TECHNICAL RESPONSE

TROPICAL FOREST

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

André Braga Junqueira,[1,2]* Carolina Levis,[3,4]* Frans Bongers,[4] Marielos Peña-Claros,[4] Charles Roland Clement,[5] Flávia Costa,[6] Hans ter Steege[7,8]

McMichael *et al*. state that we overlooked the effects of post-Columbian human activities in shaping current floristic patterns in Amazonian forests. We formally show that post-Columbian human influences on Amazonian forests are indeed important, but they have played a smaller role when compared to the persistent effects of pre-Columbian human activities on current forest composition.

In our paper (*1*), we link pre-Columbian archaeological sites in Amazonia to current forest composition. We conclude that pre-Columbian human influences are still noticeable in the forest's composition today. The main issue that McMichael *et al*. (*2*) address is the effect of post-Columbian peoples on modern forests. Although they present distribution maps of modern and pre-Columbian human populations, they did not evaluate the effects of these populations on modern forests. All over the world, humans tend to live where people did before, and Amazonia is no exception. We argue, however, that a visualization of spatial trends between modern and ancient human occupation patterns and forest plots is insufficient to "show that the observed patterns of tree species distributions […] may be better explained by the influence of post-Columbian rather than pre-Columbian human activities" as stated by McMichael *et al*. Although most other points raised by McMichael *et al*. could be answered with a careful reading of our paper, we here address some of them and provide further analyses aiming to move forward in this debate.

McMichael *et al*. criticize our list of domesticated species. In order to circumscribe this list, we used a "broad" concept of plant domestication based on Darwin (*3*), Rindos (*4*), and Clement (*5*), who argue that domestication is a process in which propagation and selection by humans yield a variety of outcomes over time. Forest management by Native Amazonians often resulted in changes in population structure and distribution

[1]International Institute for Sustainability, Rio de Janeiro, RJ 22460-320, Brazil. [2]Centre for Conservation and Sustainability Science (CSRio), Department of Geography and the Environment, Pontificial Catholic University of Rio de Janeiro, Rio de Janeiro, Brazil. [3]Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia, Petrópolis, Manaus, AM 69067-375, Brazil. [4]Forest Ecology and Forest Management Group, Wageningen University & Research, Wageningen 6700 AA, Netherlands. [5]Coordenação de Tecnologia e Inovação, Instituto Nacional de Pesquisas da Amazônia, Petrópolis, Manaus, AM 69067-375, Brazil. [6]Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Petrópolis, Manaus, AM 69067-375, Brazil. [7]Biodiversity Dynamics, Naturalis Biodiversity Center, Leiden 2300 RA, Netherlands. [8]Systems Ecology, Free University, Amsterdam 1081 HV, Netherlands.
***Corresponding author. Email: abjunqueira@gmail.com (A.B.J.); carollevis@gmail.com (C.L.)**

