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## **A Network Theory of Hunter-Gatherer Population Distribution**

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We develop a network theory of population distribution among mobile hunter-gatherers. This theory proposes that, due to the heterogeneity of resources in space and time, foragers create networks of habitats that they access through residential cycling and shared knowledge. The degree of cycling that individuals exhibit in creating networks of habitats, encoded through social relationships, depends on the relative scarcity of resources and fluctuations in those resources. Using a dynamic model of hunter-gatherer population distribution, we illustrate that increases in population density, coupled with shocks to a biophysical or social system, creates a selective environment that favors habitat partitioning and investments in social mechanisms that control the residential cycling of foragers on a landscape. The archaeological record of the Texas Coastal Plain (TCP) provides a starting point to ground our theory. A preliminary analysis of the long-term energy consumption patterns and investments in burials and grave goods on the TCP conforms to the model's predictions. Our work extends the Ideal Free Distribution the workhorse population distribution model in human behavioral ecology and illustrates a general variance reduction, safe-operating space tradeoff among mobile human foragers that drives social change.

### **Keywords:**

# A network theory of hunter-gatherer population distribution

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## Abstract

We develop a network theory of population distribution among mobile hunter-gatherers. This theory proposes that, due to the heterogeneity of resources in space and time, foragers create networks of habitats that they access through residential cycling and shared knowledge. The degree of cycling that individuals exhibit in creating networks of habitats, encoded through social relationships, depends on the relative scarcity of resources *and* fluctuations in those resources. Using a dynamic model of hunter-gatherer population distribution, we illustrate that increases in population density, coupled with shocks to a biophysical or social system, creates a selective environment that favors habitat partitioning and investments in social mechanisms that control the residential cycling of foragers on a landscape. The archaeological record of the Texas Coastal Plain (TCP) provides a starting point to ground our theory. A preliminary analysis of the long-term energy consumption patterns and investments in burials and grave goods on the TCP conforms to the model's predictions. Our work extends the Ideal Free Distribution—the workhorse population distribution model in human behavioral ecology—and illustrates a general variance reduction, safe-operating space tradeoff among mobile human foragers that drives social change.

## Introduction

The Texas Coastal Plain (TCP) contains some of the oldest and longest used hunter-gatherer mortuary sites in the Americas. Hunter-gatherer mortuary locations, rates of burial and rates of grave good deposition on the TCP all provide deep-time records with enormous potential to evaluate models of how foraging populations distribute on a landscape [1–9]. Researchers on the Texas Coastal Plain have long argued that the development of a hunter-gatherer mortuary complex between 7000 and 750 cal BP reflects specialization in the use of particular resource zones—habitat partitioning—and the development of territorial ownership [1–9]. By 7,000 cal BP, TCP foragers established small cemeteries centered on the use of resources from the Gulf of Mexico and inland along freshwater streams and uplands [1, 2]. Around 3,000 cal BP, cemeteries expanded quickly, peaking in the number of locations and the number of interred individuals between 1,000 and 750 cal BP [1, p.137] (see also [3–5, 7–9]). Importantly, during this time-period, human bone isotope evidence indicates a restricted use of resources within well delineated habitat types (e.g., riverine savanna vs.

coastal estuary) [2,10]. Why? What mechanisms led foragers to partition their use of space on the prehistoric TCP?

In this paper, we build and analyze a spatially explicit model of coupled population and resource dynamics to investigate this question. The model allows us to isolate the social-ecological conditions that may cause a population of foragers to partition in space and time, focusing on a narrow range of habitats. The model describes the distribution of foraging populations as individuals respond to seasonal changes in the availability of resources, as well as longer-term changes in climate and population. The model that we build is more complex than typical optimal foraging models, such as the Ideal Free Distribution [11–13], because the model describes important feedback relationships between resources, individual foraging and land use; however, the model is also less complex than agent based models that describe more details of particular systems (e.g., [14–16]). Building the model in this “sweet spot” of intermediate complexity makes operational a general network theory of hunter-gatherer population distributions in space and illustrates a variance reduction, safe-operating space tradeoff, in which individual decisions to maximize the stability of the food supply in the short-run creates a social-economic system vulnerable to disruption in the longer-run. Such trade-offs, we propose, provide one mechanism that causes hunter-gatherers to partition in space and adopt more labor intensive institutions and technologies. We juxtapose the model’s insights with mortuary and radiometric data from the TCP, finding initial congruence between the predictions of the model and patterns in the archaeological record.

## Population distribution, partitioning and territoriality

Our work builds upon the Ideal Free Distribution (IFD), which links individual decisions about where to locate in space with a populations’ distribution on a landscape [13]. The IFD assumes that individuals locate in the habitat where they maximize their fitness, are asocial, have complete information on the quality of the habitats that compose a landscape and are free to move between habitats [17]. Applications of the IFD to human populations illustrate that the model helps explain where individuals will first choose to reside when entering a new region, as well as differences in population density between habitats that vary in their quality [11, 12, 18]. However, the IFD fails to inform us about crucial processes relevant for understanding the distribution of human foraging populations over long spans of time and the emergence of habitat partitioning and territoriality.

First, the IFD is an equilibrium or long-run average concept, and this concept does not capture practical issues, such as the costs of information and movement. Specifically, if there are identifiable cultural groups, the IFD allows them to distribute in at least two indistinguishable ways: (1) foragers may cycle and completely mix in space and time, or (2) foragers may partition in space so that the average density over the whole space and over time is the IFD. <sup>1</sup> More concretely, the application of the IFD to explain the distribution of foragers in modern fisheries illustrates that stable and equal return rates in alternative fishing habitats can either emerge from multiple boats (individuals) cycling through habitats (mixing in space and time), or the same boats constantly fishing the same habitat (partitioning in space) [19]. A classic ethnographic example of high rates of forager cycling comes from the Kalahari, where groups of families associate with resources around particular water holes, but the composition of groups within a particular territory (nlore) fluxes as individuals and nuclear families move in and out [20, 21]. Often this flux occurs through reciprocal visiting. “Visitors join residents in the exploitation of resources, and the days take is unobtrusively distributed within the

<sup>1</sup>There is a third possibility that groups may mix in space but partition in time. This is beyond the scope of our inquiry, but could possibly occur among pastoralists.

camp at the days end...No matter where they are from, as long as people are living together in a single camp the more's food is theirs to share" [22, p. 333]. Conversely, among the Modoc of modern day California, territorial "boundaries were precisely defined and understood by the Modoc and transgression meant war" [23, 201]. Families were self-sufficient and tied to particular tracks of territory, with only the sick and elderly experiencing the freedom to move across boundaries with the ease of Kalahari foragers. Either pattern, rapid cycling (!Kung) or slow cycling (Modoc), could lead to an ideal distribution in which the mean fitness (or a proxy for fitness like return rate) of individuals is equal, in the long-run, among alternative habitats.

Second, the IFD implicitly assumes a stable forager–resource structure over the long-term, in which any given habitat is not susceptible to threshold change between multiple equilibria. The idea of multiple equilibria is a paradigm that helps describe change in real systems as potentially dichotomous and punctuated rather than smooth and continuous [24–31]. Any given habitat on a landscape may be modeled as a forager-resource system that constantly changes, but may settle into regimes that approximate stable equilibria. For example, Freeman and Anderies illustrate how either increasing population density or decreasing the the growth rate of resources in a single habitat makes that modeled forager-resource system vulnerable to a flip from a productive equilibrium into a poverty trap equilibrium in which foragers just harvest enough calories for biological maintenance [32]. This is important because, on a landscape with differences in resource endowments, the emergence of habitats that are either productive or degraded (poverty trap) for individual foragers can have a feedback on the decision making of individuals in ways that an IFD does not allow one to imagine. Freeman and Anderies argue, and illustrate evidence consistent with this position, that foragers adopt territorial ownership to reduce uncertainty about where to move on a landscape when many habitats are vulnerable to flips into a poverty trap [32,33]. Though this argument does have the advantage of relating ownership norms to long-term, nonlinear changes in resource use and predictability, it may also put "the cart before the horse." The model lacks spatially explicit dynamics and does not allow one to study the emergence of partitioning, which might logically occur prior to the emergence of territorial ownership.

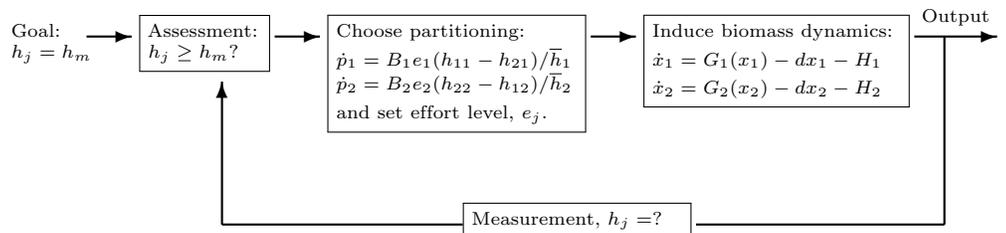
Territoriality refers to rules and norms that restrict entry into a habitat, making entrance more costly due to the existence of social norms or attacks. The degree of partitioning on a landscape refers to the mixing individuals in space and time; a shift from rapid forager cycling (as in the !Kung case above) to slow cycling–habitat partitioning–may provide a necessary condition for the adoption of territoriality (i.e., the transformation of an IFD into a so-called Ideal Despotism Distribution [13]). This is implied by the Model of Economic Defense [34], which we have elsewhere called the area reduction mechanism [33]. Many human behavioral ecologists emphasize that the productivity and predictability of resources drives territory size, and, as productivity and predictability increase, foragers reduce the size of their home-range. In turn, smaller home-ranges increase the net benefits of territoriality for individuals [35,36]. A causal chain is implicit, Chain 1: ecology  $\rightarrow$  partitioning  $\rightarrow$  territoriality. In Chain 1 as a system approaches demographic equilibrium (carrying capacity), foragers reduce their home-range to productive and predictable resources. This steady shift toward smaller home-ranges reduces incentives to cycles through multiple habitats on a landscape and, eventually, foragers partition in space and time. This partitioning increases the net benefits of adopting territoriality for individuals.

