TECHNICAL COMMENT

TROPICAL FOREST

Comment on "Persistent effects of pre-Columbian plant domestication on Amazonian forest composition"

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Levis *et al*. (Research Articles, 3 March 2017, p. 925) concluded that pre-Columbian tree domestication has shaped present-day Amazonian forest composition. The study, however, downplays five centuries of human influence following European arrival to the Americas. We show that the effects of post-Columbian activities in Amazonia are likely to have played a larger role than pre-Columbian ones in shaping the observed floristic patterns.

The extent to which pre-Columbian human activities shape modern Amazonian forests remains a matter of debate (*1*–*3*). Levis *et al.* (*4*) concluded that tree "domestication" by pre-Columbian people—the inhabitants of Amazonia prior to European arrival around 1500 C.E.—played a major role in shaping the floristic composition observed in today's forests. Several methodological biases, however, may have resulted in a misleading conclusion. Here, we use publicly available data (*5*) to show that the observed patterns of tree species distributions and tree diversity in the Amazon, to the extent that they are anthropogenic, may be better explained by the influence of post-Columbian rather than pre-Columbian human activities.

Levis *et al.*'s approach (*4*) includes a regression-based model that uses environmental characteristics, distance to river, and distance to pre-Columbian archaeological sites to predict the richness and abundance of purportedly domesticated tree species in Amazonia. They based their argument on the modern composition of 1170 plots where a complete forest inventory had been made (*6*). For many of the "domesticated" tree species chosen by Levis *et al.*, however, there is no evidence for pre-Columbian exploitation, domestication (i.e., phenotypic and/or genetic modification), or enrichment in Amazonia (*7*). For example, the most abundant non-palm species in the study, *Hevea brasiliensis*, has been widely used for rubber (latex) since the industrial era, yet there is scant evidence for its pre-Columbian cultivation or domestication.

Levis *et al*. downplay the past 500 years of colonization by European settlers and the recovering indigenous population. Much of the modern population of Amazonia is clustered around major river channels, exhibiting a similar distribution to that of known archaeological sites and the modeled distributions of pre-Columbian peoples (Fig. 1) (*5*). The activities of post-Columbian populations have had an undeniable influence on the forests around them. For example, the Amazonian rubber boom of 1850–1920 resulted in the intensive extraction of latex from *H. brasiliensis* by rubber tappers of mestizo and indigenous ancestries, accompanied by deforestation, agriculture, and agroforestry in areas that were occupied. Enrichment of forests with deliberately sown *H. brasiliensis* and edible palm species is known to have occurred during the rubber boom (*8*). The modern inhabitants of Amazonia use and maintain these edible palms. These industrial-era forest activities were concentrated along river courses (*8*–*10*), which were and still are the most accessible and resource-abundant areas of the forest (*11*). Unsurprisingly, the spatial distributions of modern and ancient people are strikingly similar. Modern population densities (Fig. 1A) mirror the modeled distributions of ancient people (Fig. 1B). Likewise, areas close to modern population centers (Fig. 1C) have a similar distribution to areas close to archaeological sites (Fig. 1D).

The locations of the Amazonian forest inventory plots used in Levis *et al.*'s study are disproportionately located near areas with the

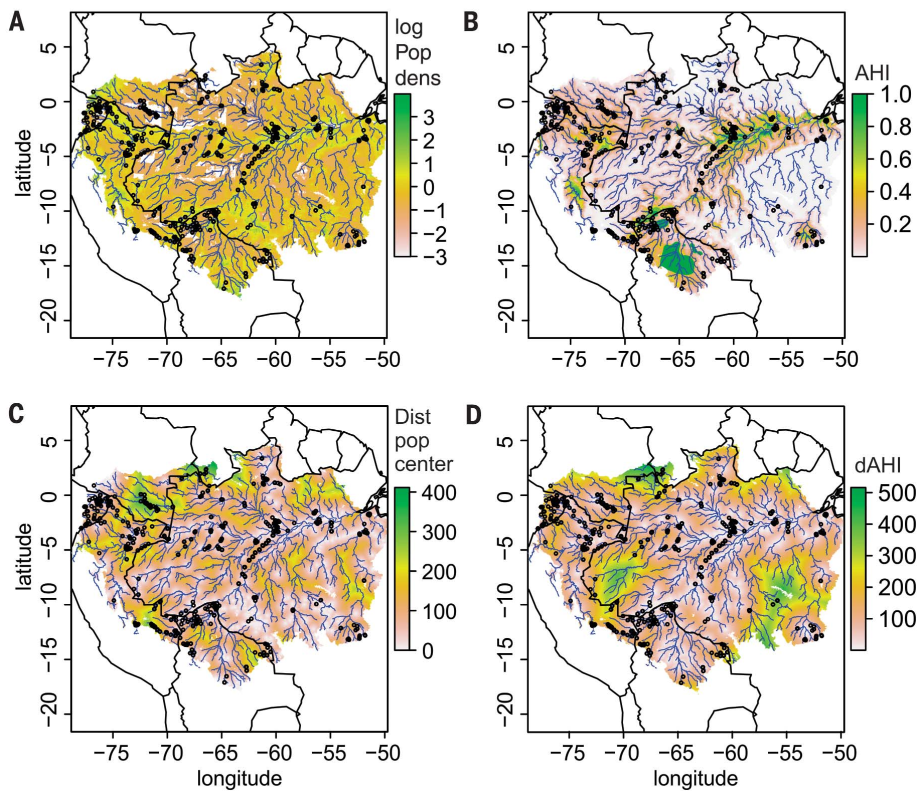

Fig. 1. The distributions of past and present people in Amazonia. Distributions are shown in relation to river networks (blue lines) and forest inventory plot locations (black circles). (**A**) Modern population densities ($\log_{10}$ scale; persons/km^2) for the years 2000–2010 (*5*). (**B**) Modeled distribution of ancient human influence (AHI) by pre-Columbian peoples, based on archaeological and paleoecological data (*1*). (**C**) Distance to modern population centers (defined here as areas with densities of ≥25 persons/km^2) (*5*). (**D**) Distance to archaeological sites containing evidence of pre-Columbian civilizations (dAHI) (*1*).

