

# **Dispersals as demographic processes: testing and describing the spread of the Neolithic in the Balkans**

Marc Vander Linden, Fabio Silva

Institute for the Modelling of Socio-Environmental Transitions

Bournemouth University

## **Abstract**

Although population history and dispersal are back at the forefront of the archaeological agenda, they are often studied in relative isolation. This contribution aims at combining both dimensions, as population dispersal is, by definition, a demographic process. Using a case-study drawn from the Early Neolithic of South-Eastern Europe, we use radiocarbon dates to jointly investigate changes in speed and population size linked to the new food production economy and demonstrate that the spread of farming in this region corresponds to a density-dependent dispersal process. The implications of this characterisation are evaluated in the discussion.

## **Keywords**

Dispersal, population, density-dependence, SPDs, Early Neolithic, Balkans

## **Introduction**

Having been relegated to the shadows of archaeological theory for decades, dispersal and population history (in particular population size) are now back under the spotlight, largely thanks to new analytical developments originating from both within (e.g. summed probability distributions, hereafter SPDs) and outside the discipline (e.g. isotopes, modern and ancient DNA). These methodological refinements have, however, not been accompanied by comparable theoretical leaps and both demographic topics, despite being intricately related, are often still considered in isolation.

The literature on the introduction of farming practices in Europe provides a good example of this situation. While scholars have bitterly debated whether or not new incoming farming communities were responsible for the introduction of domesticated plants and animals across the whole of Europe (e.g. Ammerman & Cavalli-Sforza 1984, Robb and Miracle 2007, Whittle 2007, Fort 2012) or at regional scales (e.g. McClure et al 2014, Brami 2015, Binder et al 2017, Blagojevic et al 2017, Manen et al 2019), aDNA studies have partially settled the controversy. Genetic sampling and analysis of Early Neolithic human bone samples systematically demonstrate in all regions of Europe the introduction of a new genomic component whose eventual origins can be traced back to Anatolia (e.g. Lazaridis et al. 2016, Mathieson et al. 2018). At the same time, numerous papers have reported a rise in SPDs associated with the local onset of agriculture in various parts of Europe, interpreted as the signal of a demographic regime shift triggered by the new productive economy (e.g. Shennan et al. 2013, Balsera et al. 2015, McLaughlin et al. 2016). While scholars have linked this demographic “boom” to the local immigration of a new population (especially Collard et al. 2010), few have explicitly and formally discussed the intimate relationship between the dispersal of farming populations and concurrent changes in regional population sizes (e.g. Silva and Vander Linden 2017).

This contribution argues that re-articulating population size and dispersal together is of paramount importance for archaeology. The history of migrations in archaeology can largely be read as the rise and fall of the popularity of available proxies, from pottery types during the heydays of culture-history, to a variety of scientific techniques, most noticeably modern DNA in the late 1990s, Sr isotopes in the early 2000s and now ancient DNA. It could be said that many archaeologists passively wait for past human mobility to be identified by ancient DNA studies, which has led to a dearth of archaeological methods and theories suited to characterise and explain such dispersal processes. One way to reignite such creativity is to reconsider what cognate disciplines have to offer, for instance population ecology, a field with a long tradition of mathematical modelling (e.g. Skellam 1951, Levins 1966).

With this perspective in mind, this paper focuses on density-dependent dispersals, one particular category of dispersal processes identified by population ecology. Using the spread of farming in South-Eastern Europe as case-study, we combine geostatistical interpolation of  $^{14}\text{C}$  dates and SPDs to jointly investigate changes in speed and population size linked to the new food production economy, and to identify whether or this process can be characterised as density-dependent.

### **Dispersal as a demographic process**

Population ecology is “the study of the distribution and abundance of organisms” (Turchin 1998: 1). As a dispersal is but a change in the distribution of an organism, by definition population and dispersal are intrinsically linked, though the corresponding mechanisms underlying this relationship are both complex and variable (e.g. Matthysen 2012). Here, we focus on dispersal processes whereby there is a functional relationship between population density and the rate of spread, so that the population size increases until a certain density threshold is reached, at which point the population starts redistributing itself through space under the form of an advancing wave-front (Turchin 2002: 155; see also Matthysen 2005). Such processes form the conceptual and mathematical basis of reaction-diffusion (or Fisher-Skellam) models, which have been the quantitative method of choice in archaeology for assessing and modelling dispersals with suspected demographic basis, such as farming (e.g. Pinhasi et al. 2005, Davison et al. 2006, Fort et al. 2012). Without going into mathematical details (see Steele 2009 for an excellent overview), reaction-diffusion models have two components: firstly, a reaction term based on population growth and, secondly, a diffusion term linked to the population dispersal. Under these models, the rate of spread blurs the first and second terms by being related to both the intrinsic population growth rate and the mean spatial dispersal rate. Traditionally, the archaeological focus has laid on quantifying rates of spread through statistical analyses of radiocarbon dates, as they provide precise estimates of the first date of arrival of the corresponding archaeological phenomenon at different spatial locations (Steele 2009). However, the use of reaction-diffusion is predicated on the premise of the first, reaction term which is determined by population growth. By contrast to the emphasis placed on quantifying rate of spread, within archaeological studies population growth is generally assumed, rather than empirically demonstrated, and is set using parameter values derived from instance from ethnographic or historic sources, which may or may not be good analogues for prehistoric demography (e.g. Fort 2012).

