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Socioecological Dynamics Structuring the Spread of Farming in the North American Basin-Plateau Region

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ABSTRACT

The spread of agriculture is a major driver of social and environmental change throughout the Holocene, yet experimental and ethnographic data indicate that farming is less profitable than foraging, so why would individuals choose to adopt agriculture leading to its expansion? Ideal distribution models offer one framework to answer this question: Individuals should adopt less profitable subsistence strategies and occupy more marginal environments when local population density increases competition to the point where the suitability of the best strategies and habitats becomes equal to what can be gained in poorer strategies and habitats. Coupling radiocarbon-dated archaeological sites with a validated measure of agricultural suitability, we evaluate the emergence of farming in the Basin-Plateau region of North America. Our results show that farming first occurs in the more suitable Colorado Plateau physiographic region, and only spreads into the less suitable Great Basin after population density on the Plateau increases. This produces an approximate 300- to 400-year lag between the onset of farming on the Plateau and in the Basin. These findings support the ideal distribution hypothesis for the spread of farming, and suggest a general socioecological process that may help explain global patterns in the timing and tempo of agricultural expansions.

ARTICLE HISTORY

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KEYWORDS

Ideal free distribution model; population ecology; behavioural ecology; maize agriculture; Ancestral Puebloan; Fremont Complex

Introduction

The spread of farming represents a major driver of social and ecological changes in human history (Bellwood et al., 2005; Diamond and Bellwood, 2003). Yet despite a clear global trend where farming replaces foraging, broad comparisons indicate that domesticated plants and animals are less profitable (energetic gains per unit time) than wild resources (Bowles, 2011). This raises the question: Why would anyone choose to adopt agriculture if it provides worse economic outcomes than available alternatives?

Ideal distribution models from population ecology provide a framework to answer this question (Kennett et al., 2006). Pioneered by Fretwell and Lucas (1969), ideal distribution models are now broadly applied to archaeological problems (Codding and Bird, 2015; Weitzel and Codding, this issue). The basic ideal free distribution (IFD) model assumes that individuals seek to maximise habitat suitability, have perfect knowledge of the environment, are free to settle wherever they like, and that the suitability of a habitat declines with each additional occupant. As illustrated

in Figure 1, these conditions produce a pattern where individuals should occupy the most suitable habitat until increasing population density in that habitat reduce its suitability to the point where it becomes equally profitable to occupy the next best habitat. This logic applies to subsistence strategies as well: Individuals in one location should select the most profitable strategy, until increasing competition drives down its profitability to levels near equal of the next most profitable subsistence strategy.

Applied to the emergence (i.e. domestication) and spread (i.e. migration or diffusion) of agriculture (i.e. food production with domesticates, see Smith, 2001), the ideal distribution model suggests that individuals should only switch from more profitable foraging strategies to less profitable farming strategies once local population pressure makes their expected returns near equal.

Considering domestication, individuals should only intensify (*sensu stricto*; Boserup, 1965; Morgan, 2015) their subsistence toward food-producing strategies that initiate domestication (Fuller, 2007; Smith,

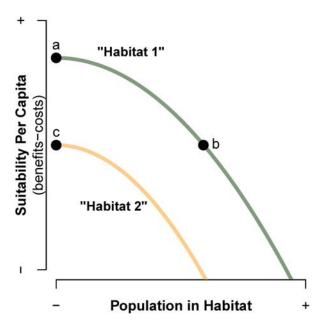


Figure 1. Graphical representation of the ideal distribution model following Greene and Stamps (2001) for a simplified two-habitat environment. Incoming agricultural populations should settle in the more suitable habitat ('Habitat 1'), only moving to the less suitable habitat ('Habitat 2') once population density reduces suitability (point a to b) to the maximum level of second habitat (point c).

2001) once local population pressure diminishes per capita suitability so much as to make the added effort worthwhile. This logic is in line with longstanding (e.g. Cohen, 1977; Flannery, 1969) and recent (Kavanagh et al., 2018; Weitzel and Codding, 2016) explanations for domestication, which suggests that initial domestication should occur first where the ratio of habitat suitability to population density is lowest. This could occur in high or low suitability habitats depending on the relationship between habitat suitability and population density.

