which some Preclassic

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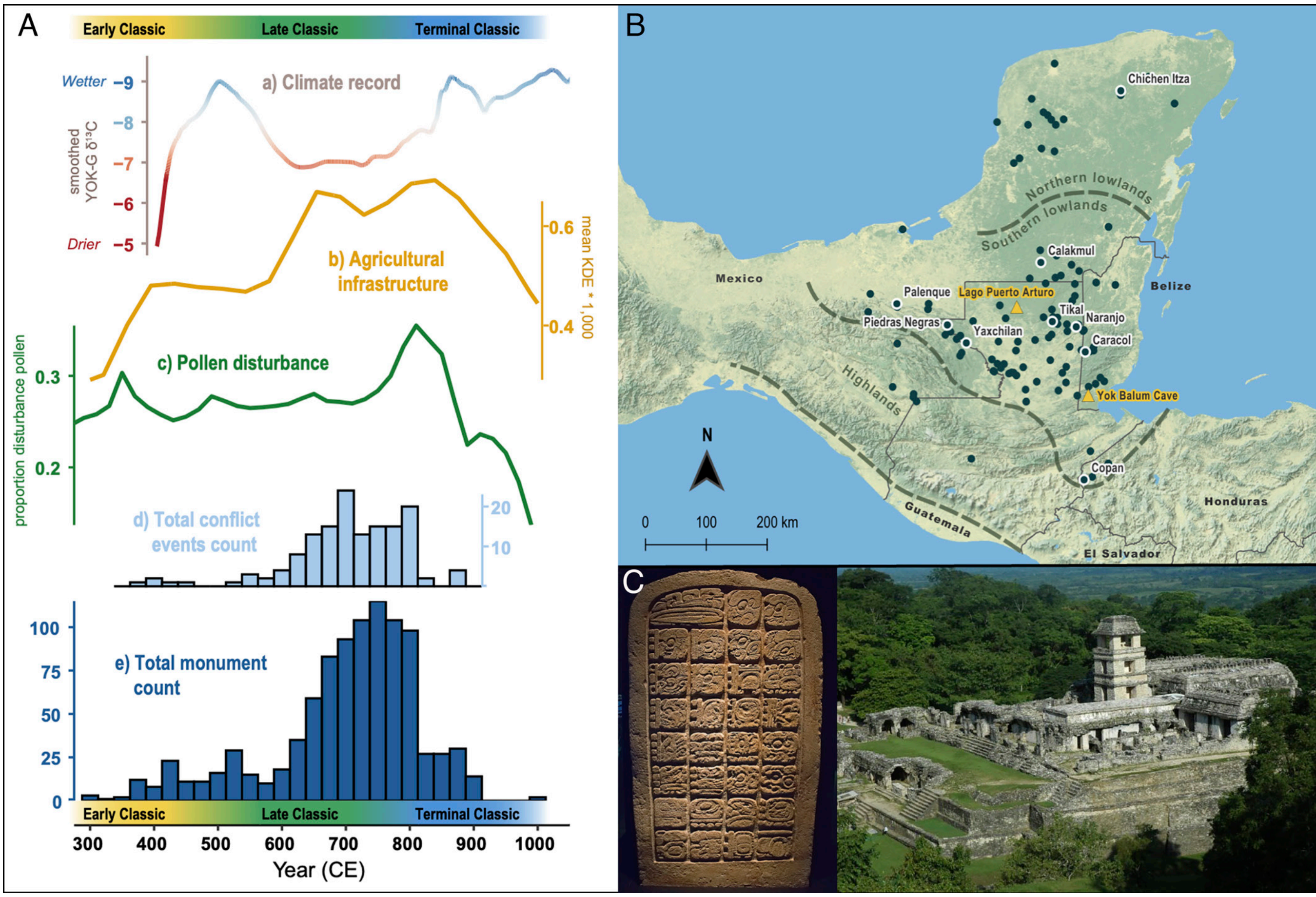

Fig. 1. (*A*) Time series stack—more details can be found in section 7.0. (*B*) Map of the study area with sampled Maya centers represented as green points. (*C*) Photo of a Classic Period Maya Stela monument (*Left*) and a photo of a Classic Period Maya Lowland urban center (Palenque) (*Right*)—Photo credit: Ymblanter (*Left*), Alfred Diem (*Right*).

urban centers persisted into the Classic Period (16–20), it is evident that numerous urban centers emerged during the Classic Period, with urbanism reaching its peak in the Late Classic (circa 650–750 CE) before declining between 750 and 900 CE (19). Crucially, throughout both the Preclassic and Classic periods, urban centers and their surrounding territories were predominantly inhabited by farmers (18, 21). Thus, the rise and fall of Maya Lowland cities reflects shifts in the aggregation or dispersal of agrarian populations. Accordingly, our theoretical model examines the conditions under which farmers would bear the seemingly paradoxical costs of living in urban areas, regardless of whether a city was newly emerging or well-established.