The original Fisher-Skellam model, however, does not encapsulate the diversity of dispersal dynamics possible – a point thoroughly discussed by Steele (2009) but largely forgotten by archaeologists since. Examples include the addition of: the Allee effect, which takes into account

that the low densities of a population at the wave-front increases its risk of extinction; a greater length of time between birth and dispersal (e.g. Fort and Mendez 1999), environmental heterogeneity in space and/or time (e.g. Silva and Steele 2014), or advection, i.e. the fact that movement is made along preferential rather than random directions (e.g. Davison et al 2006). Here we want to especially draw attention to a branch of Fisher-Skellam modifications that consider the interrelationship between dispersal and demography, namely density-dependant dispersal models. Steele et al (1998) first observed that, because the basic Fisher-Skellam model counterbalances a logistic growth term with a diffusion term, it predicts that people will disperse preferentially into adjacent regions where the population size is furthest from carrying capacity. However, this is not always the case as people may decide to disperse along greater distances depending on demographic, and hence population density dependent, pressures. When the diffusion term is allowed to be density-dependent a range of new realistic behaviours emerge (Newman 1980). One possible behaviour results from a negative correlation between population density and dispersal distance, i.e. when the dispersal distance increases with decreasing population density, as would happen, for example, when mate searching. Steele et al (1998) suggest this mechanism as responsible for the accelerated human colonisation of the Americas. Conversely, when dispersal distances increase with increasing population density, that is when there is a positive correlation between the two, then one would only expect an increase in the rate of spread when the dispersal distance is much larger than it would normally be (Steele 2009).

The argument put forward here is that SPDs offer a complimentary method to assess any correlations between demography and the timing of dispersals as they provide, admittedly imprecise and relative, means of quantifying change in population size and growth. They can therefore be used, in conjunction with other more spatial methods, to assess the demographic dynamics of dispersals which can provide clues as to what type of diffusion model best fits the archaeological dispersal process under study.

## **Data and methods**

The regional case-study chosen to illustrate our approach encompasses an area bounded between 37 N and 48.5 N and 10 E and 25 E. This region plays a key role in the dispersal of early farming as it includes the earliest occurrences of plant and animal domesticates in Europe, and the origins of the two main routes of diffusion responsible for introduction of early farming across most of the sub-continent (Bocquet-Appel et al. 2009). In order to investigate chronological and spatial trends across the area, we compiled from the existing literature a georeferenced dataset of 2267 radiocarbon determinations for 380 sites, covering the time period between 14000 and 5000 uncal BP (ie Final Pleistocene, early and middle Holocene, thus bridging the date of local introduction of domesticates by at least one millennium; see below). Although this record is more extensive than for many parts of the world, the state of the documentation remains patchy in comparison to most of Europe. The geographic distribution of samples is uneven, with areas with limited or no coverage contrasted by areas with high-density clusters of dates (Figure 1). The differential impact of recent research projects and diverging sampling strategies is particularly noticeable, with some studies focusing on extensive sampling rate of individual sites in order to achieve local high chronological resolution (e.g. Tasić et al. 2015) and others maximising geographical coverage by seeking more restricted numbers of dates across larger number of sites (e.g. Vander Linden et al. 2014).

<insert Figure 1 here>

We will first analyse the spatial structure of this dispersal by performing ordinary kriging of radiocarbon dates. This is a necessary first step in order to understand better the spatial dynamics of the dispersal process which is important to assess any correlations with demography (see Silva and Steele 2017). Selected samples include dates on domesticated archaeobotanical or zooarchaeological remains, and from archaeological cultural contexts directly associated with food production. In order to filter out noise, we superimposed a 50x50km grid on the research area and, for each cell, selected the oldest date. The resulting dataset was then used for the ordinary kriging. This analysis was done using the *gstat* package in the R statistical environment (Gräler et al. 2016, R Core Team 2020). In order to account for uncertainty in sampling, we also performed a kriging analysis on a filtered version of the dataset which only include dates on short-lived material, i.e. a priori assuming as unreliable any dates on charcoal, or any dates for which information on type of sample is not available.

In order to investigate potential fluctuations in population, we aggregated radiocarbon data into an SPD using the *rcarbon* package (Bevan and Crema 2020). Radiocarbon dates belonging to individual sites were binned using 100-year bins and all simulations were run 1000 times. We have constricted our temporal window to between 9500 and 6500 cal BP which bracket the local Neolithic. Within this window, fluctuations in SPDs are largely made sense of via statistical significance tests against theoretical population models using the *modelTest* function (Timpson et al 2014). When doing so, it is worth briefly considering the theoretical demographic implications and assumptions of the models employed (e.g. Begon et al. 1996, Turchin 2003, Rockwood 2006). The exponential model states that a closed population, i.e. one with no emigration or immigration, set in a stationary environment will grow (or decline) following an exponential trajectory (Turchin 2002: 19-22). This model is arguably simple and often unrealistic given its underlying assumptions of closedness and constancy of resources. In this sense, any significant deviation between such a model and empirical SPD indicates that other processes are at play in regulating population fluctuations, which can be due to extraneous factors (such as an epidemic causing a significant population drop) or more simply, when the exponential model's underlying assumptions are not valid. Although the quantification of deviations from the exponential model is of no help to identify these processes as such, it provides robust foundations for further modelling and thus we perform this analysis before proceeding any further.