Considering the spread of farming, agriculture should only emerge as a viable strategy when population density drives down more profitable subsistence strategies (Kennett et al. 2009; Shennan 2018). Once this occurs, individual farmers should seek to maximise their returns by occupying the most suitable habitats, only moving into adjacent less suitable habitats when the expected utility of doing so is equal to those gained by remaining in increasingly competitive habitats that are more suitable. From this perspective, it does not matter whether the spread of farming in a given region is driven by diffusion (individuals adopting neighbouring strategies and domesticates) or migration (the colonisation of a region by neighbouring agriculturalists), as either process should only occur when population densities drive down per capita suitability to a threshold where farming becomes viable in less suitable habitats.

To evaluate this ideal distribution hypothesis for the spread of agriculture, we examine the onset of

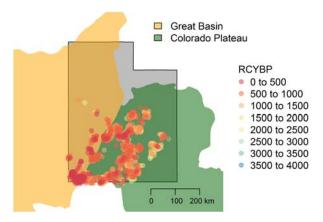


Figure 2. Map of the study area showing the distribution of Late Holocene radiocarbon dated archaeological sites relative to the Great Basin and Colorado Plateau physiographic regions across the modern state of Utah. Site coordinates are randomly shuffled by one decimal degree and colour coded by radiocarbon years before present in 500-year intervals. Sites in this sample are northwest of the Colorado River and south of 40° north.

farming in the Basin-Plateau region of western North America, specifically within the modern state of Utah (Figure 2). Here, foraging is estimated to be two to four times as profitable as farming (Simms, 1984; Barlow, 2002), suggesting that individuals should only adopt farming strategies if there were no locally unexploited wild resource patches available within their foraging radius (Mohlenhoff and Codding, 2017). Yet despite these costs, populations associated with numerous archaeological cultures, including Basketmaker (Matson, 2006), Puebloan (Kohler and Varien, 2012), and Fremont (Morss, 2009 [1931]; Madsen and Simms, 1998; Simms, 2008) all subsisted on maize for the majority of their diet (Coltrain, 1993; Coltrain and Leavitt, 2002; Coltrain et al., 2007; Coltrain and Janetski, 2013). If the ideal distribution hypothesis for the spread of agriculture is correct, then the onset of farming in the Basin-Plateau region should follow some simple predictions:

- 1) farmers should colonise more suitable habitats first
- 2) farmer population density should be higher in more suitable habitats
- 3) farmers should only settle in poorer habitats when population density increases in the better habitats, presumably to the point where the two habitats have equal suitability.

Here we test these predictions by comparing the distribution of farming adaptations across the Great Basin and Colorado Plateau physiographic provinces using the summed calibrated probability distribution of ¹⁴C dated sites as a proxy for population density and a validated moisture index (Ramankutty et al., 2002; Yaworsky and Codding, 2018) as a proxy for habitat suitability.

Materials and Methods

Study Area

The study area encompasses approximately the southern two-thirds of the modern state of Utah northwest of the Colorado River and south of 40° north latitude (Figure 2). Recent systematic reviews by Spangler et al. (2019) and McFadden (2016) offer a detailed summary of the archaeological record in the southern portion of the study area, including occupations marked by Basketmaker II-III (ca. 2200-1300 cal BP), Pueblo I-III (ca. 1300-700 cal BP), and Fremont (ca. 1800-700 cal BP) archaeological cultures. While sometimes referred to collectively as the 'Formative Period', here we simply refer to this time as the farming period. This also serves to focus this research on the continuous record of radiocarbondated sites associated with farming adaptations, rather than on discrete archaeological cultures.

Data

Environmental Data

We divide the study area into two sub-regions following the USGS physiographic province designations (USGS, 2019): Colorado Plateaus province and the Great Basin section of the Basin and Range Province (see Figure 2). As a proxy for agricultural suitability, we rely on the moisture index (MI; see Supplementary Materials), which has been validated as a global predictor of agricultural suitability by Ramankutty et al. (2002), and by Yaworsky and Codding (2018) who show that MI predicts settlement decisions among historical agricultural populations in the study area. A raster of MI values is available from Yaworsky (2016). We select this as a suitability proxy as farming production in this arid region should be moisture limited. The moisture index provides a relative estimate of available soil moisture, measured as the ratio of actual evapotranspiration to potential evapotranspiration (Ramankutty et al. 2002; Yaworsky 2016). Other factors such as growing degree-days also limit farming in the region (Yaworsky 2021), though we do not include them here. While MI surely fluctuated through time, we make the simplifying assumption that climate-driven changes in past moisture index values were spatially homogeneous so that wetter places on the landscape always had higher MI values relative to drier places.

