

toward the extracellular side of the pore, further increasing the energetic cost for ions to traverse this region. The series of TM1-TM2 tilts and TM3 rotations leads to the formation of a large 10 to 12 Å × 20 Å conductive pathway lined by the TM3a and TM3b segments; preliminary MD simulations show conduction of both cations and anions through this pore (fig. S6). These permeation pathway cross sections underlie the similarities between the open model and the MscS crystal structure (12, 13). Except for the narrowing at the intracellular end of its pore (Fig. 4C, arrows), the crystal structure could, in principle, support ion conduction and thus might represent an inactivated/desensitized conformation after opening. The structural rearrangements described here demonstrate a gating mechanism that is distinct from that of MscL (14, 17, 18) but confirms the critical role of helix tilting in transducing bilayer deformations to generate an aqueous pathway through the membrane.

Note added in proof: A recent model of open MscS (42), based on computation and single-channel analyses, is in agreement with the present conformation of TM3 (Fig. 2).

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Pre-Columbian Urbanism, Anthropogenic Landscapes, and the Future of the Amazon

Michael J. Heckenberger,^{1*} J. Christian Russell,² Carlos Fausto,³ Joshua R. Toney,⁴ Morgan J. Schmidt,⁵ Edithe Pereira,⁶ Bruna Franchetto,⁷ Afukaka Kuikuro⁸

The archaeology of pre-Columbian polities in the Amazon River basin forces a reconsideration of early urbanism and long-term change in tropical forest landscapes. We describe settlement and land-use patterns of complex societies on the eve of European contact (after 1492) in the Upper Xingu region of the Brazilian Amazon. These societies were organized in articulated clusters, representing small independent polities, within a regional peer polity. These patterns constitute a “galactic” form of prehistoric urbanism, sharing features with small-scale urban polities in other areas. Understanding long-term change in coupled human-environment systems relating to these societies has implications for conservation and sustainable development, notably to control ecological degradation and maintain regional biodiversity.

Are there “lost cities” in the Amazon that await discovery in the dense tropical forests of the region? If so, how did indigenous civilizations alter forested environments, and do past patterns provide clues to resource management today? Recent archeology, which documents large settlements (>30 ha) and extensive landscape alterations in several areas,

has sparked debate on prehistoric Amazonian urbanism (Fig. 1A) (1–3). The Upper Xingu region of the southern Amazon (Mato Grosso, Brazil) is one critical example of complex settlement and land-use patterns (4–6). Here, we report recent findings on settlement planning and supralocal integration, which document a highly self-organized anthropogenic landscape of late

prehistoric towns, villages, and hamlets, with well-planned road networks across the region. These patterns, although differing substantially from other world areas, share characteristics common of small, urban polities elsewhere.

The nature and development of prehistoric urbanism are contested issues. In recent decades, archaeological and historical studies of non-Western cases across the globe have emphasized variability, in addition to central-place and city-state forms, and substantially expanded the known distribution of urban societies [supporting online material (SOM) text] (7–9). Early urban societies are characterized by a “reasonably large and permanent concentration of people within a limited territory” but are commonly “identified with a broad-type of ritual-political centre... with small residential populations and are thus ‘marginally urban’” (10, 11). We use a definition of early urbanism that is not limited to cities, meaning megacenters (5000 or more persons) distinctive in form and function from rural or suburban communities, but that also includes multicentric networked settlement patterns, including smaller centers or towns.

Rather than ancient cities, complex settlement patterns in the Upper Xingu were characterized by a network of permanent plaza communities integrated in territorial polities (~250 km²). This

dispersed, multicentric pattern of plaza towns (~20 to 50 ha) and villages (<10 ha) was organized in a nested hierarchy, which gravitated toward an exemplary political ritual center. We refer to these hierarchical supralocal communities as galactic clusters, inspired by Tambiah's (12) "galactic polity" model, which draws attention to the basic similarities between small-to-large centers and the "radial mapping" of satellites in relation to an exemplary center. The galactic clusters existed within a regional peer polity composed of geographically and socially articulated but independent polities that shared basic features of techno-economy, sociopolitical organization, and ideology (Fig. 1B) (13).

