Quaternary Science Reviews 296 (2022) 107737

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Progress in domestication research: Explaining expanded empirical observations

Dorian Q. Fuller [a], Tim Denham [b], Logan Kistler [c], Chris Stevens [a, d, e], Greger Larson [f], Amy Bogaard [g, h], Robin Allaby [i, *]

[a] Institute of Archaeology, University College London (UCL), London, UK
[b] School of Archaeology and Anthropology, The Australian National University, Canberra, Australia
[c] Department of Anthropology, Smithsonian Institution, National Museum of Natural History, Washington, DC, USA
[d] School of Archaeology and Museology, Peking University, Beijing, China
[e] McDonald Institute of Archaeology, University of Cambridge, Cambridge, UK
[f] The Palaeogenomics & Bio-Archaeology Research Network, School of Archaeology, University of Oxford, Oxford, UK
[g] School of Archaeology, University of Oxford, Oxford, UK
[h] Santa Fe Institute, Santa Fe, NM, USA
[i] School of Life Sciences, University of Warwick, Coventry, UK

ARTICLE INFO

Article history:
Received 23 August 2022
Accepted 25 August 2022

Handling editor: Donatella Magri

Keywords:
Domestication
Archaeobotany
Archaeogenomics

ABSTRACT

Abbo and Gopher contend that we offer nothing new to the study of domestication in three recent papers (Bogaard et al., 2021; Allaby et al., 2021, Allaby et al., 2022b). They claim that we offer no "innovation, a new venue of research" and "use a new jargon to express old ideas." They further claim as erroneous our key conclusions about domestication as: protracted, co-evolutionary, comprising multiple pathways of convergent evolution, and taking place at the landscape scale. Here we defend these recent contributions as genuine progress that builds on previous ideas and hypotheses through empirical illustration and a raft of new data. Combining new data with old and new theory, we develop frameworks that suggest future directions for research.

1. Standing on the shoulders, but new heights

As opposed to our work lacking innovation, we have built-on concepts of our predecessors, based on considerable bodies of new data and data-types not previously available. Bogaard et al. (2021) point out that language used to describe domestication has its roots in 19th century European thinking. This historical background means that revised and inclusive definitions of domestication are needed. Some cultivated plants fit less easily into concepts developed initially for European cereals. This challenges us to refine and expand the vocabulary and concepts we use, especially for non-cereal crops (e.g. Denham et al., 2020). This does not mean that we can or should abandon the work of our academic predecessors; on the contrary, it is crucial to revisit 'old' influential concepts and terminology (Bogaard et al., 2021). Given the vast body of theoretical ideas pertaining to domestication produced in the last century it is not surprising we have found support for some of the concepts of our predecessors when applying hard data; for example the concept of co-evolution between crops and people of Darlington (1969) and Rindos (1980), and the landscape perspective proposed by Terrell et al. (2003). We might add that the concept of different pathways to crop domestication, such as contrasting cereals and tubers (Fuller and Denham, 2022), as well as for livestock (Zeder, 2012), was also already presaged by Harris (1977). We bring empirical evidence from excavated archaeobotanical and -zoological remains, together with revised and high precision archaeological chronologies from multiple species and world regions that illustrate these processes. Where our insightful predecessors had much less empirical basis for their theories, we offer data that both support but also move beyond previous theorizing. We integrate evidence from genomics and ancient DNA unavailable until the past few years. Our contributions provide new insights into four areas.

First, these data illustrate generally protracted and variable rates of evolution (Bogaard et al., 2021; Allaby et al., 2022a). Second, the variable rates require explanation at the population genetic level in

* Corresponding author.
E-mail address: r.g.allaby@warwick.ac.uk (R. Allaby).