Archaeological Data

The complete data set of archaeologically-derived radiocarbon dates was compiled by JDS from the published literature (e.g. Louderback et al., 2011, Massimino and Metcalfe 1999), gray literature, and personal communications. All dates will be available

on the Canadian Archaeological Radiocarbon Database (Martindale et al. 2016; Gajewski et al. 2011). We subset this database in time to the Late Holocene (those with a calibrated upper two sigma range younger than 4000 years old) and in space to sites located south of 40 degrees latitude and north and west of the Colorado River in the modern state of Utah. Lab numbers for all dates selected through this procedure are available in the supplemental material. Dates associated with farming are identified by direct dates on cultivars (e.g. Zea mays), or feature associations with farming period architecture (e.g. pithouses), ceramics (e.g. Sevier Grey) or clay figurines (e.g. Fremont figurines). While all dates during the farming period are likely associated with populations more or less reliant on agricultural, we distinguish between all dates and farming dates in order to explore the onset of farming adaptations in each sub-region.

Analysis

We run all analyses in the R environment (R Core Team, 2019). The first step couples the environmental and archaeological data: Each site is assigned to a physiographic province using the overlay function in the sp package (Bivand et al., 2013), and MI values are extracted for each site using the raster library (Hijmans, 2018).

Suitability

We refer to the MI values for each site as 'occupied MI', representing the relative suitability occupied by past populations at any one time and place indicated by a radiocarbon-dated archaeological site. The distribution of occupied MI values across each of the two sub-regions provides an empirical measure of occupied suitability to determine which sub-region is more suitable for agriculture, assuming that moisture is the greatest limiting factor. These distributions are compared graphically using box-and-whisker plots with notches that are analogous to approximate 95% confidence intervals around the sample medians, and compared statistically using a Wilcoxon rank sum test.

Population (SPD) Time Series

We evaluate predictions by generating a summed probability distribution (SPD) of calibrated radiocarbon dates from archaeological sites (e.g. Crema et al., 2016; Kelly et al., 2013; Robinson et al., 2019; Shennan et al., 2013; Timpson et al., 2014). We generate two SPDs for each sub- region: First on all dates, second only on dates associated with farming (see above). We calibrate and sum all radiocarbon dates using the rcarbon package from Bevan and Crema (2018). For all SPDs, we use a 100-year moving average to smooth over stochastic variation introduced by calibration and sampling, and a conservative bin term (h=1000) to avoid bias introduced by multiple overlapping dates from the same site (see Bevan and Crema, 2018). We select this bin term using the 'binsense' function to identify a threshold of h between 0 and 2000 where changes in the SPD level off. As shown in Section 2.4 of the supplemental material, this reduces some peaks and troughs in the SPD, though the overall shape does not change for either region. Given that both regions have similar research histories in the State of Utah, we expect the relative density of dates in each region to be similar across space, but to vary through time. We evaluate this by calculating the spatial and temporal date density for each region. We treat SPD values as a proxy for population density, but we do acknowledge that this is an imperfect measure that omits other important measures of population, such as site size. The final SPDs are nonnormalized and standardised by the size of the bounding box of each sub-region to facilitate comparison between regions (see supplemental material).

We identify the onset of continuous farming activity using non-parametric phase modelling available in the bchron package (Parnell et al. 2008; Parnell 2019). Specifically, we use the 'BchronDensity' function on all radiocarbon dates associated with farming. This approach applies a Gaussian mixture to the calibrated ages in order to estimate the overall density of radiocarbon ages (Parnell 2019). This allows us to evaluate occupation phases (e.g. d'Alpoim et al. 2016), from which we may identify discrete start and end dates at specific credible intervals. We calculate the 99% credible interval of the occupation phase associated with farming sites. By rounding each start and end date to the nearest century, we select the longest continuous phase of farming for each sub-region.

To determine if population densities are higher in the more suitable region, we randomly resample dates for each region with replacement (i.e. bootstrap) and recalculate the SPD as described above 100 times. We then calculate the 1% and 99% confidence envelope for each year in each sub-region. Non-overlapping envelopes rounded to the nearest century identify periods when farming population densities in each region meaningfully differ from one another (see supplemental material).

Results

The sample includes 505 radiocarbon dates from 125 sites in the Great Basin, and 1002 dates from 350 sites on the Colorado Plateau dating to the last 4000 years (Table 1). The area of the bounding box (see supplementary information) encompassing dated sites in the Great Basin is 39,382 square kilometres, and in the Colorado Plateau is 79,669 square kilometres (see Table 1), making the Colorado Plateau sub-region area 2.02 times larger than that of the Great Basin sub-

Table 1. Data summary for each sub-region reporting the number of sites and dates, the area and area ratio relative to one another, the moisture index (MI) mean, standard deviation (SD), median, and interguartile range (upper and lower box values; see Figure 3), and the earliest direct date on maize (median cal. BP) plus the date of the onset of persistent farming adaptations measured as the first century included in the longest continuous 99% credible interval of the summed probability distribution of calibrated radiocarbon dated archaeological sites associated with farming.