If the exponential growth model proves to be a bad fit to the empirical data, we formally and independently identify inflections in the mean of the summed density using a change-point analysis, a technique routinely used for time series such as climate variation (e.g. Beaulieu et al. 2012). This is done because, rather than immediately repeat the statistical significance test with more complex models (which, it must be stressed, will always yield a result, regardless of whether or not it makes sense to do so) we want to independently verify whether the long-term trend in the SPD time series can justifiably be described with more complex models as opposed to, for example, when short-time scale wiggles on top of an exponentially increasing background are present. It is also useful to understand how complex a model one should aim for and, therefore, it is a useful tool to avoid model overfitting. Change-point analysis of the mean of the SPD was performed using the *changepoint* package (Killick and Eckley 2014).

As the change-point analysis results justified the use of a logistic growth model (see Results below) we then rerun *modelTest* with a logistic null model. This model adds a maximum threshold for population size, known as the “carrying capacity”, that regulates growth. It is this addition that

makes the rate of growth density-dependent. When starting with a very low initial population, or in the case of invasion into a new habitat, the solution of the logistic equation exhibits a well-known S-shaped curve whereby a small population experiences a rapid phase of growth which, when a certain size threshold is reached, starts to decrease until it plateaus at the carrying capacity level (Turchin 2003: 29). Comparing a logistic model with empirical data thus allows one to assess whether or not such a phase of growth happened and, if so, its temporal brackets and amplitude. Such characterisation is a key information for assessing potential density-dependent dispersal processes, as the population growth term of reaction-diffusion equations is generally modelled as a logistic growth (Steele 2009).

However, in the above we are only looking at the meta-population across the entirety of our domain area. To understand the interrelated dynamics of dispersal and demographic within our domain we need to look at the appropriate scale, as we have argued for previously (Silva and Vander Linden 2017). To do this one must track the dispersing wave-front at a scale that is not small enough that it becomes invisible (due to, for example, low data resolution or poor sampling coverage) and not large enough that one loses the local demographic signal and instead can only observe changes to the meta-population. Here, we will use the spatial structure of the dispersal retrieved from the ordinary kriging to divide our domain into the appropriate regions (see Results below). We will then compare the demographic signals of the different geographical regions between themselves using *permTest* function (Crema et al 2016). Finally, we look at smaller-scales for localised growth rates as obtained using the *sptest* function (Crema et al 2017).

Code and data are available at the following: <https://github.com/mavdlind/density>.

## Results

Figure 2 illustrates the results of spatial interpolation. As made evident by recent studies (e.g. Lespez et al. 2013, Perlès et al. 2013, Krauß et al. 2018), early farming is documented across several river valleys of Greece and southern Bulgaria during the first half of the 9<sup>th</sup> millennium cal BP. After a period of standstill, the diffusion resumes westwards by 8200-8100 cal BP and exhibits a complex spatio-temporal structure, reminiscent of wider patterns observed across the entire European sub-continent (Bocquet-Appel et al. 2009, 2012). Across the Danube basin, the spread is overall spatially extensive and rapid, with early sites observed across the entire area. However, several regions also exhibit a delayed introduction of plant and animal domesticates. In some instances, this apparent delay seems artificial and is probably linked to lack of sampling (e.g. southern Serbia), whilst in others this pattern is backed by extensive data (e.g. lower Vrbas basin in northern Bosnia & Herzegovina: Vander Linden et al. 2014). The spread of early farming across the Adriatic basin is – counter-intuitively given the likely use of boat technology – slower and exhibits a clear SE-NW gradient. Whilst farming practices are documented along the eastern and southern Adriatic coast around 8000-7800 cal BP, it is only practised by 7600-7500 cal BP across the entire area. We can therefore identify three regions with differing dispersal dynamics (Greece, Adriatic and Danube basin) which will be used subsequently.

<insert Figure 2 here>

The results of the kriging analysis done on the high-quality samples only are highly similar, with two exceptions (Figure 1 SI). Firstly, as the distribution of dates is patchier to start with, the

predicted surfaces rely far more heavily on the interpolation process as such. Secondly, the interpolated start date for early farming in Greece appears to be delayed by several centuries, a clear methodological artefact linked to the simple filtering process adopted. Despite older discussions regarding the existence of a Neolithic phase pre-dating 8300 cal BP in continental Greece (e.g. Reingruber & Thyssen 2009), the introduction of farming is indeed now uncontroversially set at c. 8600 calBP for both northern (Dikili Tash eastern Macedonia: Lespez et al. 2013) and southern Greece (Franchthi, Argolid: Perlès et al. 2014). Although somewhat unrealistic, this short example demonstrates the perils of over-demanding data hygiene, which are as potentially damaging as all-encompassing, uncritical data collection.

