

¹

Decomposing Habitat Suitability ² Across the Forager to Farmer Transition

³ ¹, Kenneth B. Vernon^{1,2}, Peter M. Yaworsky^{1,2}, Jerry Spangler³, Simon Brewer^{4,5}, and Brian F. Codding^{1,2,5}

⁴ ¹Department of Anthropology, University of Utah, Salt Lake City, UT, 84112, USA

⁵ ²Archaeological Center, University of Utah, Salt Lake City, UT, 84112, USA

⁶ ³Colorado Plateau Archaeological Alliance, Ogden, UT 84401, USA

⁷ ⁴Department of Geography, University of Utah, Salt Lake City, UT, 84112, USA

⁸ ⁵Global Change and Sustainability Center, University of Utah, Salt Lake City, UT, 84112, USA

⁹ July 6, 2020

¹⁰ Draft submitted to *Environmental Archaeology*
¹¹ Do not distribute without permission from the authors

¹² **Abstract**

¹³ How might subsistence strategies structure the costs and benefits of habitat selection and,
¹⁴ therefore, drive settlement patterning? We explore this question within an Ideal Distribution
¹⁵ framework, arguing that (i) a habitat can be decomposed into its environmental covariates, (ii)
¹⁶ their relative contributions to suitability can vary as a function of subsistence strategy, and (iii)
¹⁷ the resulting differences will in turn lead to different population distributions across habitats. To
¹⁸ evaluate these claims, we apply a Poisson point-process modeling approach known as maximum
¹⁹ entropy (MaxEnt) to Archaic hunter-gatherer and Formative maize-farmer sites within the
²⁰ Grand Staircase-Escalante National Monument. Our results show that environmental covariates
²¹ vary in their importance for each strategy and that the strategies themselves vary in their
²² land use and habitat distribution, with Archaic foragers being widely distributed across space,
²³ Formative farmers more densely packed into areas indicative of higher maize productivity. The
²⁴ approach itself also has wide application to other subsistence strategies, including horticulture
²⁵ and pastoralism, across a range of environmental conditions.

²⁶ **Keywords:** Ideal Free Distribution, Grand Staircase-Escalante National Monument, Subsistence-
²⁷ Settlement Dynamics, Poisson Point Process Modeling, Maximum Entropy, Land Use

²⁸ **1 Introduction**

²⁹ In the context of subsistence-settlement dynamics, the order in which choices are made matters,
³⁰ for the choice of where to live introduces new subsistence constraints and the choice of how to live
³¹ introduces new settlement constraints (Binford, 1980; Bettinger and Baumhoff, 1982). While the
³² interaction of these deserves further consideration, here we focus on the latter, on how subsistence
³³ strategies might constrain habitat selection. We argue that (i) a habitat can be decomposed into
³⁴ its environmental covariates, (ii) their relative contributions to suitability can vary as a function
³⁵ of subsistence strategy, and (iii) the resulting differences will in turn lead to different population
³⁶ distributions across habitats.

³⁷ The analysis is largely motivated by two complementary ideas. The first is that intensification
³⁸ can alter the way per capita suitability responds to demographic pressure (Kennett et al., 2006).
³⁹ The second is that measures of subsistence efficiency can be applied not only to the behaviors of
⁴⁰ individuals, but to locations in space (Magargal et al., 2017). Drawing on spatial modeling techniques
⁴¹ outlined by Yaworsky et al. (in review), we implement our coupled subsistence-settlement approach
⁴² within an Ideal Distribution framework (Fretwell and Lucas, 1969) using a statistical method for
⁴³ species distribution modeling known as maximum entropy (MaxEnt) (Phillips et al., 2004, 2006;
⁴⁴ Elith et al., 2011). Archaeological applications of MaxEnt have increased over the last several years
⁴⁵ (Banks et al., 2011; d'Errico and Banks, 2013; Galletti et al., 2013; McMichael et al., 2014a,b, 2017;
⁴⁶ Kondo, 2015; d'Errico et al., 2017; Wachtel et al., 2018), so a deeper understanding of the approach
⁴⁷ is called for. To aid in this, we rely on the interpretation of MaxEnt as a Poisson point process
⁴⁸ model (Berman and Turner, 1992; Baddeley and Turner, 2000), an interpretation that has garnered
⁴⁹ a great deal of attention in the recent ecological literature (Fithian and Hastie, 2013; Merow et al.,
⁵⁰ 2013; Renner et al., 2015; Phillips et al., 2017). We evaluate our claims using the extensive record of
⁵¹ subsistence and settlement provided by the distribution of Archaic (8,500-2,500 BP) and Formative
⁵² (2,000-700 BP) sites in the contested Grand Staircase-Escalante National Monument (GSENM),
⁵³ where individuals transitioned from foraging to farming over a roughly 1500 year period, from 3000
⁵⁴ to 1500 BP (Spangler et al., 2019).

⁵⁵ **2 Theory, Methods, and Materials**

⁵⁶ Intuitively, people will live where they can make the best living, however they choose to do that.
⁵⁷ Consider Archaic hunter-gatherers, whose broad diets include a large variety of wild resources
⁵⁸ (Simms, 2008). Because those resources are widely dispersed, the foragers themselves should be
⁵⁹ widely dispersed, too. For those who transition to farming, however, settlement will likely be more
⁶⁰ clustered, especially in an area like the arid Southwest, where potential maize production is spatially
⁶¹ limited (Spangler et al., 2019). Thus, the spatial distribution of their archaeological materials should

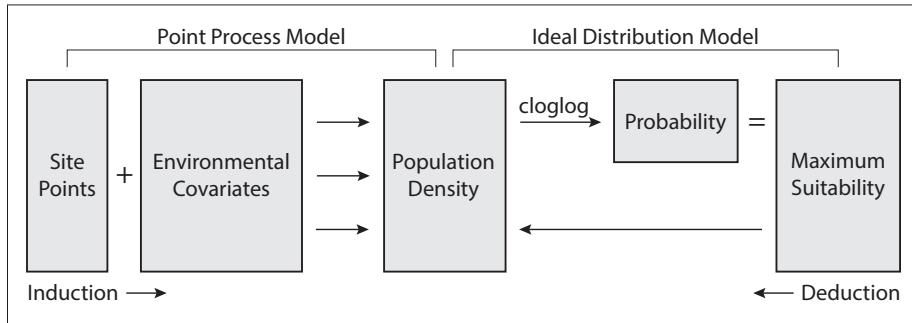


Figure 1: Methods Diagram. The conceptual relationship between Ideal Free and Point Process models. Note that the complementary log-log (cloglog) transforms an empirical density estimate into a probability of site occurrence, which we take to be an operational definition of maximum potential suitability wherever the IDM holds (discussed below and in supplement A).

62 differ as well, a fact that we can leverage to decompose their respective habitats into a number of
 63 environmental variables (precipitation, temperature, elevation, etc.), which are thought to co-vary
 64 with the suitability of that habitat. In this way, we are effectively walking a chain of inference
 65 from suitability, as defined by the theoretical Ideal Distribution Model (IDM), to the environmental
 66 covariates, whose contribution to suitability we measure with an empirical Poisson Point Process
 67 Model (PPM), as shown in Fig. 1. It is important to note that this interpretation of a PPM as an
 68 empirical model of suitability is only meaningful within the conceptual framework provided by the
 69 IDM; thus, it would be invalid in circumstances where individuals do not distribute themselves in
 70 conformity with that model.

71 2.1 Deductive Model: Suitability and Subsistence Efficiency

72 According to the IDM (Fretwell and Lucas, 1969), suitability should decline as a function of increasing
 73 population density. In the simplest case, this is because density leads to greater competition, which
 74 in turn reduces the benefit to the individual of occupying that habitat (Parker and Sutherland, 1986;
 75 McCool and Yaworsky, 2019). Given that individuals seek to maximize their own gains, the model
 76 predicts that they will settle the highest ranked habitat first, with subsequent infilling occurring up
 77 to the point where the next highest ranked habitat is of equal suitability, at which point individuals
 78 should settle both at an equal rate. This process will, thus, lead to an equilibrium distribution in
 79 which each individual experiences the same level of gain - the same actual suitability - regardless of
 80 the maximum potential suitability of the habitat they happen to occupy.

81 A simple, intuitive way to articulate these model expectations with subsistence behavior draws
 82 on Optimal Foraging Theory (Emlen, 1966; MacArthur and Pianka, 1966; Charnov, 1976a,b) to
 83 postulate an identity between the suitability of a habitat and the optimal overall caloric return-rate

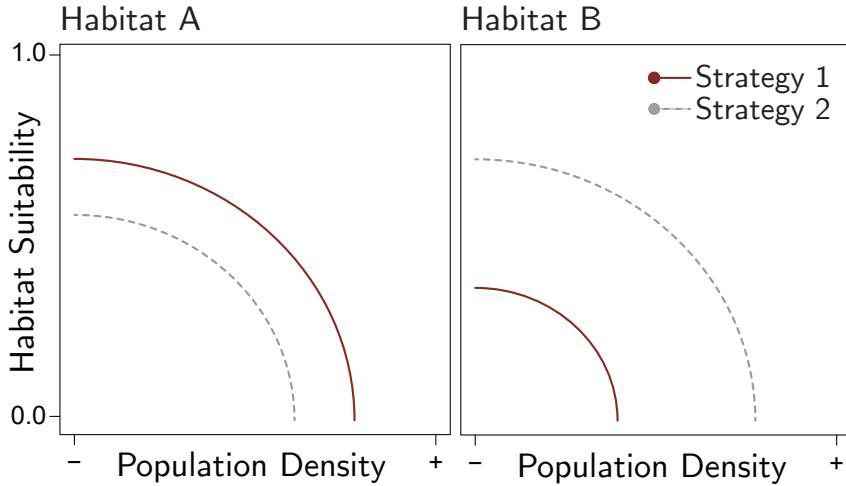


Figure 2: An IDM showing the effects of subsistence on settlement, specifically a change in the potential suitabilities and relative rankings of habitats A and B.