	Great Basin	Colorado Plateau
Sites (n)	125	350
Dates (n)	505	1002
Area (km²)	39,382	79,669
Area Ratio	0.49	2.02
MI Mean	0.073	0.105
MI SD	0.023	0.035
MI 75% Quartile	0.089	0.125
MI Median	0.062	0.097
MI 25% Quartile	0.057	0.076
Earliest Maize Date (med. cal. BP)	1809	3153
Onset of Farming Period (cal. BP)	2000	2300

region. Each sub-region has as a spatial date density of 0.13 dates per square kilometre, indicating equitable coverage per region across space. Overall, the sample has a temporal date density of 0.38 dates per year. The Great Basin has a lower temporal date density at 0.13 dates per year compared to 0.25 for the Colorado Plateau.

Which Habitat is More Suitable for Agriculture?

Comparing the distribution of occupied MI values between the Great Basin and Colorado Plateau shows that the Plateau is significantly more suitable for agriculture (W = 103368, p < 0.0001; Figure 3).

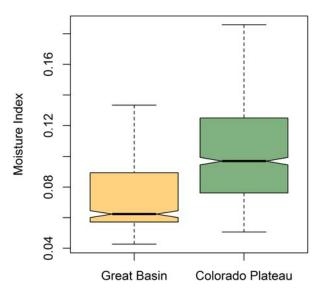


Figure 3. Variation in occupied habitat suitability (Moisture Index) sampled at radiocarbon-dated archaeological site locations in the two sub-regions. The boxes show the interquartile range (25% to 75% quartile), thick black lines show the sample medians, and notches indicate the approximate 95% confidence intervals of the median.

As summarised in Table 1, sites in the Great Basin occupy a mean MI of 0.07 (±0.023) while those on the Colorado Plateau occupy a mean MI of 0.11 (±0.035). Median MI values also differ significantly from one another, with Great Basin sites occupying a significantly lower values than the Colorado Plateau, as indicated by the non-overlapping notches (approximate 95% confidence intervals) shown in Figure 3. This suggests that the Plateau is a more suitable habitat in terms of moisture availability, and should be occupied by farmers earlier and have more numerous dates during the farming period.

Prediction 1: Farmers Should Colonize More Suitable Habitats First

The earliest direct date on maize in the study area appears on the Colorado Plateau around 3150 median cal. BP (Roberts 2018), though evidence of widespread persistent farming does not emerge until about 850 years later (Figure 4). An evaluation of the 99% credible interval for the SPD generated from farmingassociated radiocarbon dates indicates that persistent agricultural adaptations emerge first on the Colorado Plateau beginning about 2300 cal. BP, and only spread into the Great Basin after a 300-year lag by about 2000 cal. BP (Figure 4). The earliest direct date on maize in the Great Basin dates only to ca. 1800-1900 cal. BP (Landon and Roberts 2018:231). This supports the first prediction that farmers colonise the more suitable habitat first.

Prediction 2: Farmer Density Should be Higher in More Suitable Habitats

As shown in Figure 5, there are three periods where populations on the more suitable Colorado Plateau are significantly denser than in the less suitable Great Basin. These include a brief 100-year period at 3800 cal. BP, followed by two increasingly longer periods from 2300 to 2000 cal. BP - immediately following the onset of sustained farming adaptations on the Plateau - and 1700-800 cal. BP - during the peak of farming across the study area. This supports the expectation that population density is higher in the more suitable habitat, though this is not the case for every moment in time.

Prediction 3: Farmers Should Only Settle in Poorer Habitats When Population Density Increases in Better Habitats

A significant increase in population density on the Colorado Plateau follows the emergence of farming economies 2300 years ago. This precedes the onset of farming activity in the Great Basin at 2000 cal. BP, suggesting that it is only worthwhile to undertake farming strategies in the less suitable Great Basin once populations increasingly saturate the more suitable Colorado Plateau. Based on expectations from ideal distributions models, this suggests that farmers settled the Great Basin only after population density drove down suitability on the Colorado Plateau to levels that overlapped with suitability in the Great Basin (see Figure 1).