Chain 1 contrasts with the argument of Freeman and Anderies above: Chain 2: ecology  $\rightarrow$  territoriality  $\rightarrow$  partitioning. Chain 2 views high forager cycling as a system with a set of reinforcing feed backs. An IDF that is mixed in space and time reinforces itself through networks of information flow, which moderates how effectively foragers

find and harvest food. Territoriality emerges when this information flow fails because individuals who commit to territoriality stabilize flows of information, and thus resources (a proxy for fitness), initiating a new regime of partitioned land use. Evaluating the plausibility of causal chains 1 and 2 requires a spatially explicit dynamical systems model. The model that we construct allows us to run experiments and make statements about the plausibility of each causal chain that standard statistical methods do not allow from observational data alone. The issue is whether foragers can partition prior to adopting territoriality, and if they can, what does that system look like from the perspective of an average forager's fitness? In short, what social-ecological contexts result in a well mixed, rapid cycling ideal distribution of foragers or a partitioned, slow cycling distribution of foragers among habitats?

## A Spatially Explicit Population-Resource Model

To identify the social-ecological conditions under which foragers may form well mixed vs. partitioned distributions, we build a two habitat model (the spatial population distribution model or SPDm). We provide an intuitive description of the model here, and we present the formal equations in the *Model and Methods* section. The basic assumption of SPDm is that resources vary periodically due to an external driver, like fluctuations in rainfall or solar energy (seasonality). This tenet allows us to systematically analyze the consequences of breaking two of the assumptions of the IFD: The assumptions that resources do not vary in time and, by extension, the assumption that foragers have complete information on the availability of resources in alternative habitats. Systematically studying the consequences of breaking these assumptions is critical to explain the emergence of well mixed vs. partitioned distributions of foragers in which the mean fitness of residing in alternative habitats is equal.



**Fig 1.** Basic block, feedback diagram of the SPDm. Equations defined in the *Model and Methods* section. The diagram is read as follows: The goal is set outside the loop, i.e. by physiology, and enters from the left. The feedback loop then operates to iteratively assess whether the goal is being met, adjust effort and spatial partitioning which, in turn, induces biophysical dynamics producing an output (harvest) which is then measured (do I feel hungry) and compared in the next time period to the goal.

Fig. 1 summaries SPDm. In this model, every forager has the goal of obtaining a harvest of energy ( $h_j$ ) greater than a baseline energy target ( $h_m$ ) necessary for reproducing social relationships, maintaining biological function and reproducing biologically ( $h_j > h_m$ ). In order to achieve this goal, a forager chooses how much time to spend harvesting resources from either habitat one or habitat two, which are both affected by harvest pressure and an external driver of productivity (e.g., rainfall or oceanic up-welling). The harvest of resources from habitats one and two, in turn, affects how much time foragers spend in a given habitat (i.e., whether a forager remains

stationary or cycles between the two habitats). Choices about harvest and whether to cycle between habitats results in an output of resources, which foragers then assess against their baseline target and, again, make choices about harvesting and partitioning. This reciprocal system captures three fundamental processes.

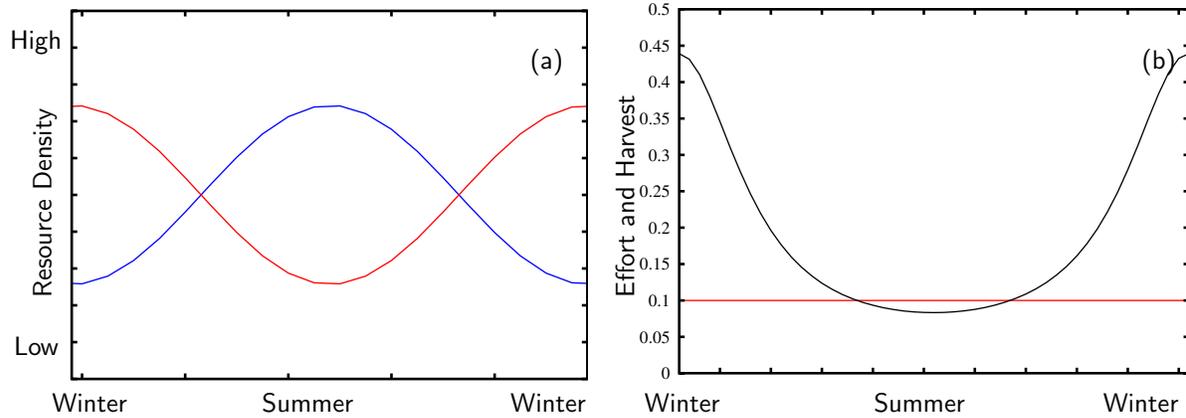
First, there are two habitats in which resources grow ( $G(x_i)$ ) and deplete due to decay ( $d_{x_i}$ ) and harvest pressure ( $H_i$ ). Importantly, the resources in each habitat vary periodically due to external drivers (seasonality). Here we assume that variation in the productivity of the habitats remains out of phase. Resources in one habitat peak during the winter (e.g., the Texas Coast) and resources in the other habitat peak during the summer (e.g., inland gallery forests on the Texas Coastal Plain). Figure 2a illustrates this dynamic. Note that the peaks of the red and blue curves are offset<sup>2</sup>.

Second, two representative agents occupy the habitats. One agent represents the mean forager in group one and one represents group two. Group one has an association with habitat one and group two with habitat two. These associations follow the convention of mobile foragers and form home-ranges. However, the association is fluid and does not represent a cost for other foragers who may move into the habitat (e.g., [22,37]), which contrasts with such costs generated by territoriality [38]. Each forager makes two types of decisions: How much to harvest in a given habitat and whether to use multiple locations and take advantage of the freedom (no coast of movement) generated by the free assumption of the IFD that we replicate. The decision about how much to harvest now in habitat  $i$  is defined by a satisfying process. Foragers simply ask: have I met  $h_m$ ? If the answer is yes, foragers use their excess time to bond socially, rest, etc. If the answer is no, foragers spend their time harvesting resources (see Equations 3-7, *Model and Methods* section). Fig 2b illustrates how this dynamic works, in particular, when forcing a forager to remain in one habitat. The black curve represents time spent harvesting resources and the red curve harvest ( $h_j$ ) in habitat one (the blue curve on Fig 2a). Note that as productivity increases (the blue curve on Fig. 2a rises), work effort declines (the black curve on Fig 2b). The red curve remains constant because, in this case, the stationary forager maintains a constant level of harvest, in response to resource variation, by adjusting their level of foraging effort up or down.

Finally, the benefits of residential cycling between habitats include the acquisition of information and a potentially more consistent supply of resources [39–42]; however, this comes with the opportunity cost of leaving known resources behind. We capture this tension between known and unknown resources by the equations that govern the degree of partitioning or how rapidly foragers mix in space and time (Equations 8-10, *Model and Methods* section). A forager changes the proportion of their time budget in a given habitat by taking into consideration their current proportion of time in a given habitat and the normalized difference in harvest per unit effort between the two possible habitats. This process captures the following heuristic: ‘Does changing my proportion of time in a habitat affect my harvest?’ If yes, then a forager is more willing to change the proportion of time they spend in a given habitat. Willingness to change, however, also depends on how well a forager knows the other habitat. If a forager spends 90 % of their time in habitat one, then they do not know much about habitat two. This uncertainty reduces the willingness to change the proportion of time in habitat one. When the proportion of time in habitat one is 50 %, foragers know both habitats well, and are more willing to alter their strategy. In short, information about alternative habitats and the difference in harvest per unit effort between alternative habitats interact. When foragers cycle between habitats and completely mix in space,

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<sup>2</sup>The assumption that resources vary 180 degrees out of phase fits the resource structure of the Texas Coastal Plain. Please note that qualitatively our results hold for a system in which resources are 90 degrees out of phase as well.



**Fig 2.** Graph (a): Resource dynamics. Red curve ( $x_1$ ) illustrates resource variation of the TCP coast and the blue curve ( $x_2$ ) resource variation inland in riverine areas of the TCP. Graph (b): Harvest dynamics among stationary (partitioned) foragers in the riverine area of the TCP: harvest (red curve) and foraging effort (black curve). The effort curve is identical except that the trough is shifted to the winter when resource density is high and the peak to the summer when resource density is low (red curve in (a)).

information remains abundant and the opportunity costs of leaving known resources low. Thus differences in harvest per unit effort more strongly influence decisions.

In sum, we have a two habitat system described by four ordinary differential equations. In this system, the change in biomass,  $\dot{x}_i$ , effort devoted to foraging for resources  $e_j$ , and the change in the proportion of time spent in a given habitat  $\dot{p}_j$  co-evolve. These equations capture the interplay between uncertainty in the productivity of resources, climate variation, decision making about how much time to spend collecting resources and how much of that time is devoted to a given habitat. The distribution of foragers in space emerges from the interplay of these decision making processes and variability in the availability of resources.

## Model Results

Our analysis illustrates subtle trade-offs and the existence of multiple regimes of land use. We find that rapid forager cycling is a highly effective regime of land use - raises carrying capacity - but also sets a system up for collapse into partitioned groups that potentially live in a “Malthusian Purgatory.”

