



Response: Commentary: Rain, Sun, Soil, and Sweat: A Consideration of Population Limits on Rapa Nui (Easter Island) before European Contact

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A response on

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by Lipo, C. P., DiNapoli, R. J., and Hunt, T. L. (2018). *Front. Ecol. Evol.* 6:25. doi: 10.3389/fevo.2018.00025

A recent commentary (Lipo et al., 2018) takes issue with some of the conclusions of our study of population potential on Rapa Nui (Easter Island) before European contact (Puleston et al., 2017). We have no objections to their vision of early Rapa Nui, and we believe it is consistent with our analyses, but we believe that they have misread our analysis substantially.

First, the commentary mistakenly asserts that we concluded “that the island once supported a population of 17,500.” We did conclude that “given rates of nitrogen accumulation that are found in other parts of Polynesia, population sizes of 17,500 and higher were theoretically possible” (p. 12). This calculation is both well supported and carefully qualified in our analysis. The purpose of our study was to evaluate the dependence of maximum population on ecological and social factors. We repeatedly emphasized that the estimates of maximum sustainable population were highly conditional on the scenario being tested and not intended to settle once and for all the question of Rapa Nui’s pre-contact population size.

Second, Lipo et al. (2018) misread our findings as an argument in favor of the pre-European “collapse” narrative. It is precisely because our estimates of quasi-equilibrium population sizes span such a wide range that we do not uncritically embrace this argument. In fact other recent work by our group demonstrated that prior to European contact, populations declined in some parts of Rapa Nui and not others. We concluded that constraint was a more appropriate framework than collapse for evaluating pre-contact Rapa Nui populations (Stevenson et al., 2015). This paper (Puleston et al., 2017) explores potential constraints quantitatively and, as noted in the abstract, our results varied depending on plausible assumptions of nitrogen availability, clustering around 3,500 individuals in the low-nitrogen case and 17,500 in the high-nitrogen case.

The commentary correctly points out that the fluxes of plant-available nitrogen accumulation on the island are poorly understood. We made this point ourselves; it is why we chose to explore two nitrogen scenarios. One represents the case where nitrogen inputs are limited to the best

available estimates of rates of dissolved N deposition in rainwater along with a small amount of biological fixation of N. The high-N case also included N fixation occurring as a byproduct of sugar cane decomposition. Cultivars of sugar cane associated with N-fixation in a study by Lincoln and Vitousek (2016) in Hawai'i are found on Rapa Nui and believed to have pre-dated European contact. Thus, we could not ignore the possibility that Rapa Nui cultivators partially overcame a nitrogen constraint through their management practices, as Hawaiian cultivators did.

Third, Lipo et al. (2018) make several perplexing misstatements about our methodology, including their assertion that our scenarios overestimate maximum population because we do not account for annual variability in food yields. Our methods section describes in detail how climate variability observed at six weather stations placed across the island by the research group informs the agricultural model, and how we captured additional rainfall variability by incorporating long-term data from the airport weather station. Perhaps (as we said in our paper) climate, and so food yield, is even more variable than our data-based analysis recognizes, but to say we ignored the influence of stochastic variability is simply wrong.

Lipo et al. (2018) also suggest that our use of arithmetic rather than geometric means is inappropriate. We strongly disagree, but in any case the use of the geometric mean would change our high-N population mean across all treatments to 16,580 individuals, a decrease of about 5%. They also suggest that our results include a hidden assumption that there must have been large numbers of workers because they were required for statue construction and transport. Our methods make clear that we made no such assumptions.

Finally, Lipo et al. (2018) assert that our models are “black boxes.” In fact we build upon a version of Century, a nutrient cycling model that has been fully accessible to the research community, widely used, thoroughly documented, and tested

since the late 1980s. The food-limited population model we used has been described and analyzed in several publications (e.g., Lee and Tuljapurkar, 2008; Puleston and Tuljapurkar, 2008; Puleston et al., 2014). It is surprising that the authors suggest our modeling was opaque, as we provided them with our population code (and Century is available from Colorado State University) and an offer to help with interpretation of any unclear portions prior to publishing their commentary. They made no request for clarification and so we must assume that our modeling was sufficiently transparent.

We stand by our methods and results, and note that the reason why we use models in human ecology is to approach complicated problems from a new direction, evaluate potential constraints, and generate hypotheses, which may then be examined and tested. Perhaps our low-nitrogen scenario, which agrees with the population estimates preferred by Lipo et al. (2018), is a better representation of pre-contact Rapa Nui than is the high-nitrogen scenario—but if so, we have to ask why cultural practices that enhanced nitrogen input elsewhere in Polynesia were not implemented on Rapa Nui. More generally, we believe that it is sometimes better to determine what might have been possible (and why) than to limit ourselves to what we believe is probable.

AUTHOR CONTRIBUTIONS

CP drafted the response. TL, SH, OC, PV, and CS made edits and additions.

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