¹Department of Anthropology, University of Florida, Gainesville, FL 32611, USA. ²Land-Use and Environmental Change Institute, University of Florida, Gainesville, FL 32611, USA. ³Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, Rio de Janeiro 20940-040, Brazil. ⁴Department of Anthropology, University of Florida, Gainesville, FL 32611, USA. ⁵Department of Geography, University of Florida, Gainesville, FL 32611, USA. ⁶Coordenação de Ciências Humanas, Museu Paranaense Emílio Goeldi, Belém 66077-830, Brazil. ⁷Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, Rio de Janeiro 20940-040, Brazil. ⁸Associação Indígena Kuikuro do Alto Xingu, Parque Indígena do Xingu (PIX), Mato Grosso, Brazil.

*To whom correspondence should be addressed. E-mail: mheck@ufl.edu

The Upper Xingu headwater basin is a lobe of tropical forest, transitional between the dense evergreen rainforests at the core of the Amazon and scrub forests and woody savannas of the central Brazilian highlands. It is part of the transition forest region that extends across the southern Amazon (14). Within core areas of the basin, our studies document several major episodes of prehistoric change within a cultural continuum extending from initial colonization, ~1500 to 1200 years before the present (yr B.P.) or earlier, to the present. Our survey and excavations have focused on the organization and development of the galactic clusters ~750 to 450 yr B.P. (table S1) (15, 16). After ~500 to 400 yr B.P., early European colonialism resulted in substantial depopulation and forest expansion.

We have identified 28 prehistoric residential sites, most or all of which are associated with two galactic clusters that represent small territorial polities (17). Our investigations demonstrate that clusters integrated large- (>40 ha) and medium-sized (<30 ha) plaza towns and smaller (<10 ha) plaza villages as well as small (nonplaza) hamlets (Fig. 2 and figs. S1 and S2) (15). Plaza towns are distinguished by major ditches (500 to >2000 m long), defining settlement boundaries and, in some cases, occurring within settlements (fig. S1) (18). Ditches range from 1 to 3 m deep and 5 to

10 m wide. They are associated with raised interior berms (formed from ditch fill) and were augmented with a wooden palisade wall (19). Extensive residential occupations are documented across interior portions of walled settlements, including structural remains (house and trash-midden areas) and ceramic cooking utensils, covering ≥20 ha in first-order settlements (figs. S3 and S4). Smaller nonwalled plaza villages are similar in size and form to larger contemporary villages (20).

Each cluster had an exemplary plaza center, although all permanent settlements had a central plaza (120 to 150 m in diameter), which, like today, served as the political ritual center and probably the cemetery of the local group. This underscores the importance of public ritual as a major integrating feature of the prehistoric polities (15). In addition to their larger size and structural elaboration, including gates, roads, and secondary plazas (possible ritual staging areas), walled towns are distinguished by their position in relation to the cluster center: The largest residential centers are located roughly equidistant (3 to 5 km) from the exemplary center to the northwest and southeast (21) and medium-sized centers to the northeast and southwest, roughly 8 to 10 km from the center. The area enclosed by the primary satellites represents the core area of