https://doi.org/10.1016/j.quascirev.2022.107737
0277-3791/

terms of selection processes, which we illustrate fits a model for competitive selection (for seed size) and environmental selection (for non-brittle rachis), but not the truncation selection that has typified selective breeding in agronomic contexts (Allaby et al., 2021, 2022a). Third, morphological changes during domestication can be compared in terms of rates across crops from different regions (grain size data in Allaby et al., 2022b), and in terms of different phenotypic traits for the same crop (Fuller et al., 2014, 2018), as well as comparing across livestock and crops from the same region (Bogaard et al., 2021). The processual, generally protracted yet dynamic, evolutionary rates cannot be understood from the evidence of any single archaeological site, rather a regional “landscape” perspective is imperative, representing something of a paradigm shift (Allaby et al., 2021). Fourth, new data raise questions about comparability of pathways to domestication, including how quantitatively documented domestication in some seed crops and livestock might differ from those of other crop types. David Harris (1977) discussed “alternative pathways to agriculture” and highlighted major differences between cereals, tubers, tree-nuts and ungulates within systems of hunter-gatherer exploitation and domestication; he saw parallelisms for which he could draw on very little zooarchaeological or archaeobotanical, and no genetic evidence. The new body of evidence supports many of Harris's insights, but also challenges us to think about language revisions and new frameworks of interpretation, such as the landscape and process philosophy.

2. Protracted rates of co-evolution under domestication

A slow fixation of non-shattering morphotypes in cereals was first suggested by Tanno and Willcox (2006) for wheat from 4 sites and barley from 2 sites. Since then, larger datasets have accumulated (Fuller, 2007; Tanno and Willcox, 2012; Arranz-Otaegui et al., 2016; Allaby et al., 2017), all of which fit with a process measured in millennia that becomes visible at a regional level of study. Grain size change, another correlate of cereal domestication, also indicates a millennial long window of change (Fig. 1). Bogaard et al. (2021) illustrated the data for einkorn wheat and Chinese rice, demonstrating a new approach for estimating variable rates of phenotypic change rather than the previous assumption of uniform rates throughout the process (Purugganan and Fuller, 2011). Genomic evidence suggests that wild barley populations throughout western Asia contributed to the domesticated population (Poets et al., 2015), while the limited ancient genomic evidence does not indicate the strong bottleneck predicted if rapid domestication had occurred (Allaby et al., 2019). Similar domestication scenarios are inferred from ancient genomes of maize (Kistler et al., 2018), sorghum (Smith et al., 2019) and rice (Ishikawa et al., 2022). Human cultures also co-evolved slowly, as seen in a gradual increase and refinement of stone sickle technology alongside and after the evolution of non-shattering in cereals in western Asia (Maeda et al., 2016), and sickle or hand-harvesting knives were adopted *after* rice was domesticated in China (Fuller, 2007). Both indicate a cultural evolution at times reactive to changes in plants.

3. Alternative selection models for domestication traits

Allaby et al. (2021, 2022a) describe three ways in which crop selection might occur. In the classic model of environmental selection, leading to change in the population at a rate proportional to the fitness difference of a trait to an environmental threshold value. The evolution of non-shattering follows such a process leading to a typical logistic curve of genotype frequency. This contrasts with selective breeding, in which individuals with a below minimum trait value are eliminated with certainty (truncated) leading to very rapid trait fixation. A third model, described formally for the first time by Allaby et al., 2022b, is competitive selection, whereby a common resource available to competing individuals is differentially acquired, such as soil resources accumulated by different sized seedlings. The increased success in one genotype exerts a resource cost to others, which increases with more advantaged individuals and intensifies the removal of less competitive individuals, despite a diminishing competitive advantage to individual advantaged genotypes. Overall this leads to a snowballing rate of change in the population, a pattern that fits with evidence for seed size change under domestication across several cereals, pulses and oilseeds (Allaby et al., 2022b).