Critically, we treat urbanization as neither inevitable nor the product of "progress," but instead seek to explain when individuals find the benefits of urbanization to outweigh the costs (3). This is important because it suggests a city's decline may result from most of its residents deciding it is to their advantage to leave (or revolt) and questions the assumption that urban persistence unwaveringly promotes human well-being.

1.1. The Study Area. The Maya Lowlands (Fig. 1*B*) are an ideal region for studying the origins and expansion of early cities. They represent one of the few independent centers of city formation in the world and encompass a diverse range of environments, including tropical rainforests in the south and semiarid savannas and dry forests in the northwest (21, 22). Across both southern and northern zones, high-quality perennial water sources are patchily distributed, rainfall is highly variable, and agricultural suitability ranges across perennial wetlands, seasonal swamps in karst depressions (bajos), upland forests, and limestone flats (23–26). These conditions divide farmers into those with access to year-round surface water and those dependent on seasonal precipitation, water storage, and dry farming—while all groups contend with water quality limitations (27). The result is considerable environmental and demographic heterogeneity, with agricultural populations unevenly distributed across the landscape. Such variability often favored dispersed settlement patterns, particularly where the concentration of surplus resources was difficult (24, 28)–yet it is precisely within this context that the formation of cities becomes a phenomenon requiring explanation.

Archaeologically visible agricultural settlements first appear circa 2000–1000 BCE as people aggregated into small farming communities in resource-rich areas, including fertile lowlands and wetlands (16, 17, 29). These communities increasingly relied on pottery technology and staple domesticates like maize, beans, squash, and manioc (30–32). This coincides with the appearance of plaza pyramid complexes in the lowlands, signaling growing density, and complexity. During the Middle Preclassic (900–400 BCE) monumental buildings increase in size and number, which along with prestige goods, suggest increasing inequality and political complexity (17). During the Late Preclassic (400 BCE–250 CE) archaeologists observe an expansion of urban centers and intensified agricultural infrastructure (16, 17, 25, 33, 34). The Preclassic ended circa 100–250 CE when several large centers were abandoned (16, 19). Nonetheless, urban centers persisted in several key lowland areas, some of which expanded into Classic Period cities (e.g., Tikal) (33).

Population size, centralization, social inequality, and the number of urban centers expanded greatly in the Early and Late Classic Periods, culminating in an urban apogee circa 650–750 CE (19). Once established, centers were connected by regional trade networks administered by kings and queens who also oversaw warfare, urban construction projects, diplomacy, subjugation, and other activities (19, 35–37). A growing number of lidar remote sensing surveys of the Maya Lowlands reveal a heavily modified landscape with extensive urban settlements and agricultural features (Fig. 1*C*) including terraces, canals, fields, reservoirs, and roads (27, 38, 39). Archaeologists observe that by 750 CE, balkanization, decentralization, and settlement abandonment occur across the polities in the Maya Lowlands, unfolding over many decades and varying by geographic locale (19, 36, 40, 41).

As centers in the Southern Lowlands were undergoing abandonment, multiple large centers in the Northern Lowlands experienced pulses of population growth and political expansion during the Terminal Classic and Postclassic periods (42–44). These new urban configurations were centered on high suitability habitats and were less numerous and less hierarchical than CPML cities (45), but many went into decline circa 1000–1100 CE (46). Dispersed farming communities remained in the southern and northern Lowlands throughout the Postclassic and beyond (47).

2. The Population Ecology of Urbanization

Settlement decisions involve selecting locations based on their intrinsic suitability, determined by resource abundance and social amenities (48–52). Models from population ecology propose that the highest suitability habitats should be settled first, with subsequent occupants settling in increasingly less suitable places as a function of increasing competition in the better habitats (negative density dependence). When individuals independently make settlement decisions to maximize their suitability, two outcomes arise: 1) high-suitability habitats have higher population densities compared to lower-quality ones, and 2) an equilibrium is reached where all individuals experience the same per capita suitability (Fig. 2*A*). This pattern is described by the ideal free distribution (IFD) model, which includes the simplifying assumption that people have complete knowledge of their local environment.