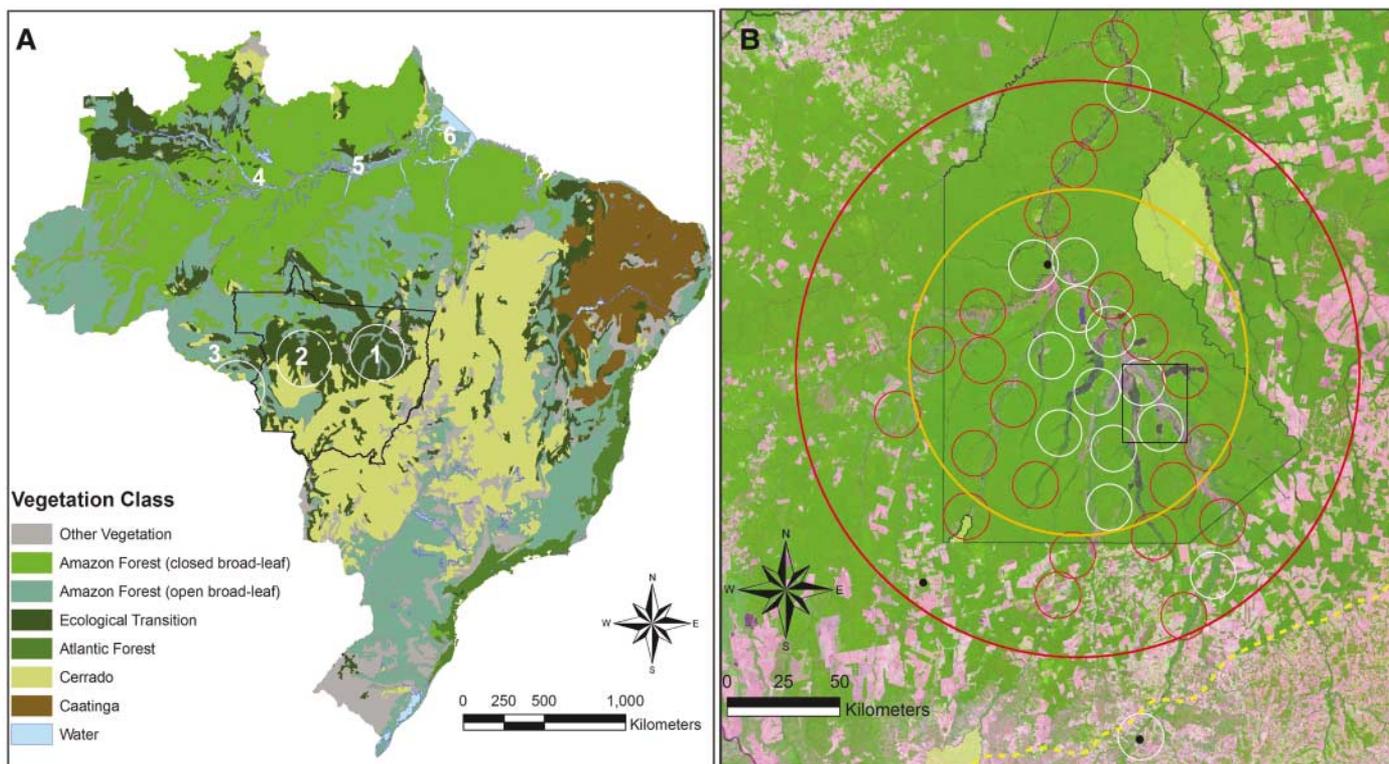


Fig. 1. (A) Map of Brazil showing major vegetative regions and areas of Amazonian complex societies, including (1) Mato Grosso state outlined; (2) blue-green forest in eastern Brazil is open broad-leaf associated with the Atlantic Forest biome. (B) Proposed cluster distributions in the Upper Xingu basin. White numbered circles are based on presence of major (>30 ha) walled centers; red unnumbered circles are hypothetical (47, 48). Area of acute anthropogenic influence is denoted by an orange circle (150 km diameter, ~17,500 km²) and

moderate to minimal anthropogenic influence by a red circle (250 km diameter, ~50,000 km²). PIX is denoted by a black line. The study area is denoted by a black box. A hatched yellow line denotes the ecological boundary between the southern Amazon forest (north) and the wooded savanna/scrub forest (south). Indigenous areas other than PIX are marked with light green. Black dots are general locations of sacred areas of Morená (north), Kamakuaka (southwest), and Sagihengu/Ahasukugu (southeast).

each polity, with smaller nonwalled settlements situated in a hinterland area.

The southern Kuhikugu cluster is centered on site X11, which was the principal political ritual center and largest residential center. The better-known northern Ipatse cluster has two major residential centers located to the north-northwest and south-southeast of the exemplary center (X13). X13 is interpreted as a primarily ceremonial center because of the paucity of domestic remains in areas outside the central plaza, the central location between X6 and X18, and the elaborated ground plan (22). The relation of X6 and X18 to X13 is similar to the orientation of high-ranking houses in the contemporary Kuikuro village, situated to the north-northwest and south-southeast of the plaza center. Secondary centers are situated to the north-northeast and south-southwest of X13.

