Identifying social learning between Roman amphorae workshops through morphometric similarity

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Abstract

The aim of this study is to identify interactive dynamics within amphorae workshops in the Roman Empire. The Baetica province (currently Andalusia, southern Spain) hosted for almost 300 years a massive infrastructure that supplied olive oil to the Western provinces of Rome. A large number of workshops produced the same type of amphora to ship the product through maritime and riverine transport networks. Despite the amount of evidence it is difficult to find an archaeological proxy able to tell us how were these workshops organised.

We apply here an evolutionary framework to understand potential links between workshops through morphometric similarities in the amphorae they produced. By exploring small yet statistical significant differences in the amphorae made in 5 different workshops the approach is able to identify how individual potters acquired and transmitted technical skills. Our approach applies multivariate statistical methods to cluster a variety of amphorae based on morphometric measurements. Other studies have developed similar approach to analyse handmade pottery but we show here that the method can be also applied to large-scale production of a standardized amphora type (i.e. Dressel 20).

Results suggest that morphometric similarity is inversely correlated with spa-

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tial distance between workshops. This outcome suggests that pottery-making techniques were transmitted through vertical transmission with little or no movement of potters between distant workshops.

The work also highlights that morphometric similarity may be an effective proxy to identify social learning dynamics even amongst workshops producing exactly the same amphoric type.

Keywords: Roman Empire; amphorae workshops; Dressel 20; social learning; cultural evolution

1. Introduction

The archaeological record can help us identify the mechanisms by which humans learn from each other (Richerson and Boyd, 2005; Schillinger et al., 2016a). Cultural transmission dynamics can be identified by analysing archaeological proxies able to capture the distinct variability generated by different social learning mechanisms (Shennan and Wilkinson, 2001; Eerkens and Lipo, 2005). This approach has been successfully applied to the material culture generated by small-scale societies but it has been seldom explored in the case of large-scale production (Shennan et al., 2015; Neff, 1992).

This paper explores the social dynamics of specialized production in the Roman Empire. We focus here on analysing large-scale production of a single amphoric type (Dressel 20) in a specific area. An evolutionary framework has been used to identify social learning dynamics between pottery-makers (Mesoudi, 2015; Shennan, 2008a). Following a large number of authors (Cavalli-Sforza and Feldman, 1981; Hosfield, 2009), pottery production can be learned on different modes of cultural transmission depending on the level of production in the communities. Vertical transmission is a mode of transmission when the teaching of the production is done from master to disciple while in horizontal transmission individuals teach pottery techniques to other individuals within the same level and those workers spread the knowledge to their community (Epstein, 1998).

Artefact variation should also be affected by geographical distance (Björklund

et al., 2010; Shennan et al., 2015; Van Strien et al., 2015). If vertical transmission is predominant then culture should be similar in nearby groups with high degrees of interaction (Hart, 2012). The underlying consequence is that it should be possible to identify interaction between workshops by quantifying similarity amongst the amphorae they produced; if apprentices moved between distant workshops then no differences would be found on this proxy while a more strict vertical transmission would be revealed by distant workshops exhibiting less similarity.

The debate on social learning processes is hindered by the challenge of detecting the different modes of transmission in the archaeological record (Roux, 2015). In the case of archaeology, several studies have analysed this process focused on the production of handmade pottery (Steele, James et al., 2010) or with stylistic variations (Neiman, 1995; Shennan and Wilkinson, 2001). Our work aims at identifying learning processes even in the case of the standardized massive olive oil production common during the Roman Empire (Gandon et al., 2014; Bevan, 2014).

Olive oil was one of the most important products of the Classical Mediterranean world as it was used in almost all aspects of daily life including cooking, lightning and hygiene (Mattingly, D.J., 1988). The Baetica province (currently Andalusia, southern Spain) developed a massive infrastructure of olive oil production to face the demands of the Roman Empire. The product was shipped in large amounts of amphorae to distant provinces all along the Western provinces. One of its most important clients was the Roman army as olive oil was supplied to tens of thousands of legionaries in places such as Britannia (Funari, 2005; Carreras Monfort, 1998) and Germania (Remesal, 1986).