The empirical SPD presents noticeable fluctuations, especially an apparent rise from 8000 to 7400 cal BP, followed by a 100-years long dip, and a return to high values from about 7200 cal BP onwards (Figure 3). The data exhibits significant deviations from the exponential null model ( $p = 0.0099$ ). In particular, two segments suggesting a lower than expected population up to 8000 cal BP, encompass both the Mesolithic period and the introduction of early farming to Greece and southern Bulgaria. Two other segments suggesting higher populations appear around 7800-7500 cal BP and 7200-7000 cal BP.

<insert Figure 3 here>

The change point analysis identifies three distinct segments in the SPD (Figure 4, top). The first segment, between 9000 and about 8000 cal BP, corresponds to the lowest mean in summed density and, as already mentioned, encompasses the Mesolithic period and the introduction of early farming in Greece and southern Bulgaria, and also matches the marked negative deviation from the exponential model. The second segment, between 8000 and 7200 cal BP, corresponds to the second episode of farming dispersal, with a marked rise until 7700 cal BP, followed by a nearly symmetrical drop until 7200 cal BP. The final segment, between 7200 to 6500 cal BP, represents the highest mean in summed density and includes a marked positive deviation from exponential model. In chrono-cultural terms, it corresponds to the local Late Neolithic, a period that we will only make occasional references to as its chronological span lies outside the remit of the present contribution (e.g. Porčić 2020).

<insert Figure 4 here>

The increasing trend identified by the change-point analysis indicates three phases, which is suggestive of logistic growth since, as discussed above, it posits an initial period of slow population uptake, followed by a period of fast growth, and closed by another period of slow uptake as the population reaches carrying capacity. We then proceeded to run *modelTest* with a logistic growth null model where we obtained a p-value of 0.001 (Figure 4, bottom). The positive deviation at the beginning of the SPD is a mere artefact of method (as the model is fitted to a given later start date). The negative deviation between 8200 and 8000 cal BP indicates that, for that part, the rate of growth of the SPD is slower than the theoretical one. A perfect coincidence between the logistic model and the empirical SPD between c. 8000 for 7500 cal BP roughly matches the second stage identified by the change-point analysis. Finally, there is a deviation from the logistic null model from c. 7400 to 7300 cal BP, as the empirical SPD does not grow continuously until the highest overall density is reached. The last segment derived from the change point analysis corresponds to the highest recorded summed density, with minimal localised positive deviations from the logistic null.

The permutation test comparing the trajectories for Greece, and the Danube and Adriatic basins shows staggered starting points for the uptake of each empirical SPD (Figure 5). For Greece, the main episode of growth occurs 8400 and 8200 cal BP, with corresponding positive deviation from the other two regions lasting until c. 7900 BP. In the Danube basin, the growth in summed density begins shortly before 8000 and reaches its peak around 7600 cal BP. This peak corresponds to the sole – positive in this instance – deviation from the other regional signals, as otherwise the empirical SPD sits within the overall envelope, suggesting it drives the overall signal. A negative deviation occurs between 7500 and 7300 calBP, corresponding to the drop in summed density reported earlier. In the Adriatic basin, the empirical SPD exhibits a rise from c. 8000 cal BP until c. 7450 cal BP although it appears as a negative deviation from the other areas until c.7600 cal BP. A positive deviation is recorded between 7500 cal BP and 7200 cal BP, as the local peak in summed density is reached here at a later stage. As in the Danube basin, this peak is followed by a drop in the empirical SPD, although it appears as a positive deviation from the other two regions, suggesting its more limited amplitude.

<insert Figure 5 here>

Regional variations in growth rates are also observed in point-based comparisons. Figure 6 shows, on the left panel, statistically significant demographic growth expressed as positive and negative local deviations from the regional norm, and on the right panel, actual values expressed in average yearly growth rate. For the period between 9000-8500 cal BP and 8500-8000 cal BP (figure 6, top), sites across Greece, the Danube basin, Southern and Eastern Adriatic all present positive growth rates, although positive deviations are only observed for southernmost Adriatic and Greece. By contrast, the Northern Adriatic is characterised by negative growth rate values and negative deviations. Between 8500-8000 and 8000-7500 cal BP (figure 6, middle), all sites exhibit a positive growth, with positive deviations distributed in south-central Adriatic, and, inland across the entire Pannonian basin and adjacent areas. Negative growth, and associated negative deviation, occurs in eastern Serbia, especially in the area of the Danube Gorges. From 8000-7500 cal BP to 7000 cal BP (figure 6, bottom), positive growth rates and deviations are confined to the western part of Danube basin and the north-western half of the Adriatic basin. Other areas exhibit a wide range of values, with negative growth and deviations present in areas located well behind the expanding front of farming, such as eastern Serbia and Greece.