Our survey and mapping of earthworks within and between settlements documented extensive planning based on standardized geometric and relational principles, which became durably fixed in settlement and road architecture. These relational principles are calibrated or “fitted” to basic ecological features, such as settlement position at wetland/upland interface. Four primary orientations have been recognized: (i) the formal road, roughly corresponding to the northeast-southwest solstice axis ($\sim 67^\circ/247^\circ$), present in all plaza settlements (23); (ii) the perpendicular north-south axis, which also forms a primary axis of regional distributions (a north-south road) (X13, X18, X19, and X20); (iii) intercardinal angles (X13); and (iv) the southeast-northwest solstice axis in the two largest residential centers (X6 and X11). Major roads in settlements (20 to 50 m wide) are contiguous with those between settlements (10 to 20 m wide), which extend up to 3 to 5 km. Traffic networks link satellites across a broader area and include wetland features such as raised causeways, bridges, and canoe canals. At the supra-local level, our survey revealed a grid-like pattern, created by regularly spaced settlements and road networks (Fig. 3A).

Our investigations of the two galactic clusters indicate that the territory of each polity was ≥ 250 km². Within each cluster, we estimate 100 to 150 ha or more of settlement space and a population in the mid-thousands (≥ 2500) distributed between walled towns, which are estimated to have 800 to 1000 or more persons [as known ethnographically from adjacent areas (24)], and smaller nonwalled villages (250 ± 100 persons). The centers of the two clusters (X11 and X13) are separated by ~ 20 km, which is also the distance separating X11 from X24, another putative cluster center, and other known centers across the region (15). The distribution of large centers indicates that the regional peer polity was composed of 15 or more clusters across an area $\geq 20,000$ km², including sites far to the north and south of the study area. We estimate a regional population of $\geq 50,000$ (> 2.5 persons/km²) (25).

The clusters of walled towns and nonwalled villages were maintained by semi-intensive resource management systems (26). Similar to villages today, these were probably focused on

manioc agriculture, with diverse lesser crops (including arboriculture), as suggested by continuity in land use and utilitarian technology, and extensive wetland management (such as fish