1. All else equal, above a critical threshold that sets the severity of seasonal changes in resources, rapid forager cycling has a higher maximum population density than slow forager cycling (habitat partitioning). Below this threshold, habitat partitioning results in a higher maximum population density.
2. Increases in the maximum population density at which foragers maintain a consistent level of calorie intake comes with tradeoffs. For example, in low amplitude environments, partitioning increases the maximum population density at which foragers can maintain a consistent intake of calories, but this requires giving-up information about opportunities to find other fitness enhancing resources and, importantly, makes foragers more vulnerable to lower frequency (decade-to-century scale) perturbations. The implication is that longer-term variation in resources favors cycling between habitats.

3. Forager-resource systems experience a general variance reduction, safe-operating space tradeoff. This means that habitat cycling increases the carrying capacity of the environment, reducing variation in the intake of calories for individuals. However, as forager populations approach the carrying capacity of a given social-technological set of strategies, the ability of the ecosystem and social system to withstand perturbations declines, and foragers become vulnerable to cascades of resource failure as they cycle between habitats. This dynamic should favor, in some environments, the adoption of territoriality, and partitioning should emerge from territoriality rather than the other way around.

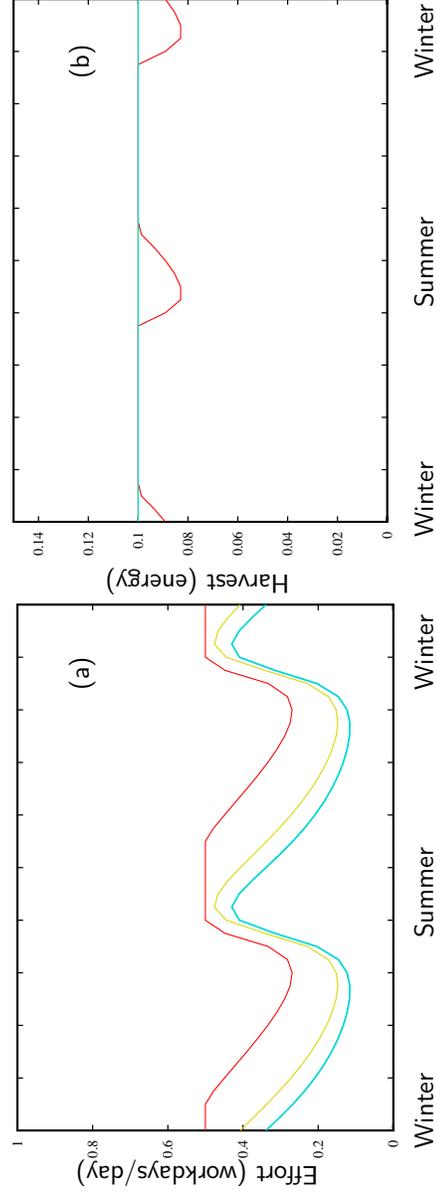
## The advantages of cycling in variable environments

Figure 3 illustrates the benefits of cycling through habitats that boom and bust at different times on a seasonal time-scale. In this case, we force habitat partitioning. This means that we force the representative agent from group one to spend 100 % of her time in habitat one and the same for group two in habitat two. At a low population density (the blue line in Figure 3), resource harvest always meets a forager’s target of calorie uptake ( $h_m$ ). It is only when scarcity emerges that the incentive to cycle on a seasonal time-scale becomes clear (shift from blue-to-yellow-to-red line). At  $N = 3.5$ , for example, during lean periods, foragers work at the max tolerable level (12 hours per day) while falling far short of their calorie target (Figure 3b). This situation is untenable, thus shifting between habitats is essential.

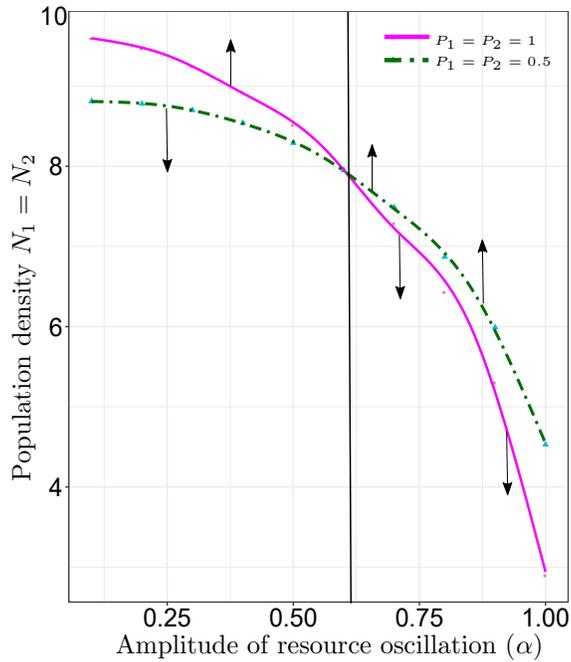
Figure 4 summarizes the result illustrated above in general. Above a threshold of  $\alpha = 0.58$  in the severity of seasonality—the degree of resource boom-bust between winter and summer—forager cycling maximizes the population density at which foragers consistently meet their calorie target ( $h_m$ ) over 50 years. Below this amplitude threshold, habitat partitioning maximizes the population density at which foragers can meet their calorie target. The arrows pointing up above the two curves indicate population densities at which the model transitions into a degraded resource state. In this range of population densities, foragers cannot consistently meet their resource target, no matter what strategy they use. The arrows pointing down from the curves indicate population densities at which both strategies, forager cycling or habitat partitioning, allow foragers to consistently meet their calorie target. The lower a realized population density is relative to the maximum values defined by the curves in Figure 4a, the wider the range of initial conditions at which partitioning and forager cycling are equivalent on an annual time-scale.

However, Figures 5a & b illustrate the recovery time of foragers when a perturbation hits habitat one (e.g., an extended dry period). The results in Figures 5b & c were generated by starting the initial biomass of habitat one at a very low level under two different population densities: one fourth the maximum density at which foragers meet their calorie target (Figure 5a) and one half of the maximum population density (Figure 5b). The x-axis records the initial degree of forager cycling (distribution of population in space), and the y-axis records the time (in years) that it takes foragers to recover from the perturbation to habitat one and converge to meeting their calorie target ( $h_j = h_m$ ). At both levels of population density, higher forager cycling results in a much faster recovery than more partitioning.

For example, in a low population density and aseasonal environment (solid magenta line, 5a), a population of foragers that spends 50 % of their time in each habitat recovers 3/4 of a year faster than a partitioned population. It would not take a very high frequency of such perturbations, perhaps one per decade, to increase fitness for foragers who cycle relative to those who partition. In sum, at small time-scales and low population densities, rapid forager cycling and partitioning seem equivalent, in terms of



**Fig 3.** Foraging effort (a) and harvest (b) over a two-year period in habitat one for increasing population levels when foragers are sedentary. Blue line- $N_i$  for all  $i=1$ ; yellow-green line- $N_i$  for all  $i=2$ ; Red line- $N_i$  for all  $i=3.5$ . The dynamics in habitat 2 are identical. Note that the resource growth rate,  $r$ , and the minimum harvest level  $h_m$ , simply set the units for (or scale the) sustainable population size. Our choice to set  $h_m = 0.1$ , sets the sustainable population size to order 1 (individuals, households, village clusters, depending on the spatial scale of the habitat implied in the units of  $x_i$ , etc.)  $\alpha = 1$ .



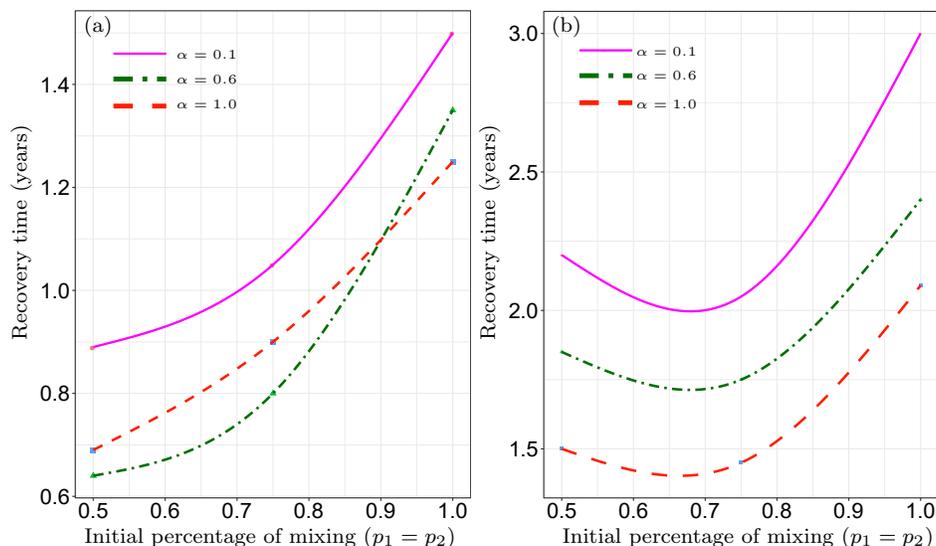
**Fig 4.** Maximum population density at which foragers can maintain a consistent diet that meets the target of  $h_m$  when partitioned ( $p_1 = p_2 = 1$ , solid magenta line) and when mixed ( $p_1 = p_2 = 0.5$ , green-dashed-dot line). In high amplitude environments, migration between habitats has a higher maximum density than no migration, and in low amplitude environments, the opposite is true.

the consistency of calorie intake, but at larger scales forager cycling has a clear advantage. Even at low population densities and in almost unrealistically aseasonal environments, forager cycling increases the consistency and mean of harvests over time. In short, we should expect ideal free distributions that are well mixed in space and time.