<insert Figure 6 here>

## **Discussion**

The analysis of radiocarbon dates for the Mesolithic-Neolithic transition in the Balkans confirms the existence of a human dispersal process contemporary with the spread of plant and animal domesticates. The spatial interpolation of the radiocarbon record demonstrates the complex spatial and temporal structure of this spread, marked by an earlier episode in Greece, followed after a standstill by an expansion phase across both the Danube and Adriatic basins. The change point analysis indicates three distinct segments in the empirical SPDs for the entire research area, the first change point chronologically coinciding with the second phase of farming dispersal. The positive deviation of the empirical SPDs from the exponential model demonstrates that this regime shift is characterised by faster than predicted growth, suggesting that the expected trajectory of the local Mesolithic population cannot account for the observed signal as already observed by Silva and

Vander Linden (2017). The comparison of the empirical SPD with the fitted logistic model reinforces this view. The lack of deviation between c. 8000 and 7500 cal BP confirms this to be when the highest phase of growth occurs. Following readings of similar signals in other European regions (e.g. Shennan et al. 2013), we interpret this “boom” in the empirical SPD as the expression of a new demographic regime enabled by the new farming economy.

The permutation test contrasting the signals for Greece, the Adriatic and Danube basins demonstrates that the spatial structure of the spread as identified by kriging of radiocarbon dates translates into changes in population size at the regional level. There is a spatio-temporal lag between the regional “boom” events, confirming previous work identifying a travelling wave-like behaviour associated with the dispersal of farming across Europe (Silva and Vander Linden 2017). Likewise, regional and temporal variation in the growth rates show that these are systematically and statistically higher at the wave-front rather than in areas behind it. Notably, our analysis highlights a correlation between wavefront (as observed in the kriging) and population density (using the SPDs as proxy) wherein, for the Danube basin both rate-of-spread and density are high, whereas in the Adriatic both are low. This observed co-variation of wave-front speed and regional population growth rates, as remarked upon above, indicates a density-dependent dispersal process rather than, for instance, spatial patterns linked to density-free processes (e.g. Jeltsch et al. 1997).

The identification of a density-dependent dispersal reinforces existing aDNA data on the presence of a new population. More fundamentally, it also provides a platform for further elucidation of the processes shaping this dispersal and the period immediately following it. It is essential to realise that the original formulation of both exponential and logistic models only relies upon endogenous factors, i.e. related to the population itself. Even under such limited conditions and without further exogenous or density-independent (e.g. environmental) factors, both models can exhibit a range of different behaviours (Rockwood 2006: 79-89). Likewise, it is known since Skellam’s seminal article (1951) that a key variable in density-dependent dispersal is the growth rate at the front. Under the reaction-diffusion model, the growth rate remains constant, leading to a constant progression of the wave-front. Discrepancies between this theoretical prediction and empirical observations for Europe have been highlighted on multiple occasions, and many scholars have sought to identify and model exogenous factors responsible for the slowing down and/or acceleration of the wave (e.g. river and sea travel: Davison et al. 2005, Silva and Steele 2014; climate: Krauß et al. 2018; see also Bocquet-Appel et al. 2012). Although there have been attempts at considering space competition and the density of foraging populations (e.g. Isern et al. 2012), to our knowledge, there have been minimal, if any, attempts at considering changes in the population density of the incoming Neolithic communities. Sullivan and colleagues’ simulations have however demonstrated that Allee effects and spatio-temporal variability of the population density behind the front can generate fluctuations in the rate of spread (Sullivan et al. 2017). From this perspective, it is worth asking whether or not SPDs can help to test this hypothesis for past density-dependent human dispersals. In turn, a more accurate understanding of the potential effects of local population density is necessary to re-assess the role of exogenous factors, such as habitat fragmentation and carrying capacity (e.g. Van Dyken & Zhang 2019), on the speed of dispersals.

Drops in the empirical SPDs after the “boom” have been observed for several European regions, although their precise start relative to the “boom” and duration vary enormously (e.g. Shennan et al. 2013: fig. 3 and table 1). A similar, very short, “bust” is recorded in the empirical SPD for the Balkans but only proves statistically significant against the logistic null model – unsurprising,



considering this model expects population to stay at carrying capacity once it reaches it. Such events have sometimes been interpreted as a sign of Neolithic farming not being successful in the long run, an argument convincingly made for Britain where the “bust” lasts for several centuries parallel to profound transformations of farming practices, settlement patterns and social practices (Colledge et al. 2019). In our study area, however, neither zooarchaeological nor archaeobotanical data show profound changes for the period under consideration (e.g. Gaastra et al. 2019). An alternative hypothesis is that this “bust” is the artefact of a travelling wave type of dispersal, as part of the local population emigrates away from this region as the dispersing travelling wave resumes its course (Silva and Vander Linden 2017). An argument towards this thesis is the contemporaneity of this drop in the SPD with the date recently suggested for the earliest dispersal of the LBK (see Jakucs et al. 2016). This being said, it is noteworthy that such oscillations in population size, ranging from dampening to chaotic, can also occur because of endogenous factors such as time-lags between population size and resource availability (i.e. amount of resources available being related to the pressure on these resources immediately before; May 1975, Begon 1996: 60-2).