84 an individual can achieve there when pursuing a particular subsistence strategy. This identity
 85 expands on the strategy employed by Magargal et al. (2017), assigning to each habitat an estimate of
 86 expected subsistence efficiency but also allowing for foraging strategies themselves to be negatively
 87 density-dependent. The identity also provides for a number of additional subsistence-settlement
 88 dynamics. As Kennett et al. (2006) show, the transition to a farming strategy can decrease the
 89 magnitude of density's effect on suitability and introduce Allee effects, or positive contributions
 90 to suitability at low density (Allee et al., 1949; Sutherland, 1996). In addition, it suggests that
 91 subsistence transitions can lead to changes in the maximum potential suitability of habitats, which
 92 can in turn lead to changes in their relative rank.
 93 Of those three, the last should have the largest effect on density distributions. As shown in Fig.
 94 2, we assume in the simplest case two habitats, H_A and H_B , and two strategies, S1 and S2. S1
 95 has greater subsistence efficiency in H_A relative to H_B and should, therefore, rank H_A above H_B .
 96 Conversely, S2 has greater efficiency in H_B relative to H_A and should, therefore, rank H_B above
 97 H_A . All else being equal, a change in maximum potential suitability should, in turn, entail different
 98 habitat distributions for each strategy. Individuals pursuing S1 should occur at higher densities in
 99 H_A , and individuals pursuing S2 should occur at higher densities in H_B . This outcome is a simple,
 100 qualitative variation of the “input matching rule” (Parker, 1978), which states that population
 101 density should be proportional to the maximum potential suitability of a habitat.
 102 Logically, the inverse of this matching rule should also hold, so that the observed density of individuals
 103 pursuing a subsistence strategy within a habitat indicates something about that habitat’s potential

¹⁰⁴ suitability for the strategy. That is, if the density of individuals pursuing strategy S1 in a habitat
¹⁰⁵ is greater than the density of individuals pursuing strategy S2 in that habitat, then the potential
¹⁰⁶ suitability of that habitat for S1 ought to be greater than its potential suitability for S2, assuming
¹⁰⁷ at least that the strategies are at equilibrium.

¹⁰⁸ Similar reasoning applies to an environmental variable's ecological utility function, where that refers
¹⁰⁹ to changes in the variable that increase or decrease a habitat's potential suitability (for how we
¹¹⁰ specify an ecological utility function, see discussion of the marginal response below and in Supplement
¹¹¹ A). Since suitability is tied to subsistence efficiency, environmental covariates should also exhibit
¹¹² different ecological utility functions for individuals pursuing different subsistence strategies, which
¹¹³ should in turn entail different habitat rankings and habitat distributions. So, just as observed
¹¹⁴ population density suggests something about potential suitability, it should suggest something about
¹¹⁵ these ecological utility functions, too.

¹¹⁶ Crucially, these inferences from observed density to both potential suitability and ecological utility
¹¹⁷ rely on the assumption that no Allee effects have occurred, that density affects both strategies
¹¹⁸ equally, and that settlement costs are the same for both. Yet, as already noted, these assumptions
¹¹⁹ are almost certainly false. Thus, without suitable actualistic research to estimate settlement costs
¹²⁰ and other subsistence related constraints and trade-offs, the naïve inference from density to potential
¹²¹ suitability is tantamount to inferring from the fact that a person occupies a low quality habitat
¹²² that they must actually prefer that habitat, which is uncharitable in the extreme (Coddington and
¹²³ Bliege Bird, 2012; Coddington and Bird, 2015). Heeding this concern, we fall back on evaluating
¹²⁴ potential suitability relative to land use itself, assuming that this must in some way relate to the
¹²⁵ underlying subsistence efficiency of each strategy.

¹²⁶ 2.2 Inductive Model: MaxEnt as a Point Process

¹²⁷ An inductive (or predictive) distribution model requires a dependent variable or response, in this
¹²⁸ case site "occurrence" data, and a set of independent variables or predictors, here environmental
¹²⁹ variables thought to co-vary with the response. Typically, archaeologists think of site occurrences as
¹³⁰ presence-absence or Bernoulli responses, thus turning to logistic regression to model the probability
¹³¹ of each outcome, which is then interpreted in terms of habitat suitability (Kvamme, 2005; Wachtel
¹³² et al., 2018). This is a somewhat awkward approach, however, for two important reasons (Warton
¹³³ and Shepherd, 2010; Phillips and Elith, 2013; Fithian and Hastie, 2013; Hastie, 2013; Renner et al.,
¹³⁴ 2015). First, systematic inventory of potential absence locations is rarely conducted, so the data
¹³⁵ we have at our disposal is overwhelmingly presence-only. This is exacerbated by the fragmentary
¹³⁶ record of archaeological sites commonly used as a proxy for past occurrences. Second, this approach
¹³⁷ often fails to recognize that probability measures are sensitive to spatial scale. If a region consists of
¹³⁸ two habitats about whose environmental conditions we know nothing save that one has twice the

139 area of the other, we should not assign to each a probability of settlement of 0.5, but rather 0.66
140 and 0.33 respectively.

141 To address these issues, we interpret site occurrences as counts or Poisson responses per unit area,
142 in short, as densities (Warton and Shepherd, 2010; Fithian and Hastie, 2013; Renner et al., 2015).
143 More precisely, we assume that archaeological sites are independent and identically distributed point
144 locations $s_p = \{s_1, \dots, s_N\}$ occurring within a larger project window W . While this assumption of
145 independence is almost certainly unrealistic, it does allow us to treat the density distribution of sites
146 as a Poisson point process and thereby formulate expectations regarding that distribution using a
147 point process model (PPM).

148 A Poisson point process can be either homogenous or inhomogenous (Baddeley and Turner, 2000;
149 Baddeley et al., 2015). For a homogenous process, the point pattern exhibits “complete spatial
150 randomness,” so there will be variation around the mean, but not variation whose direction away
151 from the mean we can estimate. Thus, our expectation regarding a habitat i ’s density (denoted
152 $\lambda(s_i)$ in the PPM literature) is just the average density of W :

$$\lambda(s_i) = \frac{N}{\text{area}_W} \quad (1)$$

153 This serves as a null model. It is equivalent to the hypothesis that individuals do not differentiate
154 habitats with respect to their land use, so that we have no reason to expect sites to occur more
155 often in one habitat as opposed to another.

156 For an inhomogenous process, the point pattern does not exhibit complete spatial randomness, so the
157 density within any habitat can be modeled as a log-linear response to a vector X of environmental
158 covariates $\{x_1, \dots, x_j\}$:

$$\lambda(s_i) = \exp(\beta_0 + \beta_1 X(s_i)) \quad (2)$$

159 where β_0 is the intercept, β_1 a vector of coefficients, and the error a Poisson distribution. A
160 fitted PPM model can be used to estimate the population density in each habitat based on its
161 environmental conditions, which is equivalent to estimating site occurrence probability for every
162 habitat size (Fithian and Hastie, 2013). We emphasize that this is only an estimate of the relative
163 density (referred to as the relative occurrence rate), as we cannot measure the total prevalence of
164 points within the window without true absence data (Fithian and Hastie, 2013; Hastie and Fithian,
165 2013; Phillips and Elith, 2013).

166 One popular form of PPM is MaxEnt (Fithian and Hastie, 2013; Merow et al., 2013; Renner and
167 Warton, 2013; Renner et al., 2015; Phillips et al., 2017), which estimates β -coefficients for Eq. 2
168 subject to the constraint that the geographic probability distribution be as close as possible to

absolute entropy (Jaynes, 1957). For the sake of clarity, we use 'MaxEnt' in this paper to refer to a particular software implementation for training a PPM and 'entropy' to refer to a particular concept in information theory (Shannon, 1948). In terms of point patterning, absolute entropy is equivalent to homogeneity or complete spatial randomness, or a geographically uniform probability distribution. Formally, MaxEnt estimates β -coefficients by maximizing the penalized log-likelihood of the following:

$$P_i/B_i = \exp(\beta_0 + \beta_1 X(s_i)) \quad (3)$$

where P_i is the probability density of covariates at presence locations and B_i is the probability density of covariates across the research area, typically estimated using background or quadrature points, also known as pseudo-absence points (Elith et al., 2011; Merow et al., 2013). The ratio is equivalent to point density in ecological as opposed to geographic space (across habitats, that is, as opposed to coordinate locations). The distance between them is the relative entropy of the point process (also known as the Kullback-Leibler or KL divergence) (Elith et al., 2011; Merow et al., 2013). Minimizing relative entropy in ecological space is equivalent to maximizing absolute entropy in geographic space, for smaller values of relative entropy suggest less differentiation in land use, which in turn entails greater homogeneity in the resulting point pattern.

One can also think of the ratio P_i/B_i as a means of controlling for a covariate's prevalence (Elith et al., 2011; Merow et al., 2013). The reason for doing so is straightforward. Though many sites may occur at some value of an environmental covariate, if that value is ubiquitous, it should be given less weight in fitting the final model, for it becomes that much harder to discern whether individuals have arrived at that value because they chose to or simply as a matter of chance.