However, individuals may decide to exclude others from their settlements to increase their own suitability. This behavior is most likely when resources that contribute to suitability are dense, predictable, and monopolizable (53–55). In such cases, populations no longer distribute freely. Instead, established residents in more suitable habitats may act as despots, excluding others and creating an ideal despotic distribution (IDD). Under an IDD, those in control of high-ranking habitats (despots) achieve greater fitness at the expense of others (48, 56, 57). In both IFD and IDD models, individuals may experience an Allee effect, where increasing population density initially raises habitat suitability up to some threshold, after which negative density dependence resumes (58, 59). Allee effects can draw in outsiders who are willing to enter a locale to take advantage of returns to scale (56). Under an IDD, Allee effects can give rise to patron–client systems, where those who initially occupied the most suitable places (despots) allow others to enter in return for a share of their labor or resources (54, 55). However, Allee effects can also occur without despots, as individuals are drawn in via mutual gains (59).

These dynamics can lead to different population-level outcomes. Under an IFD, population density should positively correlate with intrinsic habitat suitability, leading to a dispersed pattern with few large aggregations. In an IDD, individuals should seek to limit density, as those defending high ranking patches want to avoid accelerating negative density dependence. All else equal, large and stable population aggregations should only occur where activities benefit from economies of scale (Allee effects), especially under IDD conditions.

These population dynamics can interact in complicated, nonlinear ways to favor urbanism. Two temporary factors–climate/environmental shocks and intergroup conflict–may lead to ephemeral urbanism. Lasting cities are likely to require capital investments that activate latent economies of scale, promoting stable urbanism and patron–client relationships (60).

2.1. Climate Shocks. Harmful climate shocks often decrease the suitability of marginal habitats more than productive ones because of intrinsic differences in environmental characteristics. As a result, residents of low suitability habitats may try to relocate to less affected areas (61, 62). This may result in temporary aggregations where individuals seek access to high productivity areas to weather the storm. Those living in productive habitats under negative density-dependent conditions may try to exclude these newcomers (57). However, if climate shocks render marginal habitats untenable, conflicts of interest will arise between established residents seeking to limit entry and newcomers attempting to gain access to a more suitable patch. This condition should be most likely when landscapes are heterogenous and circumscribed (63, 64). Under these conditions newcomers benefit by virtue of accessing a habitat with higher suitability and established residents cannot afford the costs of exclusion. This "tolerated theft" of habitat parcels will result in population aggregation and lower per capita habitat suitability (Fig. 2*B*) (65). This dynamic may produce population aggregations that are small (dozens) or very large (thousands) depending on existing population sizes, intrinsic environmental suitability, and subsistence technologies.

If environmental conditions improve, these dynamics should dissolve, which would result in the disbanding of aggregations and a return to prior IFD conditions. Thus, the duration of these population aggregations depends on 1) the extent and duration of the climate shock, and 2) the cost of exclusion, structured by alternative options for newcomers. As a result, aggregations of this kind tend to be ephemeral due to socioenvironmental dynamics that make them unstable.

2.2. Intergroup Conflict. When intergroup violent conflict escalates, those in vulnerable, dispersed settlements may experience reduced per capita returns due to the costs associated with violence avoidance (66, 67). When economic activities are constrained or require some residents to engage in noneconomic tasks like resource guarding, individuals face diminishing marginal returns (67). If these costs become too high, moving to aggregate sites or cities is beneficial as such locations offer protection in numbers (9). This strategy constitutes a return to scale so long as the size of a population aggregation proportionately reduces the per capita costs of violence avoidance, and aggregation will persist so long as resource costs do not outweigh the costs of violence avoidance. This dynamic suggests a sigmoidal returns curve, with a minimum group size threshold needed to reduce violence avoidance costs and an upper limit where additional members lead to diminishing returns (Fig. 2*C*). Established residents (despots) control access to protected settlements and may impose costs on newcomers by forming patron–client relationships. A trade-off may arise when newcomers looking to settle near the core of protected settlements face higher access costs compared to those in more dangerous peripheries.