## Conclusion

Thanks to numerous methodological developments inside and outside the discipline, we are experiencing exciting times where an increasing number of archaeologists address topics such as dispersal and population history in general. This methodological focus should however not be made at the expense of more general theoretical considerations: there is a fundamental difference between the identification and the characterisation – yet alone understanding – of a dispersal process. Here for instance, using a combination of spatial interpolation, SPDs and explicit evaluation of theoretical demographic growth models rooted in population ecology, we conclude that the spread of early farming in the Balkans was a density-dependent dispersal. This conclusion is in many respects expected given the technological nature of this transition and implies further specific hypotheses to be tested regarding the impact of changing population size and density on the travelling wave. Furthermore, it is also worth asking if the same properties are met by later dispersals documented by ancient DNA for Europe.

Whilst SPDs offer a unique, if blurry, window into the former, the latter remains more elusive. Yet, the joint assessment of both topics is a preliminary, necessary step to assess the interplay between human populations and exogenous factors, such as habitat fragmentation or climate change. Although the temptation to focus on such rewarding “low hanging fruits” in light of modern debates is high and understandable, this should not be made at the expense of methodological and theoretical precaution.

## Figures

Figure 1: distribution map of radiocarbon dataset

Figure 2: ordinary kriging of  $^{14}\text{C}$  dates associated to the spread of farming

Figure 3: SPD and exponential null model

Figure 4: change-point analysis (top) and logistic null model (bottom)

Figure 5: regional spatial permutations

Figure 6: average yearly growth rate for different time intervals. Left: positive and negative local deviations of from the regional norm. Right: actual growth rate values.

## Acknowledgements

This paper is part of the Past Global Changes (PAGES) Paleoclimate and the Peopling of the Earth (PEOPLE3K) network. We would like to thank all members of the PEOPLE3K network for comments, and especially Jacob Freeman for the initial idea of using a change-point analysis to study SPDs. Many thanks as well to the two anonymous reviewers, and to Dr Javier Fernández-Lopez for their useful recommendations.

## References

- Ammerman AJ, Cavalli-Sforza LL. 1984 The Neolithic Transition and the Genetics of Populations in Europe. Princeton: Princeton University Press.
- Balsera V, Díaz-del-Río P, Gilman A, Uriarte A, Vicent JM. 2015 Approaching the demography of late prehistoric Iberia through summed calibrated date probability distributions (7000–2000 cal BC). *Quat. Int.* **386**, 208–211. (doi:10.1016/j.quaint.2015.06.022)
- Beaulieu C, Chen J, Sarmiento JL. 2012 Change-point analysis as a tool to detect abrupt climate variations. *Philos. Trans. A Math. Phys. Eng. Sci.* **370**, 1228–1249. (doi:10.1098/rsta.2011.0383)
- Begon M, Mortimer M, Thompson DJ. 1996. Population ecology. A unified study of animals and plants. Oxford: Blackwell.
- Bevan A, Colledge S, Fuller D, Fyfe R, Shennan S, Stevens C. 2017 Holocene fluctuations in population demonstrate repeated links to food production and climate. *Proc. Natl. Acad. Sci. U. S. A.* **114**, E10524–E10531. (doi:10.1073/pnas.1709190114)
- Bevan A, Crema ER, 2020 rcarbon v1.3.1: Methods for calibrating and analysing radiocarbon dates [URL:https://CRAN.R-project.org/package=rcarbon](https://CRAN.R-project.org/package=rcarbon)
- Binder D, Lanos P, Angeli L et al. 2017. Modelling the earliest northwestern dispersal of the Mediterranean Impressed Wares: new data and Bayesian chronicles. *Documenta Praehistorica* **44**, 54-77. (doi:10.4312/dp.44.4)
- Blagojević T, Porčić M, Penezić K, Stefanović S. 2017. Early Neolithic population dynamics in the Eastern Balkans and the Great Hungarian Plain. *Documenta Praehistorica* **44**, 18-33. (doi: 10.4312/dp.442)
- Bocquet-Appel J-P, Naji S, Vander Linden M, Kozłowski JK. 2009 Detection of diffusion and contact zones of early farming in Europe from the space-time distribution of 14C dates. *J. Archaeol. Sci.* **36**, 807–820. (doi:10.1016/j.jas.2008.11.004)
- Bocquet-Appel J-P, Naji S, Vander Linden M, Kozłowski J. 2012 Understanding the rates of expansion of the farming system in Europe. *J. Archaeol. Sci.* **39**, 531–546. (doi:10.1016/j.jas.2011.10.010)
- Brami MN. 2015. A graphical simulation of the 2,000-year lag in Neolithic occupation between Central Anatolia and the Aegean basin. *Archaeological and Anthropological Sciences* **7**, 319-327. (doi:10.1007/s12520-014-0193-4)
- Collard M, Edinborough K, Shennan S, Thomas MG. 2010 Radiocarbon evidence indicates that migrants introduced farming to Britain. *J. Archaeol. Sci.* **37**, 866–870. (doi:10.1016/j.jas.2009.11.016)