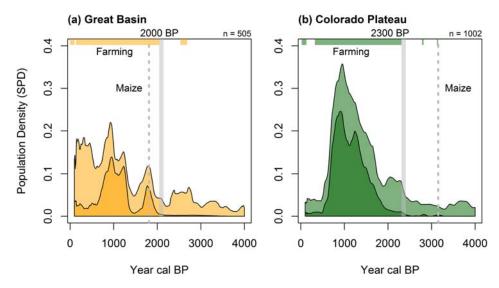


Figure 4. Population history of the (a) Great Basin and (b) Colorado Plateau sub-regions of the study area from 4000 to 100 years ago inferred from radiocarbon-dated archaeological sites. Plots show the 100-year moving average of the non-normalized summed probability distribution (SPD) of all calibrated radiocarbon dates (lighter polygon) and of those associated with evidence of farming (darker polygon) standardised by the area of each sub-region to approximate relative population densities. The dashed grey line shows the earliest direct date on maize in each sub-region. The solid grey line shows emergence of persistent farming adaptations (i.e. the farming period) in each sub-region estimated as first century included by the longest continuous 99% credible interval (CI) of the farming SPD. The coloured bars at the top of each frame show all years within the 99% CI of the farming SPD, indicating the discontinuous duration of farming.

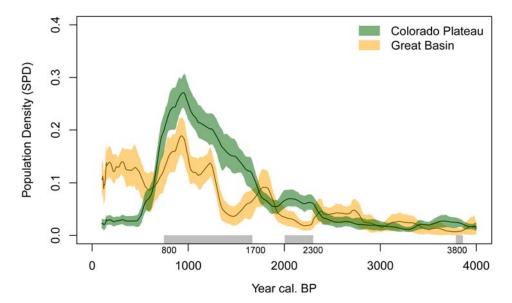


Figure 5. Summed probability distribution (SPD) of radiocarbon-dated archaeological sites across the Great Basin and Colorado Plateau (see Figure 4), each with a 1% to 99% bootstrapped confidence envelope (CE). Grey rug shows periods of non-overlapping CEs where the Plateau SPD is higher than the Basin SPD rounded to the nearest century from 3800-3900, 2300-2000, and 1700-800 cal. BP. While not examined here, the end of the record after the peak farming period shows a reversal of this trend with higher SPD values in the Basin than on the Plateau.

Discussion

The results of this study support the ideal distribution hypothesis for the spread of agriculture. The earliest sign of farming in the study area occurs in the more suitable physiographic region, the Colorado Plateau, and only expands into the less profitable Great Basin once populations increase, presumably decreasing the suitability of occupied habitats to a point where individuals could gain near equivalent yields by farming in either sub-region. These findings have implications for understanding regional prehistory, and offer support for a general framework that may be capable of elucidating global population expansions, including the spread of agriculture.

Implications for Regional Prehistory

The results of this study have direct implications for understanding the spread of maize, while also offering insights to help explain intensification events in the Early Holocene, the context of Late Holocene environmental degradation and agricultural collapse, and the processes structuring the Late Holocene migration of intensive foragers.

The Northward Expansion of Maize

The ideal distribution hypothesis for the spread of agriculture offers a possible explanation for the timing and tempo of the northward expansion of maize. As shown above, maize was already introduced to the study area, yet people did not adopt it right away. These early direct dates on maize come from the Eagle's Watch site (Roberts, 2018). While there may

be other sites like this that have yet to be discovered (Janetski, 2017), currently these early dates on maize are often interpreted as 'outliers' (Allison, 2019) as they do not represent the full emergence of agricultural economies throughout the region, but instead perhaps mark an early but short-lived migration of San Pedro farmers from southern Arizona (Roberts 2018) or an early but temporary adoption of agriculture by local populations.

This ca. 800 year lag between the arrival of maize and the emergence of wide-spread farming economies on the Colorado Plateau may be the product of individuals gaining higher returns by continuing to forage, indicating that population-driven competition did not yet drive down foraging profitability to levels near the lower returns gained from maize agriculture. Upham (1994) proposes such a process is structured the gradual emergence of sedentary farming across the Desert West. If this is true, then the delayed onset of farming adaptations in the Great Basin may be partially structured by its lower suitability for farmers, but also by higher profitability of foraging relative to the resident ('Archaic') population density. This is consistent with the near simultaneous occurrence of the first directly dated maize (ca. 1900 cal. BP) and the onset of intensive farming adaptations (ca. 2000 cal. BP) in the Great Basin, which contrasts with the delayed dynamics seen on the Plateau.

