



# Toward a theory of non-linear transitions from foraging to farming



Jacob Freeman<sup>\*</sup>, Matthew A. Peeples, John M. Anderies

Department of Sociology, Social Work and Anthropology, Utah State University, United States

School of Human Evolution and Social Change, Arizona State University, United States

School of Sustainability, Arizona State University, United States

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## ABSTRACT

The evolution of agricultural economies requires two processes: (1) the domestication of plants and (2) specialization in agricultural practices at the expense of alternative subsistence pursuits. Yet, in the literature, domestication receives the lion's share of attention while theories of specialization lag behind. In this paper, we integrate ideas from human behavioral ecology (HBE) with tools from dynamical systems theory to study the effects of ecological inheritance on levels of investment in foraging and 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 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.

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## 1. Introduction

The adoption of domesticated plants is one of the most studied problems in anthropology, particularly as an outcome of human–environment interactions (e.g., Barker, 2006; Binford, 2001, 1968; Bowles and Choi, 2013; Childe, 1928; Flannery, 1985, 1973; Hayden, 1990, 1998; Huckell, 1995; Kennett and Winterhalder, 2006; MacNeish, 1992; Piperno and Pearsall, 1998; Rindos, 1984, 1980; Rowley-Conwy and Layton, 2011; Smith, 1995, 2011a; Wills, 1988; Winterhalder and Goland, 1997, 1993). 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., Harris, 1996; Hayden, 1990; MacNeish, 1992, p. 3; Smith, 1995, p. 3; Wills, 1988, 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 (Bender, 1978; Flannery, 1968; Hayden, 1990; Hunter-Anderson, 1986; Nichols, 1987; Rindos, 1980). Thus, a fundamental question is why, once domesticated plants became available, did some

people increase their time invested in farming at the expense of hunting and gathering while others did not (Barlow, 2006; Freeman, 2012a; Hunter-Anderson, 1986; Phillips, 2009; Rindos, 1980; Smith, 2001; Vierra, 2005; Zvelebil, 1996)? In short, what dynamics explain the various levels of investment – from zero to near the total input and output of a subsistence system – in farming?

In this paper, we work within a human behavioral ecology (HBE) framework to combine an optimal foraging model with dynamical systems theory to study why individuals specialize (or not) in farming when wild resource alternatives are available as well. Our work contributes to understanding the coevolution of subsistence strategies and ecosystems. Specifically, we use the insight gained from our dynamic model of optimal foraging and farming to develop expectations for how the modification of ecosystems may result in different trajectories of change in the evolution of farming strategies. Our model, by its very structure, illustrates the importance of niche construction and ecological inheritance (discussed below) for understanding non-linear trajectories of change in human subsistence systems. We argue that HBE provides an overarching framework to understand specialization in domesticates at the expense of hunting and gathering. Within HBE, however, models that incorporate the feedback dynamics caused by niche construction are important, though under used, tools to help understand non-linear trajectories of evolution. Dynamical

<sup>\*</sup> Corresponding author at: Department of Sociology, Social Work and Anthropology, Utah State University, United States.

systems models are one tool for extending models drawn from optimal foraging theory to understand such possibilities.

## 2. Ecological inheritance, foraging models, and non-linear trajectories

A growing number of anthropologists are using niche construction theory to help explain the domestication of plants (or lack thereof) from long-term plant-herbivore interactions (Bleed and Matsui, 2010; Laland and O'Brien, 2010; Rowley-Conwy and Layton, 2011; Smith, 2007, 2011b,a, 2015; Zeder, 2015). Here we take on a different but equally important issue. Why, once domesticated plants are available, do populations make different levels of investment in these resources? For example, maize entered the southwest US by 4200 BP (Merrill et al., 2009). Although no one denies that the crop continued to evolve and become fine tuned to local environments, the marginal change in the crop's niche after 2000 BP was very small. Yet, in west Texas, the level of investment in maize remained very low, while in other parts of the southwest, such as present day Colorado, New Mexico, and Arizona, populations became specialized in the production of maize (e.g., Hard et al., 1996). At a finer scale, the Fremont archeological tradition of modern day Utah and Colorado is well known for a high degree of variation in levels of investment in maize, evidenced among sites and individuals (Simms, 2008), despite the fact that people had access to similar races and varieties of maize. This pattern is known from other archeological case studies around the world as well, for example, central western Argentina (Gil et al., 2011). Our supposition is that the evolution of disparate investments in farming is a consequence of the different ways that foraging practices and cultivating domesticated plants modify the composition and structure of ecosystems and, thus, modify the net benefits of different behaviors for producing food over time.

A key process in our supposition comes from niche construction theory: ecological inheritance. Ecological inheritance is an outcome of niche construction, which is the ability of organisms to “shape environments to states that are suited to their biology (and less frequently to states that are not)” (Odling-Smee and Laland, 2011, p. 221). Odling-Smee et al. (2013, p. 8) define ecological inheritance as:

“[t]he inheritance, via an external environment, of one or more natural selection pressures previously modified by niche-constructing organisms (Odling-Smee et al., 2003). Ecological inheritance typically depends on organisms bequeathing altered selective environments to their descendants, but other organisms, including unrelated conspecifics and members of other species that share the same ecosystem may also be affected by this legacy. Where an act of niche construction leads to a change in the species composition of the local ecological community, this too is regarded as an aspect of the ecological inheritance.”

Here we are concerned with the last aspect of ecological inheritance in the above definition, changes in the composition of an ecological community, particularly as a consequence of the optimal decisions of individuals.<sup>1</sup> We assume, as is common in HBE, that selection favors the optimal solution to a problem in any given context, whether the solution is arrived at via some “combination of genetic adaptation, physiological plasticity or culturally transmitted information” (Brown and Richerson, 2014, p. 108). To the point, the ways that humans produce food, which is constructing their niche, may affect the composition of an ecosystem; in turn, the changed

composition of the ecosystem may change the behaviors that are optimal – and, by inference, fitness maximizing – in the future. It is this feedback between the optimal behavior now, an ecosystem's structure, and optimal behaviors in the future that needs investigation to better understand variation in people's investment in farming.

### 2.1. On the importance of modeling feedbacks

In HBE, many explanations for changes in human behavior are grounded by optimal foraging models (OFM) (Bird and O'Connell, 2006; Coddling and Bird, 2015; see also Winterhalder and Smith, 2000). Such models are a useful starting point, but need extension to better explain levels of investment in farming. To see why, please consider the following example.

Barlow (2006) proposes a 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:

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

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 “ $\leq$ ” 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 Eq. (1) and rewrite Eq. (1) as

$$A(l_c) = A_s(l - l_c) + A_c(l_c). \quad (2)$$

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

$$A'(l_c) = -A'_s + A'_c = 0 \quad (3)$$

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:

$$A'_s < A'_c. \quad (4)$$

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 (Barlow, 2006, 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

<sup>1</sup> Other aspects of ecological inheritance are important and interesting; they are simply beyond the scope of this paper.

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