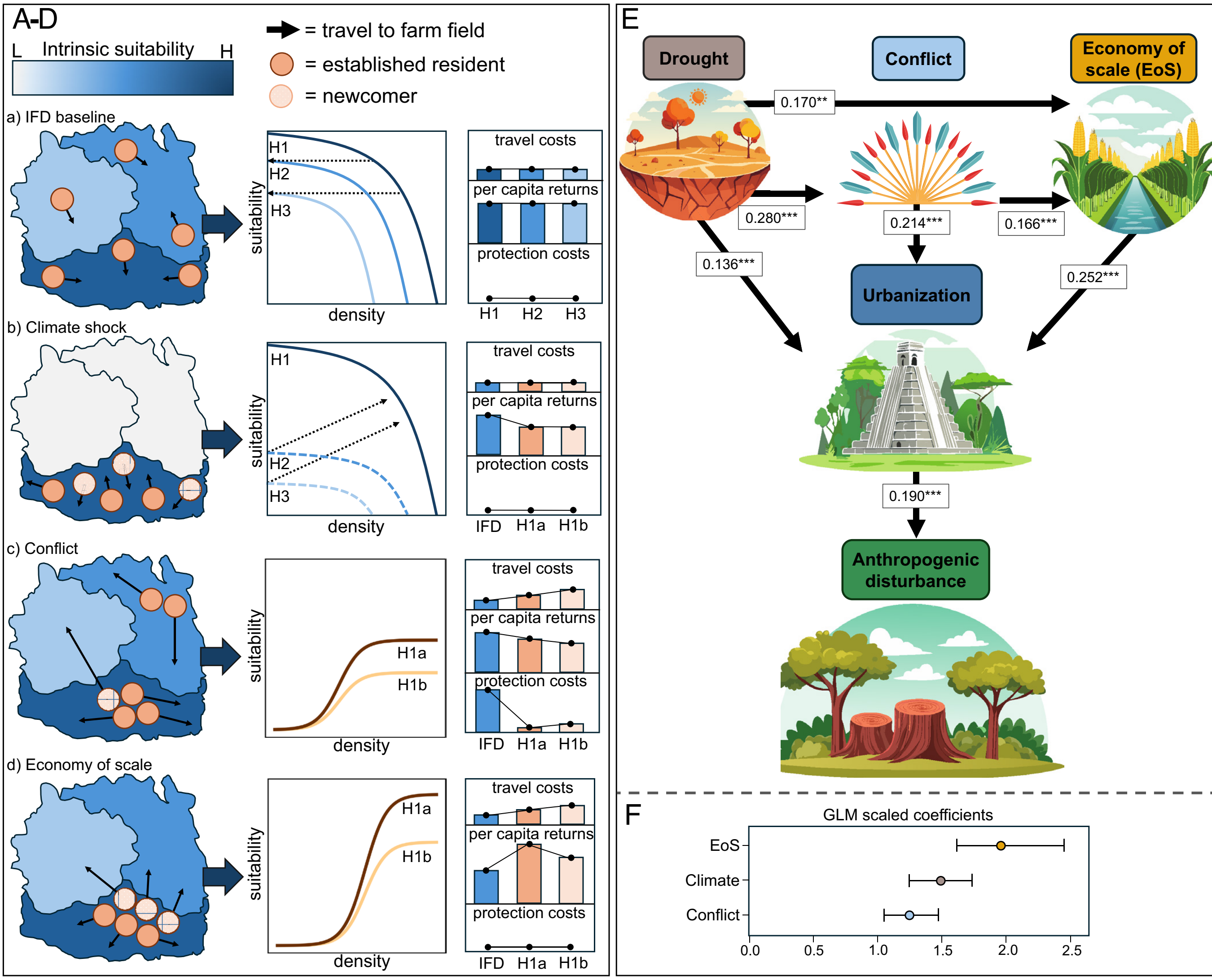

Fig. 2. (*A*) An IFD with the population at equal suitability equilibrium across the three habitats (H1-H3). We assume for comparative purposes that travel costs are low and at equilibrium. (*B*) A climate shock renders the two low-ranked habitats untenable, driving relocation to the high-ranked habitat, increasing aggregation. Negative density dependence means per capita returns in the high-ranked habitat will be lower for all. When the climate shock ends, population distribution will return to IFD (*A*). (*C*) Intergroup conflict drives aggregation, which decreases the costs of violence avoidance while increasing travel costs and competition. When conflict ends, population distribution will return to IFD (*A*). (*D*) Allee effect draws in outsiders who receive lower benefits relative to established residents. Travel costs may be lessened when farm fields are moved closer to urban areas to take advantage of agricultural infrastructure. (*E*) Theoretical predictions and the results of the pSEM showing scaled effect sizes (betas) with asterisks denoting *P*-value significance. (*F*) Negative binomial GLM scaled coefficient effect sizes with 95% CI. Note: The Images in Fig.2 E were generated using Adobe Illustrator's AI-features.

Aggregations may end or pause if 1) peace reduces violence avoidance costs or 2) further population aggregation leads to a cross-over point between diminishing protection benefits and accelerating resource costs. The latter could result in informal diffuse aggregations, where newcomers settle close to but not within a settlement core to avoid high access costs or exclusion. Despots, benefiting from conflict, may intensify regional violence (68) in-part to maintain the high costs for leaving cities.