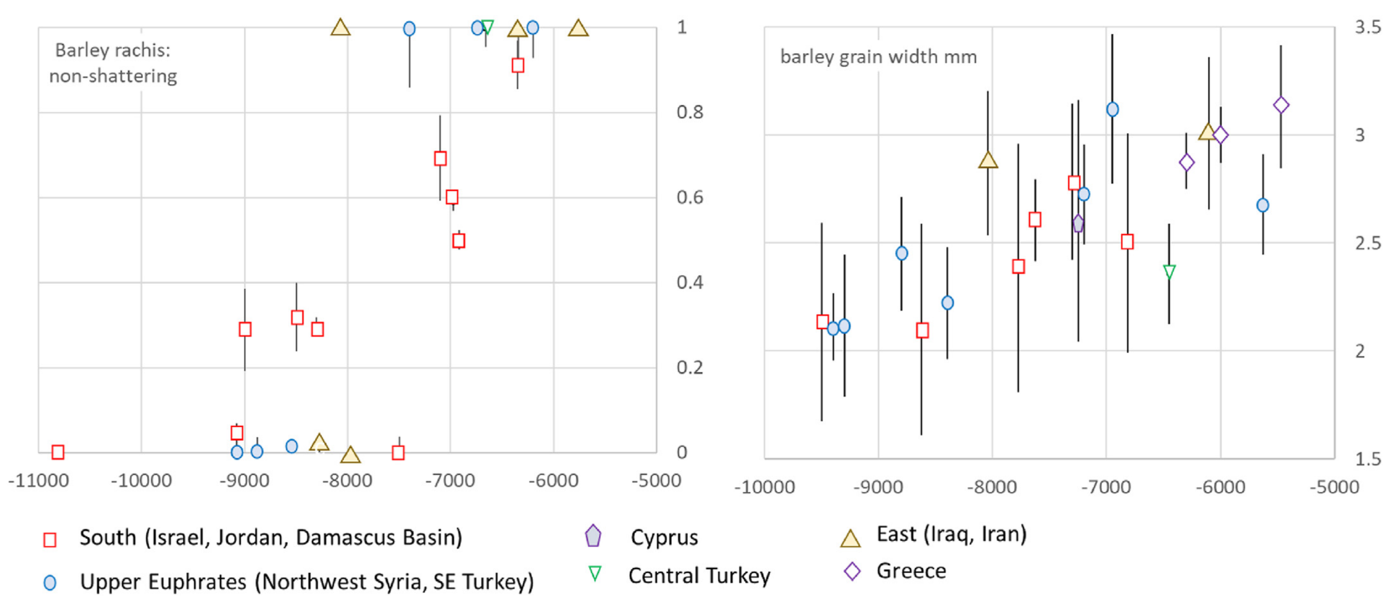

Fig. 1. Archaeobotanical evidence for barley domestication traits over time. Plotted against median age, years BCE (based on summed probability of calibrated radiocarbon dates): (left) the proportion of non-shattering rachis remains with estimated standard deviation (from Allaby et al., 2017 augmented from Riehl et al., 2013; Whitlam et al., 2020), at right, the mean and standard deviation of grain width (from Fuller et al., 2014; Colledge et al., 2018).

4. Variable rates in time and space

Variable rates of phenotypic change during the domestication process have been estimated from archaeobotanical data, marking an improvement over linear regression estimates for the entire process (Purugganan and Fuller, 2011). Allaby et al. (2017) introduced the idea that the rate of selection for non-shattering (in rice, barley, einkorn and emmer) varied over time, generally accelerating as the proportion of archaeological non-shattering increased above ~25% of the population or more, while Allaby et al. (2022a) demonstrate periods of faster and slower evolution in grain size (in 7 crops). Such patterns fit with geographical mosaics of co-evolution (Thompson, 2005), rather than conventional models of two co-evolving local populations. Hence, we argue the process is best understood at a landscape or metapopulation level (Allaby et al., 2021), drawing attention to the importance of “networks of interaction” and “broader ecological contexts” (Bogaard et al., 2021: 11). Domestication was not an event isolated in a particular field.

5. Variable pathways beyond typical cereals

Calling for a landscape perspective, Terrell et al. (2003) drew attention to the multiplicity of practices in utilization and management of different species and the continuum between foraging and cultivation (also see Yen, 1989; Latinis et al., 2000; Clement et al., 2015; Denham, 2018). They framed domestication as the cumulative effect of human actions rather than “long-range planning or clairvoyance” (Terrell et al., 2003: 333). Our framework is congruent with this, but we have brought together substantial new datasets from cereal domestication regions and from genetics. Bogaard et al. (2021) is novel in drawing attention to the hypotheses of similarities and difference between domesticates of fundamentally different kinds, as well as the variable and complex roles of human intentionality implied by the different pathways.