Settlement dynamics within the study area further elucidate the nuances of how this process may have unfolded. For example, early farming adaptations in the southwestern portion of the study area - associated with Ancestral Puebloan (Virgin Branch) populations during the Basketmaker II-III period – differ between the well-watered St. George Basin and the neighbouring arid uplands around Kanab. Despite being less suitable for agriculture, farming emerges first in the more arid uplands, appearing with few exceptions as intermittent periods of intensive agricultural land use followed by abandonment, consistent with short-term depletion of local resources resulting in abandonment and resettlement elsewhere (McFadden 2016; Spangler et al. 2019; Spangler 2021). While seemingly counter to predictions, this case helps prove the rule: Foraging persists longer in the St. George Basin because it was more profitable than early maize agriculture, while farming may have been relatively more profitable than foraging in the uplands given local population densities. However, once populations increase further throughout the region, foragers in the St. George Basin begin relying more on farming, and being tethered to well-watered locations, were more sedentary than their upland counterparts producing a more robust archaeological signature (Spangler et al. 2019; Spangler 2021). Thus the farming period starts with ephemeral agricultural sites in moderately suitable places, only later appearing much more archaeologically visible once resource competition encourages the adoption of farming in more suitable locations. If ubiquitous, this pattern may help explain the lag from the initial appearance of maize to the onset of the farming period across the study area.

In addition to being less profitable than wild resources overall, the earliest varieties of maize may have been even less productive in this temperate environment prior to about 2000 years ago with the introduction of additional varieties (da Fonseca et al., 2015) and the emergence of local adaptations (Swarts et al., 2017) that produced earlier flowering maize. These changes would have made maize more profitable, thereby reducing the threshold at which individuals may find it optimal to switch from foraging to farming.

The degree of investment required to successfully farm may also structure the timing of agricultural transitions. While maize agriculture is typically conceived of as rain-fed dry farming in the Four Corners region (e.g. Bocinsky and Kohler, 2014), it may be optimal (Boomgarden et al., 2019) if not altogether necessary (Boomgarden, 2015) to irrigate maize in the study region. While less costly subirrigation may have been possible in a few limited locations in the study area, such as wetland meadows in the arid uplands around Kanab (Roberts 2018; Roberts et al. in press), irrigating in the majority of the study area would dramatically increase the costs of farming and would likely delay the point at which individuals would find it profitable to adopt agricultural subsistence strategies.

Additional costs also surely mount with increasing resource competition. Hora-Cook (2018) leverages the

ideal free distribution model to suggest why Fremont occupants of the Uinta Basin, north of this study area, began building defensive structures following an increase in storage features. Carter et al. (2021) recently showed that increasing Fremont population density correlates with increased fire activity, suggesting that individuals were applying frequent fires to the landscape, possibly to clear fields at low elevations, and to increase encounters with declining wild resources at higher elevations.

While this study relies on a validated proxy of suitability, the moisture index is only a proxy of available soil moisture. Other factors also likely structured the suitability of farming across the study area, including nutrient availability, and critically, growing degreedays, which trades off with moisture availability (Yaworsky 2021). Future work will need to incorporate additional proxies of agricultural suitability in order to assess the specific environmental factors that constrained farming in the region.

While addressing a specific sub-region, these results offer insight into the factors that structure the spread of maize across the broader Southwest and Great Basin archaeological regions. Indeed, the process driving the spread of agriculture from the Plateau to the Basin examined in this case study is likely the same process that facilitated the northward expansion of maize agriculture from Mesoamerica.

Early Holocene Plant Intensification

If the intrinsic or 'pristine' suitability of the Colorado Plateau is higher than the Great Basin for all subsistence strategies, not just farming, then we should expect that intensification events will generally occur earlier and population densities will be higher on the Plateau than in the Basin. Evidence from the Early Holocene supports this supposition when intensive dietary and technological changes associated with small seed use occur earlier on the Colorado Plateau.

The earliest evidence for the use of small seeds occurs on the Colorado Plateau at North Creek Shelter as early as 10,500 cal. BP (Louderback, 2014), only emerging later in the Great Basin with evidence at Danger Cave at 9,700 cal. BP (Rhode et al., 2006). Likewise, coiled basketry - which is associated with small seed processing and parching (Herzog and Lawlor, 2016) - occurs first on the Plateau at Cowboy Cave beginning about 9,000 cal. BP (Geib and Jolie, 2008; Yoder et al., 2010), only emerging later in the Great Basin at Danger Cave after 8,300 cal. BP (though it might date earlier at nearby Hogup Cave, see Martin et al. 2017).

