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Plant Domestication
First come first served for ancient crops

Analysis reveals that the economic importance of crops is most influenced by their antiquity of domestication.

The evolution of plant domestication is a topic replete with paradoxes when viewed through the lens of progress. Agriculture is the pillar that supported the rise of civilization, and yet it is also associated with initial malnutrition, disease and labour traps\textsuperscript{1-3} that obfuscate the mechanisms and motivations behind the process. In this issue of *Nature Plants* Milla and Osborne add to this complex picture by attempting to answer why humans have come to rely on just twelve plant species for the bulk of their plant-based needs when thousands of species have been domesticated\textsuperscript{4}.

The diet of the hominin lineage leading to humans has been shifting over the past few million years as the ecology of humans has evolved. The expansion of savannahs several million years ago left an isotopic signature reflecting increased C4 plant consumption in hominin fossils\textsuperscript{5}, an increased level of carnivory and use of fire for cooking to externalise the first part of the digestion process is associated with the expansion of brain size\textsuperscript{6}, and during the last ice age the dietary spectrum of humans inflated to a wide range of species in the Broad Spectrum Revolution\textsuperscript{7}. Latterly, humans are still in a state of evolutionary flux adapting to the transition to agriculture\textsuperscript{8}. The story of the rise of the genus *Homo* has been one of an adapting generalist that rapidly spread around the globe with the vigour of a weed. However, as Milla and Osborne argue, the current narrow dependency on so few species for survival is the hallmark of a specialist species adapted to a specific and stable ecological niche. History has generally been unkind to specialists when it comes to extinction in the wake of environmental change.

To uncover the reasons why the human nutritional niche has become so narrow Milla and Osborne considered the factors that might help explain why some domesticates dominate. This is no mean feat since the variation of forms, origins and uses of varying importance of domesticated plants is huge. Each is wrapped up in a specific historical context, making a general system for comparison challenging. The authors took 866 domesticate species and categorized them into five principal groups based on use – herb seed, herb fruit, woody fruit, leaf and root. They then considered four principal attributes about these crops – crop importance in terms of land area used, age of domestication from archaeological evidence, climate in the area of origin in terms of seasonality in temperature or rainfall and their overall phylogenetic spread. Unsurprisingly, they find these factors influence each other and require disentanglement. The majority of domesticated crops originate from a few domestication centres around the globe of varying ages each associated with a specific climatic regime. Different domestication centres have a tendency to be associated with different crop types, partly as a consequence of climate. Similarly, there is a loose phylogenetic association with crop domestication centres, such as grasses and legumes tending to come savannah and Mediterranean climates. As many have observed before, domesticated plants as a whole are found throughout the angiosperms with little obvious phylogenetic structure. Consequently, all the factors considered are related to antiquity. Once these confounding factors are separated out there remains an
indisputable signal across all categories of crop type that the most relevant crops are biased towards older domestications.

Milla and Osborne go on to argue that the most relevant crops show a significant level of phylogenetic overdispersion - important crops do not occur in close phylogenetic proximity as much would be expected by chance. This adds an intriguing layer of insight, because it suggests that in general there has been a suppressing effect by the dominating crops preventing the rise to prominence of new crops. Frustratingly, such a nebula signal cannot yet be focussed to a specific instance of a demonstrably suppressed crop when individual crop histories are so complex. The principle, however, shines a light on a potential flaw in the progress represented by domestication – a tendency to over specialization through the repression of crop innovation. The key unanswered question and no doubt topic of ensuing debate will be why and how such suppression could have occurred. Milla and Osborne suggest priority effects in which earlier crops have had longer to adapt to the human environment and outcompete newcomers, perhaps analogous to dinosaurs hindering the rise of mammals. Such analogies raise the question of whether older crops or newer crops are generally better for the uses to which we put them. Alternatively, there may be cultural or economic inertia that prevents humans from adopting new crops to a level of high prominence.

Niche specialization is often a trait of evolutionary progression, and domestication is often viewed as a complex series of niche constructions by humans. This study suggests that humans have constructed their niche more narrowly than they could have as a consequence of legacy, which makes us vulnerable to the effects of environmental change. More optimistically, there may be a plethora of crops out there which have not been used to their potential yet simply because some other crop got there first.