But even standard linear PPMs account for the background distribution, so why use a MaxEnt PPM? This is a complicated question involving a number of modeling trade-offs. By default, MaxEnt transforms the set of covariates X into a larger set of *features* including product, quadratic, and hinge terms (described in Supplement A) (Phillips and Dudík, 2008; Elith et al., 2011; Phillips et al., 2017). It then reduces that set through regularization, which also limits overfitting by penalizing the log-likelihood (Dudík et al., 2004; Phillips et al., 2004; Elith et al., 2011). This process has the advantage of capturing complex multi-modal responses unavailable to a simple linear PPM. It also increases the model's predictive power (Elith et al., 2006; Phillips and Dudík, 2008; Wachtel et al., 2018; Yaworsky et al., in review). Unfortunately, the price of this gain in predictive power is a loss of interpretability (Phillips et al., 2006), specifically with respect to covariate importance, where linear models can leverage standardized coefficients and model diagnostics like the Likelihood Ratio Test. MaxEnt does provide alternative measures (described below), but these must be read with caution, for the underlying Poisson probability distribution is less transparent and the subsequent statistical inference more opaque. Thus, MaxEnt faces a familiar modeling trade-off between prediction and

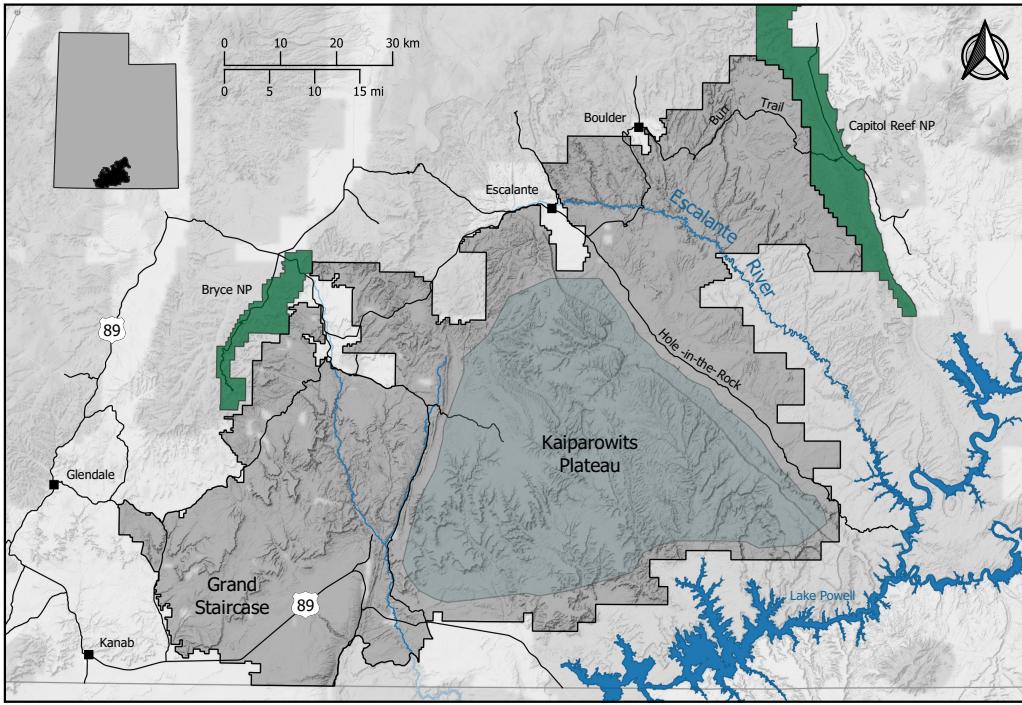


Figure 3: Reference Map for the Grand Staircase-Escalante National Monument. Includes nearby national parks, major water features, and the original boundary designation, which defines the current project window.

203 interpretability. To get some handle on this trade-off, we compare the results of a feature-restricted
 204 MaxEnt and linear PPM.

205 2.3 Archaeological Point Patterns (λ)

206 The project window from which we draw environmental and archaeological information is the
 207 GSENM, an area in south-central Utah along the western most extent of the Colorado Plateau.
 208 When these data were collected, the monument consisted of some 1.9 million acres (7.6 thousand
 209 km²) commonly subdivided into three major regions including the Grand Staircase, the Kaiparowits
 210 Plateau, and the Canyons of the Escalante, as shown in Fig 3. While mostly uniform with respect
 211 to their aridity, these regions do exhibit dramatic variation in topography and vegetation.

212 Here we focus on Archaic (AR) and Formative (FO) economies within the GSENM as they present
 213 a fairly stark contrast in their respective subsistence strategies. From roughly 8,500 to 2,500 BP, the
 214 former involved a broad-spectrum foraging strategy including everything from large game animals
 215 to less profitable resources like nuts and seeds (Simms, 2008). Beginning around 2,000 BP and

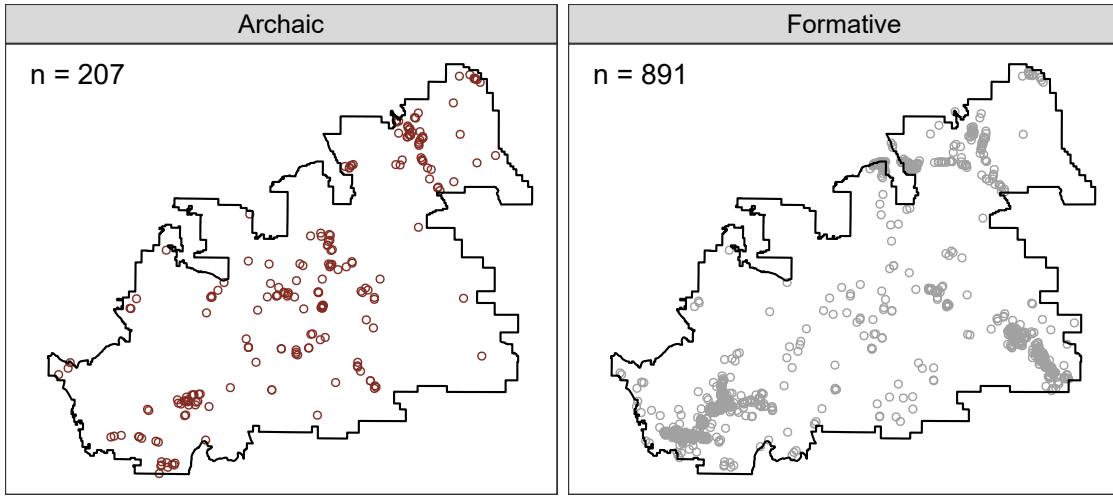


Figure 4: Point Patterns. The distribution of Archaic and Formative Sites.

216 persisting for nearly 1,300 years, the latter involved a small-scale, agricultural strategy highly reliant
 217 on maize (Coltrain et al., 2007). Importantly, Formative maize farming is a form of intensification
 218 (*sensu stricto*, Morgan, 2015), whereby higher energetic yields are gained at the expense of diminished
 219 efficiency (Barlow, 2002), producing more food per unit area (Boserup, 1965) and increasing the
 220 carrying capacity of occupied habitats. This is reflected in the relative abundance of observed
 221 residential sites associated with each time period (AR=207, FO=891).

222 Spatial data for archaeological sites and information required to associate each with Archaic and
 223 Formative time periods are drawn from records curated by the Bureau of Land Management (BLM)
 224 and the Utah State Historic Preservation Office (SHPO). These records contain field notes detailing
 225 the presence and number of formal diagnostic materials. The rules we use to infer time period
 226 affiliations from those diagnostics are outlined in detail in our report to the BLM GSENM district
 227 office (Spangler et al., 2019). We then select only residential sites (as opposed to temporary camps)
 228 defined as places of long-term habitation and indicated archaeologically by the presence of either
 229 deep hearths, habitation features, which are too costly to build when stays are short, or heavy
 230 groundstone, which are too costly to transport (Beck et al., 2002). The resulting point patterns are
 231 shown in Fig. 4. These represent spatial patterning in prehistoric foraging and farming strategies
 232 within the GSENM.

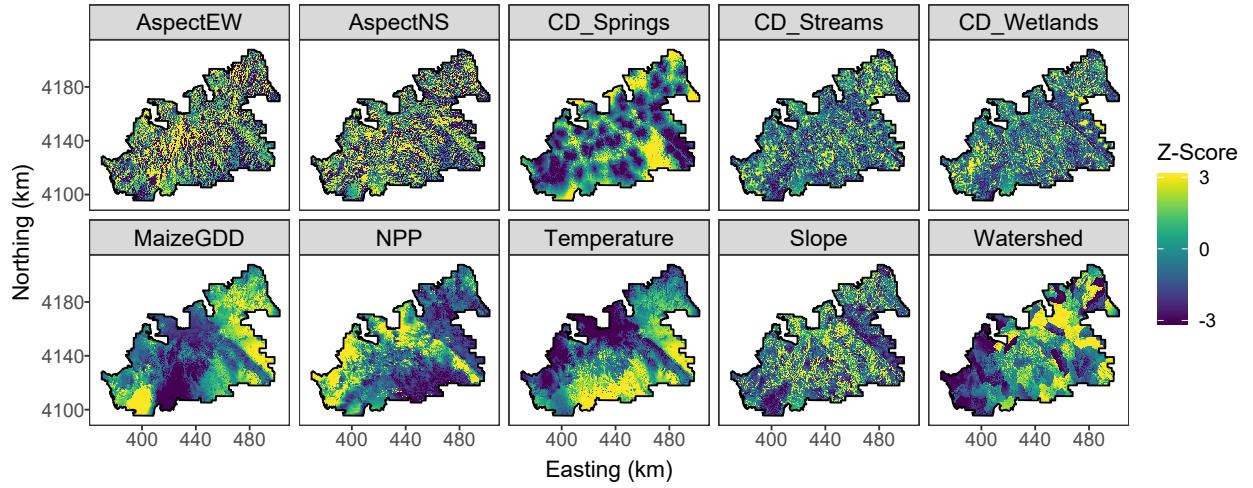


Figure 5: Environmental Covariates Projected in Geographic Space. For visualization purposes, the z-values of these covariates were compressed into a -3 to 3 range.