### A variance reduction, safe-operating space tradeoff

Fig. 6a-c displays a powerful variance reduction, safe-operating space tradeoff associated with forager cycling. Fig. 6a-c display three phase plots. Phase plots display the relationship between variables that change over time. For example, in Fig. 2a the biomass of habitats one and two vary over time and are 180 degrees out of phase (i.e., when one peaks, the other troughs). An alternative way to plot this relationship is in phase space, plotting the biomass of habitat one on the x-axis, and the biomass of habitat two on the y-axis. In this example, the graph would display a perfect negative correlation. Imagine a movie of a pencil drawing this relationship on the graph. The pencil would start in the lower right corner (habitat one high biomass, habitat two low biomass) and, over time, move along a perfect linear trajectory toward the upper left corner of the graph and then back to the bottom right corner. The pencil will just oscillate along this trajectory over time. Displaying how variables in a dynamical system relate to each other in a phase plot is a powerful tool for studying the coevolution of those variables over time and identifying emergent changes in the structure and typology of a system under different parameter values.

The x-axis on each plot of Fig. 6a-c displays the proportion of time that group one spends in habitat one, and the y-axis displays the proportion of time that group two spends in habitat two. Each plot contains five regions (highlighted on Fig. 6a). Regions

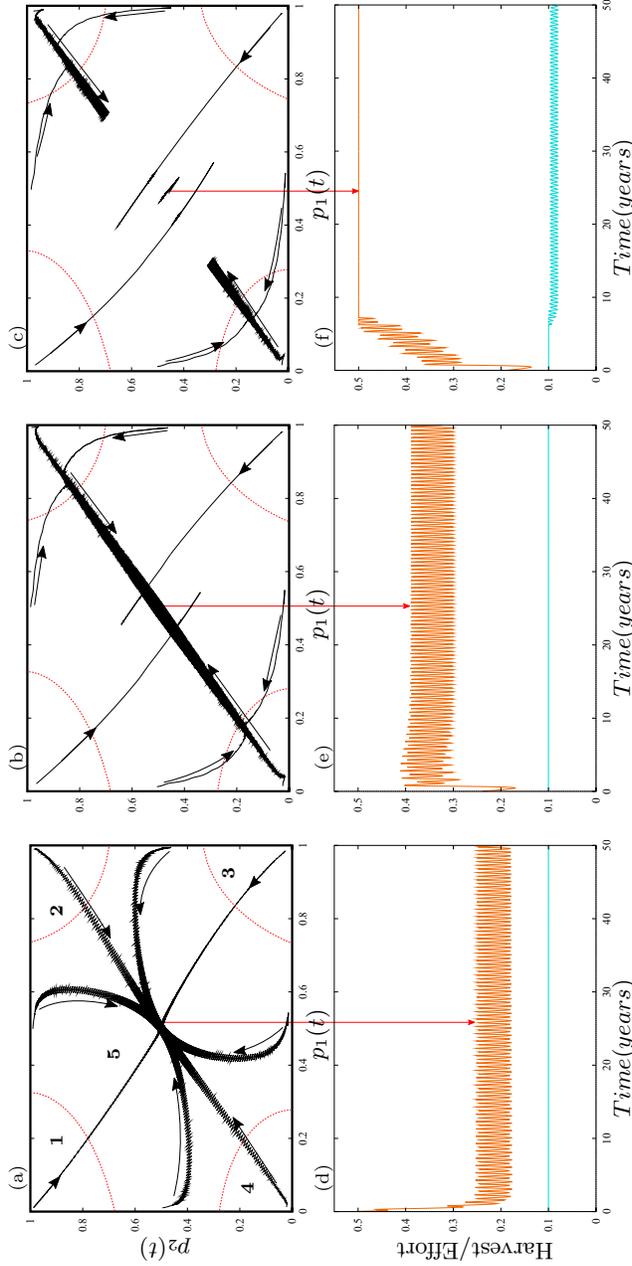


**Fig 5.** The recovery time (y-axis) it takes a population of foragers to consistently meet their calorie target following a perturbation to habitat one (a drought) for different levels of initial cycling (x-axis). Graph (a) population density is  $1/4$  of the maximum population density recorded in Figure 4 for a given level of resource oscillation ( $\alpha$ ). Graph (b) population density is  $1/2$  of the maximum recorded in Figure 4. In general, the graphics illustrate that full partitioning drastically increases recovery time from a perturbation.

1 and 3 are analogous to each other. In these regions, both representative foragers spend near 100 % of their time in the same habitat (Region 1=everyone in habitat two, and Region 3=everyone in habitat one). Regions 2 and 4 are, again, analogous to each other. In these regions, the system displays partitioning. In Region 2 the group two forager spends near 100% of her time in habitat two, and the forager from group one near 100 % of her time in habitat one. Region 4 displays the opposite. The forager from group two spends most of her time in habitat one, and the forager from group one in habitat two. Finally, Region 5 displays mixing in space and over time. At the very center of this region foragers spend, on average, 50 % of their time in each habitat.

The black curves that traverse the above five regions on Fig. 6a-c illustrate the relationship between the proportion of time spent in habitats one and two as the system changes over time. The arrows along the black curves illustrate the direction of change over time. For example, imagine a system that starts at an initial condition in Region 1 on plot Fig. 6a. In this case, the system starts with the forager from groups one and two spending almost 100 % of their time in habitat two. The arrow pointing toward the middle of the graph indicates that, over time, the mean proportion of time each forager spends in each habitat converges to a constant in Region 5, after which the system oscillates with constant mean around 0.5 (a perfectly mixed system with a forager spending 50 % of her time in both habitats).

To give some intuition in terms of foraging populations, Fig. 6 allows us to study how internal changes in the use of space, such as groups aggregating into habitat one for an important ceremony or groups completely partitioning to their associated ‘home-range’ affects the long-term evolution of the system under different population densities. Fig. 6a illustrates that when population density is low, the system is globally robust to changes in the use of space, including highly aggregated populations (e.g.,  $p_1 = 0.99$ ,  $p_2 = 0.01$ ) or highly partitioned populations (e.g.,  $p_1 = p_2 = 0.99$ ). In the



**Fig 6.** Phase plane analysis of spatial effort allocation. In all cases,  $\alpha = 1$ . graphs a-c are phase plots that illustrate changes in the proportion of time allocated to habitats one and two over time by groups one and two for different initial conditions. In graph (a)  $N_i$  for all  $i=2.5$ ; in graph (b)  $N_i$  for all  $i=4.25$ ; in graph (c)  $N_i$  for all  $i=4.5$ . Graphs d-f illustrate total foraging effort (orange curves) and the calorie harvest (blue curve) for a forager in group one when the system converges to a perfectly mixed equilibrium, on average, of  $p_1 = p_2 = 0.5$ . Graphs d-f indicate the mean hours of work a foragers must put-in to gain food and the consistency of hitting the calorie target ( $h_j = h_m$ ) over time when foragers from both groups perfectly mix in space.

parlance of sustainable human-resource systems, the system has a complete safe-operating space. The safe-operating space is literally all of the starting values of  $(p_1, p_2)$  on Fig.6a from which the system will evolve to a state where foragers consistently meet their calorie target. At lower population densities, as a system moves away from extreme values in the corners, foraging effort in habitats one and two ( $e_1(t)$  and  $e_2(t)$ ) quickly drop below the maximum tolerable work level of 0.5 and remain there, oscillating around a mean of 0.21 workdays/day, and foragers consistently meet their target harvest of calories (Fig. 6d). In short, Fig 6a illustrates a system in which forager cycling minimizes variation in the calorie intake of foragers (at multiple scales as demonstrated above) *and* has a complete safe-operating space.

Figure 6b illustrates the consequences of increases in population density to very near carrying capacity (here,  $N_1 = N_2 = 4.25$  &  $\alpha = 1$ ). This increase in population density has two consequences. First, in a perfectly mixed system (rapid forager cycling), foragers continue to meet their calorie target at equilibrium, but at a lower rate of return. For example, Fig. 6e illustrates changes in foraging effort and harvest over time when the system has converged to an equilibrium at  $p_1 = p_2 = 0.5$ . Note that the mean of the orange curve is much higher in Fig. 6e than 6d. This means that foragers are working harder to maintain a constant intake of calories (blue curves in Figs. 6d and e are constants).

Second, the increase in population density reduces the  $p_1$ - $p_2$  space in which foragers can converge to meeting their calorie target. Another way to say this is that Fig. 6e only emerges when the system initially starts within Region 5. If the system starts in Regions 1-4, the system will converge to one that is mixed, but foragers will experience long-term variation in their mean intake of calories (a result analogous to Figure 6f where the blue curve oscillates). In this environment, the processes of aggregation (everyone shifting to one habitat or another) or partitioning (individuals staying within one habitat) results in foragers not converging to meet their resource target. Outside of Region 5, harvest pressure is not allocated equally enough to keep the system from crossing a critical threshold of productivity-to-consumption. Quite literally, the safe-operating space of the system, the range of initial  $(p_1, p_2)$  values from which the strategy of cycling between habitats leads to a consistent supply of resources over the long-term, declines. If foragers become too aggregated or too partitioned, the consequence is oscillating resource shortfalls; a sequence of: good year, shortfall year, good year, shortfall year, etc.

For instance, when the system starts with everyone aggregated in habitat two (Region 1), foragers must start by working as hard as they can to harvest food. This depresses the productivity of habitat two. Because the cost to migrate is zero ( $q_{ij} = 1$  for all  $ij$ ), foragers head for habitat one, which depresses the resources in this habitat and causes foragers, again, to work as hard as they can. Over time, foragers converge back to a mixed system, but it is too late, in a sense, because the resource base in both habitats never has sufficient time to recover. Thus, foragers end up in a long-run equilibrium in which they can meet their resource needs every other year, but also would face about a 10-20 % shortfall every other year. All this is to say that although forager cycling reduces variation in the calorie intake of individuals and raises the carrying capacity of many environments, the very success of the cycling strategy (leading to population growth until near carrying capacity) reduces the ability of foragers to aggregate and disperse without causing targeted resources to vary unexpectedly as a consequence of their movements. This is known as a variance reduction, safe-operating space tradeoff. The vary strategy used to reduce variation in the intake of calories leads to a decline in the size of the safe operating-space of the system. This is not something foragers could necessarily recognize unless they experienced the negative consequences.

