Hunter-gatherer populations inform modern ecology

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Our species *Homo sapiens* is extraordinarily successful, yet we are still subject to the same environmental constraints, such as famine and disease, as all other organisms (1). Fundamental approaches from ecology and evolution have proven useful for understanding how interactions with biotic (other species) and abiotic (physical) surroundings influence humanity's trajectory (e.g., refs. 2 and 3). Additionally, disentangling the forces that have limited human populations in the past has much potential to provide novel insights into how technological innovations have shaped human societies today (4). However, the utility of studying humans to address the large-scale ecological patterns and processes that determine species' abundances (numbers) and distributions (geographic ranges) is generally overlooked. A study by Tallavaara et al. (5) in PNAS provides an instructive example of the dual value of studying human ecology.

Humans are an abundant, widely distributed, and well-studied species. We know our physiological limits. Our ecological interactions with other species, especially our diseases, are comparatively well understood. There are good data on the abundances and global distributions of humans spanning hunter-gatherers (6, 7) to modern societies (Fig. 1 *A* and *B*). Tallavaara et al. (5) leverage the former to identify the complex interactions between climatic and biotic factors that constrain hunter-gatherer densities worldwide. Their primary motivation is to test a longstanding idea proposed by archeologist and late National Academy of Sciences member, Lewis Binford (6). In doing so, Tallavaara et al. (5) also provide one of the most detailed evaluations of what may be a widespread phenomena in biogeography (see below). Their work highlights intriguing questions for understanding how humans have rapidly transitioned from a sparsely inhabited planet of hunter-gatherers to the densely populated agricultural and industrial lifestyles of today.

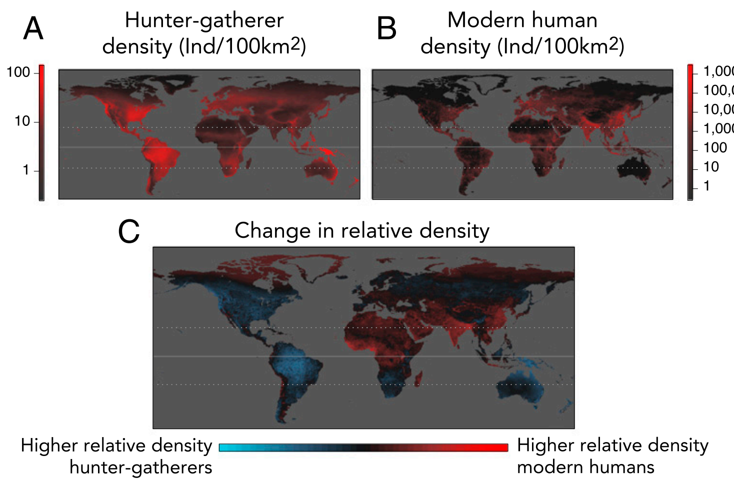

Fig. 1. Predicted densities of hunter-gatherers (*A*), modern humans in 2015 (*B*), and the difference in relative densities between the two (*C*). Note the difference in scale between *A* and *B*, with modern humans occurring at densities up to four orders-of-magnitude higher than the densest hunter-gatherers. Values in *C* are calculated as the differences between log densities in *A* and *B* after rescaling each by respective maximums. Solid gray lines indicate the Equator; dashed lines indicate the Tropics of Cancer and Capricorn. Map *A* modified from ref. 5 (https://zenodo.org/record/1069787#.Wj2SprbMzBI); map *B* is constructed using data from the Center for International Earth Science Information Network from Columbia University, 2016 (22).

Disentangling Drivers of Species Distributions

In a seminal 1950 paper titled *Evolution in the Tropics*, biologist Theodosius Dobzhansky (8) proposed the idea that biological enemies—such as competitors, predators, and diseases—are most limiting in the tropics, where biodiversity is greatest, while abiotic constraints, such as temperature and aridity, limit species in high latitudes where the physical environment is harsh. Ecologist Robert H. MacArthur (9) later extended this hypothesis by suggesting that environmental tolerances and species interactions, respectively, determine the northern and southern extents of species distributions across North America. Empirical evaluation of the Dobzhansky–MacArthur Phenomenon has been a challenge in part because measuring the effects of complex biotic and abiotic interactions over the entirety of species' ranges is difficult (10). Tallavaara et al. (5) use structural equation modeling to evaluate the context-dependence of environmental productivity,

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biodiversity, and disease on the abundance and distribution of ~300 hunter-gatherer societies from across the Earth.

Structural equation modeling has a long history in the quantitative social sciences (e.g., ref. 11) and is increasingly being used in ecology (e.g., ref. 12) to evaluate causal pathways underlying complex interactions of multiple ecological drivers [see Tallavaara et al.'s (5) conceptual model in Fig. 1]. Through a set of regression equations, hypothesized relationships can be evaluated with data to understand the direction and magnitude of direct and indirect effects of multiple factors on a response variable [e.g., in Tallavaara et al.'s (5) case, hunter-gatherer abundance or density]. Consistent with previous work [references 6–9 in the Tallavaara et al. (5) paper], Tallavaara et al. found that environmental productivity strongly affects hunter-gatherer population abundance. Interestingly, however, their study reveals how the relative importance of environmental productivity, biodiversity, and disease burdens change from high- to low-productivity environments.

