Toward a Theory of Non-linear Transitions from Foraging to Farming

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Abstract:
The evolution of agricultural economies requires two processes: 1) the domestication of plants and 2) specialization in domesticates at the expense of hunting and gathering. Yet, in the literature, domestication receives the lion’s share of attention while theories of specialization in domesticates lag behind. In this paper, we integrate ideas from human behavioral ecology with tools from dynamical systems theory to study the effects of ecological inheritance on the transition from foraging to farming. Ecological inheritance is an outcome of niche construction and our study provides a formal link between foraging theory and niche construction. Our analysis of a dynamic model of foraging and farming illustrates that strategies for the optimal allocation of effort to foraging and farming can lead to the emergence of multiple stable states. The consequence of this is that low-level farming optimizes subsistence (e.g., minimizing the effort required to meet a subsistence goal) in a forager-resource system over a few years, but makes the whole system vulnerable to punctuated change over decades due to rare events. We use the insights of our model to propose a general ecological framework to explain the evolution and diversity of transitions from foraging to farming.

Keywords:
Agricultural change, Niche construction, Human behavioral ecology, Foraging theory, Resilience
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Niche construction and its legacy—ecological inheritance—are integral to explain the adoption of domesticated plants by hunter-gatherers [1–9]. This is intuitive. The adoption of domesticated plants is one of the most studied problems in anthropology, particularly as an outcome of human-environment interactions (e.g., 4, 7, 10–28). The long standing justification for this intensity of research is that the adoption of domesticated plants underlies major changes in the evolution of human societies, such as the emergence of inequality and sociopolitical hierarchies (e.g., 29; 17; 21, p. 3; 25, p. 3; 26, p. 1). However, the evolution of political hierarchy and inequality are not correlated with the adoption of domesticated plants per se, but are often coincident with specialization in the production of domesticated plants at the expense of hunting and gathering [17, 24, 30–33]. Thus, a fundamental question is why, once domesticated plants became part of the subsistence base, did some people increase their time invested in farming at the expense of hunting and gathering while others engaged in a persistent mix of foraging and low-level farming [24, 32, 34–39]?

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In this paper, we integrate ideas from human behavioral ecology (HBE) and dynamical systems theory to study why individuals specialize in the production of domesticated plants at the expense of hunting and gathering. Our integration of ideas from HBE and dynamical systems theory allows us to investigate the effects of ecological inheritance. Ecological inheritance is a process whereby the behavior of individuals today modifies an ecosystem; and, in turn, the fitness of individuals’ behaviors in the future is effected by the modified ecosystem that they ‘receive’ from their ancestors [40, p. 13]. Ecological inheritance is product of niche construction, which is simply the ability of organisms to “shape environments to states that are suited to their biology (and less frequently to states that are not)” [41, p. 221].

Our work contributes to understanding the coevolution of subsistence strategies and ecosystems. Specifically, we use the insight gained from a dynamic model of optimal foraging and farming to develop expectations for how ecological inheritance may result in different evolutionary trajectories of food production strategies. We argue that HBE provides an overarching framework to understand specialization in domesticates at the expense of hunting and gathering. However, the feedback dynamics caused by niche construction can generate non-intuitive trajectories of evolution, and dynamical systems models are a critical tool for extending models drawn from optimal foraging theory to understand such possibilities.

Foraging models, Ecological Inheritance, and Non-linear Trajectories

In HBE, many explanations for changes in human behavior are grounded by optimal foraging models (OFM) (42, 43; see also 44). Such models are a useful starting point, but are not sufficient to explain specialization in domesticates at the expense of hunting and gathering. To see why, please consider the following example.

Barlow [34] proposes an OFM to describe investment in the production of domesticates at the expense of hunting and gathering. With just a few assumptions, this model provides a partial explanation for when foragers will choose to invest in farming at the expense of foraging. Most relevant here: 1) Individuals can invest their time in two mutually exclusive food producing activities, cultivating maize (the dominant domesticated plant in prehistoric North America) and foraging for wild foods. 2) individuals only have so much time that they can use to produce food, thus $l_s + l_c \leq l$. Where $l$ is the maximum amount of effort (in units of time) that an individual can devote to producing food, and $l_s$ and $l_c$ are the effort spent foraging and cultivating, respectively. (3) Individuals attempt to maximize their rate of energy gain because this maximizes their fitness.

Given these assumptions, we can rewrite Barlow’s [2006] model in a compact form. Individuals obtain an output of energy described by the following equation:

$$A(l_s, l_c) = A_s(l_s) + A_c(l_c)$$  (1)

where $A(l_s, l_c)$ is the total energy gained from foraging and farming; $A_s(l_s)$ is a function that describes the energy gained from foraging; and $A_c(l_c)$ is a function that describes the energy gained from cultivating. When individuals maximize output subject to the time allocation constraint above, it is assumed that they fully utilize their labor. Thus, the “≤” in the labor constraint becomes equality which leads to $l_s + l_c = l$ or $l_s = l - l_c$. Hence, we can eliminate $l_s$ from equation...
(1) an rewrite equation (1) as

$$A(l_c) = A_s(l - l_c) + A_c(l_c).$$

(2)

Differentiating output with respect to $l_c$ yields the first order conditions for a maximum, i.e.

$$A'(l_c) = -A'_s + A'_c = 0$$

(3)

which leads to a well-known condition in economics: at the optimal labor allocation, the marginal productivity of labor in different occupations is equal, (i.e. $A'_s = A'_c$). From this basic result comes Barlow’s [2006] decision rule for when to cultivate maize:

$$A'_s < A'_c.$$  

(4)

This rule stipulates that individuals allocate effort to the cultivation of maize once the marginal gain from the next unit of effort so spent is greater than the opportunity cost of that unit of effort spent foraging [34, p. 96]. Thus, a decline in the marginal returns from foraging should spur investment in cultivating maize and *vice versa*.

While a productive start, the model above needs further development. The most relevant reason to our discussion is as follows. The model does not explicitly describe why the marginal returns from either foraging or farming may increase or decrease. The causes of such changes could be either endogenous or exogenous processes that change much more slowly than decisions about how much time to invest in foraging and farming. For instance, on the foraging side of the equation, we can imagine that climate change may drive the productivity of important wild resources down, leading to the adoption of more agriculture (if the climate change did not similarly affect the marginal productivity of cultivating maize). Alternatively, population growth could lead to the depletion of wild resources, which would decrease the marginal rate of return from foraging relative to farming; this possibility invokes ecological inheritance as a causal mechanism [3, p. 315].

A qualitative appeal to ecological inheritance as a causal mechanism glosses over the possibility that ecological inheritance results in non-linear trajectories of change in many systems [40, p. 20-21]. Equation (4) assumes that foraging and farming are mutually exclusive, both as activities and *in their effects on ecosystems*. For an individual who makes decisions over a time scale of months, this might be reasonable. However, over decades, the foraging and farming decisions of many individuals likely creates interactions and interdependencies between foraging, farming and ecosystems. For example, clearing land to plant crops over decades might positively or negatively effect the productivity of wild resources; in turn, this interaction effect would determine how individuals should best allocate their effort to foraging or farming. The interdependency of foraging and farming decisions with the productivity of an ecosystem could result in strong non-linearities and threshold effects in the dynamics of human-environment interactions.