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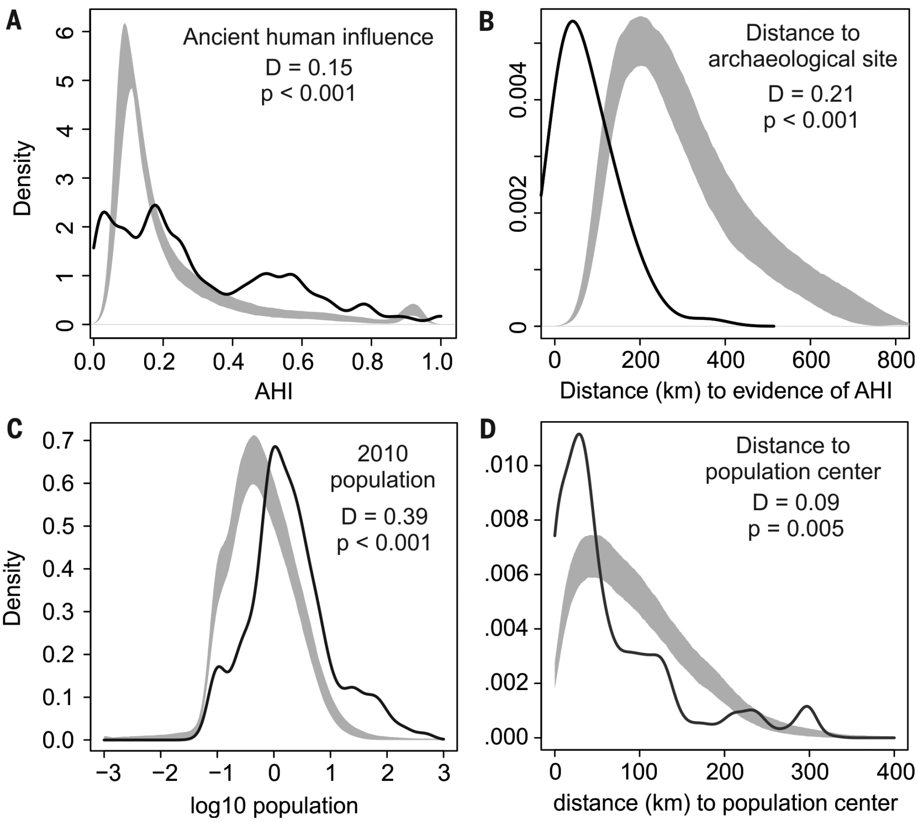

Fig. 2. Probability density distributions of Amazonian forest plot locations. (**A** to **D**) Distributions of forest inventory plots (black lines) are compared with random expectations (grayscale curves) for (A) modeled ancient human influence (AHI); (B) distance to archaeological or paleoecological sites with evidence of ancient humans; (C) modern population size ($\log_{10}$ scale; persons/km^2); and (D) distance to modern population centers (≥25 persons/km^2). The width of the gray curves indicates the 95% confidence interval. For detailed methods, see (*1*).

highest abundances of archaeological sites; the plots are also located in areas where the modeled pre-Columbian populations are highest (Fig. 2, A and B). Our analysis, based on an equivalent probability-density function, reveals that the forest inventory plots are also spatially biased toward areas with higher modern population densities, and are closer to modern population centers than would be expected by chance (Fig. 2, C and D). Given these biases toward forests with high probabilities of disturbance by both pre- and post-Columbian peoples, is it reasonable to attribute the observed floristic patterns to pre-Columbian plant domestication? Likewise, given these sampling biases and the lack of data from more-remote forests, we must question the conclusion that tree domestication broadly shapes Amazonian forests.

The analysis by Levis *et al.* also ignores the naturally patchy distributions of many Amazonian plant species (*6*). All of the tree species that they consider domesticates are native species that would be abundant in some areas regardless of human intervention. Regardless, the authors broadly consider all occurrences of trees identified as domesticates as being related to human activity. For example, *Mauritia flexuosa* is a heavily utilized Amazon palm species and is classified as a domesticated species in Levis *et al.*'s analysis, yet it is also a naturally dominant species in swamp forests (aguajales) (*12*). Without identifying species' natural (non–human-influenced) abundance paterns, the magnitude of human influence remains unquantifiable.

Finally, most of the edible trees in their study are early-successional species that are not expected to persist as dominant forest elements for hundreds of years after the population collapse. This observation makes it even more probable that the modern legacy of people on Amazonian forest structure is recent rather than prehistoric, although in some cases it is likely cumulative. A more nuanced approach is needed to disentangle the persistent effects of pre- and post-Columbian peoples on the Amazon and to understand the legacies of all people who have inhabited these forests throughout the Holocene.

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