- Colledge S, Conolly J, Crema E, Shennan S. 2019 Neolithic population crash in northwest Europe associated with agricultural crisis. *Quat. Res.* **92**, 686–707. (doi:10.1017/qua.2019.42)
- Crema ER, Habu J, Kobayashi K, Madella M. 2016. Summed Probability Distribution of 14 C Dates Suggests Regional Divergences in the Population Dynamics of the Jomon Period in Eastern Japan. *PLOS ONE* **11**, e0154809. (doi:10.1371/journal.pone.0154809)
- Crema ER, Bevan A, Shennan S. 2017. Spatio-temporal approaches to archaeological radiocarbon dates. *Journal of Archaeological Science* **87**, 1-9. (doi:10.1016/j.jas.2017.09.007)
- Davison K, Dolukhanov P, Sarson GR, Shukurov A. 2006 The role of waterways in the spread of the Neolithic. *J. Archaeol. Sci.* **33**, 641–652. (doi:10.1016/j.jas.2005.09.017)
- Fort J. 2012 Synthesis between demic and cultural diffusion in the Neolithic transition in Europe. *PNAS* **109**, 18669-18673. (doi:10.1073/pnas.1200662109)
- Fort J, Méndez, V. 1999 Time-delayed theory of the Neolithic transition in Europe. *Phys. Rev. Lett.* **82**, 867–870.
- Fort J, Pujol T, Vander Linden M. 2012 Modelling the Neolithic transition in the Near East and Europe. *American Antiquity* **77**, 203-219. (doi:10.7183/0002-7316.77.2.203)
- Gaastra JS, de Vareilles A, Vander Linden M. 2019 Bones and Seeds: An Integrated Approach to Understanding the Spread of Farming across the Western Balkans. *Environ. Archaeol.* (doi:10.1080/14614103.2019.1578016)
- Gräler B, Pebesma E, Heuvelink G. 2016. Spatio-Temporal Interpolation using gstat. *The R Journal* **8**, 204-218.
- Jakucs J *et al.* 2016 Between the Vinča and Linearbandkeramik Worlds: The Diversity of Practices and Identities in the 54th-53rd Centuries cal BC in Southwest Hungary and Beyond. *J World Prehist* **29**, 267–336. (doi:10.1007/s10963-016-9096-x)
- Isern N, Fort J, Vander Linden M. 2012 Space competition and time delays in human range expansions. Application to the neolithic transition. *PLoS One* **7**, e51106. (doi:10.1371/journal.pone.0051106)
- Jeltsch F, Müller MS, Grimm V, Wissel C, Brandl R. 1997 Pattern formation triggered by rare events: lessons from the spread of rabies. *Proc. Biol. Sci.* **264**, 495–503. (doi:10.1098/rspb.1997.0071)
- Killick R, Eckley IA. 2014 changepoint: An R Package for Changepoint Analysis. *Journal of Statistical Software* **58**, 1-19. (doi:10.18637/jss.v058.i03)
- Krauß R, Marinova E, De Brue H, Weninger B. 2018 The rapid spread of early farming from the Aegean into the Balkans via the Sub-Mediterranean-Aegean Vegetation Zone. *Quat. Int.* **496**, 24–41. (doi:10.1016/j.quaint.2017.01.019)
- Lazaridis I *et al.* 2016 Genomic insights into the origin of farming in the ancient Near East. *Nature* **536**, 419–424. (doi:10.1038/nature19310)
- Lespez L, Tsirtsoni Z, Darcque P, Koukouli-Chryssanthaki H, Malamidou D, Treuil R, Davidson R, Kourtessi-Philippakis G, Oberlin C. 2013 The lowest levels at Dikili Tash, northern Greece: a missing link in the Early Neolithic of Europe. *Antiquity.* **87**, 30–45. (doi:10.1017/s0003598x00048602)
- Krauß R, Marinova E, De Brue H, Weninger B. 2018 The rapid spread of early farming from the Aegean into the Balkans via the Sub-Mediterranean-Aegean Vegetation Zone. *Quat. Int.* **496**, 24–41. (doi:10.1016/j.quaint.2017.01.019)
- Levins R. 1966 The strategy of model building in population biology. *Am. Sci.* **54**, 421–431.