For this reason, this ancient province became an important support for the production and distribution of olive oil to the rest of the Empire during three centuries (Chic, 2005; Berni, 1998; Remesal, 1998). Baetica provided a strong connectivity through riverine transport that allowed inland producers to use an important trade network through the Mediterranean and Atlantic (García Vargas, 2010). The exponential production growth required the creation of over

a hundred amphora workshops supporting olive oil shipment. These workshops were located along the Guadalquivir river and its tributaries. The majority of amphorae produced in this area are classified as Dressel 20 type divided into a variety of subclasses (Berni, 2008; Martin-Kilcher, 1987). Dressel 20 were used mostly to transport olive oil for around 300 years in order to satisfy the demand within Roman Empire (Remesal, 1977).

This specialized production was highly standardized both in terms of products and processes and did not vary much. The same type of amphora was produced over 300 years with small differences while similar stamps and information was recorded on them Rubio-Campillo et al. (2017).

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Despite our knowledge of the process little is known on how learning was organised in these workshops. Did they have different traditions and apprentices worked in the place where they were trained? Did potters work in more than one workshop? Were changes in production decided by workshops or by external actors? All these questions are linked to the social learning processes that took place in the workshops.

If the system was organised based on vertical transmission mechanisms with no potters moving to distant workshops then amphorae produced in nearby workshops might share more similar traits than with the rest of the production. On the other hand, if horizontal dynamics were common then this correlation with spatial coordinates should not be present as workers would share their methods (Hosfield, 2009).

The paper can be summarized as follows. The next section introduces the dataset and the methods used to analyse it. Section three presents the results while the last part discusses the outcomes and highlights the main conclusions of the work.

2. Material and methods

2.1. Workshops

Our sample consisted of 413 Dressel 20 amphorae collected from the 5 Dressel 20 workshops that have been more intensively excavated in the last decades. The workshops were located at Malpica, Cerro del Belén (hereafter, Belén) (Díaz Trujillo, 1992), Parlamento (García Vargas, 2000), Villaseca(García Vargas and Morena, fourthcoming) and Las Delicias (Fernández et al., 2001; Mauné et al., 2014) (see Figure 1).

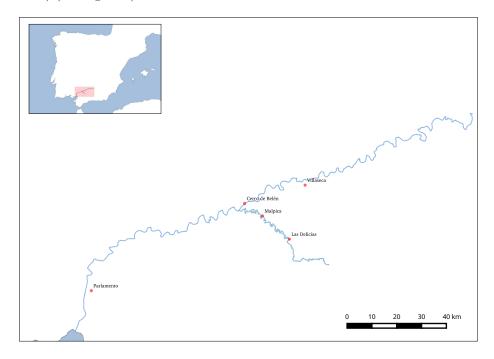


Figure 1: Map from Baetica province during the Roman Empire depicting the location of the 5 analysed workshops. Dressel 20 workshops were mostly distributed along the rivers Gualdalquivir and Genil.

The sample was roughly uniformly distributed amongst the 5 workshops (80-100 samples for each of them). These workshops were located a diversity of locations so spatial dynamics could be potentially identified. All of them had overlapping long chronologies so differences in amphorae could not be inherently

explained by temporal variation. This trait is reinforced by the fact that the Dressel 20 type did not show any remarkable change in shape for almost three centuries (Berni and García Vargas, 2016). We analysed Dressel 20 of the three most abundant variants spanning three centuries (Dressel C, Dressel D, Dressel E) (Berni, 2008; Martin-Kilcher, 1987). All the variants were found in the 5 workshops so no intrinsic bias was generated by them.