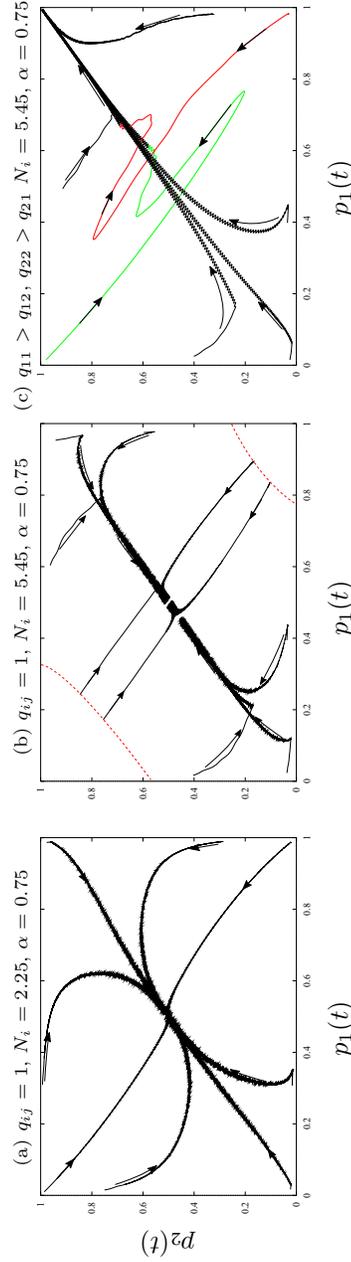
Figure 6c illustrates a population density above the carrying capacities identified in

Figure 4a ( $N_1 = N_2 = 4.55$  &  $\alpha = 1$ ) and, in this case, there is no safe-operating space. All initial values of  $(p_1, p_2)$  lead to a situation in which foragers do not meet their calorie target, regardless of whether they cycle or partition. In the long-run, effort is maxed ( $e_i(t) = e_x$ ), and harvest is less than the preferred target ( $h_j(t) < h_m$ ) for some time intervals in the annual cycle (Figure 6f). This opens up a region in  $p_1 - p_2$  space that cannot be reached from all initial conditions (i.e., generates habitat partitioning). In this setting, the long run mean proportion of time spent in a given habitat depends on initial conditions, creating a barrier between Regions 2 and 4 because the capacity of the internal dynamics of the system to reach well mixed states is limited, and only exogenous forcing (e.g., climate variation beyond normal seasonality) can temporarily mix the system.

Bottom line: foragers have overshot carrying capacity and entered a “Malthusian Purgatory.” No matter whether they cycle or not, they cannot meet their desired energy target. Thus, initial conditions determine the degree of partitioning. More technically, when foragers work as hard as tolerable, their choices about foraging in different habitats decouple from variation across habitats. Put another way, under conditions of relative abundance ( $e_i(t) < e_x$ ) foragers adjust effort to create a match between their calorie uptake and desired calorie uptake (move  $h_j(t)$  toward  $h_m$ ). This decision impacts biomass ( $x_i$ ) which, in turn, impacts foraging effort ( $e_i(t)$ ), which starts the cycle anew. Thus, foraging effort ( $e_i(t)$ ) depends on both the proportion of time in a given habitat ( $p_i$ ) and biomass ( $x_i$ ), coupling their dynamics in such a way as the average over an annual cycle of  $p_1$  and  $p_2$  become equal. However, when foraging effort equals the maximum tolerable effort ( $e_i(t) = e_x$ ), foraging effort  $e_i(t)$  no longer depends on time in a habitat ( $p_i$ ) and biomass ( $x_i$ ), it is simply a constant. This weakens the coupling between the proportion of time in a habitat and the biomass of a habitat. Thus, a distribution of foragers in space that is mixed (cycling) bifurcates into one that is potentially partitioned, depending on initial conditions.

A subtle lesson with important consequences emerges from the comparison of Fig. 6b and c. In the environment defined by 6b, foragers are vulnerable to a cascade of oscillating resource failures. If foragers respond to, say a drought in habitat one, by aggregating in habitat two for a season, then in a system where movement is free, this behavior generates a cascade of resource failures over the following years. But, the resource system still has enough stocked-up biomass that, if a bumper year hits in which productivity is above normal, the system can transition back into one in which individual foragers consistently meet their calorie target. There is still the capacity for foragers to learn that their high cycling strategy is vulnerable and, thus, adjust their strategies to reduce the chances that they experience a sequence of resource shortfalls again. In the environment defined by Fig. 6c, foragers have crossed into a Malthusian Purgatory. Partitioning follows from overshooting the carrying capacity of the environment. The only way to deal with this is a massive migration or suffer prolonged negative fitness for generations, until population is, again, well below carrying capacity and the resource base can recover sufficiently. In order for partitioning to proceed territorially, the system must cross into Malthusian purgatory, and foragers must respond by adopting territoriality. As Cowgill noted long ago, changes in strategy are unlikely in such a situation; rather depression and stagnation are likely because individuals lack adaptive capacity [43]. Who wants to claim ownership over a habitat with negative fitness for an average forager?

Partitioning in real systems is not likely a simple consequence of changes in equilibrium resource abundance and competition among foragers in different habitats—Chain 1 in the introduction. Rather, partitioning results from a complex interaction of resource abundance, the perception of foragers, the dynamics of knowledge creation and movement.



**Fig 7.** Phase plane analysis of spatial effort allocation; curves represent the  $p_1 - p_2$  space in which foragers can converge to consistently meeting their resource target  $h_m$ . As population density increases from (a) to (b), the  $p_1 - p_2$  space in which foragers can converge to consistently meeting their resource target  $h_m$  declines. Graphs (c) illustrates the effect of territorial ownership. Territorial ownership enlarges the  $p_1 - p_2$  space in which foragers can converge to the resource target. In all cases,  $e_x = 0.5, r_p = 1$ . In graphs (a)-(c), the amplitude of variation in  $x_1$  &  $x_2$  is held constant at  $\alpha = 0.75$ .

## Territoriality

Fig. 7a-c replicates Fig. 6a-c except in two crucial respects. First, foragers occupy a slightly less variable environment, and, second, in Fig. 7c we keep population density equal to Fig. 7b and break the cardinal assumption of the IFD that it is free to move between habitats due to territorial norms. In particular, we assume that searching for resources within one's home-range is free, but searching for resources outside of one's own home-range has a slight cost (either avoiding attack or securing a ritual gift). In Fig 7a and b, we observe, again, that increasing population density reduces the  $p_1$ - $p_2$  space in which foragers can converge to meeting their resource target. In Fig 7a, again population density is low, and the safe-operating space of the system encompasses all potential values of  $(p_1, p_2)$ . Increasing population density to the level in Fig 7b, decreases the safe-operating space of the system. The black curves on Fig 7b define the safe-operating space. If foragers aggregate beyond the red lines, they will experience cascades of resource short fall that oscillate over time, unless a perturbation increases the productivity of the system.

In this slightly less seasonal environment, territorial ownership has the consequence of enlarging the  $p_1$ - $p_2$  space in which foragers can converge to meeting their calorie target, though the system now always converges to one that is partitioned. This is illustrated by Figure 7c, which introduces a cost for group one to access habitat two and for group two to access habitat one. This cost slows the flow of foragers between habitats in response to differences in harvest per unit effort. In turn, as foragers spend more time in their own habitat, they lose information on the other and discount traveling there relative to harvesting resources in one's own 'home-range.' This dynamic leads to complete partitioning of groups in space and time. Such partitioning based on territorial ownership cannot happen when  $\alpha = 1$  because partitioning creates too much concentrated harvest pressure on a given habitat. However, where  $\alpha = 0.75$  ownership norms allow individuals to consistently meet their resource target, whether they are partitioned or highly aggregated. Foragers can partition because the resource base in each habitat can withstand more intense harvest and foragers can aggregate because territorial ownership prevents a massive swing of population from one habitat to another, slowing down the movement of foragers on a landscape. The adoption of territorial ownership, in an emergent way, stabilizes the harvests of individual foragers by reducing the risk of leaving a system's safe-operating space.

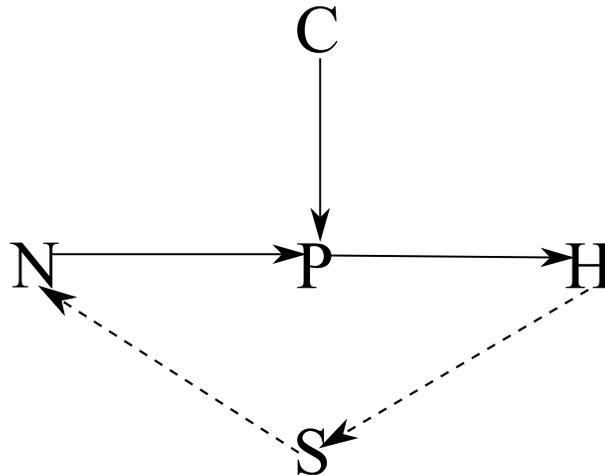
## Discussion: Social Change and Partitioning on the TCP

Our analysis of the SPDm allows us to explore the question posed in the introduction: What potential mechanisms drove habitat partitioning on the TCP? In particular, in a non-linear dynamical system in which the harvest of resources by individuals, biomass production and the degree of partitioning are interdependent, can we identify the chain of interactions that leads to partitioning and territoriality? A powerful way to gain insight into the processes that may lead to high cycling vs. partitioned populations of foragers is to modify the Ideal Free Distribution (IFD) within the framework of the SPDm. In the SPDm, we modify the assumption that foragers have complete information on the resources among alternative habitats on a landscape and that mean resource abundance is stable over time. These modifications move the model closer to the reality that forgers face without attempting to replicate all of the decisions that real foragers face in particular environments. Thus, the SPDm, though more complex than the IFD, retains generality.