Supporting predictions of the Dobzhansky–MacArthur Phenomenon, disease burdens are a stronger limiting factor on hunter-gatherer populations in highly productive areas, such as the lowland wet tropics. However, in less-productive environments, such as deserts and tundra, biodiversity [calculated in the Tallavaara et al. (5) study as the number of birds, plants, and mammals] matters more. This result is in line with the idea that biodiversity promotes ecosystem stability (e.g., refs. 13 and 14), which could be important for maintaining reliable access to resources in hunter-gatherer populations. Perhaps most fascinating, the Tallavaara et al. (5) model reveals the ecological "sweet spot" for humans: the temperate and subtropical biomes (e.g., Eastern North America, Western Europe, and Southeast Asia) where the balance between abundant resources and low disease burdens supports the highest hunter-gatherer abundances.

How Many Hunter-Gatherers Could the Earth Support?

The Tallavaara et al. (5) model provides a baseline estimate from which to understand the unique cultural and technological innovations that have allowed human expansion. Based on their model using three environmental variables, we estimate the global population of hunter-gatherers to be on the order of ~10 million. However, it should be noted that this approximation does not consider a number of potentially important factors. For example, the authors use only terrestrial productivity, although hunter-gatherers were not restricted to just land resources. Productive coastlines provide humans with access to marine resources that are driven by factors separate from those on land (15). Additionally, hunter-gatherers used food-storage technologies—such as sealing, smoking, and drying (16)—to take advantage of seasonal or patchy resources. Fruitful areas for future research include incorporating the roles of: (*i*) marine productivity, (*ii*) storage technologies (e.g., drying), and (*iii*) proto-agriculture (e.g., slash-and-burn) in boosting hunter-gatherer abundance. Nevertheless, estimating hunter-gatherer population size serves as a useful benchmark to compare modern human population.

Technology and Human Expansion

Cumulative cultural evolution in humans has produced innovations that have allowed us to push back many of the constraints that limited hunter-gatherers (17, 18). Preindustrial agricultural societies occurred at densities on the order of 100 times higher than the most abundant hunter-gatherers, even in the absence of fossil fuels (19). Comparing the estimated densities of hunter-gatherers across the globe to the modern distribution of human density (Fig. 1) illuminates how technology has continued to push ecological limits even further. Interestingly, distribution maps of ~10 million hunter-gatherers and today's 7.6 billion people share some important similarities. Many of the regions that supported the highest densities of hunter-gatherers still host some of the largest populations today (e.g., the Pacific Coast and Eastern North America, parts of temperate Eurasia, and much of Southeast Asia), albeit at densities several orders-of-magnitude higher than hunter-gatherers.

In other ways, these distribution maps display striking differences. Many regions where high disease burdens previously limited hunter-gatherers to low densities (e.g., equatorial Africa, India, and eastern China) are now some of the most densely populated areas on the planet (Fig. 1*C*). This suggests that in addition to agriculture, mitigating diseases has been an important factor in allowing continued expansion in human population. Despite this progress, however, our species has not completely escaped the ecological impact of diseases on human development. The enduring legacy of disease burdens is evident by the latitudinal gradient in income (20) that persists today, where the tropics are generally poor and many economies at high latitudes have flourished. Disease-driven poverty traps (21) may still inhibit economic development in tropical regions today.

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Human population expansion and increased standards of living in mid and high latitudes suggest that overcoming low environmental productivity may be easier than combating diseases. Consider, for example, the disproportionate increases in human density in some of the most arid regions, such as North Africa, the Middle East, the American Southwest, and the Central Pacific Coast and Altiplano of South America (Fig. 1*C*). Plant and animal domestication, along with irrigation, have allowed dry areas such as these to support densely inhabited civilizations for thousands of years. Populations in low productivity regions, including high latitudes, are also supported by importing resources from more productive regions. Today, this is accomplished through high inputs of fossil fuels to power global trade networks.

Perspectives and Conclusions

The Tallavaara et al. (5) paper illustrates the utility of studying humans using macroecological tools, in addition to highlighting pressing problems that lie at the intersection of traditional disciplinary boundaries. Their model supports predictions of the Dobzhansky–MacArthur Phenomenon, suggesting that hunter-gatherers were subject to similar ecological drivers that may act generally across species. At the same time, their work exemplifies how studying human ecology provides important insights into the extent that ecological factors and technology influence populations and economies today. Their estimates of hunter-gatherer populations provide a useful baseline for understanding how the human species has alleviated environmental constraints and transitioned from hunter-gatherer lifestyles to agriculture and now industrial-urban societies in just the past

~10,000 y. Understanding how culturally driven technologies continue to abate the multiple ecological drivers that restricted hunter-gatherers remains a grand challenge for both science and society.

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