6. Repeated, data-free critiques

Abbo and Gopher (2022) is the latest iteration in a decade long series of similar criticisms (Abbo et al., 2010, 2012; Abbo and Gopher, 2020), in which they insist that domestication was directed as a conscious selection process, rapid (a few human generations), and took place rarely, i.e., in one or a few chosen communities. Despite claiming this for two decades (since Lev-Yadun et al., 2000), no well-dated archaeobotanical or zooarchaeological assemblage from an archaeological site or regional cluster of sites from Southwest Asia or any other region of early domestication (Africa, China, Mesoamerica, New Guinea, South America), has yet been excavated to support their claims. The accumulation of data over the past 20 years points increasingly to the paradigm of protracted domestication, a co-evolutionary process at the landscape scale. Their posited rapid domestication leads to the expectation of truncation selection (associated with intentional selective breeding) and strong bottlenecks; yet this is contradicted by the available genomic evidence, including ancient genomes (Allaby et al., 2019), and is not supported by archaeological evidence that provides timescales for domestication processes for numerous crops (at least 34 instances documented in Fuller et al., 2014, and several since then: Murphy and Fuller, 2017; Fuller et al., 2017; Kistler et al., 2018; Stevens et al., 2020; Mueller, 2019; Clements et al. 2015) and numerous animals (e.g. Arbuckle and Hammer, 2019; Arbuckle and Kassenbaum, 2021; Peters et al., 2022).

Rather than offering evidence or new analyses, our critics seem intent on making the study of domestication political or politically correct. While it is important to critically evaluate the language used to represent our data and how these categories developed (as explored in Bogaard et al., 2021; Clement et al., 2021; Iriarte et al., 2021), in the end our understanding of domestication must be informed and constrained by empirical observations—the evidence excavated from archaeological sites that represents the past fragmentarily, and the evidence revealed through the analysis of crop and livestock genomes present and past. Our recent papers have modified and renewed interpretative frameworks to accommodate this growing empirical record.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

References

Abbo, S., Gopher, A., 2020. Plant domestication in the neolithic near east: the humans-plants liaison. Quat. Sci. Rev. 242, 106412.
Abbo, S, Gopher, A, 2022. On partnerships, responsibilities, and political correctness reflections on plant domestication at the landscape level. Quat. Sci. Rev. (this issue).
Abbo, S., Lev-Yadun, S., Gopher, A., 2010. Agricultural origins: centers and non-centers; a Near Eastern reappraisal. Crit. Rev. Plant Sci. 29 (5), 317–328.
Abbo, S., Lev-Yadun, S., Gopher, A., 2012. Plant domestication and crop evolution in the Near East: on events and processes. Crit. Rev. Plant Sci. 31 (3), 241–257.
Allaby, RG, Stevens, CJ, Kistler, L, Fuller, DQ, 2022a. Genetic Revelations of a New Paradigm of Plant Domestication as a Landscape Level Process. Plant Breeding Reviews 45, 321–343.
Allaby, R.G., Stevens, C., Lucas, L., Maeda, O., Fuller, D.Q., 2017. Geographic mosaics and changing rates of cereal domestication. Phil. Trans. Biol. Sci. 372 (1735), 20160429.
Allaby, R.G., Ware, R.L., Kistler, L., 2019. A re-evaluation of the domestication bottleneck from archaeogenomic evidence. Evolutionary Applications 12 (1), 29–37.
Allaby, R.G., Stevens, C.J., Fuller, D.Q., 2022b. A novel cost framework reveals evidence for competitive selection in the evolution of complex traits during plant domestication. J. Theor. Biol. 537, 111004.
Allaby, R.G., Stevens, C.J., Kistler, L., Fuller, D.Q., 2021. Emerging evidence of plant domestication as a landscape-level process. Trends Ecol. Evol. 37, 268–279.
Arbuckle, B.S., Hammer, E.L., 2019. The rise of pastoralism in the ancient Near East. J. Archaeol. Res. 27 (3), 391–449.
Arbuckle, B.S., Kassenbaum, T.M., 2021. Management and domestication of cattle (Bos taurus) in neolithic Southwest Asia. Animal Frontiers 11 (3), 10–19.
Arranz-Otaegui, A., Colledge, S., Zapata, L., Teira-Mayolini, L.C., Ibáñez, J.J., 2016. Regional diversity on the timing for the initial appearance of cereal cultivation and domestication in southwest Asia. Proc. Natl. Acad. Sci. USA 113 (49), 14001–14006.
Bogaard, A., Allaby, R., Arbuckle, B.S., Bendrey, R., Crowley, S., Cucchi, T., Denham, T., Frantz, L., Fuller, D., Gilbert, T., Karlsson, E., 2021. Reconsidering domestication from a process archaeology perspective. World Archaeol. 53 (1), 56–77.
Clement, CR, Casas, A, Parra-Rondinel, FA, Levis, C, Peroni, N, Hanazaki, N, Cortez-Zarraga, L, Rangel-Landa, S, Martinez-Balleste, A, Lemes, G, Lotero-Velasquez, E, Bertin, VM, Mazzochini, GG, 2021. Disentangling Domestication from Food Production Systems in the Neotropics. Quaternary 4 (1), 4.
Clement, C.R., Denevan, W.M., Heckenberger, M.J., Braga Junqueira, A., Neves, E.G., Teixeira, W.G., Woods, W.I., 2015. The domestication of Amazonia before European contact. In: Proceedings of the Royal Society B: Biological Sciences. https://doi.org/10.1098/rspb.2015.0813, 07 August 2015.
Colledge, S, Conolly, J, Finlayson, B, Kuilt, I, 2018. New insights on plant domestication, production intensification, and food storage: the archaeobotanical evidence from PPNA Dhra‘. Levant 50, 14–31.
Darlington, C.D., 1969. The silent millennia in the origin of agriculture. In: Ucko, P.J., Dimbleby, G.W. (Eds.), The Domestication and Exploitation of Plants and Animals. Duckworth, London, pp. 67–72.
Denham, T.P., 2018. Tracing Early Agriculture in the Highlands of New Guinea: Plot, Mound and Ditch. Routledge, Oxford.
Denham, T.P., Barton, H., Castillo, C., Crowther, A., Dotte-Sarout, E., Florin, A., Pritchard, J., Barron, A., Zhang, Y., Fuller, D.Q., 2020. The domestication syndrome in vegetatively propagated field crops. Ann. Bot. 125, 581–597.
Fuller, D.Q., 2007. Contrasting patterns in crop domestication and domestication rates: recent archaeobotanical insights from the Old World. Ann. Bot. 100 (5), 903–924.