The key result of our analysis is the existence of a variance reduction, safe-operating

space tradeoff in the SPDm. This tradeoff is a special type of tradeoff under the more general umbrella of robustness-fragility tradeoffs. This type of tradeoff emerges from individual decisions about the use of habitats and the responses of individuals to changes in resource density. Forager cycling between habitats stabilizes the intake of calories for individuals in the short-run, but the very success of this adaptation may lead to population growth and the emergence of vulnerability to climate change and internal social dynamics in the longer-run (a reduction in safe-operating space). Robustness-fragility tradeoffs are a common feature of social-ecological systems [24, 32, 44–49], and, we argue, under-appreciated mechanisms that drive social change. Such tradeoffs do not determine the form of social change, but set the preconditions for large shifts in strategies for interacting with the environment.

For example, our analysis illustrates that the severity of seasonality and population density interact on smaller time-scales. When population density is low, foragers may partition or cycle between habitats. The two strategies are equivalent (Figs. 3 and 5), if the goal is to maintain a stable supply of calories. Of course, in a low population density environment other incentives beyond a consistent supply of resources at a seasonal time-scale exist to cycle, like finding mates. Similarly, even in aseasonal environments, climate perturbations, like droughts that occur at decade frequencies, generate an incentive to cycle for individuals (Fig. 4). The Texas Coastal Plain is a temperate environment with a moderate-to-high degree of seasonality. Thus, we would expect, at low densities, climate variation on a seasonal and decade scales to favor high cycling (lots of visitation, shifting of group residence and so forth). However, if population density were to increase relative to resources at a landscape level (multiple habitats), rapid forager cycling would insure a consistent diet, but would also cause the safe-operating space of the whole system to decline.



**Fig 8.** Proposed causal diagram of the factors that lead to partitioning. N=Population density, P=productivity, C=climate variation, H=Harvest, and S=Strategy.

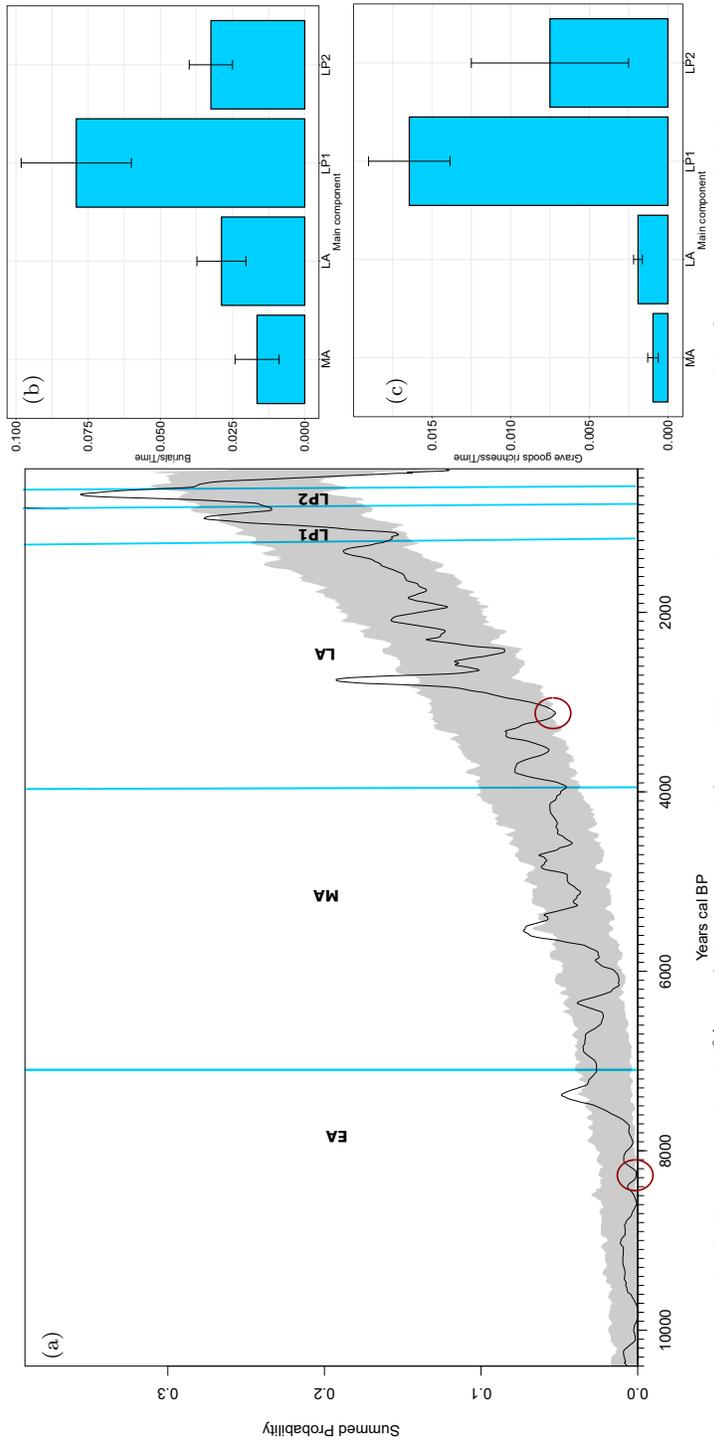
Fig. 8 summarizes a proposed causal chain for the TCP. Population (N) and Climate (C) affect the productivity of resources (P). Foragers apply knowledge to harvest resources and generate a harvest (H) of calories. Harvest feeds back to population, mediated by the strategy (S) used by foragers to monitor the flow of foragers on a landscape (open access, free to cycle vs. ownership, higher cost to cycle). In this loop, forager cycling leads to consistent harvests, in spite of climate shocks, which leads to population growth and, in turn, growth affects productivity and leads to the variance reduction, safe-operating space tradeoff. Two mechanisms might lead to partitioning. The first is descent into Malthusian Purgatory (Fig. 6c). In this case, population would

overshoot carrying capacity and the system of land use would bifurcate into one in which foragers work 12 hours per day where ever they happen to locate. No incentive exists to move. As noted earlier, there would also be very little incentive to adopt territoriality in this situation as it would mean a lot of effort just to maintain a potentially less negative level of fitness. Fitness would still be negative, however. Population migration and long-term depression should follow such a Malthusian overshoot.

Second, climate variation may generate a ‘signal’ to individual foragers a la [32] that they should adapt to stabilize their flow of resources. One form of adaption is territorial ownership, which would lead to habitat partitioning. The role of information in moderating decisions about the proportion of time to spend in any given habitat underlies this mechanism. Recall, rapid cycling creates a more consistent intake of calories and raises the carrying capacity of human foragers on a landscape (Figure 2 & 4), in part through the acquisition of information that makes accessing resources more efficient. Indeed, if foragers were to engage in the exchange of goods and form networks on top of local kin based relationships, this would generate even more bang for the cycling buck. Knowledge infrastructure would generate ever more efficient flows of information and, at least initially, as population density increased foraging would become more efficient [50]. Thus, incentives en-train rapid cycling in foraging economies, even those undergoing increases in population density. The trick to understanding the emergence of partitioning is understanding that even though a rapid cycling strategy is resistant to increases in population density, the safe-operating space of the whole system declines.

A decline in safe-operating space proves a paradox. Reductions in the safe-operating space set foragers up for cascades of resource failure. However, such a process also provides a potential Boserupian escape from Malthusian overshoot. In terms of the TCP, one might imagine a spurt of sea-level rise along the coast that inundates estuaries with salt water. This would depress productivity for a few years as species adjust their ranges and so on, stimulating foragers to aggregate among inland habitats (e.g., Region 1 on Fig. 6). At low population density, no problem. However, as the system approaches carrying capacity and the safe-operating space declines, this behavior would generate resource short-falls that oscillate over time generating a successful year, bad year, successful year, etc. sequence. This very pattern provides a signal that the knowledge infrastructure so integral to cycling between habitats is worthless. The incentive thus arises for foragers to shift their social norms of land use, generating partitioning in an emergent way on the landscape. Crucially, in this scenario the resource system still has enough biomass capital relative to population size that, if a bumper year of productivity hits, the system could transition back into one in which individual foragers consistently meet their calorie target. The capacity exists for foragers to learn and adjust their strategies to reduce the chances that they experience a sequence of resource shortfalls again. This is the basic causal chain for the emergence of a new regime of land use: ecology  $\rightarrow$ territoriality $\rightarrow$ partitioning (or N and C  $\rightarrow$ H $\rightarrow$ S in Fig 8).

We can evaluate the above argument, in an illustrative way, by observing the association between investments in place and changes in the energy output of human foragers on the TCP over the last 10,000 years (cal BP). If a general variance reduction, safe-operating space tradeoff mechanism were at work, we would expect foragers to respond to population growth by intensifying their cycling between habitats and networks of information exchange, but this would lead to vulnerability, to either climate shocks or internal fission-fusion dynamics that might cause higher variance in the intake of calories to emerge at the level of the individuals. In response, we should see more investments in territorial behavior/ownership because this would stabilize the return rates of individual foragers more than continuing with a rapid forager cycling strategy, inadvertently raising the carrying capacity of the TCP and starting the dynamic a new.



**Fig 9.** (a) SPD against time, grey shaded area is the 95% confidence interval from 500 exponential regression models from re-sampled data following the procedure outlined by [51]; (b) Burials per unit of time by each cultural historical period (MA=Middle Archaic, LA=Late Archaic, LP1=Late Prehistoric 1, and LP2=Late Prehistoric 2. (c) Exchange items deposited per unit of time by cultural historical periods.

In short, we should see periods of growth in the foraging systems of the TCP, punctuated disruptions followed by a shift in regime to a higher energy output state and more investment in place by foragers.