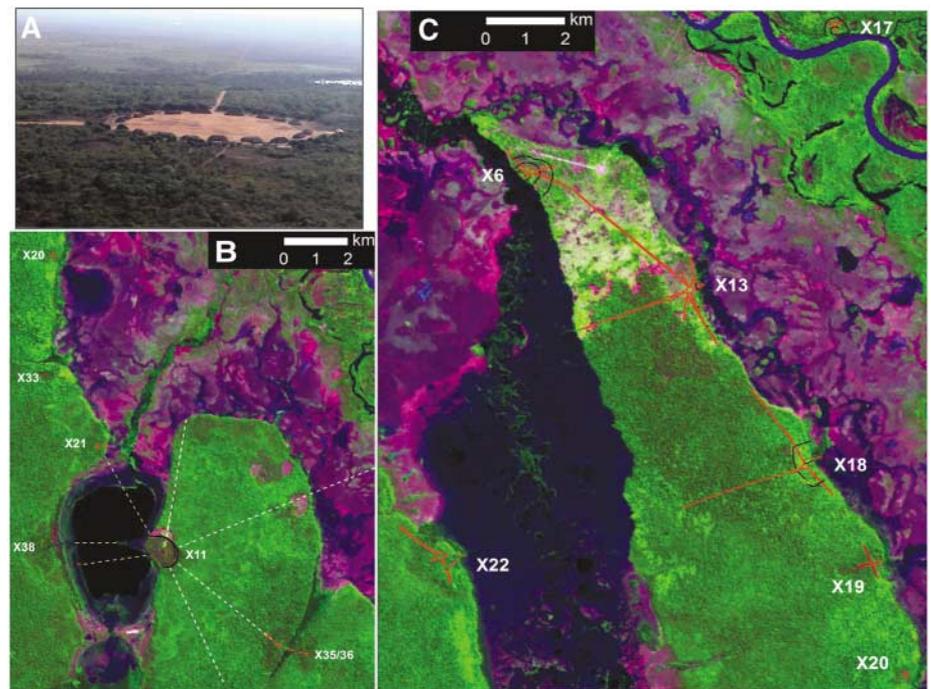


Fig. 2. (A) Contemporary Kuikuro village (2003). (B) Southern (Kuhikugu) cluster (hatched lines are projected from mapped village earthworks). (C) Northern (Ipatse) cluster sites. Global Positioning System (GPS)-mapped earthworks are denoted by red lines for road and plaza berms and black lines for ditches in (B) and (C). Pronounced anthropogenic “scarring” is found around areas of prehistoric sites. The location of Kuikuro village in (C) is just right of X6.

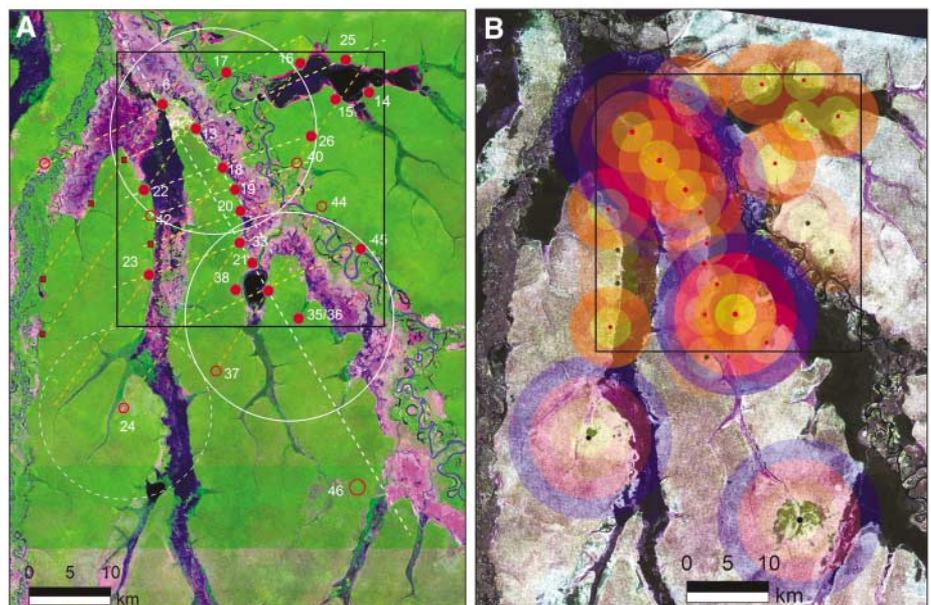


Fig. 3. (A) Regional road networks, extrapolated from GPS-mapped earthworks in and between sites (Fig. 2 and fig. S2). Northern and southern clusters are denoted by large white circles; GPS-mapped sites by small solid red circles; sites lacking GPS coordinates by open red circles; hypothetical site locations by squares; putative cluster by the dashed white circle; and extrapolated road orientations by dashed lines. (B) Overlapping concentric use areas of 2.5-km (yellow), 5.0-km (orange), and 10-km (blue) diameters positioned over pre-Columbian sites; black dots are sites that lack GPS coordinates.

farming), as indicated by the presence of earthen dams and artificial ponds (15, 27–29). Contemporary land use can be roughly divided into three concentric zones: village agricultural countryside (~2.5 km from settlements), a more remote but active resource use zone (~5 km), and deep forest. The density of prehistoric settlements created overlapping zones with far more extensive and intensive land use (Fig. 3B) (26). Mosaic landscapes alternated between areas or islands of acute human influence (in settlements, along roads, and in agricultural countryside) and less affected areas between settlements, between cluster cores and satellites, and particularly between clusters in the regional peer polity, characterized by large tracts of high forest. Intrasettlement production included large compost areas, characterized by anthropogenic dark earth and large open areas (devoid of domestic refuse), probably used for manioc cultivation (15, 30, 31).