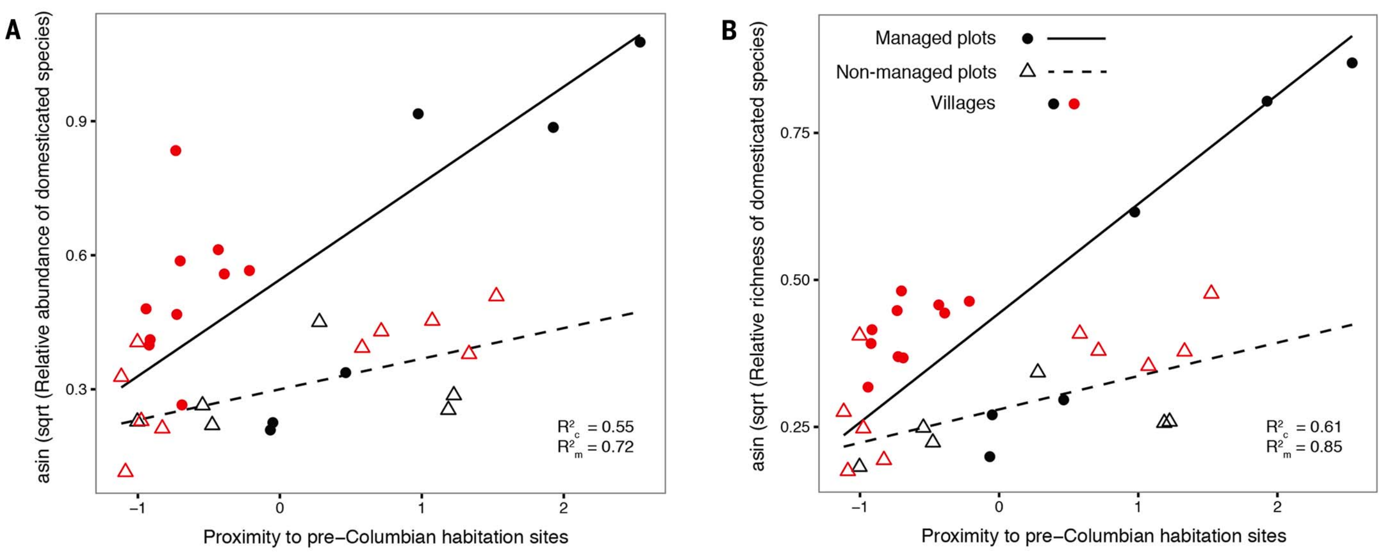

Fig. 1. Post- and pre-Columbian human impacts on forests along the middle Madeira River, Central Amazonia. (**A** and **B**) Effect of post- and pre-Columbian management activities on the relative abundance (A) and relative richness (B) of domesticated species in 32 0.1-ha forest plots. "Proximity to pre-Columbian habitation sites" was assessed from the degree of soil modification, assuming that soils with the highest fertility and density of ceramic fragments were ancient habitation sites (*12*). The *x* axis was obtained from a principal components analysis, summarizing the variation in soil chemical and physical parameters. Information on current management was obtained from interviews with local residents. Regression lines are the result of linear mixed-effect models [response variable ~ proximity to pre-Columbian habitation sites × current management + (1|village)]. "Village" was included as a random factor because our plots were distributed in two different sites ("villages") with contrasting soil properties; plots in the village denoted by black symbols were in general located in more fertile soils (i.e., closer to pre-Columbian habitation sites) than those in the village denoted by red symbols (especially in the "non-managed" treatment). In both models, the probabilities of all fixed factors are < 0.001. R^2_m and R^2_c refer to the fit of the fixed factors and of the whole model (fixed + random), respectively.