2.4 Environmental Covariates (X)

For this analysis, we decompose suitability into a set of ten environmental covariates (5), which we derive from a larger set through Principal Component Analysis to reduce spatial covariance (Yaworsky et al., in review). These group roughly into landscape attributes, climate values, environmental productivity, and resource distribution. Landscape attributes include aspect (both east-west and north-south), slope, and watershed size, with the first two being extracted from a digital elevation model (U.S. Geological Survey, 2019) and the latter provided by Utah’s Automated Geographic Reference Center (AGRC Staff, 1984). Our sole climate covariate is thirty-year average temperature (PRISM Climate Group, 2019). Indicators of environmental productivity include maize growing-degree days (GDD) (Coop, 2014) and net primary productivity (NPP) (Numerical Terradynamic Simulation Group, 2013). Finally, we define resource distributions as cost-distance to water features computed using Tobler’s hiking function (Tobler, 1993), specifically cost-distance to springs, streams, and wetlands. The rasters encoding these covariates are projected to a 50-m x 50-m resolution. For more details regarding these covariates, see supplement B.

Climate and productivity covariates in our dataset are measures of modern variation within the GSENM, so we must assume that the relative differences across space for each category are largely representative of relative differences in the past. For example, if it is hotter in the eastern part of the GSENM today, then it was hotter in the eastern part of the GSENM during the times in question. While further work is required to test this assumption, we proceed with this analysis

252 without introducing additional bias that would come with using spatially-explicit reconstructions of
253 past climate and environment (Coddington and Jones, 2013).

254 **2.5 Hypotheses**

255 We argue that these environmental covariates will contribute differentially to suitability as a function
256 of subsistence strategy - in this case, Archaic foraging and Formative farming - and that this will
257 lead to differences in the downstream distribution of those strategies. Transposed into the language
258 of point processes, these claims amount to the following null and alternative hypotheses:

259 H_0 Archaic and Formative point patterns are homogenous.

260 H_1 Archaic and Formative point patterns are inhomogenous.

261 H_2 Archaic and Formative subsistence strategies differ significantly in (a) the ecological
262 utility of covariates, (b) the potential suitability of habitats, and (c) the spatial
263 clustering of sites.

264 We stress that we are evaluating these hypotheses relative to land use as we have no independent
265 control on subsistence-settlement constraints and trade-offs. In general, however, we expect that
266 environmental covariates more conducive to maize agriculture will play a greater explanatory role in
267 Formative site patterning. Because individuals pursuing a more intensive farming strategy have more
268 to gain by reducing handling rather than search costs (Bettinger and Baumhoff, 1982; Kelly, 1992;
269 Hawkes and O'Connell, 1992; Morgan, 2015; Parker et al., 2018), we also expect that Formative
270 individuals will be more sedentary, with residential sites exhibiting greater levels of clustering around
271 maize-promoting covariate values. Conversely, those pursuing a more general and less intensive
272 Archaic foraging strategy should be more mobile, with residential sites trending toward a homogenous
273 point pattern spread out across a wider range of covariate values.

274 **2.6 Analytical Methods**

275 To test these hypotheses, we center and scale our covariates, subtracting by the mean of each and
276 dividing by their standard deviations, which makes estimated β -coefficients directly comparable. To
277 estimate the background distribution of these covariates for model training, we generate a spatially
278 uniform or gridded quadrature scheme of 100,000 points based loosely on a rule recommended by
279 (Renner et al., 2015) (for more details, see Supplement A).

280 We then use the spatstat package in R (Baddeley et al., 2015) to fit three linear PPMs: (a)
281 a stationary or homogenous PPM that measures the average density for each strategy; (b) a
282 strategy-insensitive, inhomogenous PPM of all the points, both Archaic and Formative; and (c) a
283 strategy-sensitive, inhomogenous PPM that treats time period as a categorical interaction term

with two levels, Archaic and Formative. These are nested models, allowing Analysis of Variance (ANOVA) to evaluate whether each model is significantly better than its simpler alternative. The results will tell us whether the respective point patterns are different than a homogenous point process (H_0 and H_1) and whether they are different than each other (H_2). PPM (iii) also provides a de facto Wald test of significant differences in the linear importance of each covariate for each subsistence strategy (H_{2a}). A graphical Ripley's L test (Ripley, 1977) accompanied by a Maximum Absolute Deviation (MAD) test (Baddeley et al., 2014) evaluates potential for significant clustering in foraging and farming point patterns (H_{2c}) (further details in Supplement A). These will give us an idea of their “notional” habitat size as well as their density of occupation within it.

Next we use the dismo package in R (Hijmans et al., 2017) to fit a MaxEnt PPM for each subsistence strategy, restricting its default feature expansion to hinge and quadratic terms so that only the additive contributions of each covariate are measured, which eases interpretation of MaxEnt’s estimates of covariate importance. Through iterations of fitting a PPM, MaxEnt tracks changes in the empirical log-loss associated with changes in each feature, which is assigned to the corresponding covariate. Once a model is fitted, the total contribution to the log-loss for each covariate is divided by the sum of all covariate scores, and then multiplied by one hundred to give a percent contribution score (Phillips, 2017). MaxEnt then randomly permutes each covariate and evaluates the loss in model performance, measured using the area under the receiver operating characteristic curve (AUC) (for a discussion of the AUC, see Yaworsky et al., in review). Again, these measures are divided by the total loss across all covariates, and then multiplied by one hundred to give a permutation importance score (Phillips, 2017). Together these measures provide some indication as to the importance of each covariate to the final model and by extension to the corresponding subsistence strategies (H_{2a}). To validate these scores, we also conduct a spatial random bootstrap and fit MaxEnt PPMs to the resulting data. This includes building ten models for each time period and in each case removing approximately one quarter of the presence and background points within spatially defined quadrats (further details in Supplement A). An ANOVA tests whether the results are significantly different.

We generate marginal response plots (Fig. 8) for each covariate by holding all other covariates at their zero-centered means and predicting the density from a MaxEnt PPM using all the data. That is then converted into a probability using the complementary log-log transform (cloglog) (Baddeley et al., 2010; Phillips et al., 2017). The marginal response shows how potential suitability (operationalized as probability of occurrence) responds to changes in a covariate within the average habitat as represented in ecological space and relative to a subsistence strategy, so they are graphical representations of strategy-specific ecological utility functions (see Supplement A for the actual formulas estimated by MaxEnt). We compare these plots to probability density functions for covariates at Archaic and Formative presence locations and background locations to show how MaxEnt’s probability estimates

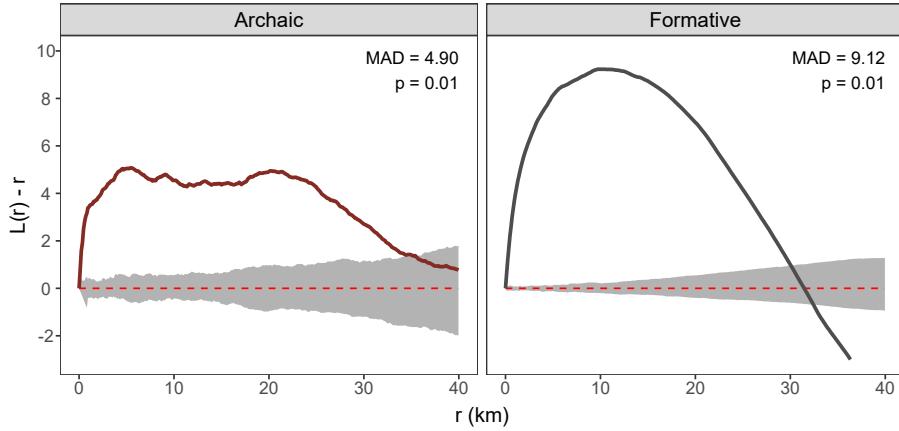


Figure 6: Ripley’s L Test. Values greater than expected by the null mode (represented by the red dashed line) indicate spatial clustering. Values less than expected by the null model indicate spatial repulsion. The gray ribbon represents Monte Carlo simulations of the null mode. Where the line enters the gray ribbon, it is no longer significantly different than complete spatial randomness. The MAD statistic measures the maximum distance between observed values and the null model.

320 relate to the ratio P_i/B_i , with B_i being estimated using the quadrature points.

321 Finally, we use a MaxEnt PPM (iii) to estimate the density at each geographic location within the
 322 GSENM. MaxEnt’s raw predictions are point density estimates standardized by the total number
 323 of occurrence locations. Although we do not know the true prevalence of each strategy, to get a
 324 sense of the difference in population density distributions we take the product of MaxEnt’s raw
 325 output and the total number of sites for each strategy. Again, the standardized estimates are
 326 converted into probabilities using cloglog. Being transformations of the underlying density, these
 327 probability estimates are not susceptible to issues of scale (Fithian and Hastie, 2013) and thus
 328 provide a suitable means for operationalizing habitat suitability. Although they are not observations,
 329 strictly speaking, they are pair-wise estimates, so we can use a Wilcoxon Signed-Rank Test to see if
 330 the model suggests significant differences in the spatial distribution of potential suitability (with
 331 respect to land use) between Archaic hunter-gatherers and Formative maize-farmers (H_2b). While
 332 there are more sophisticated techniques for map comparisons (Wilson, 2011), this test is sufficient
 333 for current purposes.

334 All statistical analyses are conducted in the R programming environment (R Core Team, 2019) with
 335 code and further discussion reported in the supplementary material.