Late Holocene Environmental Impacts and Agricultural Collapse

While this paper focuses on the emergence of agricultural economies and their spread throughout the region, the end of this record marks a collapse and retraction of agricultural economies (Madsen and Simms, 1998; Simms, 2008). This transition is most often attributed to climatic change which limited agricultural production (e.g. Benson and Berry, 2009; Benson et al., 2007; Thomson et al., 2019; Finley et al., 2020). Applying the logic of the ideal free distribution model may provide further opportunities to elucidate this process.

Specifically, the model assumes that habitat suitability is negatively correlated with population density (Figure 1). Also referred to as negative density dependence, if true, this would imply that (a) higher population densities push individuals into less suitable habitats, and (b) individuals will lower the suitability of their local environment regardless of the original level of suitability. Both of these conditions will make individuals less resilient to climate change at higher population densities.

Here we provide evidence supporting the former: Our results show that individuals only began farming in the less suitable Great Basin after populations grew on the Colorado Plateau. However, as shown in Figure 4, the end of the record shows that populations in the Great Basin were more numerous than those on the Colorado Plateau. There are at least two possible explanations for this. First, it may be that the Great Basin is more suitable for hunting and gathering than the Colorado Plateau, so that the return to foraging adaptations allowed hunter-gatherer populations to persist at higher densities in the Basin than on the Plateau. This would not be surprising given that different subsistence strategies evaluate suitability differently (Vernon et al., this issue; also Yaworsky et al. 2020). If this is true, then the delayed onset of farming in the Great Basin may also be a partial product of denser 'Archaic' populations subsisting on more profitable wild resources at the time when farming is emerging on the Plateau; though more research is needed to evaluate this. Alternatively, this result may be an artifact of our study area: Growing season precipitation is higher in the southern portion of our study area, and our southernmost sites are in the Great Basin because we exclude sites south of the Colorado River on the Colorado Plateau; as such, the pattern could result from enduring farmers living at relatively high density. Agricultural adaptations may have persisted in this southwestern portion of the study area because Southern Paiute were irrigating fields in select locations along riverbanks (Allison et al., 2008), thereby buffering them from climatic shocks. Future work will investigate the persistence of farming in this region in more detail.

Prior research supports the latter prediction that individuals deplete resources in their local environment, either through direct hunting (e.g. Janetski, 1997) or broader patterns of environmental

degradation such as deforestation (e.g. Kohler, 1992), either of which may lead to decreased ecosystem resilience (Crabtree et al., 2017). Thus, even individuals in the most suitable habitats likely experienced decreasing resource profitability as a function of increasing population densities, which may have led to the adoption of more intensive subsistence strategies, thereby further accelerating the dynamic relationship between population growth and declining suitability, perhaps eroding the sustainability of these strategies. Under increasing competition in degraded habitats, even minor climate perturbations may have pushed individuals over a threshold where agriculture was no longer profitable. Such climate-driven perturbations may reset the equilibrium between populations and resources, leading some to migrate elsewhere, further reducing local competition, and encouraging a return to foraging economies by those who choose to remain.

Late Holocene Intensification

These same dynamics may also elucidate the timing and tempo of Late Holocene migrations across the region, including the proposed expansion of Numicspeaking populations in the last 1000-500 years (Lamb, 1958; Madsen and Rhode, 1994). While debated (e.g. Thomas 2019), many propose that Numic-speaking people migrated from the southwestern Great Basin (Bettinger and Baumhoff, 1982). This process marks the onset of intensive foraging economies at the expense of more mobile Archaic Period hunter-gatherers in the western Great Basin (Bettinger and Baumhoff, 1982; Hildebrandt, 2016; Magargal et al., 2017), and possibly of agricultural populations in the eastern Great Basin (Ambler and Sutton, 1989). The latter populations may have already been in decline because of climatic changes limiting agricultural production (Benson and Berry, 2009; Thomson et al., 2019), as discussed above.