There are several potential reasons that the evolution of food production strategies may exhibit such dynamics. However, our concern here is the potential effect of a specific type of non-linear feature in social-ecological systems–the emergence of multiple stable states and thresholds–on the evolution of subsistence strategies (e.g., 15, 45–49). Multiple stable states refers to the idea that there are discrete ways that an ecological or social-ecological systems could be organized under the same environmental conditions (e.g. hunting and gathering or agriculture) [50–54]. The emergence of multiple stable states is important because their presence in a system could lead to transitions.
from foraging to farming that are punctuated, difficult to anticipate, and very costly to reverse. Thus, the emergence of multiple stable states under some regimes of ecological inheritance and not under others is likely a factor that determines why systems of low-level food production follow different evolutionary trajectories (e.g., smooth and continuous versus punctuated).

Multiple stable states

Figure 1 is a heuristic for understanding how systems with multiple stable states differ from those with a single state or equilibrium. An equilibrium for a dynamical system is the “state” to which the system tends over long time periods (e.g., a pendulum, after given an initial push will eventually end up still, and hanging down). The value of this state can change as parameters that define the system change (e.g., the length of the pendulum or the gravitational constant). The curves in figures a-c show how the equilibrium of a system may change as an ecological parameter changes, and the blue dots represent the equilibrium solution for a dynamical system for a given value of the ecological parameter (e.g. solar flux, soil fertility, temperature, etc.).

In systems with a single possible equilibrium, there is a continuum of states that the system can occupy (Figure 1a and 1b). The consequence is that evolutionary change is continuous and reversible. Alternatively, in a system with multiple stable states (Figure 1c), there are multiple equilibria that a system may occupy (i.e., multiple potential solutions to a system of equations for a given set of parameters, two blue dots for the same parameter value). The consequence is that evolutionary change is sometimes continuous and reversible, but may also be punctuated, difficult to reverse, and difficult to anticipate. To illustrate these differences between systems, please consider the following two examples.

First, assume that the choice an individual has to make in Barlow’s [2006] model is whether to allocate time to cultivating maize or harvesting mesquite beans (a seed that falls from a mesquite tree). Abstracting away from the issue of processing time for the moment, the marginal rate of energy gained from mesquite is determined by the density of mesquite trees. This is because the density of trees determines how long people must search for beans. By analogy, the density of mesquite trees is the ecological parameter in Figure 1a or b (the x-axis) and time devoted to mesquite collection is the state variable (y-axis). This implicitly assumes that the density of mesquite changes much more slowly (e.g., years) than decisions about the effort to invest in collecting beans (e.g., days-to-months). The black curves, again by analogy, represent the equilibrium time invested in collecting mesquite at each given density of mesquite trees. As the density of mesquite declines, selection pressures should favor decreasing labor, at equilibrium, in the collection of mesquite (the blue dot moves down an to the right in 1a or 1b). Given the assumption of the model, a decline in effort devoted to mesquite at equilibrium necessarily implies an increase in the production of maize. In sum, there is a continuum of unique labor allocations to the collection of mesquite determined by the density of mesquite; the change in investment is continuous and reversible, and, thus, labor allocation to farming also changes along a continuum.

Second, let’s continue the mesquite and maize theme to provide a concrete illustration of the dynamics summarized in Figure 1c. Flannery [15] proposes that there are tradeoffs between clearing mesquite forests to plant maize and collecting mesquite beans. Flannery [15, p. 505] states, “With maize crossing the the 250 kg/ha threshold, a new loop in the system was established; mesquite trees were cut down to make way for maize, and although preceramic...
Figure 1: Figures designed after Scheffer [53]. The black curves represent all of the possible equilibrium states of a system for a given ecological parameter. The blue dots represent a unique equilibrium solution. The arrows indicate the direction that the system will move over time if it is not in equilibrium.
peoples continued to collect mesquite pods, they were harvesting from ever dwindling Prosopis groves. Instead of propagating mesquite seeds by their collecting and threshing behavior, they were propagating maize kernels by eliminating mature mesquite."

In this example, the ecological parameter is the productivity of maize controlled by the selective breeding practices of early Mesoamerican forager-farmers. The equilibrium state is the amount of area covered by mesquite, which determines the abundance of mesquite beans.

Now we can analogize Flannery’s proposition to Figure 1c. An increase in the average productivity of maize (x-axis) causes a decrease in the level of effort devoted to the collection of mesquite at equilibrium (the blue dot moves down and to the right). This occurs because individuals choose to plant more maize and cut down mesquite as the productivity of maize increases. In this case, the 250 kg/ha threshold is marked by the thick red line. Once maize productivity hits this threshold, farmers rapidly shift toward a low effort invested in collecting mesquite at equilibrium (all of the points on the lower right thick curve to the right of the shaded area. In Flannery’s proposition, the reason the shift between equilibria occurs is because, once maize productivity hits 250 kg/ha, deforestation and seed consumption decrease the rate of mesquite reproduction past a critical threshold. The implication is that farmers move from a low level of effort to a high level of effort devoted to the production of maize, and skip over intermediate levels of investment (the dashed curve). In this case, the shift from low-level farming to intensive farming is punctuated and costly to reverse. However there is more to the story.

Figure 1c helps illustrate that Flannery’s proposition is missing a crucial element. When the ecological parameter (here the productivity of maize) falls within the shaded zone, the system is vulnerable to a variance induced transition. This is because deforestation and consumption decisions are not solely controlled by the productivity of maize (the ecological parameter). There are shocks that constantly perturb an ecological system generated by dynamics such as El Nino-La Nina weather cycles and pest cycles. For example, a disease outbreak could shock a mesquite forest and cause a decline in mesquite forest cover. In the shaded area of Figure 1c, this shock would stimulate individuals to compensate by growing more maize despite the fact that productivity is, on average, below the 250 threshold. This behavior, in turn, would drive the rate of mesquite reproduction too low for the forest to recover. Forager-farmers would then end up in an environment with a low density of mesquite trees, and their high investment in the production of maize would keep the forest from recovering. In this situation, the transition is not only punctuated and difficult to reverse, but also difficult to anticipate based on forager-farmers’ prior knowledge of the system.

The coupled processes of niche construction and ecological inheritance can lead to multiple stable states and critical thresholds. The consequence of multiple stable states is that two mechanisms may generate a punctuated shift from foraging to farming: 1) crossing a parameter threshold (e.g., the 250 kg/ha line) through a slow process internal to a subsistence system, like seed selection, or 2) crossing a state variable threshold (the dashed black curve) via a fast external shock like a La Niña episode. This second mechanism is captured in the example above when forager-farmers, combined with a pest outbreak, deplete the density of mesquite just enough (past the dashed curve in the shaded area) that they cause a regime shift. In short, the emergence of multiple stable states—due to niche construction and ecological inheritance—may effect the trajectory of evolution that a system follows.
Questions

Two questions follow from our discussion: 1) Under what ecological and social conditions might the optimal allocation of effort to foraging and food production cause multiple stable states to emerge? And, if multiple stable states emerge, 2) what variables could create different trajectories that the evolution of food production follows? To contribute to answering these questions we develop and analyze a dynamic model in the spirit of Barlow’s OFM and Flannery’s insights regarding the interdependency of humans and ecosystems. Our questions hone in on the consequences of niche construction and ecological inheritance for the evolution of food production at the expense of hunting and gathering.

A Dynamic Model of Time Allocation to Foraging and Farming

Our goal is to construct a model with the simplest possible assumptions to capture the biological realism of niche construction and ecological inheritance. In particular, we want to capture, in a minimal way, the interdependencies of foraging, farming, and the productivity of an ecosystem. As we note in section six below, our stylized model has the analytical power to explore alternative scenarios of niche construction and ecological inheritance. A more complex model would make this more difficult because complexity necessitates a sacrifice of analytical power. For our argument here, analytical power is more important than model complexity, and, thus, we have chosen to keep the model as simple as possible.