- Manen C, Perrin T, Guilaine J, et al. 2019 The Neolithic Transition in the Western Mediterranean: a Complex and Non-Linear Diffusion Process - The Radiocarbon Record Revisited. *Radiocarbon* **61**, 531-571. (doi:10.1017/RDC.2018.98)
- May RM. 1975 Biological populations obeying difference equations: stable points, stable cycles, and chaos. *J. Theor. Biol.* **51**, 511–524. (doi:10.1016/0022-5193(75)90078-8)
- McClure SB, Podrug E, Moore AMT, Culleton BJ, Kennett DJ. 2014. AMS 14C chronology and ceramic sequences of early farmers in the Eastern Adriatic. *Radiocarbon* **56**, 1019-1038. (doi:10.2458/56.17918)
- McLaughlin TR, Whitehouse NJ, Schulting RJ, McClatchie M, Barratt P, Bogaard A. 2016 The Changing Face of Neolithic and Bronze Age Ireland: A Big Data Approach to the Settlement and Burial Records. *Journal of World Prehistory* **29**, 117–153. (doi:10.1007/s10963-016-9093-0)
- McLaughlin TR. 2019 On Applications of Space–Time Modelling with Open-Source 14C Age Calibration. *Journal of Archaeological Method and Theory* **26**, 479–501. (doi:10.1007/s10816-018-9381-3)
- Mathieson I *et al.* 2018 The genomic history of southeastern Europe. *Nature* **555**, 197–203. (doi:10.1038/nature25778)
- Matthysen E. 2005 Density-dependent dispersal in birds and mammals. *Ecography* **28**, 403–416. (doi:10.1111/j.0906-7590.2005.04073.x)
- Matthysen E. 2012 Multicausality of dispersal: a review. In: Clobert J, Baguette M, Benton TG, Bullock JM (eds). *Dispersal ecology and evolution*. Oxford: Oxford University Press: 3–18.
- Newman, W. I. 1980. Some exact solutions to a nonlinear diffusion problem in population genetics and combustion. *J. Theor. Biol.* **85**, 325–334. (doi:10.1016/0022-5193(80)90024-7)
- Pinhasi R, Fort J, Ammerman, AJ. 2005 Tracing the Origin and Spread of Agriculture in Europe. *PLoS Biology* **3**, 2220-2228. (doi: 10.1371/journal.pbio.0030410)
- Perlès C, Quiles A, Valladas H. 2013 Early seventh-millennium AMS dates from domestic seeds in the Initial Neolithic at Franchthi Cave (Argolid, Greece). *Antiquity* **87**, 1001–1015. (doi:10.1017/s0003598x00049826)
- Porčić M. 2020 Observations on the origin and demography of the Vinča culture. *Quat. Int.* (doi:10.1016/j.quaint.2020.04.012)
- R Core Team 2020 *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>
- Reingruber A, Thissen L. 2009 Depending on 14C Data: Chronological Frameworks in the Neolithic and Chalcolithic of Southeastern Europe. *Radiocarbon*. **51**, 751–770. (doi:10.1017/s0033822200056071)
- Robb J, Miracle P. 2007 Beyond ‘migration’ versus ‘acculturation’: new models for the spread of agriculture. *Proceedings of the British Academy* **144**, 99-115.
- Rockwood LL. 2006. *Introduction to population ecology*. Oxford: Blackwell.
- Shennan S, Downey SS, Timpson A, Edinborough K, Colledge S, Kerig T, Manning K, Thomas MG. 2013 Regional population collapse followed initial agriculture booms in mid-Holocene Europe. *Nat. Commun.* **4**, 2486. (doi:10.1038/ncomms3486)
- Silva F, Steele J. 2014 New methods for reconstructing geographical effects on dispersal rates and routes from large-scale radiocarbon databases. *Journal of Archaeological Science* **52**, 609-620. (doi:10.1016/j.jas.2014.04.021)

- Silva F, Vander Linden M. 2017 Amplitude of travelling front as inferred from 14C predicts levels of genetic admixture among European early farmers. *Sci. Rep.* **7**, 11985. (doi:10.1038/s41598-017-12318-2)
- Skellam JG. 1951 Random dispersal in theoretical populations. *Biometrika* **38**, 196-218.
- Steele J. 2009 Human Dispersals: Mathematical Models and the Archaeological Record. *Human Biology* **81**, 121-140. (doi:10.3378/027.081.0302)
- Steele J, Adams, J, Sluckin, T. 1998 Modeling Paleo-Indian dispersals. *World Archaeology* **30**, 286–305. (doi:10.3378/027.081.0302)
- Sullivan LL, Li B, Miller TEX, Neubert, MG, Shaw AK. 2017 Density dependence in demography and dispersal generates fluctuating invasion speeds. *Proc. Nat. Acad. Of Sci.* **114**, 5053-5058. (doi:10.1073/pnas.1618744114)
- Tasić N *et al.* 2015 The end of the affair: formal chronological modelling for the top of the Neolithic tell of Vinča-Belo Brdo. *Antiquity* **89**, 1064–1082. (doi:10.15184/aqy.2015.101)
- Timpson A, Colledge S, Crema E, Edinborough K, Kerig T, Manning K, Thomas MG, Shennan S. 2014 Reconstructing regional population fluctuations in the European Neolithic using radiocarbon dates: a new case-study using an improved method. *Journal of Archaeological Science* **52**, 549-557. (doi:10.1016/j.jas.2014.08.011)
- Turchin P. 1998. Quantitative analysis of movement. Measuring and modeling population redistribution in animals and plants. Sunderland: Sinauer Associates.
- Turchin P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton: Princeton University Press.
- Vander Linden M, Pandžić I, Orton D. 2014 New radiocarbon dates for the Neolithic period in Bosnia & Herzegovina. *Godišnjak Centar za Balkanološka ispitivanja. Jahrbuch. Zentrum für Balkanforschungen* **43**, 7-34.
- Van Dyken JD, Zhang B. 2019 Carrying capacity of a spatially-structured population: Disentangling the effects of dispersal, growth parameters, habitat heterogeneity and habitat clustering. *J. Theor. Biol.* **460**, 115–124. (doi:10.1016/j.jtbi.2018.09.015)
- Whittle, A. 2007. Going over: people and their times. In: Whittle A, Cummings V (eds). *Going over: the Mesolithic-Neolithic transition in north-western Europe*. London: British Academy: 617–628.