2.3. Capital Investment. Allee effects (59), also termed economies of scale, agglomeration effects, and superlinear scaling in economic and urban geography (6, 7, 69), can emerge through capital investments, which become worthwhile when competition-driven declines in habitat suitability can be overcome by intensification. Prime examples among preindustrial agrarian societies include infrastructure projects like canals, terraces, raised fields, and reservoirs (49, 70–73), often referred to as landesque capital (74). However, because these projects have high startup costs (70), they may only become viable after population pressure or an exogenous shock justifies the initial investment costs (54, 75). Thus, agricultural strategies that provide strong economies of scale may remain latent for some time. Before carrying capacity is reached, farmers will further intensify production (*sensu,* 75) because 1) alternative strategies will incur Malthusian penalties (76) and 2) strategies that benefit from an economy of scale suggest a sigmoidal shaped returns curve, such that once the system is established individual returns will exceed input costs (69, 77), at least up to some threshold (Fig. 2*D*). Assuming complete ecological knowledge, economies of scale then attract outsiders who gain higher per capita payoffs compared to dispersed locations (60). This sigmoidal payoff structure should also 1) foster collective action as large-scale infrastructure projects require organized and cooperative labor to generate and maintain the returns to scale (78, 79), which benefit all participants, but often not equally (69), or 2) promote the development of social structures that facilitate collective action by reducing free-riders and other social dilemmas (80, 81), which could produce Allee-like benefits that are distributed more evenly across a population (e.g., refs. 80 and

82). With strong economies of scale newcomers may abandon dispersed locations to set up farms near urban centers with access to agricultural infrastructure. This process can increase inequality, as early settlers benefit more from infrastructure than later arrivals (21, 51), and accelerate aggregation and conflicts of interest, as newcomers vie for land close to amenities (12). In all cases, established residents (despots) can leverage first mover advantages (83–85) to establish patron–client relationships by controlling access to land and resource infrastructure.

Aggregation will continue as long as 1) economic returns to scale for newcomers surpass access costs and returns in dispersed areas or alternative cities, and 2) the costs of enforcing patron–client relationships do not outweigh the benefits for despots. Aggregation then persists and grows as long as newcomers receive marginally higher returns relative to dispersed locations, and despots receive disproportionately higher payoffs, thus fueling the coevolution of cities and systemic inequality.

2.4. The Rise of Cities. From this framework city formation should result from a large and stable population aggregation characterized by a strong, enduring economy of scale and an environment that can produce a substantial surplus. Despots may co-opt a disproportionate share of this surplus to further their interests, ultimately leading to the development of state-like institutions including organized labor to construct status-enhancing monumental structures, a taxation bureaucracy, market and manufacturing sectors, standing militaries, etc. (see refs. 2 and 4). Without a robust and stable economy of scale, population aggregations are unlikely to reach the size and compactness necessary for city formation and the creation of tax-fed formal institutions.

What defines a city follows from what drives its formation. Most definitions emphasize either population size or functional roles like governance and coordination (86, 87). While both are necessary, neither is sufficient: Towns may exhibit functional centrality, and population thresholds are inherently arbitrary. We define a city as a large population agglomeration exhibiting functional centrality. Urbanization in this view is an outcome of aggregation such that the core paradox holds across scales, with cities being on the upper end. In contexts of uniformly low settlement density, the urbanization paradox does not arise. However, where overall density is low but locally clustered, our model remains applicable, particularly to the low-density, agglomerated centers typical of Maya cities (88).

2.5. The Fall of Cities. Interruptions or reversals in the processes driving early city formation can promote deurbanization. Drivers include pull factors such as favorable climate change, reduced regional violence, or reduced inequality elsewhere, and push factors such as anthropogenic ecological disruption near cities, declining returns to scale, urban disease, or elite overexploitation. These processes likely interact as complex systems susceptible to tipping points that trigger changes like urban abandonment (45). We propose five alternative outcomes based on these interactions: 1) Cities experience a “natural death” with a slow exodus due to improved rural conditions and/or urban ecological or economic decline. 2) If rural conditions become more appealing, reduced inequality may allow a city to persist due to rising per capita returns for commoners. Elite concessions are most likely when commoners have bargaining power, which is most common when land is plentiful and labor scarce (83, 89). 3) If elites refuse concessions and increase exit costs, revolt may occur, leading to either a new less exploitative elite or urban abandonment and collapse (43, 45). 4) Civil strife may invite a unified competitor to invade, resulting in the destruction of a city or takeover by new elites. 5) Resource-limited density-dependent conditions or disease led to population declines via reduced fertility, increased birth spacing, or mortality (90, 91). These outcomes can also co-occur, as seen in the Maya Lowlands during the Terminal Classic Period (40, 92, 93).

