

From domestication genomics towards molecular ecology of human environments

Anders Bergström

Ancient Genomics Laboratory, The Francis Crick Institute, NW1 1AT London, UK

e-mail: anders.bergstrom@crick.ac.uk

The domestication of animals, plants, fungi and microbes has transformed human societies. By taking control of the evolution of other organisms, domestication represents an extreme on a spectrum of interactions with our environments. This spectrum includes a wide range of intentional and unintentional modifications of ecosystems, intensifying over the last few millennia but with deep roots in human prehistory (Boivin et al. 2016). Humans are therefore an important variable in studies of the ecology and evolution of many organisms (Sullivan et al. 2017). But in a reciprocal fashion, by detailing the consequences of human niche construction activities, studies of the evolutionary histories of other organisms can inform on past human behaviours, lifestyles and ranges. Domesticates, being intimately associated with humans and often undergoing dramatic human-directed biological change, are a natural starting point in this broader effort of learning about the human past by studying the natural world that surrounds us.

A fundamental lesson learnt during the ancient DNA revolution of the last decade is that it's very challenging to uncover the details of human population histories using present-day genetic variation alone. Early events are often obscured by multiple layers of later processes. As there is no *a priori* reason to believe that our domesticates will have less complex histories, ancient DNA will be key in understanding these too. Fortunately, most domestication processes occurred in the Holocene, a period well-suited for ancient DNA. Studies in the last few years have demonstrated the value of ancient genomics in reconstructing the histories of domesticates

(Frantz et al. 2020), and this potential will be unleashed even further as the number of ancient genomes start to reach into the hundreds.

A particularly exciting opportunity offered by ancient DNA is the dissection of the very early stages of domestication, which for most domesticates is shrouded in uncertainty. If genomes dating to before and during these stages can be recovered, we can begin to answer questions in detail about the process by which wild populations were turned domestic. From what geographical areas were wild individuals initially sourced? When did human-associated populations develop a distinct genetic ancestry, and how gradually did this happen? To what extent, and for how long, did further wild individuals continue to be sourced? Was there a loss of genetic diversity or increased inbreeding in the human-associated individuals, and if so, when during the process did this happen?

Answering many of these questions will require some understanding of the natural structure and diversity of populations prior to domestication. Ancient genomes from wild individuals predating or coinciding with domestication have so far only been recovered in small numbers from a handful of species, including horses, goats, wolves, cattle and pigs (Frantz et al. 2020). Present-day wild populations might be able to serve as a proxy for natural diversity, and have greatly informed on the geographical origins and history of many domesticates, including pigs, maize and rice. However, changes in the structure of wild populations since domestication, including the possibility of domestic gene flow, and in some cases even extinction in the wild, means that present-day genomes will

hardly ever be as informative as ancient genomes predating domestication.

Furthermore, genomes even from very early domestic individuals do not necessarily allow us to conclude where the geographical origin, or origins, of domestic ancestry lies — it's difficult to rule out the existence of even earlier domestic individuals elsewhere that have yet to be sampled. Observing how domestic ancestry fits into a wild population structure, however, provides insights into origins in a fashion that is not particularly dependent on sampling very early domestic populations. In both goats and cattle, even small numbers of wild genomes have revealed asymmetries in the relationships of these to domestic animals, implying that more than one source population must have contributed ancestry (Daly et al. 2018; Verdugo et al. 2019). Recovering genomes from ancient, wild populations should thus be a priority for domestication genomics.

We only have conclusive evidence of domestication for those organisms that still live alongside humans, but ancient DNA might provide opportunities to study discontinued and 'semi-domestication' processes falling on various points further along the interaction spectrum. Some non-wolf canids in South America were likely used for hunting prior to the arrival of European dogs (Stahl 2013). Even in the absence of zooarchaeological evidence of human-induced biological change, genomic features — such as distinct human-associated ancestry or reduced diversity — could address to what extent such populations were domesticated as opposed to repeatedly tamed. Genomes from the earliest archaeologically known domestic horses, kept by the Central Asian Botai culture, surprisingly revealed that they were not the progenitor of today's domestic horses (Gaunitz et al. 2018), and might instead have represented a domestication dead end.

A key grey zone that remains poorly understood is how human hunter-gatherers started to manage plants. Early cultivation practices have long been studied archaeologically, but have received less attention from the point of view of plant population histories. For how long did human activity, intentional or not, influence the

evolution of the plant populations that would later become domesticated? Did deliberate deforestation or seed dispersal initiate demographic expansions of these crops before active management started? Plant remains generally preserve DNA less well than animal skeletons, but progress has nonetheless been made for several species, including maize, barley and wheat (Kistler et al. 2020). A potentially promising source of data is environmental DNA from sediments, which often contains both animal and plant DNA. Environmental DNA can be used to track the presence or absence of species across space and time, and is increasingly also being used to study genome-wide ancestry.

Moving further down the interaction spectrum, many animals, such as elephants and various birds of prey, have long been repeatedly captured from the wild and tamed. If tamed individuals are not contributing genetically to the wild source populations, these interactions with humans are unlikely to leave a genomically visible record. Nonetheless, the cultural and economic importance to human societies of some of these species has likely influenced their histories and geographical distributions, and they might represent an underappreciated chapter in the human story. Even some entirely wild organisms, including several species of deer, have had their habitats expanded by prehistoric humans through deliberate translocation. This became more widespread starting in Neolithic cultural contexts (Hofman and Rick 2018) and might have been a somewhat intuitive extension of a management mindset associated with the practice of agriculture. A few examples predating agriculture are also known, including the Mesolithic translocation of hares to the Baltic island of Gotland (Hofman and Rick 2018). Some species of cuscus marsupials appear to have been translocated to new islands throughout the Melanesian archipelago, in a co-dispersal process potentially going back to the late Pleistocene (Heinsohn 2003).

Towards the opposite end of the interaction spectrum, genomic studies even of organisms outside any form of human management could

contribute to the big picture of how past humans fit into ecosystems. The population dynamics of hunted animals might inform on the extent to which these influenced human demographic and migration trajectories. Observing whether human population history events coincide with those of other organisms of various kinds could point to shared environmental drivers. As an example of lifestyle insights from sediment DNA, a sudden decline in the abundance of common juniper in Icelandic sediments after human arrival suggests heavy exploitation of this tree by early settlers, e.g. for grazing or other purposes (Alsos et al. 2021).

At least conceptually, a long-term ambition for molecular anthropology might thus be for a branch of it to merge into the study of ecology. Armed with a background of reconstructed population histories for a range of other species, we could even begin to ask questions about the ways in which human evolution has been typical or atypical within a broader natural history context. Perhaps such a future science might describe how, due to our behavioral versatility and intelligence, the forces of ecology, geography and climate imposed weaker constraints on the evolutionary trajectories of human populations than those of other animals. Our ability to adapt to and modify a wide range of environments, in the extreme even taking control of the evolution of other organisms, might have made us a very unusual leaf on the tree of life.

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