Our stylized model has two components: forest reproduction and growth and time allocation to foraging or farming. We couple these two components to develop a dynamic model of time allocation to foraging and farming in a forest ecosystem under three basic assumptions.

1. The individuals in our model are households. The household is a basal cooperative economic unit in many forager-farmer and forager societies. In particular, a male and female pair or pairs form the core of a group who performs complimentary subsistence activities. For example, Holmberg [1950, p. 124] states “the nuclear family...is the fundamental economic unit among the Siriono.” He goes on: “Hunting is largely a family affair, as are fishing collecting and agriculture” [55, p. 124]. These types of observations are common from diverse places such as the American Southwest, as among the Yavapai [56] to the the islands of Indonesia, as among the Nuaulu [57].

2. We assume that households may choose to produce two staple resources: seeds produced by trees (e.g., nuts like acorns or the mesquite beans mentioned above) and/or a domesticated plant, which, for concreteness we call maize. It is common in the ethnographic record for seeds or hearts produced from trees to provide a staple of forager and forager-farmer diets. Examples include Piñyon pine nuts in the Great Basin of North American [58], palm hearts in South America and the Pacific (e.g., 55, 57, 59), and acorns in California [60]. The keys here are 1) decisions are interdependent because clearing trees for agriculture effects the production of seeds, and 2) there is a decision to make: How much effort is best allocated to the production of each?

3. Territory is open access. Open access means that there are no rules that limit who, when, and where trees may be cleared to plant and who, when, and where seeds may be collected. Our
implicit rules are simply ‘you harvest, you own’ and ‘you clear, you own.’ This means that once a resource is harvested, or a plot of land is cleared, the resource is used by the household that did the harvesting or clearing. For example, among Shoshoni foragers in the Great Basin of North America, Steward [1938, p. 253] tells us that “once work had been done upon the products of natural resources they became the property of the person or family doing the work.” Again, among the Siriono Holmberg [55, p. 44] states that property is “limited to the immediate possession, by a family, of a garden plot, by virtue of having cleared and planted it.”

<table>
<thead>
<tr>
<th>State Variables</th>
<th>Interpretations</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s(t)$</td>
<td>The density of seeds (biomass/area) at time $t$</td>
</tr>
<tr>
<td>$p(t)$</td>
<td>The density of trees (biomass/area) at time $t$</td>
</tr>
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<table>
<thead>
<tr>
<th>Parameters</th>
<th>Interpretations</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_j$</td>
<td>The rate of resource regeneration where $j \in {p, s}$</td>
</tr>
<tr>
<td>$K_p$</td>
<td>Carrying capacity of trees</td>
</tr>
<tr>
<td>$d_s$</td>
<td>Natural seed depletion rate</td>
</tr>
<tr>
<td>$N$</td>
<td>Density of households</td>
</tr>
<tr>
<td>$d_c$</td>
<td>Rate of tree clearance</td>
</tr>
<tr>
<td>$c$</td>
<td>Land cleared of trees (under cultivation)</td>
</tr>
<tr>
<td>$K$</td>
<td>Minimum daily energy return rate</td>
</tr>
<tr>
<td>$h_i$</td>
<td>Per capita harvest of resource $i$ in $s, c$</td>
</tr>
<tr>
<td>$A_i$</td>
<td>The productivity of labor in resource $i$ in $s, c$</td>
</tr>
<tr>
<td>$\beta$</td>
<td>Decay in returns to labor due to search time</td>
</tr>
<tr>
<td>$l_i$</td>
<td>Labor directed toward resource $i$ in $s, c$</td>
</tr>
<tr>
<td>$l$</td>
<td>Total available per capita labor</td>
</tr>
</tbody>
</table>

Table 1: Model state variables and parameters

**Forest reproduction and growth**

We define the density of seeds and trees at time $t$ with a set of ordinary differential equations:

$$\dot{s} = r_sp - d_ss$$

$$\dot{p} = r_ps(1 - p/K_p).$$

This set of equations captures a minimal set of processes to generate a biologically defensible story about the reproduction and growth of trees. The change in seed biomass ($\dot{s}$) is the intrinsic production of seeds ($r_s$) multiplied the density of trees in a forest ($p$) less the rate of seeds depleted by animals and decay ($d_ss$). In turn, the change in tree biomass per unit area ($\dot{p}$) is the logistic growth function. The intrinsic growth of trees increases in proportion to the density of seeds in the forest ($r_ps$), and the growth limiting effects of intraspecific competition ($K_p$) constrains the growth of trees. Here $K_p$ sets the area that households can use at time $t$. This means that when we speak
of the number of households at time \( t \) \((N(t))\), we are referring to a density. \( N(t) \) is best thought of as the ecological footprint of households, given their technology; when \( N(t) = 0 \), humans have no footprint in the forest.

### Harvest and time allocation

Now that we have defined the ecosystem, we posit a set of rules that define an evolutionarily sensible strategy for how households allocate their effort to the production of seeds or maize. To determine the best allocation of effort to foraging and farming, we must first define the harvest of seeds and maize.

We make three additional assumptions to define the per capita harvest of households. First, seed output displays diminishing returns. Diminishing returns occur because the more seeds that one gathers, the farther one must travel to gather more seeds (e.g., 61, 21-33; 62). Thus, as seeds are depleted, an ever higher proportion of time is devoted to searching, which decreases the marginal productivity of effort. Second, we assume that agricultural technology exhibits constant returns to scale and that large scale cooperation is not necessary (like maintaining large irrigation ditches) to produce maize. All else equal, this means that one extra day of labor invested in the cultivation of maize results in a one unit increase in yield. The consequence of this assumption is that decisions about how much time to invest in cultivation at the level of each individual household adds up reasonably well to the aggregate level of cultivation by all household. Finally, we assume that households minimize their time devoted to the production of sufficient food to meet their demands (which is equivalent to maximizing the rate at which they gain energy).

Given these assumptions, we define \( h_s(t) \) and \( h_c(t) \) as the per capita harvest from cultivation and seed gathering, where:

\[
h_s(t) = A_s(s) l_s^\beta \quad \text{and} \quad h_c(t) = A_c(p) l_c.
\]

In these equations, \( l_s \) and \( l_c \) are the time devoted to gathering seeds and cultivating maize. \( A_s \) and \( A_c \) are functions that represent the productivity of effort spent foraging and farming, and \( 0 < \beta < 1 \) captures the decreasing marginal productivity of seed gathering. We assume that \( A_s(s) = s \) because, for a given level of effort, lower seed density implies a lower number of seeds gathered, and \( A_c(p) = p \), which implies that soil fertility scales linearly with tree density. This soil fertility assumption follows from the idea that lower tree density is associated with shorter fallow periods and, thus, shorter times for trees to regenerate soil nutrients. The effect of these last two assumptions is that we can replace \( A_s(s) \) and \( A_c(p) \) with \( s \) and \( p \), respectively. Thus, \( h_s(t) = s l_s^\beta \) and \( h_c(t) = p l_c \). The per capita harvest of seeds and maize depends on the abundance of seeds \((s)\) and trees \((p)\) (which we defined in equations (5) & (6)) multiplied how much effort that a household invests in foraging \((l_s^\beta)\) or farming \((l_c)\), respectively. These simple harvest functions allow us to capture, in a minimal way, the interdependency of foraging and farming—or at least the harvest of seeds and cultivation of maize.