2.6. Predictions. Following the model pathways outlined above we predict (Fig. 2*E*) urbanization should positively covary with 1) harmful climate change leading to reduced agricultural productivity 2) increasing frequency of conflicts, and 3a) the construction of agricultural infrastructure to take advantage of economies of scale, 3b) increasing population size, which itself should nonlinearly scale with agricultural infrastructure. We also predict mediating relationships between these pathways as outlined in Section 2.5. Finally, we predict that urbanization will correlate with increased anthropogenic ecological disruption. More information is available in the *Materials and Methods*.

3. Results

The results of negative binomial generalized linear models testing direct effects (*SI Appendix*, Supplement 2 (S2) and section 8) strongly support model predictions. The emergence and expansion of CPML cities positively covaries with 1) dry conditions, which are known to decrease agricultural yields in the Maya Lowlands (91, 94–97), providing support for pathway one; 2) the frequency of Maya conflicts, supporting pathway two; and 3) the development of intensive agricultural capital infrastructure, supporting pathway three. Scaled effect sizes (Fig. 2*E*) show that economies of scale have the largest effect, followed by climate, and the frequency of Maya conflicts. pSEM (Fig. 2*E* and *SI Appendix*, Supplement (S2) and section 10) show numerous moderating effects, with dry conditions positively covarying with the frequency of Maya conflicts and the development of agricultural infrastructure. The frequency of Maya conflicts also positively correlates with the development of agricultural infrastructure. The findings of a generalized additive model (GAM) examining the nonlinear effect of Lowland population size on agricultural infrastructure reveal a significant superlinear relationship, indicating a robust scaling effect *SI Appendix*, Supplement (S2). Finally, the expansion of Classic Maya cities has a significant positive covariance with ecological disturbance even when climate change is controlled for (Fig. 2*E*). More details are available in *SI Appendix*, Supplement (S2).

4. Discussion

Results broadly support our theoretical model and illustrate complex interactions between climate, conflict, and economies of scale. CPML urbanization is a prime example of a largely agrarian population creating some of the most complex urban centers in the precontact New World. The expansion and scale of urban growth is likely due to the interaction between the three model pathways, as climate, conflict, and capital investments all interact and consistently predict the emergence, growth, and collapse of cities in this region.

Climate change had direct and indirect effects throughout the socioecological system. Dry conditions covary with the expansion of early Classic Maya cities and their Late Classic apogee (650–800 CE). This suggests that agricultural productivity in marginal areas was disproportionately impacted by dry conditions relative to locations of Maya centers, which could take advantage of perennial wetlands or fertile soils (90, 95, 98). The strength of the scaled climate effect in our structural equation models (pSEM) suggests that drought was a key trigger for CPML urbanization and its apogee during the Late Classic. Dry conditions also promoted Classic Period conflict, likely over scarce resources and productive arable land. Last, dry conditions predict the growth of agricultural infrastructure, suggesting economies of scale were preferentially leveraged during adverse climate intervals when water management infrastructure was crucial (98).

The frequency of Maya conflicts recorded on stone monuments links to both the emergence and expansion of Classic Maya cities, suggesting people were drawn into areas of urban control for protection. The frequency of Maya wars in historical records begins to increase during the Early Classic Period (250–600 CE) but peaks during the 7th century CE when urbanization was at its zenith (Fig. 1*D*). Results show that warfare itself was likely triggered by regional aridification, suggesting climate and conflict played an interacting role in the emergence of Classic Period urban centers. Nonetheless, warfare continues throughout the Classic Period, perhaps perpetuated by exploitative elites who benefited from endemic warfare (68, 99). Warfare continues into the early Terminal Classic (~800 CE) with the abandonment of CPML centers (Fig. 1*D*), suggesting warfare also influenced regional destabilization (19). Whether or not conflict occurred prior to the Classic period or declined with the fall of Classic centers is, however, debatable, as intergroup warfare may have persisted before and after wars were recorded on stone monuments. As such, we recognize that this is an underestimate of warfare events and future research may reveal additional linkages.