We can estimate energy output by using a summed probability distribution of radiocarbon ages from the TCP [52]. A summed probability distribution aggregates the radiocarbon ages associated with human activity and provides a measure of waste output, which is related to both population size and economic activity [53, 54]. We can estimate the degree of investment in place using two simple measures, burials per unit time and exchangeable goods (such as shell beads and pendants) deposited in graves per unit of time. More burials and more exchangeable goods per unit of time associate with territoriality and suggest more investment in particular locations and trade between discrete locations [4–9, 55].

Figure 9a illustrates the change in radiocarbon frequencies over time. The grey shaded area is a 95 percent confidence interval generated by running 500 non-linear exponential regressions of time on the summed probability values. The red circles indicate periods of social-economic disruption not likely due to sample bias or calibration effects. Figures 9b and c illustrate burials and grave goods deposited per unit of time respectively during the cultural historical periods of the Early, Middle and Late Archaic, as well as periods that we call here the Late Prehistoric I and II. Combined, the three graphs in Figure 9 paint a picture consistent with the results of the SPDm.

First, the trend is one of increasing energy consumption through time, and presumably populations as well. Second, a major shift in rates of burial and grave good deposition follow one of the only periods of rapid, short-lived socio-economic disruption that falls outside the 95 % confidence interval. This short-lived disruption around 3200 cal BP follows 6500 years of sustained growth of TCP foraging systems. The spike in the SPD at 3100 cal BP, just following this disruption, is suggestive of a regime shift to a social-ecological system with a higher energy output. If we were witnessing overshoot and collapse dynamics, the SPD would cease sustained growth and begin to display oscillations, but the sustained growth continues until 700 cal BP. Note that burials also spike in the Late Prehistoric period, coincident with an additional SPD spike. The Spike beginning in Late Prehistoric I again occurs just after a period of disruption. This short disruption does not transgress the arbitrary 95% interval, but does exceed the 90th percentile, perhaps indicating another fundamental shift in social-ecological regime. In sum, investments in higher degrees of separation in space on the TCP follow periods of disruption/rapid decline in the energy output signal of TCP foraging economies. And, the foraging economies of the TCP continue to exhibit sustained growth throughout the whole 10,000 year period, until a potential sustained collapse beginning 690 cal BP.

## Directions for future research

The intent of our empirical analysis above should not be construed as a definitive statement. Rather, we would like to emphasize that the data exist to begin evaluating arguments that rely on complex feed backs for the emergence of territoriality and habitat partitioning. Two potential directions for future research include:

1. Rigorously distinguish between population overshoot and collapse vs. a system that experiences a disruption from crossing a safe-operating space boundary, but the individuals still have the capacity to adapt and find new strategies that fundamentally change the system. A true Malthusian system would not experience a regime shift to a higher energy output (higher carrying capacity system), rather the functional relationships between variables would not change. Conversely, our argument for territoriality would imply a fundamental regime shift in the relationship between population growth and land use. Detecting regime

shifts in empirical time-series is a growing area of research and a key to distinguishing between these two scenarios [56–58].

2. A second area of research concerns middle range research on the potential for multiple regimes among ethnographically recorded hunter-gatherers [57]. Again, if our argument has purchase, then we should observe fundamentally different relationships between land use and population among ethnographically documented hunter-gatherers due to partitioning generated by the adoption of territorial norms. The fundamental change in ownership norms should change the way that information moderates land use. Among open access societies, information flow should lead to groups highly resistant to declines in the number of habitats they use, in response to increases in population density.

## Conclusion

In this paper, we have proposed a network theory of mobile hunter-gatherer population distribution, and made this theory operational with a spatial population distribution model (SPDm) built to answer a specific question: What mechanisms might drive the evolution of habitat partitioning? The Ideal Free Distribution served as a starting point for answering this question. The IFD helps explain where migrants into a new landscape will first reside, and the mean population densities of alternative habitats, at equilibrium, on a landscape over long-time spans. With respect to mobile foraging economies, however, the model does not allow one to distinguish between a stable distribution of mean population densities formed as individuals cycle among habitats and social groups vs. a stable distribution of mean population densities composed of stable groups of individuals partitioned to particular habitats. The ability to predict when individuals will cycle among social groups and, thus, habitats, vs. partition is critical for explaining not only the evolution of territorial norms of ownership, but also the intensification of production and emergent inequalities in hunter-gatherer societies. We argue that major changes in the distributions of hunter-gatherers relate to the efficacy of different strategies for maintaining a consistent supply of resources. Cycling among habitats and social groups is a form of cooperation dependent upon building diverse social networks and sharing information. A rapid forager cycling equilibrium is highly resistant to increases in population density, and should only change as foragers find the flow of information to degrade and must rely more on their own and cooperative labor in more local contexts to maintain a consistent flow of resources.

## Model and Methods

Formally, the resource dynamics of the SPDm are given by

$$\dot{x}_1(t) = G_1(x_1) - dx_1 - H_1 \tag{1}$$

$$\dot{x}_2(t) = G_2(x_2) - dx_2 - H_2 \tag{2}$$

where the change in the abundance of resources in habitat one ( $\dot{x}_1$ ) is the growth of the resource ( $G_1(x_1)$ ) in habitat one less the natural decay  $dx_1$ , less the total biomass harvested by foragers,  $H_1$ . The total harvest in habitat  $i$  is the sum of the harvests from each group, i.e.  $H_i = H_{i1}(x_i, e_{i1}) - H_{i2}(x_i, e_{i2})$ . The equation for habitat two is the same as for habitat one.

The growth of resources in each habitat,  $G_i(x_i)$  is defined by the logistic function  $G_i(x_i) = x_i r (1 - x_i / (K_i + I_i))$ ; where  $r$  is the growth rate of a resource base, and scales

the response of a given ecosystem to an external driver, which scales the variation of the resource, and  $K_i$  is the initial carrying capacity of a resource base. In a two habitat model, we have two inflows (external drivers),  $I_1$  and  $I_2$ . These inflows represent an influx of energy or water that seasonally change the carrying capacity,  $K_i$  of a resource base, and these inflows are sinusoids with a mean of 1. For example, if  $I_1 = 1 + \alpha \sin(2\pi t)$  and  $I_2 = 1 - \alpha \sin(2\pi t)$ , then  $I_1$  and  $I_2$  are 180 degrees out of phase, which may represent summer–winter peaks and valleys in the availability of resources, respectively; while  $\alpha$  is the amplitude of the peaks and valleys (Figure 2a).

The variable  $H_{ij}$  is the total harvest from habitat  $i$  by group  $j$  ( $H_{11}$ ,  $H_{21}$ , etc.). We define the harvest of an individual as  $h_{ij} = q_{ij}e_{ij}x_i$ , where  $e_{ij}$  is the effort an individual from group  $j$  spends harvesting in habitat  $i$ . The parameter  $q_{ij}$  defines the “harvestability” of the resource per unit of resource, per unit of effort of an individual from group  $j$  in habitat  $i$ . Total harvests are, then, individual harvest multiplied by population size:  $H_{ij} = N_j h_{ij}$ , where  $N_j$  is the population size of group  $j$ . The parameter  $q_{ij}$  scales (sets the units on) the sustainable population size of a given habitat. We set, initially,  $q_{ij} = 1$  for  $i = j$  and  $q_{ij} = q$ . This means that there is no cost to access resources within habitats or between habitats (the free assumption of the IFD), either in terms of mobility or participating in a gift exchange ceremony to access a habitat (e.g., [38]). The notion of territorial rights can be operationalized mathematically as  $q_{11} > q_{12}$  and  $q_{22} > q_{21}$ . Under this condition, it is more costly for an individual in group one to enter the home-range of group two than forage in their own home-range.

Two basic assumptions guide how we model foraging effort (time spent harvesting food). The first is that there exists some social convention that links individuals (kin or networks of kin) and that these social conventions are tied to home-ranges via a shared knowledge system [22]. Second, because we are interested in aggregate-level organizational patterns, we keep the individual model of decision making ecologically bounded. We model a representative agent that wants to meet their minimum harvest target,  $h_m$ . Once this is met, foraging effort stops. A reasonable assumption among foragers who do not store food [59].

We assume that foragers attempt to meet a target resource uptake rate with a minimum expenditure of labor because this maximizes the time available for other fitness enhancing activities. Figure 2b shows the target resource level (the red curve) and the effort level necessary to achieve a constant resource target (black curve) for a population in habitat one that is stationary. When resources are scarce during the winter (blue curve in Figure 2a is at a minimum), effort is at a maximum. The dynamic is: Stationary foragers adjust their work load to compensate for variation in the resource and, by doing so, maintain a constant intake of food.

In cases where variation in the availability of resources occurs out of phase, foragers may have incentives to migrate, in addition to adjusting their habitat specific foraging effort, to a habitat with more abundant resources to smooth out variation in their effort and returns from labor. To investigate this dynamic, we let  $e_j$  represent the total harvest effort of a representative agent from group  $j$ , and  $p_j$  the proportion of time individuals in group  $j$  spend in their “home-range.” Thus,

$$e_{11} = p_1 e_1, \quad e_{21} = (1 - p_1) e_1, \quad e_{12} = (1 - p_2) e_2, \quad e_{22} = p_2 e_2. \quad (3)$$

Where  $e_{11}$  is the effort (time) expended to harvest resources in habitat one by group one, which is the effort expended on foraging by group one multiplied by the proportion of time spent in habitat one ( $p_1$ ). The term  $e_{21}$  is the effort expended to harvest resources in patch two by group one and so on.