We determine how much effort should be allocated to foraging and farming by solving a constrained optimization problem:

\[
\begin{align*}
\text{minimize} & \quad l_c + l_s \\
\text{subject to:} & \quad l_c + l_s \leq l \\
& \quad A_c l_c + A_s l_s^\beta - K \geq 0
\end{align*}
\]
where \( l \) is the total time available, and \( K \) is the minimum caloric goal per person per day to meet biological, reproductive and social needs. The constrained optimization problem simply says: given that you have \( l \) total units of labor available per time period, produce \( K \) for that time period with as little of your time budget allocated to foraging and farming as possible.

Box 1 presents the solution to the constrained optimization problem households face. The solution defines a set of decision rules for allocating effort to foraging and farming. Our decision set is a heuristic that tells a household, at each time step, to check the optimal allocation of effort and then allocate effort optimally if doing so does not violate the effort or minimum calorie constraints noted above. The heuristic allows a household to converge on the best mix of foraging \((l_s)\) and farming \((l_c)\) that meets \( K \) in the shortest amount of time whenever possible.

[BOX 1 HERE]

For example, Figure 2 illustrates five potential cases or ways that a household might allocate labor at any given time \( t \), given the productivity of the ecosystem at that time. The value \( l_s^* \) is the point at which the marginal productively from cultivating is greater than the marginal productivity from gathering seeds. In case 1 a household can meet their energy constraint, \( K \) at a point that is less than \( l_s^* \); thus, the household is a hunter-gatherer household. In case 2, it is optimal for a household to gatherer seeds until \( l_s^* \) and then cultivate maize until their energy constraint is met, \( K \). Thus, the household is a low-level food producer. In the model, a household could move continuously between cases until they converge to some kind of an attractor. The main point is that the optimal allocation of labor changes over time as the productivity of the ecosystem changes. We define the interdependency of foraging, farming, and the ecosystem below.

![Figure 2: Graphic depiction of the optimization problem faced by households. When the marginal benefit of cultivation (slope of blue line) exceeds the marginal benefit of gathering seeds (slope of tangent to red curve) switch to cultivation. This occurs at \( l_s^* \), equation (16), Box 1. 1: Highly productive wild resource, never cultivate, set \( l_s = l_c \), subsistence constraint \( K \) easily met. 2: Set \( l_s = l_s^* \) and \( l_c = l \). It pays to cultivate, and the subsistence constraint \( K \) is met. 3: Set \( l_s = l_s^* \) and \( l_c = l - l_s^* \). It pays to cultivate, but the subsistence constraint \( K \) is not met. Cases 4 and 5: It never pays to cultivate because \( l < l_s^* \). The subsistence constraint \( K \) may (case 4) or may not be met (case 5) depending on the productivity of the resource.](image-url)
Coupling the ecosystem with harvest and time allocation

The production of food creates two niche constructing activities in our model (i.e., feedbacks between time allocation and the ecosystem): gathering seeds $h_s(t)$ and the harvest of maize $h_c(t)$. The effect of gathering seeds on the dynamics of the forest is obvious, the more seeds that individuals gather, the lower the reproductive rate of trees in the forest. The total harvest of seeds in the model is $Nh_s(t)$; the number of households multiplied by each household’s harvest of seeds. Similarly, given our production function of $h_c(t) = pl_c$, to cultivate maize a household must choose how many trees to clear, which effects the reproductive rate of the forest, as well as the fertility of soil. Thus, households make a clearing decision: If the amount of cleared land is insufficient for the desired production of maize, then land must be cleared. We define $c(t)$ as a household’s rate of land clearing at time $t$. Total tree clearing, $Nc(t)$ is the number of households multiplied by each household’s rate of clearing. Finally, we assume that land is cleared at a rate proportional to the difference between the desired cleared area and the available cleared area: $c(t) = d_c (A_{cd}/A_{ca})$. Where $d_c$ is a measure of how effectively a household clears trees per unit effort and how responsive they are to deviations of $A_{cd}/A_{ca}$, the ratio of area that needs cleared to the area already cleared, away from $K_p$.

We can now couple the behavior of households with the growth and reproduction of the forest:

$$\dot{s} = r_s p - d_s s - Nh_s \tag{10}$$
$$\dot{p} = r_p s (1 - p/K_p) - Nc. \tag{11}$$

Given seed and tree densities, $s(t)$ and $p(t)$, at time $t$ households make a decision about how much effort to allocate to foraging ($l_s$) and farming ($l_c$), which determines $h_s(t)$ and $c(t)$. In turn, $h_s(t)$ and $c(t)$ affect the future values of $s(t)$ and $p(t)$ through equations (10) and (11) and, thus, the best allocation of effort towards foraging and farming in the future. In sum, the fitness of a household’s decisions now depends, in part, on the forest that it “inherits.”

The Evolution and Resilience of Low-level Food Production

Our analysis indicates that 1) as our model households attempt to behave optimally, their niche construction and its legacy, ecological inheritance, generate multiple stable states: a productive state and an impoverished state. Once multiple stable states emerge, households face the risk that they may get pushed into the impoverished state. This risk is a feature of the ecosystem inherited from previous generations. 2) As households cultivate more maize, the resilience of the productive state decreases, and the risk of the system flipping into the impoverished state increases. Thus, in the short-run (a few years), it is optimal to allocate effort to the cultivation of maize as a strategy to mitigate diminishing returns from foraging; however, in the longer-run (decades), the system is more vulnerable to a punctuated state change that is difficult to anticipate. 3) It is less costly for households to reverse between foraging and farming when cultivation is 1-40% of the diet. However, once the 40% threshold is approached and crossed, it is likely difficult to go back to low-level food production.

[BOX 2 HERE]
The emergence of multiple stable states

Figure 3 is a set of phase plane plots that illustrates the inter-relationships between seed and tree density over time for three different values of population \( N \): \( N = 0 \), \( N = 1.1 \), and \( N = 1.85 \). The green and orange curves on each of the graphs are the isoclines. The isoclines are all of the points at which seed density or tree density are not changing (i.e., \( \dot{s} = 0 \) or \( \dot{p} = 0 \)). Where these curves intersect, the system is in equilibrium because \( \dot{s} = 0 \) and \( \dot{p} = 0 \). An equilibrium may be stable, also known as an attractor, or unstable, also known as a repellor. An attractor is a collection of equilibria to which a system is likely to return over the long-term if perturbed. A repellor is a collection of equilibria that a system is likely to move away from over the long-term, if perturbed.

Figure 3a has one attractor where the isoclines intersect \( (\bar{s} = 1, \bar{p} = 1) \) and, thus, one stable state. The stable state is “pristine” because, at \( N = 0 \), humans do not have an ecological footprint in the system. The stable state is globally resilient. Resilience refers to how much environmental change a system can absorb and still maintain its feedback structure \([63]\). For example, the black arrowed curves on Figure 3 illustrate how a system evolves over time for a given set of initial conditions. To illustrate, please follow the curve labeled “I” on Figure 3a. This system starts at a seed density of \( s = 0.25 \), and a tree density of \( p = 0.3 \). Over time, the trees produce seeds, which sprout and grow into trees and the forest recovers toward the pristine state \( (\bar{s} = 1, \bar{p} = 1) \). In the long-run, the stable state in this environment is globally resilient because no matter where we start the system, it will always move toward \( \bar{s} = 1, \bar{p} = 1 \) over the long run.

Please hold-on to the idea that resilience is a long run characteristic of an attractor. In real systems, perturbations constantly occur, for example, a pest outbreak in a forest that drives tree and seed biomass down.