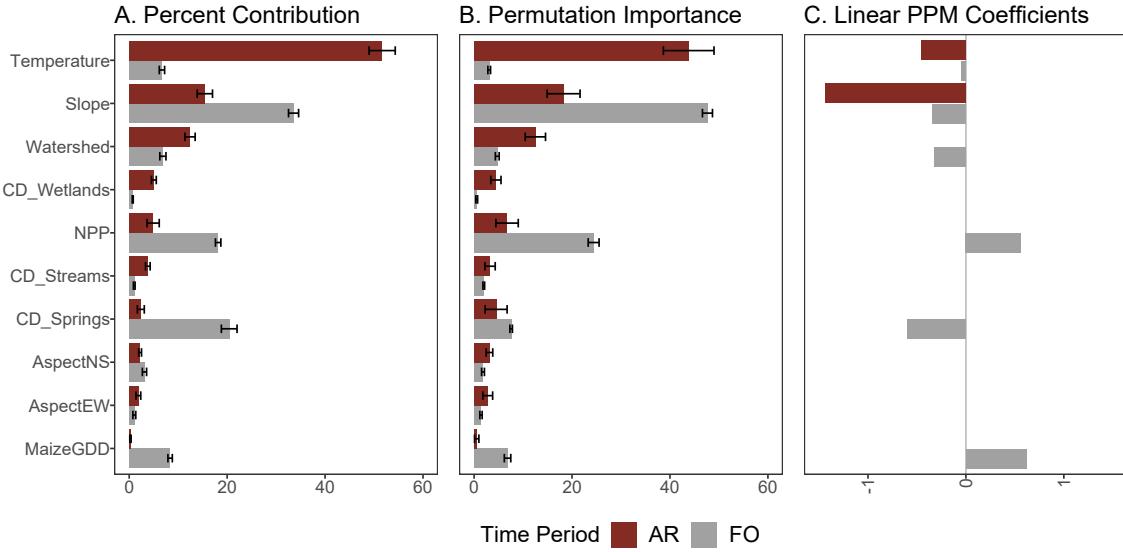


Figure 7: MaxEnt and Linear PPM Measures of Covariate Importance. These are estimated for both Archaic (AR) and Formative (FO) subsistence strategies. (A,B) ANOVAs indicate that all differences between strategies are significant. (C) For comparative purposes, the log- β 's for linear PPM (c) are reported. In general, (A) and (B) speak to the magnitude of importance, (C) to its direction.

3 Results

The results of the ANOVA show significant improvement in model fit for each incremental increase in model complexity, from stationary (a) to strategy-insensitive (b) ($\chi^2(10) = 960, p < 0.0001$) and from strategy-insensitive (b) to strategy-sensitive (c) ($\chi^2(11) = 642, p < 0.0001$). This shows that there are significant differences in land use patterns between the two strategies (H_2 is true), and that they are not homogenous (H_0 is false and H_1 is true). Results of the graphical Ripley's L and MAD tests are shown in Fig. 6. Together, these indicate that Archaic hunter-gatherers and Formative maize farmers exhibit clustering over the same range of approximately 30 kilometers, which is suggestive of their notional community size. Over that range, however, Formative maize farmers exhibit higher densities than Archaic hunter-gatherers (MAD FO = 9.12, MAD AR = 4.90).

Spatial bootstraps of MaxEnt measure spatial variation in percent contribution and permutation importance scores for each covariate, as shown in Fig. 7. Relatively speaking, temperature appears to be most important to Archaic hunter-gatherers, followed by slope and watershed size. For Formative maize-farmers, it is slope followed by NPP, cost-distance to springs, and maize GDD. ANOVAs comparing the distributions of percent contribution and permutation importance for each covariate and time period suggest that all are significantly different. As evidenced by the linear coefficient, Archaic individuals gravitate towards PRISM temperatures below the mean ($\mu = 10.77^\circ\text{C}$).

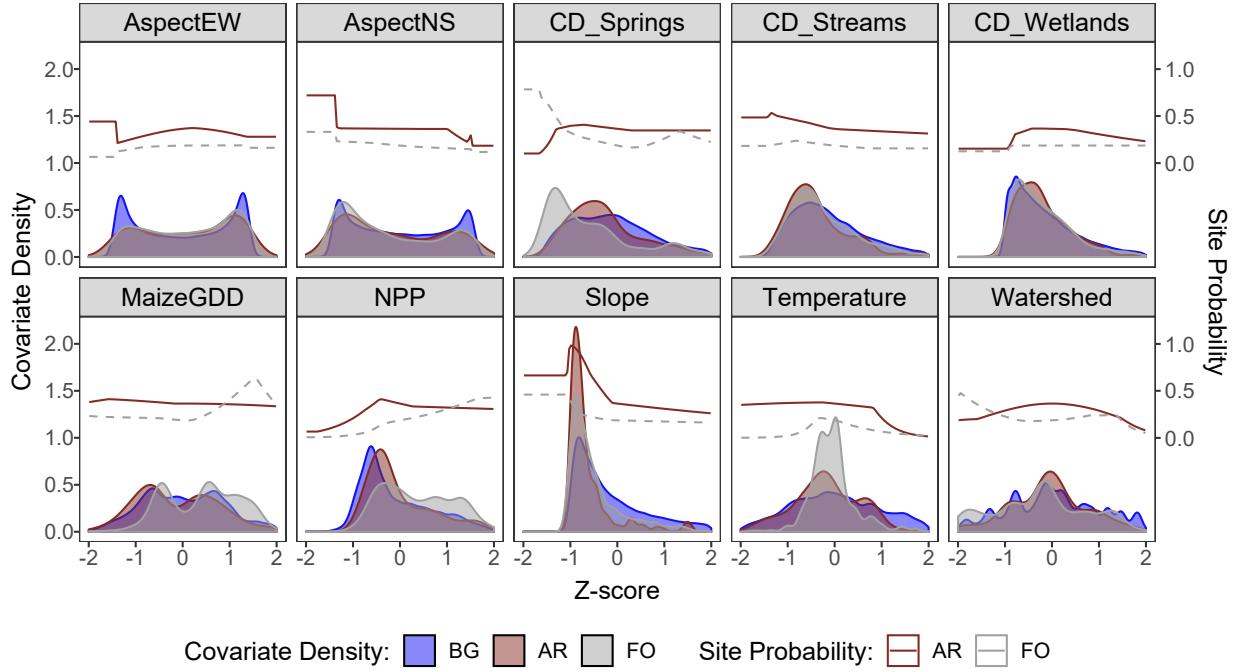


Figure 8: Covariate Density and Marginal Response Plots in Ecological Space. MaxEnt models P_i/B_i , the ratio of covariate density at presence locations (AR and FO) to covariate density at background locations (BG), with regularization to avoid over-fitting. MaxEnt then converts that ratio into a probability using the cloglog transform. The result is a marginal response plot, a line showing the response of each subsistence strategy (solid red for AR and dashed gray for FO) to change in the covariate at the margin, the “average” habitat in this case, or the point at which other covariates are held at their zero-centered mean.

353 Higher values of NPP ($\mu = 1325.29 \text{ kg-C/m}^2/\text{year}$) and Maize GDD ($\mu = 2896.54^\circ\text{F-sum}$) attract
354 agriculturalists.

355 Probability density functions and marginal response plots are shown together in Fig. 8. In general,
356 the greater the relative entropy (i.e., the greater the KL divergence between the probability densities
357 of a covariate at presence and background locations), the greater the probability of occurrence. For
358 instance, Formative sites tend to be closer to springs than the average background location within
359 the GSENM, as shown by the gray spike around -1.1 standard deviations from the mean. That
360 fact also corresponds to the change in MaxEnt’s modeled response, with higher probabilities of a
361 Formative site occurring at the same z-score value of the covariate, as shown by the grey line. The
362 overall trend is also indicated by the negative log- β in linear PPM (c).

363 Fig. 9 shows the geographic distribution of probability estimates, which serves as a proxy for the
364 potential suitability of each location with respect to the Archaic and Formative. The Wilcoxon Sign-

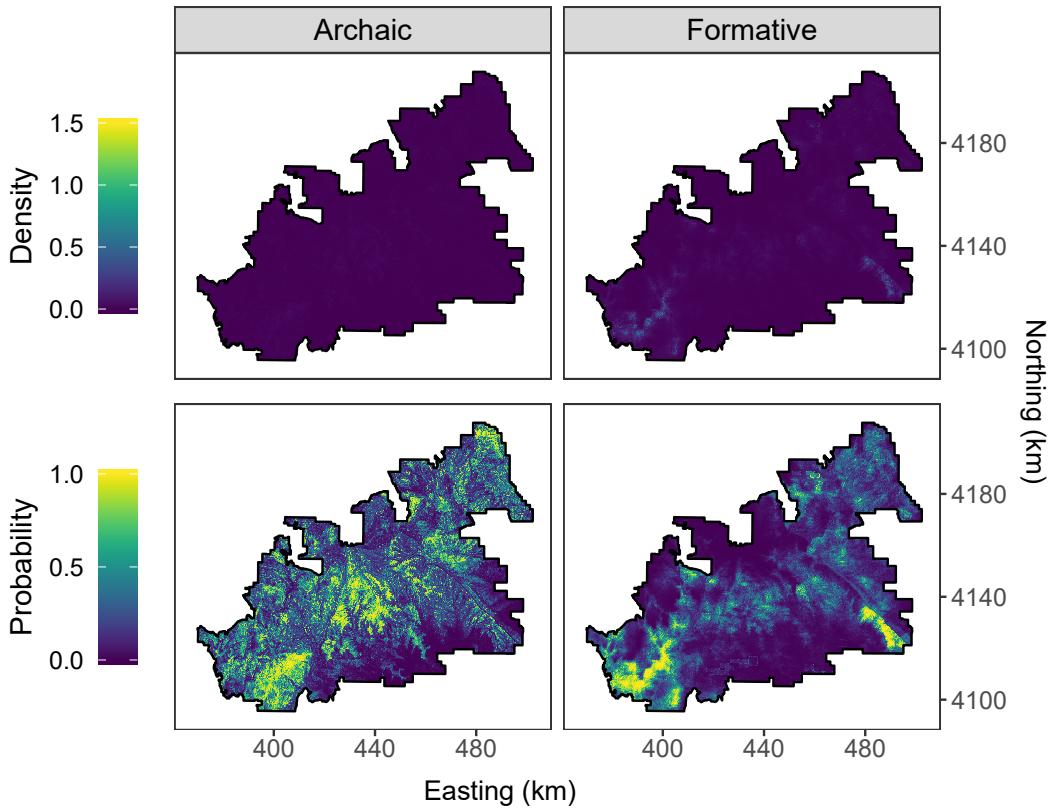


Figure 9: Site Density and Site Probability in Geographic Space. MaxEnt’s raw output is a density estimate standardized by the total number of points in the project area, so these density maps were produced by first multiplying by the total number of points for each time period. The probability at each location represents the potential suitability of that habitat, interpreted as its importance to land use behavior.