2.2. Spatial Distance

100

The approach required us to compute a pairwise matrix of spatial distances between workshops. All these workshops were located near a river as the amphorae were shipped by boat after being made and filled with olive oil. Given the relevance of riverine transport it was decided that the best proxy for spatial distance between workshops was the one observed following the river course, as summarized in Table 1

Workshops	Malpica	Belén	Villaseca	Las Delicias	Parlamento
Malpica	-	11	50	17	108
Belén	11	-	33	29	98
Villaseca	50	33	-	67	133
Las Delicias	17	29	67	-	126
Parlamento	108	98	133	126	-

Table 1: Distance matrix between workshops (in km.)

2.3. Measurements

Eight different measurements were taken from each amphora. The metrics were focused on the rim sherds as this section presents the best preservation for most archaeological contexts and they present good indicators of variation (Berni, 2008). Other interesting proxies such as handles and bases were found in lesser quantities and for this reason they would be less useful for quantitative approaches due to low sample size. The measurements can be seen in Figure 2;

they were divided into exterior diameter, inside diameter, rim height, rim width, shape width, rim inside height, rim width 2 and protruding rim.

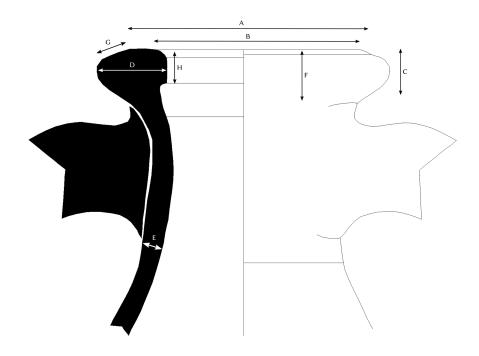


Figure 2: The 8 morphometric measurements taken for all amphorae. A: External diameter. B: Inside diameter. C: Rim height. D: Rim width. E: Shape width. F: Rim inside height. G: Rim width 2. H: Protruding rim

2.4. Exploratory Data Analysis

Principal Component Analysis (PCA) was used to explore the variation of measurements over the different workshops. PCA is a common method in archaeology in scenarios studying within-sample variation (Shennan, 2008b; Li et al., 2014; Schillinger et al., 2016b). The method allowed us to visualize the dataset by focusing on a small number of Principal Components (PCs) while retaining a majority of the variation which was in essence what we wanted to explore (Jolliffe, 2002).

2.5. Morphometric similarity

Exploratory Data Analysis was followed by the measurement of pairwise dissimilarity between the amphorae made in different workshops. The approach presented here is based on the idea that if most amphorae made in two workshops are difficult to distinguish then the workshops are making similar artefacts; on the other hand if the probability of distinguishing the production place of most amphorae is high then there are remarkable morphometric differences between the objects. This goal could be achieved by 1) training a clustering algorithm with the dataset 2) using the model to predict the workshop of the same dataset and 3) computing a confusion matrix.

The choice of clustering method was Linear Discriminant Analysis (LDA). The entire dataset was used both for the training and prediction steps as we were interested on how well workshop attribution could be predicted relying exclusively on morphometric measures. A Confusion Matrix was then computed as a quantification of the extent to what amphorae of different workshops can be identified. The Confusion Matrix computes this quantity as the number of misclassifications between each pair of groups in the dataset (i.e. the workshops). This method has already been used in similar scenarios aiming at identifying differences in artefact production (Charlton et al., 2012; Thorpe et al., 1984; Aguilera, 1998). If the amphorae made in two workshops were easily confused then their average measures must be similar; on the other hand, if the rate of misclassification between two workshops is very low then the amphorae made in these locations are distinctively different.

The diagonal of the confusion matrix (i.e. correct classifications) was removed and the number of confusions per each workshop was then divided by the total number to get the percentage of errors from a given workshops to the rest of the sample. These values were finally normalized to generate a pairwise distance matrix of morphometric measurements.