Fuller, D.Q., Denham, T.P., 2022. Coevolution in the arable battlefield: pathways to crop domestication, cultural practices and parasitic domesticoids. In: Schultz, T.R., Gawne, R., Peregrine, P.N. (Eds.), The Convergent Evolution of Agriculture in Humans and insects.. The Vienna Series in Theoretical Biology. The MIT Press, Cambridge, MA, pp. 177–208.
Fuller, D.Q., Denham, T.P., Arroyo-Kalin, M., Lucas, L., Stevens, C.J., Qin, L., Allaby, R.G., Purugganan, M.D., 2014. Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. Proc. Natl. Acad. Sci. USA 111 (17), 6147–6152.
Fuller, D.Q., Colledge, S., Murphy, C., Stevens, C.J., 2017. Sizing up cereal variation: patterns in grain evolution revealed in chronological and geographical comparisons. In: Fernández Eraso, J., Mujika Alustiza, J.A., Valbuena, A.A., Díez, M.G. (Eds.), Miscelánea en homenaje a Lydia Zapata Peña (1965-2015). Servicio Editorial Universidad Del País Vasco, Bilbao, pp. 131–149.
Fuller, D.Q., Lucas, L., Carretero, L.G., Stevens, C.J., 2018. From intermediate economies to agriculture: trends in wild food use, domestication and cultivation among early villages in Southwest Asia. Paleorient 44 (2), 59–74.
Harris, D.R., 1977. Alternative pathways toward agriculture. In: Reed, C. (Ed.), Origins of Agriculture, pp. 179–243. The Hague: Mouton.
Iriarte, J, Elliot, S, Maezumi, SY, Alves, D, Gonda, R, Robinson, M, de Souza, JG, Watling, JG, Handley, J, 2021. The origins of Amazonian landscapes: Plant cultivation, domestication and the spread of food production in tropical South America. Quat. Sci. Rev. 248, 106582.
Ishikawa, R., Castillo, C.C., Htun, T.M., Numaguchi, K., Inoue, K., Oka, Y., Ogasawara, M., Sugiyama, S., Takama, N., Orn, C., Inoue, C., 2022. A stepwise route to domesticate rice by controlling seed shattering and panicle shape. Proc. Natl. Acad. Sci. USA 119 (26), e2121692119.
Kistler, L., Maezumi, S.Y., Gregorio de Souza, J., Przelomska, N.A., Malaquias Costa, F., Smith, O., Loiselle, H., Ramos-Madrigal, J., Wales, N., Ribeiro, E.R., Morrison, R.R., 2018. Multiproxy evidence highlights a complex evolutionary legacy of maize in South America. Science 362 (6420), 1309–1313.
Latinis, D.K., 2000. The development of subsistence system models for island Southeast Asia and Near Oceania: the nature and role of arboriculture and arboreal-based economies. World Archaeol. 32 (1), 41–67.
Lev-Yadun, S., Gopher, A., Abbo, S., 2000. The cradle of agriculture. Science 288 (5471), 1602–1603.
Maeda, O., Lucas, L., Silva, F., Tanno, K.I., Fuller, D.Q., 2016. Narrowing the harvest: increasing sickle investment and the rise of domesticated cereal agriculture in the Fertile Crescent. Quat. Sci. Rev. 145, 226–237.
Mueller, N.G., 2019. Documenting the evolution of agrobiodiversity in the archaeological record: landraces of a newly described domesticate (*Polygonum erectum*) in North America. J. Archaeol. Method Theor 26 (1), 313–343.