Whether this process represents migration (Bettinger and Baumhoff, 1982) or in situ adaptation (Thomas, 2019), it marks an economic transition to more intensive foraging practices. As others have illustrated (Hildebrandt, 2016; Magargal et al., 2017), this process can be explained using logic derived from the ideal distribution model: If more intensive economies only expand once population growth drives down local suitability, then intensive Numic adaptations should only be profitable once competition increases. Building a spatially-explicit prey choice model to estimate possible return rates across the region, Magargal et al. (2017) leverage archaeological data from Hildebrandt (2016) to show that variation in suitability relative to subsistence strategy may explain the timing of the emergence of these intensive foraging practices. Additionally, suitability correlates strongly with territory size, and may help explain why more-intensive populations in smaller territories privatized resource



patches (Parker et al., 2019; also see Codding et al. 2019).

Implications for the Global Population Expansions

The Great Human Diaspora

The ideal distribution hypothesis also provides insights into other prehistoric expansions including the human diaspora out of Africa, which Eriksson et al. (2012) show follows a pattern partially driven by variation in past suitability and population density. Drawing on this model to address the rapid global expansions of modern humans about 50,000 years ago, O'Connell and Allen (2012) suggest that upon entering unoccupied landscapes, individuals should target the most profitable resources and habitats, rapidly moving into adjacent highly suitable habitats as populations drive down suitability. This suggests that in environments where highly profitable habitats are abundant and do not have barriers between them, individuals should respond to even minor reductions in suitability by quickly moving to adjacent unoccupied habitats, thereby accelerating migration. O'Connell and Allen (2012) argue this is the engine driving the rapid expansion of populations across Sahul (Pleistocene Australia and New Guinea), which appears archaeologically as a near simultaneous occupation of highly profitable habitats throughout the continent (O'Connell et al., 2018). This may also help elucidate the tempo of colonisation in the Americas (e.g. Codding and Jones 2013; Giovas and Fitzpatrick, 2014; Winterhalder et al. 2010), though this has yet to be systematically tested on a continental scale.

The Global Spread of Agriculture

The spread of agriculture is a hallmark of Holocene prehistory (Bellwood et al., 2005; Diamond and Bellwood, 2003). The ideal distribution hypothesis offers one framework to explore variation associated with the timing and speed of these expansion events (Shennan 2018). Specifically, the rate at which farming spreads should be a product of local population density and growth rates, the functional response of suitability to population density, the relative profitability of local foraging alternatives, and the suitability of adjacent habitats.

The rate of population growth resulting from local Neolithic demographic transitions (Boquet-Appel 2011) will have a profound impact on the tempo at which farming spreads. Page et al. (2016) show that populations that are either more sedentary or more reliant on agricultural resources will have both increased child mortality and increased fertility, but with fertility outpacing child mortality, the result would be rapid population growth of agriculturalists. However, the difference in population growth rates between mobile foraging and sedentary farming populations should vary depending on the distribution and density of high suitability habitats. This may help explain why the Neolithic demographic transition in the Southwestern United States varied across subregions (Kohler and Reese 2014).

Considering the distribution of habitat suitability across a landscape, and holding all else constant, agriculture should spread more rapidly in regions where adjacent habitats have smaller differences in suitability, and should be delayed where there are greater differences in suitability. This idea is supported by evidence of the spread of agriculture through Europe, where Neolithic farmers targeted specific ecological zones (e.g. Krauß et al., 2018), leading to accelerated expansions along major river drainages and coastlines that were more suitable for agriculture, and associated delays in other adjacent habitats (Davison et al., 2006; see also Shennan 2007, 2018). Similarly, this could help explain habitat-associated lags that characterise the mid-Holocene Bantu expansion in Africa (Grollemund et al., 2015), where the colonisation of rainforest patches lags savanna patches by about 300 years. If Bantu farming strategies were more profitable in savanna habitats, then individuals should not begin farming in the rainforest patches until increasing competition rendered their suitability equal.

Examining other expansion events systematically should help explain global patterns as well as local variation in the spread of agriculture. Coupling comprehensive databases of radiocarbon-dated sites with local estimates of agricultural suitability should facilitate this future research.

Conclusion

The ideal distribution hypothesis for the spread of farming offers a general framework to evaluate the timing and tempo of agricultural expansions globally. Here we evaluate this hypothesis looking at the expansion of maize agriculture from the more suitable Colorado Plateau to the less suitable Great Basin. The results support the hypothesis indicating a ca. 300-year lag between the emergence of maize farming in these physiographic regions. Farming only spreads to the Basin after increasing population density diminishes local suitability on the Plateau, presumably to a point where expected returns in both regions are equal. This evaluation is possible through the coupling of a comprehensive radiocarbon database with a validated measure of agricultural suitability. Given the dramatic growth of both records globally, we hope this case study will help structure future empirical evaluations of this hypothesis on broader spatial and temporal scales.

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