2.6. Dissimilarity correlation

The last step of this method was the comparison of morphometric and spatial distance matrices. A significant correlation between these dissimilarity matrices would suggest processes of isolation-by-distance typical from vertical transmission (Crema et al., 2014). The evaluation of these two distance matrices (morphometric distance and spatial distance) was computed using a Mantel test. Mantel test evaluates the degree of pairwise correlation between two matrices and has been particularly useful in archaeology to explore the spatial dimension of cultural change (Mantel, 1967; Diniz-Filho et al., 2013; Crema et al., 2014).

160 3. Results

3.1. Principal Component Analysis

The loadings for the two main Principal Components of the dataset are listed in Table 2

Variables	PC1	PC2	
Exterior diameter	0.877	0.312	
Inside diameter	0.404	-0.887	
Rim height	-	-	
Rim width	0.149	0.119	
Shape width	-	-	
Rim inside	-	-	
Rim width 2	0.133	0.142	
Protruding rim	-0.159	-0.272	

Table 2: Two main Principal Components. Diameter values and the protruding rim seem to capture the majority of variation.

A exploratory visualization for these two main Principal Components can be seen in Figure 3. The plot suggests that each workshop exhibits slightly different dynamics for PC1 while PC2 is distinctively different for the two most distant sites (Villaseca and Parlamento). Additionally, the first PC also tends to display more similar values for amphorae made in nearby workshops such as Belén and Malpica.

3.2. Linear Discriminant Analysis

LDA's prediction generated an accuracy of 56.6%. For this method the accuracy of the clustering algorithm is not as relevant as the distribution of errors which can be seen in the Confusion Matrix of Table 3.

	Belén	Delicias	Malpica	Parlamento	Villaseca
Belén	48	11	16	4	6
Delicias	10	81	24	8	0
Malpica	12	12	49	1	6
Parlamento	6	10	9	25	10
Villaseca	12	5	13	4	31

Table 3: Confusion Matrix of errors in predicted classifications between workshops. The sample analysed gave an accuracy percentage of 56.6% with p-value <0.01.

A tentative glance to these results suggest that workshops with a minor spatial distance such as Malpica, Belén and Las Delicias made amphorae that are more difficult to distinguish due to their similarity.

3.3. Mantel correlation test

Mantel test between morphometric and spatial dissimilarity matrices generated a correlation of 0.51 with p-value under 0.01. The analysis shows that morphometric distance of the amphorae are strongly correlated with the spatial distance of workshops. Accordingly closer workshops tend to be more similar than the rest: when geographic distance is low, as the example of Belén and Malpica, the morphometric distance seems more similar whereas when distance is higher, as Parlamento, the morphometric distance displays differences with the rest of workshops. Thus, the results suggest that the variability on the making-techniques processes might depend on the spatial distance.

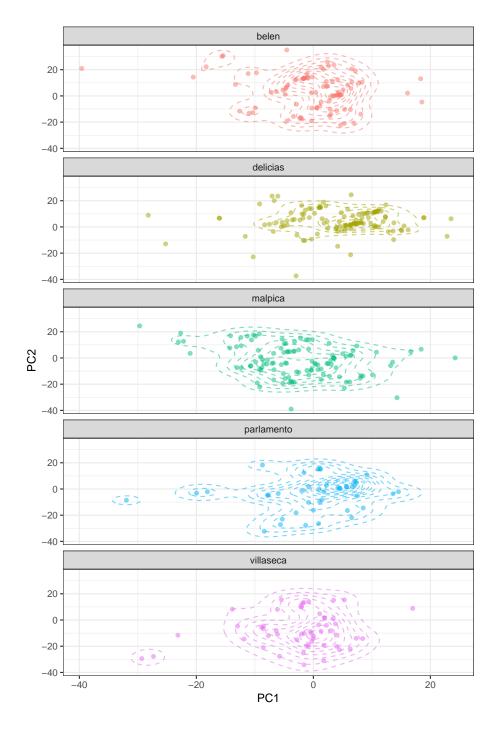


Figure 3: Scatter and density plot for the First and Second PCs. Sample is split by workshop

4. Discussion and Concluding remarks

210

Differences on the making techniques processes among workshops show a variability correlated with spatial distance. The analysed morphometric traits suggest that the similarity between amphorae decreases with the spatial distance between the workshops where they were produced. As a result, amphorae made in nearby workshops share more similar traits than amphorae made in distant workshops where contact was less frequent.