The harvest per unit effort in each habitat depends on resource abundance and the transaction costs associated with gaining access to those resources, which, holding effort

**Table 1.** Model state variables and parameters

<b>State Variables</b>	<b>Definitions</b>
$x_i(t)$	The density of resources (biomass/area) in habitat $i$ at time $t$
$p_i(t)$	The proportion of effort spent in habitat $i$ at time $t$
$e_{ij}(t)$	The effort spent in the harvest of resources in habitat $i$ by group $j$ at time $t$
<b>Parameters</b>	<b>Definitions</b>
$\alpha$	The amplitude of resource variation (the severity of boom-busts)
$r$	The mean intrinsic rate of resource growth ( $\text{yr}^{-1}$ )
$K_i$	The maximum abundance of resources in habitat $i$
$I_i$	The inflow of energy into habitat $i$
$d$	The natural decay of resources
$q_{ij}$	The transaction cost of accessing habitat $i$ for group $j$
$N_j$	The population of foragers in group $j$
$h_m$	The energy target per forager
$r_p$	The strategy adjustment rate

equal, was represented above as:  $h_{ij} = q_{ij}x_i$ . Where  $q_{ij}$  is, as defined above, the harvestability of resources in habitat  $i$  by group  $j$ . Thus,

$$h_1 = e_{11}h_{11} + e_{21}h_{21} \quad (4)$$

$$h_2 = e_{12}h_{12} + e_{22}h_{22} \quad (5)$$

where  $h_1$  and  $h_2$  are the total harvests of a representative agent in group one and two, respectively.

An individual's strategy about how much effort to expend ( $e_j$ ) and how to divide effort between habitats ( $p_j$ ) adjusts according to the following heuristic: First, "Do I feel hungry (is  $h_j < h_m$ )?" If so, increase  $e_j$  until either  $h_j = h_m$  or foraging effort reaches a maximum tolerable level  $e_x$ . Assuming that the decision to adjust foraging effort occurs on a smaller time-scale (days-months) than migration decisions (months-years), we formalize the change in foraging effort as an instantaneous process relative to the proportion of time spent in either habitat, and, thus, represent changes in foraging effort algebraically. That is, given  $p_j$ , agents choose  $e_j$  such that  $h_j = h_m$  subject to constraint  $e_j < e_x$ ,

$$e_1 = \min\left(\frac{h_m}{p_1h_{11} + (1-p_1)h_{21}}, e_x\right) \quad (6)$$

$$e_2 = \min\left(\frac{h_m}{(1-p_2)h_{12} + p_2h_{22}}, e_x\right). \quad (7)$$

Equations (6) and (7) state that each representative agent minimizes their foraging effort in a given habitat to obtain their desired level of calories, unless this exceeds the maximum tolerable effort ( $e_x$ ).

Second, "does changing my proportion of time in a habitat ( $p_j$ ) affect my harvest?" That is, is  $h'_j(p_j)$  positive or negative? If it is positive, then a forager is more willing to change  $p_j$ . Willingness to change, however, also depends on how well a forager knows the other habitat. If  $p_j$  is high, foragers do not know much about the other non-home-range habitat. If  $p_j$  is low, foragers have been away from their home-range a lot, and don't know it as well. This uncertainty reduces willingness to change  $p_j$ . When  $p_j$  is an intermediate value (e.g., 0.5), foragers spend roughly equal time in both habitats, know both well, and are more willing to alter their existing strategy. The simplest way to say this is that information moderates decisions about whether to change habitats, which are made based on resource differences.

There are a number of specific ways the comparison between habitats could be made by foragers. To avoid the problem of the *overall scale* of resource productivity impacting the comparison *between* habitats, we normalize by the average background productivity per unit effort. This is similar to the Marginal Value Theorem in which a forager compares their current return rate with the overall mean of all potential patches in an environment. That is, let

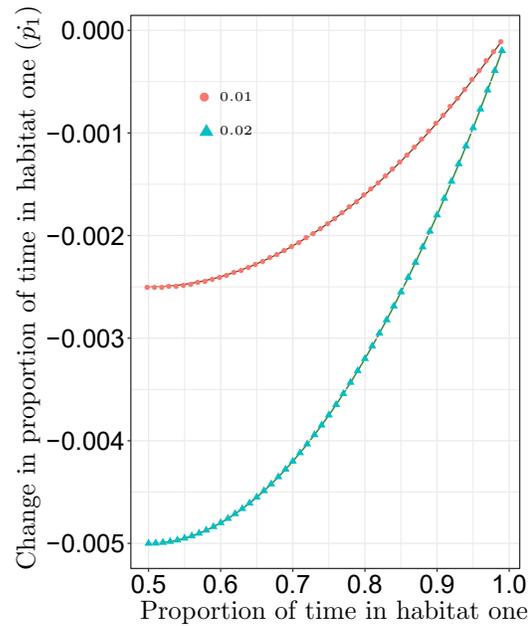
$$\bar{h}_j = \frac{h_{1j} + h_{2j}}{2} \quad (8)$$

where the average harvest of group  $j$  equals their harvest in habitats one and two divided by two. Thus, adjustments in  $p_j$  are described by

$$\dot{p}_1 = B_1 e_1 (h_{11} - h_{21}) / \bar{h}_1 \quad (9)$$

$$\dot{p}_2 = B_2 e_2 (h_{22} - h_{12}) / \bar{h}_2 \quad (10)$$

where  $B_1$  and  $B_2$  are the balance of time currently spent in both habitats for the representative agent from group one and two respectively. More formally,  $B_1 = r_p(p_1)(1 - p_1)$ , and  $B_2 = r_p(p_2)(1 - p_2)$  where  $r_p$  is the strategy adjustment rate. When  $r_p$  is higher, a forager adjusts to differences in normalized harvest per unit effort more strongly, placing less importance on information as  $r_p$  increases. Here we set  $r_p = 1$ . Fig. 10 provides an illustration of the moderating effect of the balance of time spent in habitat one on how the forager from group one responds to normalized differences in harvest per unit effort between habitats one and two. In this case, we hold the difference in harvest per unit effort constant at two values: Habitat two provides a 0.01 and 0.02 greater harvest per unit effort than habitat one. Thus, the forager from group one should decrease the proportion of time they spend in habitat one ( $p_1$ ). The main point is that when the balance of time between the two habitats is equal at 0.5, a forager more quickly decreases the proportion of her time spent in habitat one because information is abundant on habitat two. However, as the proportion of time in habitat one approaches 1, the forager more strongly discounts the potential for resources in habitat two due to uncertainty about those resources. Thus, a smaller change in the proportion of time spent in habitat one.



**Fig 10.** Illustration of how the proportion of time in a habitat moderates the effect of normalized differences in harvest per unit effort upon the change in proportion of time devoted by the group one forager to habitat one. In this case, harvest per unit effort is higher in habitat two than habitat one at two constant levels 0.01 (orange dots) and 0.02 (blue triangles). Thus, the group one forager decreases the proportion of time spent in habitat one (y-axis), and this is moderated by the current balance of time spent in habitat one (x-axis). As the proportion of time spent in habitat one decreases, the forager discounts the potential value of resources in habitat two less and adjusts her balance of time toward habitat two more strongly.

## Methods of analysis

We analyze the SPDM numerically in XPPAUT [60], which is specialty software for analyzing non-linear dynamic systems models, and report our results at two different time scales. The smaller-time scale illustrates the mechanisms that drive the behavior of the model and subtle tradeoffs associated with rapid cycling through multiple habitats vs. habitat partitioning. The larger time-scale illustrates the conditions under which rapid cycling and habitat partitioning should emerge from individual decisions about how to best maintain a consistent supply of food in a variable environment. Our analysis of the larger-time scale focuses on two different perturbations that affect foraging economies: (1) declines in the availability of resources due to, for instance, a dry period, and (2) the process of periodic aggregations of foragers for important ceremonies or due to a climate perturbation. We used XPPAUT to run simulations and generate the phase plots illustrated in Figs. 6 and 7. We used R to make simple graphs of the relationship between model parameters and simulated outcomes.

To analyze the TCP radiocarbon record, we collected all available radiocarbon dates from the Texas Coastal Plain, which are available here [61]. We cleaned the data to eliminate geological ages and ages on bulk sediments, as well as ages not directly associated with human activity. We also removed dates without a lab number. To construct the summed probability distribution of the dates we used the rcarbon package in R [51]. We calibrated the dates in this package using the the IntCal13 calibration curve [51]. We then used the BinPrep and ModelTest functions in rcarbon to average ages from the same site within a 100 calibrated years of each other. This controls for over sampling features (e.g., five similar ages from the same feature on the same site). Next, we fit an exponential regression of time on the summed probability of radiocarbon dates smoothed to 50 year averages. We use 50 years because this is about the generation step-time of a human population. Using the ModelTest function in rcarbon, we ran 500 Monte Carlo simulations to construct a confidence interval for the exponential model of time regressed on the summed probability distribution. We fit an exponential regression because inspection of the summed probability distribution indicated an exponential like trend in the mean of the data over time. The confidence interval allows one to make statements such as: we can be 95 % sure that a particular peak or trough in the summed probability distribution is not due to calibration or sample bias [62]. Note that peaks and troughs within the confidence interval may also be important to consider, but a model of what processes drive those peaks and troughs is required to interpret and pull apart the relative effects of calibration bias vs. other processes [63].

Finally, to document burials per unit time and exchange goods per unit time, we collected data from cemeteries on the TCP. We simply followed Ricklis [1] in identifying the main components of cemeteries and classifying these cemeteries as Early, Middle, Late Archaic, Late Prehistoric I or Late Prehistoric II. We then divided the number of burials and exchangeable grave goods during these time periods by the number of years in a given time period. Where cemeteries had multiple burial components identified by the excavators, we separated these components into their respective time-periods. Exchangeable goods include, beads, shell, necklaces, and shaped stones. We did not include projectile points. All data are available as supplementary files. The data are clearly aggregated at a coarse temporal grain. The radiocarbon record will allow for more fine grained time-series of burials and associated grave goods in the future.

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