Land-use planning and modification of local and regional ecology were no less remarkable or sophisticated than in other areas of early urban societies worldwide. As elsewhere, urbanism resulted in a landscape “compositionally more heterogeneous, geometrically more complex, and ecologically more fragmented” (32) than those associated with small-scale societies traditionally viewed as typical of the region. Regardless of scale, such areas of semi-intensive land-use have very different ecological parameters than those characteristic of small-scale indigenous groups in recent times (SOM text).

The Upper Xingu is another case that underscores the need to move beyond narrow typological approaches, which conflate early urban societies with full-blown cities or the state, and to focus instead on degrees and kinds of urbanism, including dispersed, multicentric urban settlements (7–9). In Amazonia, there is little evidence for the type of large, singular centers considered cities in other world areas. Substantial variability characterized this vast region, including cycling between more centralized and more diffuse settlement patterns in certain areas (34), but the largest settlements rarely exceed 50 ha (1–3). Our findings support claims that ancient civilizations in broadly forested regions, such as temperate Europe, eastern North America, and the Amazon basin, are generally more dispersed and less centralized than classical (oasis) civilizations in Egypt, Mesopotamia, and Indus River areas or, in the South American case, coastal desert or arid highland river valleys (35, 36).

Long ago, Howard (37) proposed a model for lower-density urban development, a “garden city,” designed to promote sustainable urban growth. The model proposed networks of small and well-planned towns, a “green belt” of agricultural and forest land, and a subtle gradient between urban and rural areas. The pre-Columbian polities of the Upper Xingu developed such a system, uniquely adapted to the forested environments of the southern Amazon. The Upper Xingu is one of the largest contiguous tracts of transitional forest

in the southern Amazon [the so-called “arc of deforestation” (38)], our findings emphasize that understanding long-term change in human-natural systems has critical implications for questions of biodiversity, ecological resilience, and sustainability. Local semi-intensive land use provides “home-grown” strategies of resource management that merit consideration in current models and applications of imported technologies, including restoration of tropical forest areas (39–42). This is particularly important in indigenous areas, which constitute over 20% of the Brazilian Amazon and “are currently the most important barrier to deforestation” (43). Finally, the recognition of complex social formations, such as those of the Upper Xingu, emphasizes the need to recognize the histories, cultural rights, and concerns of indigenous peoples—the original architects and contemporary stewards of these anthropogenic landscapes—in discussions of Amazonian futures.

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- Of 30 radiocarbon dates, 12 were hand-collected from the interface of stratified pre-earthwork and earthwork construction deposits (overburden) and date major site reformation at X6, X11, and X13, ~750 to 700 ± 100 yr B.P. (table S1) (15).
- The study area conforms to the territory of the Kuikuro Amerindian community, one of eight primary subgroups of the contemporary Xinguanian nation.
- Earlier occupations had major earthworks, but expansion and structural elaboration of settlements ~750 to 650 yr B.P. reworked many earlier deposits.
- Standing structures are suggested by funnel-shaped ditch bases (<50 cm base), interpreted as footings for tree-trunk walls, and a large vertical “hollow” in ditch 10, interpreted as a rotted trunk (fig. S4). Indigenous oral history and regional ethnohistory also describe palisaded settlements.
- Recent Xinguanian villages are <6 ha (maximum of <3 ha domestic area) and range up to ~350 persons in 25 houses, averaging 250 m² (Fig. 2A and fig. S6).

- X20 is situated to the north-northeast of X11, but the larger residential center of X38 is located to the west.
- X13 was apparently a smaller occupation site, similar in size to the early occupations of X6 (concentrated within the innermost ditch), which was reconstituted as the cluster center, ~750 yr B.P.
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- Many suggested cluster locations (red circles) in Fig. 1A are supported by indigenous knowledge of major sites with ditches.
- Research was sponsored by the Museu Nacional, Universidade Federal do Rio de Janeiro, and Museu Paraense Emílio Goeldi. We acknowledge support by NSF Archaeology Program (grants BCS 0004487 and 0353129), the William T. Hillman Foundation, and the University of Florida.

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Materials and Methods

SOM Text

Figs. S1 to S7

Table S1

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