The results suggest that vertical transmission could be the main cultural mechanism to explain the variability between workshops.

The different morphological traits among workshops seem to reveal low frequency of contact between potters from other workshops. The equilibrium of this dynamic for a long time span (over three centuries) can be interpreted as a high-fidelity social learning mechanism vertically transmitted within each of the workshops. The disciples could have remained working at the same workshops where they were trained.

Horizontal transmission or high mobility do not seem to match with the results of the analysis. Scenarios with frequent contact between potters or workers moving from workshop to workshop would have generated larger homogeneity in the technical practises with low intensity of isolation-by-distance processes. As a consequence workshops sharing a network of potters would have employed the same production techniques, thus generating similar amphorae. The fact that isolation by distance can be identified suggests limited mobility strictly linked to nearby workshops.

Despite these results the diversity of social learning processes is always complex. The transmission of technical skills between master and disciples and their limited mobility does not mean that no horizontal transmission process also played a relevant role. It can be a process where this vertical transmission dominated at first in the same workshops but consequently this transmission would be affected by workers who exchanged ideas or workers moving to other workshops.

To conclude, the method presented here provides a framework to identify social learning mechanisms between production centres based on morphometric measurements of artefacts. The method has proven valuable even in the case of the highly standardized amphoric production of the Roman Empire. The suggested method could also offer a good comparison with other analytical methods such as archaeometry; we believe that a framework integrating and comparing multiple sources of evidence could be extremely effective on the process of characterization of production sites and places of consumption. Our analysis provides a useful guideline for the exploration of the social learning processes related with amphora production in the Roman Empire. Hence, the results have lightened to understand the link between social learning and archaeological evidence in a diversity of scenarios.

5. Acknowledgments

The research was funded by European Research Council Advanced Grant EPNet (340828). We are grateful to Enrique García Vargas and Simon Carrignon for helpful suggestions and constructive comments on previous versions of the paper. The Museum of Écija (Antonio Fernández Ugalde), Museum of Palma del Río (Reyes Lopera and Emilio Navarro), Museum of Córdoba and Museum of Seville for kindly allowing us access to their information. Data were collected, performed and analysed in R version 3.2.4. statistical language and implemented with the package MASS and vegan. Map was done by QGIS 2.8 Wien with Pleiades template.

References

Aguilera, A., 1998. Análisis multivariable: una nueva vía para la caracterización cerámica. Pyrenae 29, 117–134.

Berni, P., 1998. Las ánforas de aceite de la Bética y su presencia en la Cataluña romana. volume 4. Col .lecció Instrumenta. Universitat de Barcelona.

Berni, P., 2008. Epigrafía anfórica de la Bética. Nuevas formas de análisis. volume 29. Col .lecció Instrumenta. Universitat de Barcelona.

245

- Berni, P., García Vargas, E., 2016. Dressel 20 (Guadalquivir Valley). URL: http://amphorae.icac.cat/amphora/dressel-20-guadalquivir-valley.
- Bevan, A., 2014. Mediterranean Containerization. Current Anthropology 55, 387-418. URL: http://www.jstor.org/stable/info/10.1086/677034, doi:10.1086/677034.
 - Björklund, M., Bergek, S., Ranta, E., Kaitala, V., 2010. The effect of local population dynamics on patterns of isolation by distance. Ecological Informatics 5, 167–172.
- Carreras Monfort, C., 1998. Britannia and the imports of Baetican and Lusitanian amphorae. Journal of Iberian Archaeology 1, 159–172.
 - Cavalli-Sforza, L.L., Feldman, M.W., 1981. Cultural transmission and evolution: a quantitative approach. Princeton University Press.
- Charlton, M.F., Blakelock, E., Martinón-Torres, M., Young, T., 2012. Investigating the production provenance of iron artifacts with multivariate methods.