365 Ranked Test indicates that the probability maps exhibit significantly different spatial distributions
 366 ($p < 0.0001$). The dispersed area in the central monument along the northwestern most extent of
 367 the Kaiparowits Plateau appears to be highly suitable to Archaic individuals, as is the area around
 368 the Escalante River, the Burr Trail, and Capitol Reef in the northeast of the monument. Values of
 369 PRISM temperature are high in this area, with springs and streams cost-distance evidently being
 370 highly variable. The concentrated area of high probability along Fiftymile Mountain in the southeast
 371 of the monument is evidently highly conducive to maize agriculture. The Vermillion Cliffs area in
 372 the southwest of the monument looks to be a high suitability area across the range of subsistence
 373 strategies explored here. This region is high in Maize GDD, low in levels of slope and cost-distance
 374 to springs and wetlands, and average in conditions for all other covariates.

375 **4 Discussion**

376 Our results show that Archaic hunter-gatherers and Formative maize farmers differ significantly
377 with respect to their land use patterning in the GSENM. Not only are their point patterns not
378 spatially random, they are also significantly different from each other. These two facts together allow
379 us to leverage the spatial distribution of observed density for each strategy to assess the relative
380 importance of environmental covariates (percent contribution, permutation importance, and linear
381 β s) as well as the potential suitability of locations within the GSENM, at least with respect to land
382 use. Presumably, high probability areas for the Formative are also those most conducive to maize
383 agriculture. This may be because lower values of slope and cost-distance to springs indicate ease of
384 irrigation and maize GDD, obviously, more opportunities for production.

385 Our results also have important implications for the region's archaeology. Here we note two. First,
386 according to the Ripley's L test, Formative maize farmers and Archaic hunter-gatherers exhibit
387 clustering at the same range, but at different densities. This seems to be slightly at odds with
388 regional trends, as well as theory, where we expect farmers to be more concentrated in a smaller area
389 owing to their reliance on a single crop and hunter-gatherers to be more dispersed over a larger area
390 owing to their less restrictive dietary requirements. This may be a result of the landscape imposing
391 constraints on neighborhood size, in which case the different strategies are only reflected in the
392 densities within those neighborhoods. In this case, "neighbors" are sites that occur closer together
393 than one would expect by chance, and the "neighborhood" is the spatial extent of that clustering. A
394 landscape constraint then would be something like a canyon that sets an upper limit on the size of a
395 neighborhood, but still allows for different numbers of neighbors within it. Alternatively, this result
396 could be a limitation of the Ripley's L statistic, which does not account for potential differences in
397 the underlying processes generating the spatial patterning we see (Baddeley et al., 2000).

398 Second, reconstructing habitats for each strategy offers an additional avenue to investigate the
399 transition from foraging to farming, allowing us to say with greater confidence whether an "Early
400 Agricultural" site (Spangler et al., 2019; Geib, 1996; McFadden, 2016) is affiliated with a more
401 foraging-like or more farming-like economy. In this case, if we know where Archaic sites are more
402 likely to occur, then absent other dating methods, the occurrence of a site there would suggest
403 an Archaic affiliation; similarly, for the Formative. An example of this would be the Kaiparowits
404 Plateau in the central area of the monument. As shown in Fig. 9, this is a high probability area for
405 the Archaic, but not the Formative; hence, a site there is more likely to be associated with hunting
406 and gathering rather than farming.

407 MaxEnt's marginal response plots in Fig. 8 provide a graphical illustration of the ecological utility
408 function for each covariate and subsistence strategy, showing how suitability varies as a function
409 of the covariate, though importantly without the costs explicitly measured. Note, too, that the

410 probability density function for the covariate at presence locations is analogous to the resource-
411 utilization niche as defined by MacArthur and Levins (1967). The marginal response is, thus, that
412 niche weighted by the background density, which allows us to consider land use choices within the
413 range of alternatives actually available. The probability maps are then those niches projected into
414 habitats found in geographic space, which gives us an idea of their potential suitability.

415 We may also interpret the marginal response as a background-weighted representation of niche-
416 breadth, overlap, and divergence (MacArthur and Levins, 1967). Temperature, for example, shows a
417 unimodal response for both the Archaic and Formative. However, the temperature niche-breadth
418 – the range of the covariate where the probability of occurrence is above a certain threshold – is
419 much narrower for the Formative than it is for the Archaic. As the peaks are centered near zero,
420 this suggests greater sensitivity among agriculturalists to deviations from the mean. Niche-overlap –
421 here defined as the range of the covariate where each strategy has a probability of occurring above a
422 certain threshold – and its complement, niche-divergence, can also be extracted from these results.
423 NPP is a good example of the former, with Archaic and Formative niches overlapping at high values.
424 Watershed size is an interesting example of the latter, with Archaic centered around the mean
425 and flanked by two Formative niches. Were these contemporaneous strategies, niche-overlap and
426 divergence would point to potential locations of resource competition.

427 These points serve as well to highlight an important cautionary tale, that inferences regarding land
428 use will be spurious when insensitive to differences in subsistence efficiency. As Fig. 9 shows quite
429 clearly, individuals who practice different subsistence strategies will use land differently and thus
430 distribute themselves differently across the landscape. This is reinforced by the ANOVA comparing
431 strategy-sensitive and insensitive PPMs. Thus, archaeological applications of the IDM may need to
432 alter proxies of suitability when evaluating settlement across subsistence transitions.

433 We have also shown that modeling the spatial distribution of the density within a Poisson point
434 process framework sheds light on the underlying environmental features composing a habitat
435 and that measures of their importance provide a means of estimating the potential suitability of
436 those habitats. In this sense, PPM is the inductive arm of the deductive IDM. Where the latter
437 structures our expectations regarding optimal settlement behavior, the former tests our hypotheses
438 regarding important constraints and trade-offs. In a related way, the cloglog transform serves as our
439 mathematical inference from density to potential suitability, with the important caveat that these
440 are restricted to land use patterning.

441 With few exceptions (Winterhalder et al., 2010) most ethnographic (Moritz et al., 2013), historic
442 (Yaworsky and Codding, 2017), and archaeological (Kennett, 2005) applications of the IDM begin by
443 establishing proxies of habitat suitability *a priori* and then evaluate qualitative model predictions
444 using settlement data. Here instead we begin by assuming that settlement behavior conforms to

445 the IDM, which is reasonable given broad empirical support (Coddington et al. this issue; Weitzel et
446 al. this issue, Jazwa et al. this issue), and then leverage this assumption to decompose suitability
447 into its environmental covariates. Future studies could expand on this Poisson point process
448 approach by evaluating population-suitability dynamics in archaeological contexts iteratively over
449 time (Winterhalder et al., 2010), and further validating its use with ethnographic cases where
450 individual return rates (E/T) are known, as others have called for (Coddington and Bird, 2015).

451 Before concluding, we emphasize several important confounds that may bias this analysis. First, we
452 constrain our sample of the archaeological record to Archaic and Formative residential sites defined
453 by the presence of certain costly architectural features and heavy groundstone. Obviously, this is
454 an imperfect definition, as it obscures differences in mobility between foragers and farmers, which
455 biases our estimate of the true population density for each strategy. Related to this is the fact that
456 we have flattened variation in the rate of occupation across time, assuming in other words that
457 all sites affiliated with a specific strategy are occupied at the same time. Since the Archaic lasted
458 nearly 6000 years, the Formative only 1500, this is almost certain to further bias our estimate of the
459 true density. To mitigate these worries, we suggest that these would not change the differences we
460 have found, only their magnitude, in fact, exaggerating the differences, with Archaic sites being
461 less densely packed and more dispersed, Formative site more densely packed and less disperseseed.
462 Nevertheless, additional empirical work is needed to evaluate that claim.

463 Another potential confound concerns the fact that data are provided by archaeological records
464 generated from surveys which exhibit bias in sampling effort and detection. Fortunately, ecologists
465 have methods for handling these biases (Warton et al., 2013; Fithian et al., 2015), and those should
466 be applied in future work. Finally, there is the issue of interactions in the point process, where the
467 occurrence of an individual in one location serves either to attract or repel others from distributing
468 themselves in proximity, both spatially and temporally. This is a violation of the independence
469 requirement in the Poisson process, and is highly likely to have occurred given our social tendencies.
470 PPMs have sophisticated tools for accommodating these interactions (Baddeley and Turner, 2000;
471 Baddeley et al., 2015), and future studies should investigate their potential.