The significant link between urban agricultural infrastructure and the rise of CPML cities strongly suggests agricultural economies of scale were major pull factors during early Classic urban phases and throughout the Classic Period and were both extensified and intensified as conditions were drying (98). This is supported by the observed superlinear scaling between CPML population size and agricultural infrastructure (*SI Appendix*, Fig. S10). The correlation between dry conditions and the initial spread of agricultural economies of scale likely relates in part to water availability and control (94, 95). As agricultural productivity declined, early population centers intensified production, including the expanded construction of large water management features that can take advantage of latent economies of scale. During the Late Classic drought, agricultural infrastructure intensified in and around cities while urban populations peaked. Urban elites then continued to coordinate the construction of agricultural infrastructure to further encourage urbanization even as climate became more favorable in the Terminal Classic and urban inequality increased. Nonetheless, the continued reliance on agricultural production in environmentally constrained settings likely shaped the unique form of many Classic Maya cities. Unlike dense, market-driven cities in other urban systems, Maya centers often took the form of low-density agrarian urbanism—spatially expansive settlements where agricultural infrastructure was interwoven with residential and civic architecture (88, 100). This pattern is consistent with the demographic and environmental limits on surplus concentration, even as elites leveraged economies of scale to intensify production and encourage population aggregation.

The interplay of these processes fostered conditions that stimulated the formation of patron–client relationships and systemic inequality. Economies of scale, in particular, both stemmed from and exacerbated urban inequality. This suggests that, even in some ancient cities, the benefits of urban scaling were disproportionately funneled to the elite. As long as elites provided sufficient concessions to ensure clients fared marginally better in cities than in nonurban areas, they could expect both urbanization and social stratification to persist. When climate shocks, conflicts, or circumscription rendered dispersed areas untenable, elites could increase exploitation as the costs of leaving cities peaked. The allowance of extreme forms of exploitation may in-part explain the eventual evolution of the Classic Maya kingship system, where hereditary rulers exercised a strong degree of power and authority (36).

Yet while urbanism and systemic inequality expanded during the Classic Period, these processes unfolded within a highly variable environmental and political landscape. Frequent climatic shocks may have interrupted the consolidation of generational wealth (91), while the continued dispersal of farming populations may have limited the capacity of elites to enforce centralized extraction (101, 102). Under such conditions, elite authority often depended on negotiated relationships—sustained through concessions, persuasion, and theatrical display—rather than on direct coercion (34). These dynamics likely contributed to periodic turnover among elite factions and may help explain the episodic volatility of urban trajectories during the Late and Terminal Classic periods (92).

The processes of climate change, conflict, and economies of scale in reverse may help explain the dissolution of CPML cities during the Terminal Classic (800–1000 CE) when 1) climate was favorable, which would increase yields in rural dry farming areas, 2) state-level warfare was declining, which may have made areas outside of city control less dangerous, 3) agricultural practices led to legacy effect ecological disruptions around cities that reduced local productivity (see below), and 4) agricultural infrastructure was in rapid decline, suggesting declining scaling benefits. The systematic ecological disruption and neglect of ecosystem services, long-recognized among the Classic Maya (24), reduced the long-term carrying capacity of near-urban landscapes through canopy loss, soil loss and diminishing soil nutrients, habitat loss for wild fauna, and more (45, 98, 103, 104). As ecological disruption coincided with reduced returns to scale and processes that made rural areas more attractive, a tipping point was reached when urban residents would have benefited from moving out of cities or forcing substantial concessions from established elites. Indeed, Postclassic cities were less hierarchical and lacked the kingship systems dominant during the Classic Period (43, 45, 95). While some Classic Period cities persisted, and a few experienced gradual deurbanization, most went into rapid decline between 750 and 850 CE, likely as the result of complex interactions between urbanization pathways leading to system-wide tipping points that drove disaggregation. These dynamics also coincided with broader demographic contractions, possibly linked to the cumulative effects of food insecurity, disease, and outmigration (104).

In conclusion, our empirical results show that unfavorable climate conditions, high costs of conflict avoidance, and the construction and maintenance of urban agricultural capital investments that benefited from economies of scale structured Classic Period Maya urbanization. Each of these nonlinear pathways contributed to the rise and apogee of Classic Period Maya Lowland urbanization, and these processes in reverse can partially explain both the demise of many Lowland cities, and the diversity in outcomes. We contend that simple population ecology models can accommodate complex, nonlinear urban dynamics, particularly with the addition of economies of scale (Allee effects) and their effects on systemic inequality.

We argue that the models presented here are generalizable and can be applied to all cases of urbanization, thus providing a unified theory that can account for one of the greatest paradoxes in human history. This is not just relevant to the past: By gaining a broader understanding of why cities emerge and expand, we are better equipped to predict when they can be sustained, or when they will decline. This is critical for understanding the conditions when urbanization is likely to increase or diminish human well-being under future climatic and demographic scenarios.