The black arrowed curves on Figure 3 help us imagine the consequences of perturbations. In the case of the curve labeled “I”, we can imagine that a pest outbreak killed-off a bunch of trees in one year, thus setting the initial conditions for the next year at \( s = 0.25 \), \( p = 0.3 \). In the short-run, the pest outbreak depresses the biomass of the forest, but, at longer time scales (over a decade), the forest moves toward the pristine attractor. In a real system, biomass may never actually get to the pristine state because perturbations are constant. However, the system is globally resilient because, over time, it continues to move back toward our “pristine” stable state. Thus, the black arrowed curves help us understand the sets of initial conditions for which the forest will tend to evolve toward a particular stable state.

In Figure 3b, we add some humans to the ecological system \( (N = 1.1) \). Now, the collection of seeds and, potentially, the clearance of forest by households can affect the long-run biomass of the ecosystem. There are two consequences.

First, the pristine stable state is no longer pristine; the attractor moves down and to the left. At this ‘productive’ attractor, it is optimal for households to expend 12% of their total available effort (i.e., 12% of their subsistence time-budget) to gather seeds; and this allocation of effort allows households to achieve their daily caloric goal \( (K) \) in a minimum amount of time. In the productive state, households do not work very long and can invest a lot of time in other activities that enhance fitness.

Second, when \( N = 1.1 \), the system displays multiple stable states, and the harvest behavior of households (collecting seeds) introduces the subtle risk that a perturbation may drive the system into an ‘impoverished’ attractor. The impoverished attractor on Figure 3b is separated from the productive attractor by a repellor (the blue square). In this multiple stable state environment, now
**Figure 3:** Phase plots: All parameters are held constant at default values except population ($N$). a-$N = 0$; b-$N = 1.1$; c-$N = 1.85$. The circles highlight stable attractors. The square in graph b highlights a repellor. Each phase plot is paired with a stability landscape (a-d; b-e; c-f).
if a pest outbreak reduces tree and seed biomass to the point labeled $I_2$, the system will move
toward the impoverished attractor over the long-run. This occurs because as the biomass of the
forest goes down, it suddenly becomes optimal for households to invest in both clearing forest to
plant maize and collecting seeds (e.g., a shift from case 1 to case 2 in Figure 2). If the biomass of
the forest decreases too far (all sets of $(s,p)$ left of the dashed blue line), a feedback loop between
seed gathering and clearing is initiated. Lower tree density leads to fewer seeds which means it
is optimal for households to clear more land to plant maize. The short term decision to clear land
leads to lower tree density which reduces seed density over the longer term. One can imagine how
this viscous feedback cycle could lead to the destruction of the forest.

However, at $N = 1.1$ the impoverished state is only impoverished in terms of the ability of
households to collect seeds. Each household can still obtain $K$; they simply are doing it by working
a lot harder than they would as pure foragers in the productive state. At the impoverished attractor,
households spend 71% of their subsistence budget cultivating maize and 29% gathering seeds.

In short, when $N = 1.1$, there are two stable states. In the productive state, households are
pure foragers who need not work very long. In the impoverished state, households are committed
farmers and work long hours. Note: if the system were hit by a large enough perturbation, we
would observe a regime shift from pure foraging at the productive attractor to fully committed
farming at the impoverished attractor! There is more to this story, however. The impoverished
attractor is not very resilient to further environmental change.

Figure 3c illustrates how sensitive the impoverished attractor is to increases in the ecological
footprint of households. In this setting, we have increased $N$ to 1.85 and the system bifurcates.
The only attractor is the impoverished attractor, very near $s = 0, p = 0$. The destruction of the
forest occurs, in part, because of the feedback noted above where clearing decreases tree and seed
biomass, which makes cultivating a more optimal strategy so people clear more forest. The other
assumption that leads to the deconstruction of the forest is that soil fertility is proportional to
tree biomass. As the biomass of trees declines, the yield of maize per unit area declines. The
consequence: people need to clear ever more area to meet their desire for maize, but the fertility
of the soil is just too low to ever get enough food to meet $K$. Hence, once people flip to the
impoverished attractor, any small increase in population or decline in the productivity of trees ($r_s$
& $r_p$) will cause large declines in the productivity of maize and decimate the productivity of the
ecosystem.

The long-run effect of low-level food production

The emergence of multiple stable states has a subtle but profound consequence. It is often optimal
for a household to engage in low-level food production at the productive attractor; however, when
households adopt low-level farming, the system loses resilience and becomes more vulnerable to
a flip from the productive to the impoverished state.

Figure 4 is a bifurcation diagram analogous to Figure 1c. This diagram is a tool for illustrating
how, holding other parameters equal, $N$ affects the structure of the system. On the $x$-axis we have
plotted $N$, and on the $y$-axis we have plotted the percent of diet obtained from foraging ($h_s/K$)
when the system is at equilibrium (i.e., $s = 0$ and $p = 0$). The thick black curves are all of the
productive and impoverished attractors that would emerge for given values of $N$. The dashed
curved is the collection of repellors that emerge for given values of $N$ and separates the productive
and impoverished curves. The shaded area defines all of the values of $N$ for which the system has
three equilibria (two attractors and a repellor).

Figure 4: Summary of the relationship between $N$ and the proportion of the diet obtained from seeds at equilibrium. The upper solid line represents all of the productive attractors; the dashed middle line, all repellors (unstable branch), and the lower solid line all of the impoverished attractors. Shaded area defines the parameter space in which a perturbation can cause the system to flip between attractors.

Figure 4 demonstrates that low-level food production is often optimal over the short term, but also creates conditions that may lead to the rapid and difficult to reverse process of adopting agriculture at the expense of hunting and gathering over the longer run. Reading from left-to-right, as $N$ increases, households in the productive state (the top left branch) remain pure foragers until a threshold of about $N = 1.25$. At $N = 1.25$ households begin to cultivate maize as a minor component of their diet, and the proportion of the diet from foraging begins to decline. Once households begin to optimize by cultivating maize, small increases in $N$ lead to fast decreases in the proportion of the diet that comes from foraging (the productive harvest branch bends down and to the right). However, foragers can only replace a maximum of about 40% of their diet with maize before the system bifurcates, and the only attractor is the impoverished state (i.e. the system crosses a parameter threshold).

It is intuitive that households can replace declining returns from seeds with maize with little
disruption to their foraging system over the short run [34]. However, cultivating maize in response
to declining returns from foraging (caused here by increases in $N$ relative to $r_p$ and $r_s$) means
that the system is more likely to flip over the long-run (i.e. cross a state variable threshold).
Given enough time, a big enough shock is sure to occur in most environments. To elaborate:
we can estimate the resilience of the productive attractor by estimating the size of the attractor.
We estimate size by calculating the Euclidean distance between the productive attractor and the
unstable harvest branch (the repellor) in Figure 4 [50]. As the size of the productive attractor
declines, the probability that a perturbation induces a regime shift increases. the point here is
that a one unit decline in the proportion of diet from foraging, at the productive attractor, induces
a decline in the size of the productive attractor that is greater than one. Thus, a perturbation of
similar size is more likely to induce a regime shift from the productive to impoverished attractor
as households supplement foraging with farming at the productive attractor.

In sum, the optimal allocation of effort to foraging and farming can make a system of low-level
food production vulnerable to a ‘flip’—caused, in part, by the very rules that allow individual’s
optimize their production of food. If the system flips into the impoverished state, the ecosystem
is vulnerable to degradation. The implication is that if a system flips, households either abandon
the area or engage in classic Boserupian responses. Boserupian responses are strategies that invest
labor in new niche construction activities and increase the productivity of land per unit area, as
well as decrease the need to further harvest trees (thereby improving soil fertility). Hence, at the
productive attractor, it is likely not very costly to increase or decrease effort in farming as pertur-
bations (droughts, etc.) dictate year-to-year. However, if environmental variation initiates a flip
into the impoverished state, households have to leave or lock-in to a run away niche construction
strategy that mitigates declines in soil fertility. A central issue is whether households might ascer-
tain from their knowledge of the environment that the risk of getting pushed into the impoverished
state is a novel feature of their social and ecological world. If so, they might be able to adapt to
longer-term variation and modify how they allocate effort in the short term; if not: look out!