472 5 Conclusion

473 The Ideal Distribution Model is a deductive framework within which to investigate variation in
474 prehistoric settlement decisions. When alternative strategies exhibit differences in their efficiency
475 across habitats, those habitats will also differ in their ecological utility and potential suitability, here
476 interpreted as measures of importance for overt land use behavior. Those differences will in turn lead
477 to downstream differences in the spatial occurrence of individuals pursuing different strategies, as
478 well as the distribution of their respective archaeological materials. As it models the distribution of

⁴⁷⁹ populations across habitats, a Poisson point process approach like MaxEnt provides a sophisticated
⁴⁸⁰ set of tools for applying these and other extensions of the IDM framework to actual empirical cases,
⁴⁸¹ such as the forager to farmer transition in the GSENM.

482 References

- 483 AGRC Staff (1984). Utah Automated Geographic Reference Center. Data retrieved August 2019.
- 484 Allee, W. C., Park, O., Emerson, A. E., Park, T., and Schmidt, K. P. (1949). *Principles of animal*
485 *ecology*. W.B. Saunders Company, Philadelphia, PA.
- 486 Baddeley, A., Berman, M., Fisher, N., Hardegen, A., Milne, R., Schuhmacher, D., Shah, R., and
487 Turner, R. (2010). Spatial logistic regression and change-of-support in poisson point processes.
488 *Electron. J. Statist.*, 4:1151–1201.
- 489 Baddeley, A., Diggle, P. J., Hardegen, A., Lawrence, T., Milne, R. K., and Nair, G. (2014). On tests
490 of spatial pattern based on simulation envelopes. *Ecological Monographs*, 84(3):477–489.
- 491 Baddeley, A., Rubak, E., and Turner, R. (2015). *Spatial Point Patterns: Methodology and Applications*
492 with R. Chapman and Hall/CRC Press.
- 493 Baddeley, A. and Turner, R. (2000). Practical maximum pseudolikelihood for spatial point patterns.
494 *Australian & New Zealand Journal of Statistics*, 42(3):283–322.
- 495 Baddeley, A. J., Møller, J., and Waagepetersen, R. (2000). Non-and semi-parametric estimation of
496 interaction in inhomogeneous point patterns. *Statistica Neerlandica*, 54(3):329–350.
- 497 Banks, W. E., Aubry, T., d'Errico, F., Zilhão, J., Lira-Noriega, A., and Peterson, A. T. (2011).
498 Eco-cultural niches of the badegoulian: Unraveling links between cultural adaptation and ecology
499 during the last glacial maximum in france. *Journal of Anthropological Archaeology*, 30(3):359 –
500 374.
- 501 Barlow, K. R. (2002). Predicting maize agriculture among the Fremont: An economic comparison
502 of farming and foraging in the American Southwest. *American Antiquity*, 67:65–88.
- 503 Beck, C., Taylor, A. K., Jones, G. T., Fadem, C. M., Cook, C. R., and Millward, S. A. (2002).
504 Rocks are heavy: transport costs and paleoarchaic quarry behavior in the great basin. *Journal of*
505 *Anthropological Archaeology*, 21(4):481 – 507.
- 506 Berman, M. and Turner, T. R. (1992). Approximating point process likelihoods with glim. *Journal*
507 *of the Royal Statistical Society. Series C (Applied Statistics)*, 41(1):31–38.
- 508 Bettinger, R. L. and Baumhoff, M. A. (1982). The Numic spread: Great Basin cultures in competition.
509 *American Antiquity*, 47:485–503.
- 510 Binford, L. R. (1980). Willow smoke and dogs' tails: Hunter-gatherer settlement systems and
511 archaeological site formation. *American Anthropologist*, 82(4):4–20.
- 512 Boserup, E. (1965). *The Conditions of Agricultural Growth: The Economics of Agrarian Change*
513 *under Population Pressure*. Aldine, Chicago, Illinois.
- 514 Charnov, E. L. (1976a). Optimal foraging: attack strategy of a mantid. *The American Naturalist*,
515 110(971):141–151.
- 516 Charnov, E. L. (1976b). Optimal foraging, the marginal value theorem. *Theoretical Population*
517 *Biology*, 9:129–136.
- 518 Codding, B. F. and Bird, D. W. (2015). Behavioral ecology and the future of archaeological science.
519 *Journal of Archaeological Science*, 56:9–20.

- 520 Codding, B. F. and Bliege Bird, R. (2012). Should I stay or should I go now? the spatial dynamics
521 of foraging and diminishing returns. *Australian Archaeology*, 74:18–19.
- 522 Codding, B. F. and Jones, T. L. (2013). Environmental productivity predicts migration, demographic
523 and linguistic patterns in prehistoric California. *Proceedings of the National Academy of Sciences*,
524 110:14569–14573.
- 525 Coltrain, J. B., Janetski, J. C., and Carlyle, S. W. (2007). The stable- and radio-isotope chemistry
526 of western basketmaker burials: Implications for early puebloan diets and origins. *American
527 Antiquity*, 72(2):301–321.
- 528 Coop, L. (2014). US Degree-Day Mapping Calculator. Data retrieved August 2017.
- 529 Dudík, M., Phillips, S. J., and Schapire, R. E. (2004). Performance guarantees for regularized
530 maximum entropy density estimation. In Shawe-Taylor, J. and Singer, Y., editors, *Learning
531 Theory*, pages 472–486, Berlin, Heidelberg. Springer Berlin Heidelberg.
- 532 d'Errico, F. and Banks, W. E. (2013). Identifying mechanisms behind middle paleolithic and middle
533 stone age cultural trajectories. *Current Anthropology*, 54(S8):S371–S387.
- 534 d'Errico, F., Banks, W. E., Warren, D. L., Sgubin, G., van Niekerk, K., Henshilwood, C., Daniau,
535 A.-L., and Goni, M. F. S. (2017). Identifying early modern human ecological niche expansions and
536 associated cultural dynamics in the south african middle stone age. *Proceedings of the National
537 Academy of Sciences*, 114(30):7869–7876.
- 538 Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R.,
539 Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion,
540 G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A.,
541 J. Phillips, S., Richardson, K., Scachetti-Pereira, R., E. Schapire, R., Soberón, J., Williams,
542 S., S. Wisz, M., and E. Zimmermann, N. (2006). Novel methods improve prediction of species'
543 distributions from occurrence data. *Ecography*, 29(2):129–151.
- 544 Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., and Yates, C. J. (2011). A statistical
545 explanation of maxent for ecologists. *Diversity and Distributions*, 17(1):43–57.
- 546 Emlen, J. M. (1966). The role of time and energy in food preference. *The American Naturalist*,
547 100(916):611–617.
- 548 Fithian, W., Elith, J., Hastie, T., and Keith, D. A. (2015). Bias correction in species distribution
549 models: pooling survey and collection data for multiple species. *Methods in Ecology and Evolution*,
550 6(4):424–438.
- 551 Fithian, W. and Hastie, T. (2013). Finite-sample equivalence in statistical models for presence-only
552 data. *Ann. Appl. Stat.*, 7(4):1917–1939.
- 553 Fretwell, S. D. and Lucas, H. L. (1969). On territorial behavior and other factors influencing habitat
554 distribution in birds I. theoretical development. *Acta Biotheoretica*, 19:16–36.
- 555 Galletti, C. S., Ridder, E., Falconer, S. E., and Fall, P. L. (2013). Maxent modeling of ancient and
556 modern agricultural terraces in the troodos foothills, cyprus. *Applied Geography*, 39:46 – 56.
- 557 Geib, P. (1996). Early agricultural period: Transition to farming. In Geib, P., editor, *Glen Canyon
558 Revisited*, volume 119 of *University of Utah Anthropological Papers*, pages 53–77.

- 559 Hastie, T. (2013). Generalized additive models. v1.09 <http://cran.r-project.org/web/packages/gam>.
- 560 Hastie, T. and Fithian, W. (2013). Inference from presence-only data; the ongoing controversy.
Ecography, 36(8):864–867.
- 562 Hawkes, K. and O'Connell, J. F. (1992). On optimal foraging models and subsistence transitions.
Current Anthropology, 33:63–66.
- 564 Hijmans, R. J., Phillips, S., Leathwick, J., and Elith, J. (2017). *dismo: Species Distribution Modeling*.
R package version 1.1-4.
- 566 Jaynes, E. T. (1957). Information theory and statistical mechanics. *Phys. Rev.*, 106:620–630.
- 567 Kelly, R. L. (1992). Mobility/sedentism: Concepts, archaeological measures, and effects. *Annual
Review of Anthropology*, 21:43–66.
- 569 Kennett, D. J. (2005). *The Island Chumash: Behavioral Ecology of a Maritime Society*. University
570 of California Press, Berkeley.
- 571 Kennett, D. J., Anderson, A. J., and Winterhalder, B. (2006). The ideal free distribution, food
572 production, and the colonization of oceania. In Kennett, D. J. and Winterhalder, B., editors,
Human Behavioral Ecology and the Origins of Agriculture, pages 265–288. University of California
573 Press, Berkeley.
- 575 Kondo, Y. (2015). An ecological niche modelling of upper palaeolithic stone tool groups in the kanto-
576 koshinetsu region, eastern japan. *The Quaternary Research (Daiyonki-Kenkyu)*, 54(5):207–218.
- 577 Kvamme, K. L. (2005). There and back again: Revisiting archaeological locational modeling. In
578 *GIS and archaeological site location modeling*, pages 23–55. CRC Press.
- 579 MacArthur, R. H. and Levins, R. (1967). The limiting similarity, convergence, and divergence of
580 coexisting species. *The American Naturalist*, 101(921):377–385.
- 581 MacArthur, R. H. and Pianka, E. R. (1966). On optimal use of a patchy environment. *The American
582 Naturalist*, 100:603–609.
- 583 Magargal, K. E., Parker, A. K., Vernon, K. B., Rath, W., and Codding, B. F. (2017). The ecology of
584 population dispersal: Modeling alternative basin-plateau foraging strategies to explain the numic
585 expansion. *American Journal of Human Biology*, 29(4):e23000–n/a. e23000.
- 586 McCool, W. C. and Yaworsky, P. M. (2019). Fight or flight: An assessment of fremont territoriality
587 in nine mile canyon, utah. *Quaternary International*, 518:111 – 121. SI: Territorial Behavior and
588 Ecology.
- 589 McFadden, D. A. (2016). *Formative Chronology and Site Distribution on the Grand Staircase-
590 Escalante National Monument*, volume 28 of *The Utah Bureau of Land Management Cultural
591 Resource Series*.
- 592 McMichael, C. H., Palace, M. W., Bush, M. B., Braswell, B., Hagen, S., Neves, E. G., Silman, M. R.,
593 Tamanaha, E. K., and Czarnecki, C. (2014a). Predicting pre-columbian anthropogenic soils in
594 amazonia. *Proceedings of the Royal Society B: Biological Sciences*, 281(1777):20132475.