5. Materials and Methods

5.1. Paleoclimate Proxy. Classic Period hydroclimate variability is estimated using annually resolved $\delta^{13}C$ data from a speleothem taken from Yok Balum Cave (YOK-G) located in the southern Maya Lowlands (89) (Fig. 1*A* and *SI Appendix*, Supplement 1 (S1)). Recent research shows that the YOK-G $\delta^{13}C$ proxy provides a representative record of hydroclimate variability for the Maya Lowlands, and suggests alternative records, such as YOK-I, are more complicated proxies of climate (see ref. 89).

5.2. Agriculture Infrastructure. Published and unpublished radiocarbon dates (n = 173, S1) from agricultural infrastructure features such as raised fields, canals, aquifers, etc. were compiled using MesoRAD (105) along with additional sources and combined into a composite kernel density estimate (CKDE) with 1,000 unique KDEs to account for uncertainty in calibrated radiocarbon probability densities. The mean KDE was calculated for use in inferential models and estimates the frequency of agricultural infrastructure construction or expansion events throughout the Classic Period (Fig. 1*B*).

5.3. Urban Ecological Disturbance. Ecological disturbance data were derived from a pollen record from Lago Puerto Arturo (S1) in the Peten of the Southern Maya Lowlands (see refs. 106 and 107). Pollen taxa were classified as disturbance or tropical forest vegetation types following the Torrescano-Valle and Islebe (108) classification of pollen taxa from a vegetation record in the Yucatan Peninsula (*SI Appendix*). Pollen sums were converted to proportions for each vegetation type. To compare the pollen record with the other time series we resampled the data to achieve annual resolution. An inverse distance weighted interpolation function was applied to impute unsampled time points by assigning more weight to values from nearby sampled points (109). By applying this function across the data points the technique smooths out variations and fills in gaps, enabling the creation of a continuous, uniformly spaced time series with a fixed annual interval (Fig. 1*C*). Trends apparent in the Lago Puerto Arturo record correlate with those seen in other Maya Lowland vegetation records spanning the Classic Period (103), suggesting the observed patterns are robust.

5.4. Maya Conflict Events. The Maya war time series derives from the Maya Hieroglyphic Database (MHD, 110) and the supplemental materials from Carleton et al. (19, 111). It consists of 144 recorded Classic Period warfare events throughout the CPML (S1). Each warfare event is associated with a historical monument inscription and Classic Maya calendar date (Fig. 1*D*).

5.5. Maya Monument Construction. Data from the MHD were used to estimate the frequency of monument production for the CPML and the number of sites engaged in monument production as a proxy for the rise and demise of cities (19, 40). Within the MHD, a search was conducted for monuments (dedicatory stelae, altars, or other noneasily portable texts like hieroglyphic stairways and murals) recording calendar dates associated with their creation (as opposed to dates associated with historical events transcribed on the monuments). Monuments with creation dates recorded as either long count dates or other calendar dates (e.g., calendar round, initial series, and distance numbers) that can be confidently correlated with the long count calendar were included. The long count dates were converted to the Gregorian calendar using the Goodman-Martinez-Thompson correlation constant. In total, the dataset contains 882 dedicatory monuments from 115 sites throughout the Maya Lowlands during the Classic Period (Fig. 1*E*, S1). These monuments document more than 1,900 events over the course of the Classic Period.

5.6. Maya Lowland Population Size. Published radiocarbon dates (n = 2,290) excluding dates from agricultural infrastructure features were compiled using MesoRAD (105) (S1) and combined into a CKDE with 1,000 unique KDEs to account for uncertainty in calibrated radiocarbon probability densities (*SI Appendix*, Supplement 3 (S3)). The mean KDE was calculated for use in inferential models and estimates Lowland population size throughout the Classic Period (Fig. 1*B*). The mean KDE significantly correlates with the total monument construction count (rho = 0.55, $P < 0.001$), suggesting the mean KDE estimate tracks populations sizes in urban centers where monuments were constructed.

5.7. Statistical Models. To test our predictions, we fit a generalized linear model with a negative binomial distribution appropriate for overdispersed count data. To determine whether our predictor variables have mediating effects, we employ pSEM using the piecewiseSEM package (112) in R. pSEMs combine multiple variables into a causal network, permitting simultaneous tests of multiple hypotheses. The pSEM technique explicitly assumes causal linkages between exogenous (predictor) and endogenous (response) variables and can quantify scaled direct and indirect effects. Finally, a GAM was specified to capture nonlinear effects between the logged population size and agricultural infrastructure variables All analyses are conducted in the R programming environment and language (113). For additional details about our analysis see *SI Appendix*, Supplements (S2) and (S3).

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

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