So What?

Our work is motivated by a basic question. Why, once domesticated plants became part of the
subsistence base, did some people increase their time invested in farming at the expense of hunting
and gathering while others engaged in a persistent mix of foraging and low-level farming? One
way to answer this question is to use the tools of foraging theory and ask: When does an individual
maximize their fitness by investing in farming at the expense of foraging, and this has been a
productive line of research (e.g., 20, 64–67). However, the foraging models that anthropologists
typically use can benefit from further development (e.g., 27, 68). Foraging models, often, do
not account for the feedbacks caused by niche construction and, thus, the process of ecological
inheritance. Ecological inheritance is known to cause non-linear trajectories of evolution. An
important possibility is that ecological inheritance may result in multiple stable states, or ways that
humans could be organized to obtain food in a given environment. Multiple stable states can lead
to transitions that are punctuated, difficult to anticipate, and very costly to reverse.

Therefore, we have combined an optimization model with a dynamical systems model to study
the effects of niche construction and ecological inheritance. We asked two specific questions.
Under what ecological and social conditions might the optimal allocation of effort to foraging and
low-level food production cause multiple stable states to emerge, and if they do, what variables should create different trajectories that the evolution of food production follows? The analysis of our model provides an answer to the first question, and creates a more informed position to propose an argument that may help answer the second question.

The model generates multiple stable states when the ecological footprint of households increases beyond a critical threshold (Figures 3b & 4). The emergence of multiple stable states has four implications.

1. When a household behaves optimally in the short-run, this act exposes all of the households to the risk of flipping from a productive state to an impoverished state over the longer run.

2. The risk of the system flipping emerges when households are still pure foragers, which opens up the possibility that households may suddenly transition from full-time foraging to full time farming. However, the full time farming at our impoverished attractor is very sensitive to increases in population density or declines in the productivity of wild resources. Any slight change will cause the system to move toward a completely denuded state.

3. The adoption of low-level food production in the productive state makes the whole system more vulnerable to perturbations. The implication is that low-level food production is costly to maintain (but see below).

4. The dynamics of our model provide a theoretical basis for defining low-level food production with domesticates as a space defined by a diet between 1 and 40% dependence upon domesticates. Note: The 40% threshold is not a universal. The exact value would vary from system to system, depending on the specifics of particular ecosystems. The key is the qualitative insight that there is a parameter threshold, and it will likely fall somewhere between 1 and 40% in many particular systems. Incidentally, there is empirical evidence that major changes in the way households organize labor occurs cross-culturally at a threshold of about 35% dependence on domesticated plants [35].

The issue now is: Why do systems follow different trajectories of evolution on the path from foraging to farming? To begin to use the insights from our model to answer this question, we consider the transition from foraging to farming in the piñon-juniper forests of the Colorado Plateau in the American Southwest. Our argument for this specific place then provides a point of departure to speculate about why systems of food production may follow different evolutionary trajectories.

An example to help consider the broader implications of the model

The Colorado Plateau is an arid region with elevations ranging between 1,500 and 3,000 meters. The region is drained by the Colorado River and its tributaries, and is also dissected by numerous small perennial and seasonal drainages. Many of these drainages form deeply incised canyons bordered by high upland mesa tops. The upland mesa tops are, in most locations, dominated by piñon and juniper trees. Over the course of prehistory, these highland mesa tops became the primary settings occupied by prehistoric farmers across much of the Plateau.
The Colorado Plateau spans two archaeological cultures; the Ancestral Puebloan and the Fremont. Both Ancestral Puebloan and Fremont populations engaged in farming. One major distinction, however, is that while populations in the Ancestral Puebloan region were committed agriculturalists by about A.D. 700 or earlier in some places, populations in the Fremont region relied on hunting and gathering, in many locations, throughout prehistory [64, 69]. Thus, while the transition to agricultural dependence appears to have been relatively complete in the Ancestral Puebloan region, the occupation of the Fremont region represents more of a mosaic with different strategies being used in different places over the long term. Our concern here is not with the initial arrival of agriculture but the increased investment in agriculture and the development of new strategies, including upland cultivation. The transition to upland cultivation occurred on several parts of the Colorado Plateau, such as: the Mesa Verde/Northern San Juan region, Cedar Mesa, portions of the Mogollon Rim, and areas along the Fremont and Green Rivers. This transition was variably timed but primarily occurred between about A.D. 200 and A.D. 750 in the four corners (70, p. 128-129; 71) and as late as A.D. 1000 further north in portions of the Fremont region [72, 73].

Based on paleobotanical and settlement data, many researchers have suggested that the prehistoric agricultural systems in the piñon-juniper woodland mesa tops along the Colorado Plateau involved a type of shifting cultivation. This method of cultivation involved the clearing of small field areas, likely with fire, followed by planting in the cleared areas. This was followed by a long fallow period when the woodland plots were allowed to regrow and soil nutrients regenerate (e.g., 71, 74–81). Local transitions from foraging and other forms of agriculture to extensive cultivation of upland mesa tops are interesting because explanations for this change are not straightforward. Extensive shifting cultivation is less efficient than many other types of agriculture and foraging [64, p. 80], it is risky [70, p. 135-136], and it is not locally sustainable [74–76]. So why did the shift to extensive cultivation occur?

One way that we might answer this question is to directly analogize from the dynamics of our model. Recall that we observed the possibility of a regime shift from pure foraging to farming, where over 70% of a household’s time budget was devoted to cultivation and the forest cover severely declined (Figure 3b). In this argument, prehistoric foragers would have inadvertently backed into the adoption of extensive cultivation. If this occurred on the prehistoric Colorado Plateau, we would expect to see the punctuated adoption of extensive agriculture and a punctuated denuding of piñon-juniper forests on mesa tops. Although, there does seem to be a punctuated increase in commitment to extensive cultivation, particularly in upland contexts [71, 76, 82], declines in forest cover seem to have occurred much more slowly, as people became more committed to agriculture. Further, in some locations, the coordinated use of high frequency fires by households may have maintained a dynamically stable forest structure that was good for disturbance loving plants such that are integral species in almost all agroecological systems in North America (e.g., 83). This suggests that a more subtle argument is required to understand why people may shift from low-level food production in which cultivation supplements foraging to a subsistence system in which foraging compliments farming—where labor is organized first around the intensive management of small patches to insure against risk, even though foraging may still provide substantial calories.
To build our argument, we combine the insights of our model with two empirical statements that relate the structure of ecosystems to tradeoffs in the knowledge economies necessary to obtain a reliable supply of food as a mobile forager versus a farmer.

First, Holling [84] provides empirical evidence that ecosystems are organized into a hierarchy of structures (i.e. leaf, tree, patch of trees, habitat, landscape, biome) controlled by a handful of processes that operate at distinct scales of space and time. The consequence is that animals face a decision hierarchy [85]. Second, in part because of the hierarchical structure of ecosystems, humans face a knowledge tradeoff. Farmers plant fields at the scale of a patch. The successful production of crops depends on having a detailed knowledge of the soil conditions, flow of water, and timing of temperature changes in the few patches where fields are planted. Mobile foragers, alternatively, use landscapes. Thus, knowledge of different landscapes, each composed of multiple habitats that are, in turn, composed of multiple patches is essential for human foragers to consistently produce food [86]. In short, farmers need a fine grained knowledge of patches, and foragers need a coarse grained knowledge of landscapes to make decisions about where to locate in space and time and invest effort to produce food.