Murphy, C, Fuller, DQ, 2017. Seed coat thinning during horsegram (Macrotyloma uniflorum) domestication documented through synchrotron tomography of archaeological seeds. Sci. Rep. 7 (1). https://doi.org/10.1038/s41598-017-05244-w.
Peters, J., Lebrasseur, O., Irving-Pease, E.K., Paxinos, P.D., Best, J., Smallman, R., Callou, C., Gardeisen, A., Trixl, S., Frantz, L., Sykes, N., 2022. The biocultural origins and dispersal of domestic chickens. Proc. Natl. Acad. Sci. USA 119 (24), e2121978119.
Poets, A.M., Fang, Z., Clegg, M.T., Morrell, P.L., 2015. Barley landraces are characterized by geographically heterogeneous genomic origins. Genome Biol. 16 (1), 1–11.
Purugganan, M.D., Fuller, D.Q., 2011. Archaeological data reveal slow rates of evolution during plant domestication. Evolution: International Journal of Organic Evolution 65 (1), 171–183.
Riehl, S., Zeidi, M., Conard, N.J., 2013. Emergence of agriculture in the foothills of the zagros mountains of Iran. Science 341 (6141), 65–67.
Rindos, D., 1980. Symbiosis, instability, and the origins and spread of agriculture: a new model [and Comments and Reply]. Curr. Anthropol. 21 (6), 751–772.
Smith, O., Nicholson, W.V., Kistler, L., Mace, E., Clapham, A., Rose, P., Stevens, C., Ware, R., Samavedam, S., Barker, G., Jordan, D., Fuller, D.Q., Allaby, R.G., 2019. A domestication history of dynamic adaptation and genomic deterioration in *Sorghum*. Nature Plants 5, 369–379.
Stevens, C.J., Shelach-Lavi, G., Zhang, H., Teng, M., Fuller, D.Q., 2020. A model for the domestication of Panicum miliaceum (common, proso or broomcorn millet) in China. Veg. Hist. Archaeobotany 30, 21–23.
Tanno, K.I., Willcox, G., 2006. How fast was wild wheat domesticated? Science 311 (5769), 1886-1886.
Tanno, K.I., Willcox, G., 2012. Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East. Veg. Hist. Archaeobotany 21 (2), 107–115.
Terrell, J.E., Hart, J.P., Barut, S., Cellinese, N., Curet, A., Denham, T., Kusimba, C.M., Latinis, K., Oka, R., Palka, J., Pohl, M.E., 2003. Domesticated landscapes: the subsistence ecology of plant and animal domestication. J. Archaeol. Method Theor 10 (4), 323–368.
Thompson, J.N., 2005. The Geographic Mosaic of Coevolution. University of Chicago Press, Chicago.
Whitlam, J., Valipour, H.R., Charles, M., 2020. Cutting the mustard: new insights into the plant economy of Late Neolithic Tepe Khaleseh (Iran). Iran 58 (2), 149–166.
Yen, D.E., 1989. The domestication of environment. In: Harris, D.R., Hillman, G.C. (Eds.), Foraging and Farming: the Evolution of Plant Exploitation. Unwin Hyman, London, pp. 55–75.
Zeder, M, 2012. The broad spectrum revolution at 40: resource diversity, intensification, and an alternative to optimal foraging explanations. J. Anthropol. Archaeol. 31, 241–264.