- 595 McMichael, C. H., Palace, M. W., and Golightly, M. (2014b). Bamboo-dominated forests and pre-
596 columbian earthwork formations in south-western amazonia. *Journal of Biogeography*, 41(9):1733–
597 1745.
- 598 McMichael, C. N. H., Matthews-Bird, F., Farfan-Rios, W., and Feeley, K. J. (2017). Ancient human
599 disturbances may be skewing our understanding of amazonian forests. *Proceedings of the National
600 Academy of Sciences*, 114(3):522–527.
- 601 Merow, C., Smith, M. J., and Silander Jr, J. A. (2013). A practical guide to maxent for modeling
602 species' distributions: what it does, and why inputs and settings matter. *Ecography*, 36(10):1058–
603 1069.
- 604 Morgan, C. (2015). Is it intensification yet? current archaeological perspectives on the evolution of
605 hunter-gatherer economies. *Journal of Archaeological Research*, 23(2):163–213.
- 606 Moritz, M., Scholte, P., Hamilton, I. M., and Kari, S. (2013). Open access, open systems: Pastoral
607 management of common-pool resources in the chad basin. *Human Ecology*, 41:351–365.
- 608 Numerical Terradynamic Simulation Group (2013). MODIS Global Evapotranspiration Project
609 (MOD16). Accessed August 2017.
- 610 Parker, A. K., Parker, C. H., and Codding, B. F. (2018). When to defend? optimal territoriality
611 across the numic homeland. *Quaternary International*.
- 612 Parker, G. and Sutherland, W. (1986). Ideal free distributions when individuals differ in competitive
613 ability: phenotype-limited ideal free models. *Animal Behaviour*, 34(4):1222 – 1242.
- 614 Parker, G. A. (1978). Searching for mates. In *Behavioural Ecology*, volume 1, pages 214–244. Oxford,
615 UK: Blackwell Scientific.
- 616 Phillips, S. (2017). A brief tutorial on maxent. Available from url:
617 http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on 2019-6-13.
- 618 Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., and Blair, M. E. (2017). Opening the
619 black box: an open-source release of maxent. *Ecography*, 40(7):887–893.
- 620 Phillips, S. J., Anderson, R. P., and Schapire, R. E. (2006). Maximum entropy modeling of species
621 geographic distributions. *Ecological Modelling*, 190(3):231 – 259.
- 622 Phillips, S. J. and Dudík, M. (2008). Modeling of species distributions with maxent: New extensions
623 and a comprehensive evaluation. *Ecography*, 31(2):161–175.
- 624 Phillips, S. J., Dudík, M., and Schapire, R. E. (2004). A maximum entropy approach to species
625 distribution modeling. In *Proceedings of the Twenty-first International Conference on Machine
626 Learning*, ICML '04, pages 83–, New York, NY, USA. ACM.
- 627 Phillips, S. J. and Elith, J. (2013). On estimating probability of presence from use–availability or
628 presence–background data. *Ecology*, 94(6):1409–1419.
- 629 PRISM Climate Group (2019). Parameter-elevation Regressions on Independent Slopes Model
630 (PRISM). Data retrieved August 2019.
- 631 R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for
632 Statistical Computing, Vienna, Austria.

- 633 Renner, I. W., Elith, J., Baddeley, A., Fithian, W., Hastie, T., Phillips, S. J., Popovic, G., and
634 Warton, D. I. (2015). Point process models for presence-only analysis. *Methods in Ecology and*
635 *Evolution*, 6(4):366–379.
- 636 Renner, I. W. and Warton, D. I. (2013). Equivalence of maxent and poisson point process models
637 for species distribution modeling in ecology. *Biometrics*, 69(1):274–281.
- 638 Ripley, B. D. (1977). Modeling spatial patterns. *Journal of the Royal Statistical Society, Series B.*,
639 39:172–212.
- 640 Shannon, C. E. (1948). A mathematical theory of communication. *The Bell System Technical*
641 *Journal*, 27(3):379–423.
- 642 Simms, S. R. (2008). *Ancient Peoples of the Great Basin and the Colorado Plateau*. Left Coast
643 Press.
- 644 Spangler, J. D., Yaworsky, P. M., Vernon, K. B., and Codding, B. F. (2019). *Hisatsinom of the*
645 *High Plateaus: A Class I Overview of Prehistoric Cultural Resources in Grand Staircase-Escalante*
646 *National Monument*. Bureau of Land Management.
- 647 Sutherland, W. J. (1996). *From Individual Behaviour to Population Ecology*. Oxford University
648 Press, New York, NY.
- 649 Tobler, W. R. (1993). Three presentations on geographical analysis and modeling: Non-isotropic
650 geographic modeling, speculations on the geometry of geography and, global spatial analysis.
651 Technical Report 93 (1), National Center for Geographic Information and Analysis.
- 652 U.S. Geological Survey (2019). The national map, 3dep products and services: The national map,
653 3d elevation program web page. accessed 2019.
- 654 Wachtel, I., Zidon, R., Garti, S., and Shelach-Lavi, G. (2018). Predictive modeling for archaeological
655 site locations: Comparing logistic regression and maximal entropy in north Israel and north-east
656 China. *Journal of Archaeological Science*, 92:28 – 36.
- 657 Warton, D. I., Renner, I. W., and Ramp, D. (2013). Model-based control of observer bias for the
658 analysis of presence-only data in ecology. *PLOS ONE*, 8(11):1–9.
- 659 Warton, D. I. and Shepherd, L. C. (2010). Poisson point process models solve the “pseudo-absence
660 problem” for presence-only data in ecology. *Ann. Appl. Stat.*, 4(3):1383–1402.
- 661 Wilson, P. D. (2011). Distance-based methods for the analysis of maps produced by species
662 distribution models. *Methods in Ecology and Evolution*, 2(6):623–633.
- 663 Winterhalder, B., Kennett, D. J., Grote, M. N., and Bartruff, J. (2010). Ideal free settlement of
664 California’s Northern Channel Islands. *Journal of Anthropological Archaeology*, 29:469–490.
- 665 Yaworsky, P. M. and Codding, B. F. (2017). The ideal distribution of farmers: Explaining the
666 euro-american settlement of utah. *American Antiquity*, page 1–16.
- 667 Yaworsky, P. M., Vernon, K. B., Spangler, J. D., Brewer, S. C., and Codding, B. F. (in review).
668 Advancing predictive modeling in archaeology: An evaluation of regression and machine learning
669 methods on the grand staircase-escalante national monument. *PLOS ONE*.

670 **Author Biographies**

671 **Kenneth Blake Vernon** is pursuing a PhD in Anthropology at the University of Utah and is the
672 assistant director of the University of Utah Archaeological Center. His research explores variation in
673 human behavior within the framework of behavioral ecology. Currently, he is using geographic and
674 spatial modeling techniques to investigate the nexus of climate, conflict, and human migration in
675 the prehistory of the American Southwest. In addition, he is working to advance data management
676 and data science in archaeology. \

677 **Peter M. Yaworsky** is a Ph.D. candidate in Anthropology at the University of Utah. His research
678 uses insights from behavioral ecology to explore the variation in both past and present human
679 behavior. Peter is particularly interested in decisions people make regarding land use on regional
680 scales. His current research focuses on the distribution of archaeological sites in the Grand Staircase-
681 Escalante National Monument, Utah and the site placement of early agriculturalists in Nine Mile
682 Canyon, Utah as a function of risk mitigation. \

683 **Jerry Spangler** is the Director of the Colorado Plateau Archaeological Alliance. He specializes in
684 the prehistoric archaeology of the Colorado Plateau and has extensive experience synthesizing records
685 across the region. His current research includes the compilation of a comprehensive radiocarbon
686 database for the Basin-Plateau region. \

687 **Simon Brewer** is Assistant Professor of Geography at the University of Utah. He specializes
688 in understanding past and present climate and vegetation change through the application of
689 paleoecological methods and environmental modeling. Current research explores the functional
690 diversity of past ecosystems relative to climate and fire regimes. \

691 **Brian F. Codding** is Associate Professor of Anthropology and Director of the Archaeological
692 Center at the University of Utah. His research examines human-environment interactions in the
693 past and present through the lens of behavioral ecology. Current research is focused on explaining
694 the dynamics structuring subsistence and land use decisions, and the feedbacks these decisions have
695 on social and ecological systems and across western North America.