 Journal of Archaeological Science 39, 2280–2293.
 - Chic, G., 2005. El comercio de la Bética altoimperial. Habis 36, 313–332.
 - Crema, E.R., Kerig, T., Shennan, S., 2014. Culture, space, and metapopulation: a simulation-based study for evaluating signals of blending and branching. Journal of Archaeological Science 43, 289–298.
 - Díaz Trujillo, O., 1992. Excavación arqueológica de urgencia en el Cerro de Belén: Palma del Río, Córdoba, in: Anuario Arqueológico de Andalucía. Junta de Andalucía, pp. 121–129.

- Diniz-Filho, J.A.F., Soares, T.N., Lima, J.S., Dobrovolski, R., Landeiro, V.L.,
 Telles, M.P.d.C., Rangel, T.F., Bini, L.M., 2013. Mantel test in population genetics. Genetics and Molecular Biology 36, 475–485.
 - Eerkens, J., Lipo, C., 2005. Cultural transmission, copying errors, and the generation of variation in material culture and the archaeological record. Journal of Anthropological Archaeology 24, 316–334.
- Epstein, S.R., 1998. Craft guilds, apprenticeship, and technological change in preindustrial Europe. Journal of Economic History 58, 684–713.
 - Fernández, P.S., Muñoz, J.T., Vargas, E.G., de la Vega, S.G.D., 2001. Excavación arqueológica de urgencia en el alfar romano de las Delicias (écija, Sevilla) 1997., in: Anuario arqueológico de Andalucía 1997. Junta de Andalucía, pp. 562–575.
 - Funari, P., 2005. The Economic history of Roman Britain: olive oil contribution to the debate. História e economia 1, 29–46.

- Gandon, E., Roux, V., Coyle, T., 2014. Copying errors of potters from three cultures: predictable directions for a so-called random phenomenon. Journal of Anthropological Archaeology 33, 99–107.
- García Vargas, E., 2000. Ánforas romanas producidas en Hispalis: primeras evidencias arqueológicas. Habis 31, 235–260.
- García Vargas, E., 2010. Formal Romanisation and the Atlantic Projection of Amphorae from the Guadalquivir Valley, in: The Western Roman Atlantic Façade: A study of the economy and trade in the Mar Exterior from the Republic to the Principate. archaeopress ed.. Oxford, England. number 2162 in BAR International Series, pp. 55–66.
- García Vargas, E., Morena, J.A., fourthcoming. La excavación del alfar de ánforas Dr. 20 de Villaseca (Córdoba). Unpublished.

- Hart, J.P., 2012. The effects of geographical distances on pottery assemblage similarities: a case study from Northern Iroquoia. Journal of Archaeological Science 39, 128–134.
 - Hosfield, R., 2009. Modes of transmission and material culture patterns in craft skills, in: Pattern and Process in Cultural Evolution. Origins of Human Behavior and Culture, 2. University of California Press, pp. 45–60.
 - Jolliffe, I., 2002. Principal component analysis. Wiley Online Library.