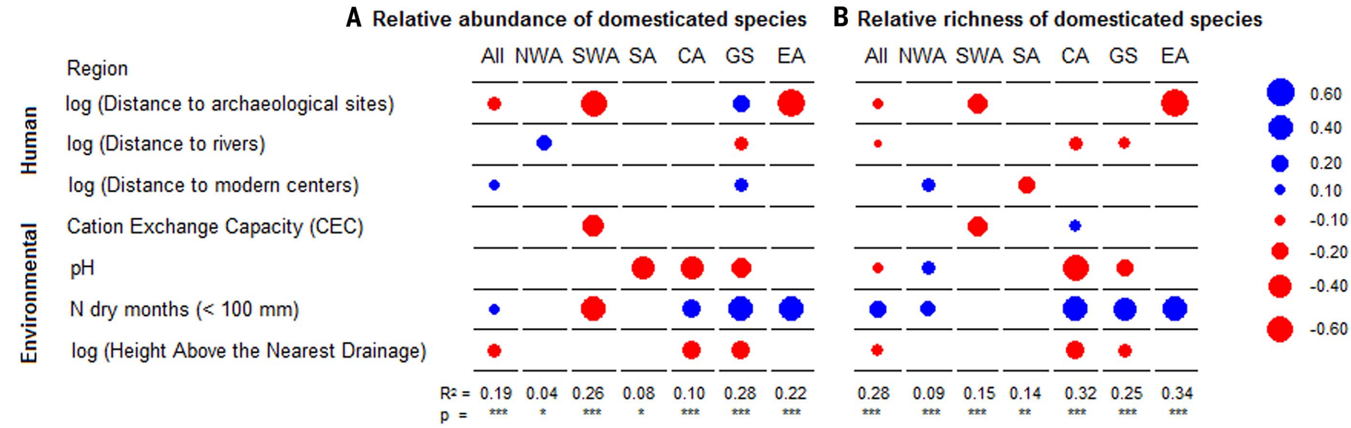

Fig. 2. Relative abundance and richness of domesticated species as a function of human (pre- and post-Columbian) and environmental variables. (**A** and **B**) Standardized regression coefficients for the relative abundance (A) and relative richness (B) of domesticated species as a function of pre-Columbian human factors (distance to archaeological sites, distance to navigable rivers), modern human occupation (distance to modern population centers), and environmental conditions (soil cation exchange capacity, pH, number of dry months, and height above the nearest drainage). Circle size indicates the relative contribution of each predictor to the regression model (only significant relations are shown; $^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$). Red and blue circles indicate negative and positive effects, respectively. For details of the models, see (*1*). Modern population centers are equal to grid cells of ≥25 persons/km^2 for the year 2000 (*10*). Abbreviations for geographical regions: NWA, northwestern Amazonia; SWA, southwestern Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia.

of trees and palms without necessarily resulting in populations with clear signs of morphological selection (*4*–*6*). In our list of 85 domesticated species, we included 51 "incipiently domesticated" species for which there is ample evidence for their management and cultivation through time. Although our list is extensive, it is still conservative, given that 301 of the species found in our plots are useful and have been documented under cultivation (*7*) (see http://mansfeld.ipk-gatersleben.de) and that there are at least 3500 plant species with documented uses in Amazonia (*8*).

McMichael *et al.* state that we "downplay the past 500 years of colonization by European settlers and the recovering indigenous population." We explicitly acknowledged the potential role of post-Columbian plant management in current floristic patterns [(*1*), p. 930]. It is indeed likely that the distribution and abundance of some economically important species (e.g., *Hevea brasiliensis*) have been modified during the past two centuries. We recognize as well that disentangling "recent" from pre-Columbian human impacts on forests is an important next step requiring approaches different from those used so far. We have started to explicitly address the issue of present and past human effects at a landscape scale. We found that old-growth forests along the middle Madeira River located on archaeological sites maintain a higher richness and abundance of domesticated species, even when they have not been intensively managed in the past 120 to 150 years (Fig. 1, A and B). This shows that human impacts older than the rubber boom can persist in forests without recent management, and that recent forest management by modern people has an effect similar to that of forest management by ancient peoples. Thus, ancient and recent forest management continuously shape the forests we see today.

The distributions of modern and past human populations and of forest plots are indeed concentrated in accessible areas [see fig. S2 of (*1*)] (*9*). Still, the correlation between the distance of our plots to archaeological sites and the distance of our plots to modern population centers is weak (Spearman rank correlation = 0.27), because numerous archaeological sites and forest plots in our database are far from modern population centers. We added distance to modern population centers (*10*) as a variable in an expanded model, in addition to the variables used in (*1*). We found that distance to modern population centers has no effect on relative richness of domesticated species at the Amazon-wide level (although it has contrasting effects depending on the geographical region, positive for northwestern Amazonia and negative for southern Amazonia; Fig. 2B) and a small positive effect on relative abundance of domesticated species (particularly in the Guiana Shield; Fig. 2A). The effect of distance to archaeological sites on both relative richness and abundance of domesticated species is much stronger and consistently negative (particularly in southwestern and eastern Amazonia), similar to the results of our previous model (*1*). These results indicate that post-Columbian activities are indeed relevant, but contrary to McMichael *et al.*'s claim, these play a smaller role than pre-Columbian activities in shaping current forest compositions.

The transformation of Amazonian forests by humans is an ongoing process, and the current flora holds signatures of the interplay of ecological and anthropogenic processes in both pre- and post-Colombian times. Despite the complexity of this process, we disagree with McMichael *et al.*'s observation that it is impossible to quantify human influence on forests "without identifying species' natural (non–human-influenced) abundance patterns." The use of well-designed plant inventories, combined with paleoecological, archaeological, ecological, and other human-related variables, is shedding light on basin-scale patterns that show substantial past human impacts on forests (*1*), mirroring patterns found at local and landscape scales (e.g., Fig. 1) (*11*). Although the effects of post-Columbian human influences are important and deserve to be investigated in detail, our expanded analysis shows that they are insufficient to downplay the persistent effects of pre-Columbian peoples in shaping Amazonian forests.

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Data on the distribution of modern population centers are available from (*10*).

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