The difference in the knowledge economies necessary to forage versus farm is significant. As one uses more levels in the ecosystem hierarchy, the number of processes that affect the distribution of resources increases. The consequence is that foragers need a generalizable system of knowledge to encode information across many scales of space and time while farmers need a more partitioned and textured knowledge of ecosystems. For example, Brown [87] documents that farmers living in the same environment as hunter-gatherers partition their knowledge of plants and animals into much finer categories. That is, for a forager, a flower is a flower, but for a farmer, a flower is a red rose, yellow rose, daffodil, etcetera. The costs of obtaining information in the nested hierarchy of ecosystem structures that humans exploit is very instructive for understanding this difference. Foragers minimize the costs of collecting information across many levels of the ecosystem hierarchy by generalizing. In contrast, farmers minimize the risk of planting at the wrong time or in the wrong location by investing in a fine grained knowledge of lower levels in the hierarchy, like patches.

In our model, once foragers adopt low-level food production (less than 40% of the diet from domesticates), the net effect of this behavior is to make the system vulnerable to a flip from the productive to the impoverished state. In the context of the nested hierarchy of ecosystem structures that human foragers encounter; we can extend this insight to make two related propositions. 1) The effects of cultivating to supplement the diet obtained from foraging at the level of ecosystem patches, scales-up to make habitats (much larger tracks of an ecosystem) vulnerable to a flip from the productive to impoverished state. 2) The consequence of this is that while over a few of years it appears optimal to supplement foraging with a little farming; this behavior makes it harder to maintain a foraging system over decades based on coarse grained knowledge about a landscape. The reason is this: now foragers must know how likely habitats are to flip into the impoverished state in addition to everything else. Further, it may be very difficult to predict such flips. An easy solution is to just farm more, but using the low-level strategy that we presumed in our model will simply degrade natural capital and make a flip more likely. In this context, selection and copying should favor a fine grained knowledge system that allows individuals to shift their subsistence system to one committed to farming at or above the 40% line and minimizes the short to medium
term (years to decades) impact of farming practices on the degradation of the forest.

In the context of the Colorado Plateau, we might expect that once domesticates were introduced to mesa top forests, the shift to minimally committed agriculturalists may have been quite rapid, stabilizing major tree depletion and more effectively allocating effort. However, once in this committed agriculture regime was established, it may have locked-in and slowly evolved toward ever more committed agriculture. In this regard the Fremont provides an interesting contrast. 1

Holding all else equal, it may be that the adoption of agriculture was most rapid in the areas with the densest forests, and foraging remained dominant in other areas because of diverse ecosystem types, including highly productive wetlands not characteristic of the Southwest US in general. In the deserts of the Southwest US and Northern Mexico, only the eastern half of the Mexican state of Chihuahua has somewhat analogous wetland formations, and maize was never adopted in this area prehistorically. The bifurcation of a foraging and farming regime could have provided the adaptive space for individuals to move between systems and give the impression of a stable low-level food production system as described by our model (i.e., a system where household diet is between 1 - 40% dependent on agriculture) in the Fremont area.

Macroecology and Macroevolution

Our argument above provides a starting point from which to generalize. If low-level food production decreases the resilience of forager-resource systems, in general, across the hierarchy of ecosystem organization: we propose that low-level food production is only weakly stable. Either an increase in the costs of processing information will stimulate individuals to shift to a committed agricultural way of life based on a knowledge system with a finer grained texture, or they will abandon an area all together. The sum result is that low-level food production should be quite rare in human societies.

Figure 5 demonstrates that low-level food production with domesticates is very rare in human societies. Figure 5 is a histogram of the societies recorded in the Ethnographic Atlas [88] that have subsistence information. There is a gap between hunting and gathering on the one hand and farming on the other. Detailed study of this gap suggests that major changes occur in societies’ use of resources at a threshold of about 30-35% dependence on farming. Farmers above this threshold grow a high diversity of crops, seemingly set by the tolerance limits of crops in their environment; however, farmers below this threshold only grow a few crops, usually a subset of crops grown by their neighbors [89]. Further, above the threshold, farming societies tend to have one or more formal weeding periods, and below this threshold no such formal institutions are observed [35, p. 3011-3012]. These data do not test whether foraging regimes and committed farming regimes are more resilient than low-level farming regimes, but they do something equally important. They warrant the development of more rigorous study. Nonetheless, our model combined with our

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1The idea that coordinated, high frequency burning maintains an open forest in a kind of dynamically stable state [83] fits very well with the kind of transition that we argue occurs in knowledge economies—even though wild foods still dominate the diet. The shift to a high management strategy and fine grained knowledge economy may increase the resilience of a forest to shocks or at least keep resilience from going down any further. But the Upper Colorado system discussed by Sullivan et al. [83] obviously was abandoned at some point. There may have been limits to how much this strategy could effect the resilience of the forest across scales and, thus, reduce the uncertainty of food production. Given a big enough shock (perhaps the Little Ice Age) many levels of the system might have experiences a flip and contributed to abandonment.
knowledge argument indicates that low-level farming is a less resilient strategy than foraging and committed farming.

![Figure 5: Histogram of the density of societies per binned level dependence on agriculture (domesticated plants only).](image)

Smith [2001] has warned us not to discount the groups in the “gap” in Figure 5, and he is correct. One reason that low-level food production regimes may develop and persist is that variation in vegetation communities causes the effects of ecological inheritance on foraging economies to diverge in space and time. For example, our model is a case in which niche construction causes a particular directional effect on the productivity of wild resources and domesticates (controlled by soil fertility). The directional effect is a double negative, harvesting seeds and clearing the forest depletes the future productivity of trees and the soil. Ecological inheritance need not occur in this manor. There are four possibilities: $++$, $+-$, $-+$, and $--$. We propose that holding other factors equal, the trajectory of evolutionary change varies in predictable ways based on the directional effect of ecological inheritance in an ecosystem. That is, if two populations adopt low-level farming, the trajectory of evolution for the population living in an environment with a double positive will be different from the trajectory of the population living in an environment with a double negative. There are two ways to evaluate this proposition.

First, we could ask: what changes to the assumptions of the model developed above are necessary to generate large basins of attraction for low level farming? Using this strategy, the challenge would be to build reasonable assumptions about the harvest behavior of forager-farmers that generate the four possible scenarios listed above. This strategy allows for the possibility of a more precise description of what happens in each case (e.g., $++$ vs. $+-$) in terms of the trajectories.
of change in different systems. For example, the systems might generate oscillations or chaotic attractors, as opposed to stable equilibria, which may have physical meaning in some contexts.

Second, we could start with two empirical propositions 1) In the case of double positive effects, the resilience of a low-level farming regime should be enhanced, and, thus, be more likely to withstand perturbations. For example, the Nualulu of Indonesia might live in a double positive setting. They plant and tend both wild and domesticated sego palms. The wild segos increase in productivity in response to low-level clearing and burning conducted to cultivate domesticated segos [57]. 2) In the case of a double negative, as in our model, the resilience of the low-level food production regime should decline and we should see a bifurcation between ‘pure’ foraging and minimally committed farming subsistence regimes. We could then take a representative sample of the Ethnographic Atlas and classify each case according to the likelihood that low-level cultivation will deplete vs. increase the key wild resources in an environment, and the effect of low-level cultivation on soil fertility. This would be a coarse grained analysis, but it would allow us to divide the sample into $++$, $+-$, $-+$, and $--$ sets of cases. We would expect the frequency of low-level food production to be highest in $++$ settings, second highest in $+-$ and $-+$ settings, and lowest in $--$ settings.