- Li, X.J., Bevan, A., Martinón-Torres, M., Rehren, T., Cao, W., Xia, Y., Zhao, K., 2014. Crossbows and imperial craft organisation: the bronze triggers of China's Terracotta Army. Antiquity 88, 126–140.
- Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27, 209–220.
 - Martin-Kilcher, S., 1987. Die römischen Amphoren aus Augst und Kaiseraugst. Ein Beitrag zur römischen Handels- und Kulturgeschichte, 1. Die südspanischen Ölamphoren (Gruppe 1). volume 7/1. Forschungen in Augst.
- Mattingly, D.J., 1988. Oil for export? A comparison of Libyan, Spanish and Tunisian olive oil production in the Roman Empire. Journal of Roman Archaeology 1, 33–56.
 - Mauné, S., García Vargas, E., Bourgeon, O., Corbeel, S., Carrato, C., García Dils, S., Bigot, F., Vázquez Paz, J., 2014. L'atelier d'amphores à huile Dr. 20 de Las Delicias à Écija (prov. de Séville, Espagne), in: SFECAG, Actes du Congrés de Chartres, pp. 419–444.
 - Mesoudi, A., 2015. Cultural Evolution: A Review of Theory, Findings and Controversies. Evolutionary Biology 43, 481–497. URL: http://link.springer.com/10.1007/s11692-015-9320-0, doi:10.1007/s11692-015-9320-0.
- Neff, H., 1992. Ceramics and evolution. Archaeological Method and Theory 4, 141–193.

- Neiman, F.D., 1995. Stylistic variation in evolutionary perspective: inferences from decorative diversity and interassemblage distance in Illinois Woodland ceramic assemblages. American Antiquity 60, 7–36.
- Remesal, J., 1977. La economía oleícola bética: nuevas formas de análisis.

 Archivo Español de Arqueología 50, 87–144.
 - Remesal, J., 1986. La annona militaris y la exportación de aceite bético a Germania. Editorial Complutense.
- Remesal, J., 1998. Baetican olive oil and the Roman economy. Journal of Roman Archaeology - Suppl. series 29, 183–200.
 - Richerson, P.J., Boyd, R., 2005. Not by genes alone. How culture transformed Human Evolution. Chicago: University of Chicago Press.
 - Roux, V., 2015. Standardization of ceramic assemblages: Transmission mechanisms and diffusion of morpho-functional traits across social boundaries.

 Journal of Anthropological Archaeology 40, 1–9.

- Rubio-Campillo, X., Coto-Sarmiento, M., Remesal, J., 2017. Bayesian analysis and free market trade within the Roman Empire. Antiquity 91, 1241–1252.
- Schillinger, K., Mesoudi, A., Lycett, S.J., 2016a. Copying error, evolution, and phylogenetic signal in artifactual traditions: An experimental approach using "model artifacts". Journal of Archaeological Science 70, 23–34.
- Schillinger, K., Mesoudi, A., Lycett, S.J., 2016b. Differences in Manufacturing Traditions and Assemblage-Level Patterns: the Origins of Cultural Differences in Archaeological Data. Journal of Archaeological Method and Theory 24, 640–658. doi:10.1007/s10816-016-9280-4.
- Shennan, S., 2008a. Evolution in Archaeology. Annual Review of Anthropology 37, 75-91. URL: http://www.annualreviews.org/doi/abs/10.1146/annurev.anthro.37.081407.085153, doi:10.1146/annurev.anthro.37.081407.085153.

- Shennan, S., 2008b. Quantifying archaeology. Edinburgh University Press.
- Shennan, S.J., Crema, E.R., Kerig, T., 2015. Isolation-by-distance, homophily, and "core" vs. "package" cultural evolution models in Neolithic Europe. Evolution and Human Behavior 36, 103–109.
 - Shennan, S.J., Wilkinson, J.R., 2001. Ceramic Style Change and Neutral Evolution: A Case Study from Neolithic Europe. American Antiquity 66, 577–593. URL: http://www.jstor.org/stable/2694174.

- Steele, James, Glatz, Claudia, Kandler, Anne, 2010. Ceramic diversity, random copying, and tests for selectivity in ceramic production. Journal of Archaeological Science 30, 1–11.
- Thorpe, O.W., Warren, S.E., Nandris, J., 1984. The distribution and provenance of archaeological obsidian in Central and Eastern Europe. Journal of Archaeological Science 11, 183–212.
 - Van Strien, M.J., Holderegger, R., Van Heck, H.J., 2015. Isolation-by-distance in landscapes: considerations for landscape genetics. Heredity 114, 27–37.