**Conclusion**

It is trivial (almost tautological) to state that niche construction and ecological inheritance partly determine the evolution of food production. Our goal in the work presented here is to understand why the process of ecological inheritance, which is an outcome of niche construction, might cause different evolutionary trajectories. We have read with great interest the recent debate over whether human behavioral ecology provides an overarching framework for studying the adoption of domesticated plants (7–9, 90–92; see also 15 & 27 for an earlier version of the argument). We argue that HBE provides an overarching framework to understand specialization in domesticates at the expense of hunting and gathering. However, the feedback dynamics caused by niche construction may cause non-intuitive trajectories of evolution, and dynamical systems models are a critical tool for improving our understanding of such possibilities. In this paper, we have shown that multiple stable states occur when we include the process of ecological inheritance (caused by niche construction) in a optimization model drawn from foraging theory/microeconomics. This model illustrates that the optimality of individual foraging decisions over shorter time scales and the resilience of a system over longer time scales are both important for understanding the evolution of food production.

**Acknowledgments**

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**Box 1: Constrained Optimization**

We solve the constrained optimization problem to determine how households should allocate effort to minimize the total effort required to meet $K$. First, we form the Lagrangian $L(l_c, l_s, \lambda)$

$$L(l_c, l_s, \lambda) = l_c + l_s - \lambda (A_c(p)l_c + A_s(s)l_s^\beta - K)$$  \hspace{1cm} (12)

which yields the first order conditions

$$\frac{\partial L}{\partial l_c} = 1 - \lambda A_c(p) = 0 \Rightarrow \lambda = \frac{1}{A_c(p)}$$  \hspace{1cm} (13)

$$\frac{\partial L}{\partial l_s} = 1 - \lambda (\beta A_s(s)l_s^{\beta - 1}) = 0 \Rightarrow \lambda = \frac{1}{\beta A_s(s)l_s^{\beta - 1}}.$$  \hspace{1cm} (14)

Both equation (13) and (14) define $\lambda$. Equating these expressions for $\lambda$ yields the following expression

$$A_c(p) = \beta A_s(s)l_s^{(\beta - 1)}$$  \hspace{1cm} (15)

which relates the labor allocated to seed gathering, $l_s$, and the system state, $p$ and $s$. This relation simply says that at the optimal value of $l_s$, the marginal productivity of labor in agriculture and gathering are equal just as in equation 3. Some algebra yields an expression for the optimal amount of labor to be directed toward gathering:

$$l_s = \left(\frac{\beta A_s(s)}{A_c(p)}\right)^{(1/\beta)}$$  \hspace{1cm} (16)

Note that the expression above is insensitive to the fact that $l_s$ may be greater than the total labor available, $l$, or whether $K$ is met. To account for these constraints, we define the *unconstrained* optimal labor allocation given in equation (16) as $l^*_s$ and the *constrained* optimum, described below, as $\overline{l}_s$. Applying the subsistence constraint yields

$$\overline{l}_s = \max\left(\frac{K - A_s(s)(l^*_s)^\beta}{A_c}, 0\right)$$  \hspace{1cm} (17)

where $\overline{l}_s$ is the *constrained* optimal labor allocation to cultivation. If $\overline{l}_s$ is zero, this means that $l^*_s$ is sufficient to meet $K$ and cultivation is forgone. Put another way, the point at which it pays to devote the next unit of labor to cultivation occurs after output is higher than $K$. In this case,

$$\overline{l}_s = \left(\frac{K}{A_s(s)}\right)^{(1-\beta)}$$  \hspace{1cm} (18)

Finally, the labor constraint must be checked to ensure that $\overline{l}_c + \overline{l}_s \leq l$. The conditions in (16) and (18) tell a household to first determine the best allocation of effort to foraging and farming, then follow the decision heuristic below.

1. If $l^*_s$ is sufficient to meet $K$ (i.e. $\overline{l}_s = 0$), then attempt to gather seeds until $K$ is met (i.e. set $l_s = \overline{l}_s$).
   
   If the effort required to meet $K$ via gathering is greater than the maximum ($\overline{l}_s > l$), then devote all available available effort to gathering (set $l_s = l$).

2. If $l^*_s$ is not sufficient to meet $K$, then set $l_s = \min(\overline{l}_s, l)$. and $l_c = \min(\overline{l}_c, \max(l - \overline{l}_s, 0))$.

3. If the quantity of land to accommodate the effort allocated to cultivation by the rule above is available, cultivate it. Otherwise, cultivate what is available and devote some effort to clearing more land in the effort to meet the required cultivable land area.
Box 2: Model Analysis

We provide additional background to interpret Figures 3 & 4. Our model is a non-linear dynamical system. A non-linear dynamical system can be studied analytically and/or numerically using software (in our case a program called XPPAUT). Both approaches can be used to determine how many solutions there are in a system (i.e. equilibria) and the qualitative stability of each solution. One determines qualitative stability by linearizing the the non-linear system around equilibrium points. Only very near equilibria can we treat the system as if it is linear. We have used XPPAUT to numerically determine the eigenvalues. If any of the real parts of the eigenvalues \( > 0 \), then an equilibrium is unstable. If the real parts of all the eigenvalues \( < 0 \), then the equilibrium is stable. We have used this theory to determine whether an equilibrium is an attractor or repellor.

For example, absent humans (N=0), our model has one equilibrium (see Figure 3a). We can show analytically that, at this equilibrium, the long-run seed and tree densities, denoted as \( \bar{s} \) and \( \bar{p} \) are \( \bar{s} = r_sK_p/d_s \) and \( \bar{p} = K_p \). This means that when seed density is not changing, the density of seeds is determined by a ratio: The production of seeds divided by the decay of seeds. That is, if we double \( K_p \), we double the seed density because we are looking at twice the area. This is a common feature of mathematical models. Ratios control the dynamics of the model. However, we must note that when we choose the value of \( K_p \), this defines the scale of other parameters. For example, setting \( K_p = 1 \) and \( r_s = 2 \) means that the seed generation rate of trees is twice as fast as the rate at which seeds are used up.

A non-linear dynamical system has both global and local properties. When we say that an equilibrium is either stable or unstable, we are talking about a local property. When we say that our model has one or three equilibria, we are talking about a global property of the system. For example, when \( N = 0 \), the equilibrium seed and tree density \( (\bar{s} = r_sK_p/d_s, \bar{p} = K_p) \) defines a stable equilibrium. This means that if the system is perturbed it will always move back toward this point. The system is globally stable because there is only one equilibrium. Figure 3d is a metaphor for these statements. On the valley bottom, the slope of the landscape is zero-signifying that the system is in equilibrium. The valley walls represent the slope or how quickly a system returns to equilibrium if perturbed. In this case, there is one valley (basin of attraction) signifying that there is only one equilibrium in the model. In Figure 3b, N is equal to 1.1 and the global structure of this system is defined by three equilibria. Two are locally stable (what we call the productive and impoverished states), the other is unstable. Notice on Figure 3e that the system may flip from one valley to the other. In Figure 3e the hill between the valleys represents the unstable equilibrium. At the top of the hill the slope is zero (the equilibrium). Any small perturbation will initiate feedback loops that lead the system into one of the adjacent valleys.