

Feedbacks, Critical Transitions and Social Change in Forager-Resource Systems
An Integrated Modeling and Ethnoarchaeological Analysis

by

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ABSTRACT

My dissertation contributes to a body of knowledge useful for understanding the evolution of subsistence economies based on agriculture from those based on hunting and gathering, as well as the development of formal rules and norms of territorial ownership in hunter-gatherer societies. My research specifically combines simple formal and conceptual models with the empirical analysis of large ethnographic and environmental data sets to study feedback processes in coupled forager-resource systems. I use the formal and conceptual models of forager-resource systems as tools that aid in the development of two alternative arguments that may explain the adoption of food production and formal territorial ownership among hunter-gatherers. I call these arguments the Uncertainty Reduction Hypothesis and the Social Opportunity Hypothesis. Based on the logic of these arguments, I develop expectations for patterns of food production and formal territorial ownership documented in the ethnographic record of hunter-gatherer societies and evaluate these expectations with large ethnographic and environmental data sets. My analysis suggests that the Uncertainty Reduction Hypothesis is more consistent with the data than the Social Opportunity Hypothesis. Overall, my approach combines the intellectual frameworks of evolutionary ecology and resilience thinking. The result is a theory of subsistence change that integrates elements of three classic models of economic development with deep intellectual roots in human ecology: The Malthusian, Boserupian and Weberian models. A final take home message of my study is that evolutionary ecology and resilience thinking are complementary frameworks for archaeologists who study the transition from hunting and gathering to farming.

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Chapter 1

INTRODUCTION

The dissertation before you contributes to understanding the evolution of subsistence economies based on agriculture from those based on hunting and gathering and the development of formal rules and norms of territorial ownership in hunter-gatherer societies. My research specifically combines formal and conceptual models with the empirical analysis of large ethnographic and environmental data sets to study feedback processes in coupled social-ecological systems (SES). I use simple models of social-ecological systems as tools that aid in the development of two alternative arguments that may explain the adoption of food production and formal territorial ownership among hunter-gatherers. My approach combines the intellectual frameworks of evolutionary ecology and resilience thinking. The result is a theory of subsistence change in hunter-gatherer SES that integrates elements of three classic theories of economic development with deep intellectual roots in human ecology: the Malthusian (Malthus, 1888), Boserupian (Boserup, 1965) and Weberian (Weber, 1927) theories. The take home message of my study is that evolutionary ecology and resilience thinking are complementary frameworks for studying cultural evolution. In fact, I argue that evolutionary ecology needs resilience thinking. The reason is simple. Social-ecological systems are dynamic entities characterized by feedbacks between individuals and resources. The only way to study such feedback processes with scientific rigor is by using the intellectual tools of dynamical systems theory and dynamical systems theory lies at the core of resilience thinking.

The Arguments

The meat and potatoes, if you will, of this dissertation is my construction of two arguments that may explain the adoption of food production and ownership rules (chapters 3 & 4). I call these two arguments the Uncertainty Reduction Hypothesis (URH) and the Social Opportunity Hypothesis (SOH). Here, I use the term hypothesis in a general sense, meaning an argument proposed to explain some group of phenomena. My goal is to evaluate the fit of these two arguments with patterns of food production and territorial ownership documented in the ethnographic record. In turn, the data analysis is designed to identify the general mechanisms that drive social and technological change in hunter-gatherer SES.

The URH proposes that subtle changes in the net productivity-to-population density ratio (r/p) of a forager-resource system have strong effects on the costs and benefits of individual foraging strategies. When the r/p ratio is really high, population is low relative to natural capital (resources). In this context, variation in the availability of resources is modulated by large scale ecosystem structures that change at time scales slower than the times scales at which perturbations shock resources and human foragers make decisions. Decrease the r/p ratio and foragers can maintain a supply of energy that is robust to environmental change by simply working a little harder. However, once the r/p ratio crosses a critical threshold, a forager resource-system is suddenly characterized by multiple stable states: a productive and a degraded state. In this situation, the strategy of working harder to achieve an energy goal creates a stochastic common pool resource dilemma in which the aggregate behavior of foragers creates the risk that every forager in a system is unable to find their desired level of food. I argue that in this ecological context natural capital accumulated at large scales (although still quite abundant) no longer effectively modulates variation in the ability of foragers to meet their desire for food and foragers experience increasing stress on their capacity to process information about the distribution of resources

in space and time. In turn, selection and copying pressures favor strategies that substitute technological and social capital for natural capital to reduce the uncertainty associated with achieving a desired level of resources.

The SOH proposes that there is a Goldilocks environmental zone where investments in the production of food provides individual foragers with an immediate benefit. This benefit is a predictable budget of non-subsistence time less sensitive to short-term climate variations at the level of a resource patch. In this Goldilocks zone, the immediate benefits of non-subsistence time favor the directional copying of strategies that increase the productivity of food in an ecosystem. This copying scales the effects of ecosystem management up to the habitat level where foraging populations have an incentive to adopt ownership institutions. Ownership institutions allow foragers to more efficiently achieve their energy target. At the landscape level, the r/p ratio increases and so does the robustness of foragers' supply of food to potential shocks. Landscape level systems where the food supply is robust to shocks have higher rates of population growth and expand at the expense of less resilient systems at the landscape scale. In this scenario, the very harvest strategies of foragers transform the social and biophysical environment across levels of ecological organization and drive the future evolution of a hunter-gatherer SES.

Based on the logic of the URH and SOH, I develop expectations for patterns of food production and formal territorial ownership documented in the ethnographic record of hunter-gatherer societies (chapter 5). I then evaluate the consistency of the URH and SOH with patterns of food production and territorial ownership in the ethnographic record. In the end, the URH is more consistent with the patterns of food production and territorial ownership in the ethnographic record. Thus, I argue that the URH provides a more robust foundation of knowledge for understanding the evolution of hunter-gatherer social-ecological systems. The URH is particularly relevant for studying the evolution of agricultural subsistence strategies at the expense of strategies based on hunting and gathering. I briefly suggest

how the URH might be used to understand this process in the prehistoric American Southwest. At a conceptual level, I argue that major shifts in how foragers manage resources, including the adoption of domesticated plants, sometimes occur as regime shifts. In the context of this dissertation, a regime shift describes an abrupt or discontinuous change in the ways that forager-resource interactions are organized. My research indicates that regime shifts may be propagated through populations of foragers as individuals respond to seemingly slight changes in their demography or the net productivity of wild resources. These kind of evolutionary dynamics, I propose, lead to mosaics of human-resource systems that coevolve and structure the opportunities and constraints that individuals must cope with (Thompson, 2005).

Motivation

My primary motivation is to help clarify the potential relationship between the adoption of agriculture and formal rules of territorial ownership. I define agriculture as a set of strategies used to grow food by managing disturbance and succession dynamics, as well as the distribution of soil nutrients and water in space and time in an ecosystem. From this perspective, agriculture falls on the far right of a continuum of strategies that humans might use to manage ecosystem processes and affect the availability of food. On the far left of the continuum is simply the harvest of wild resources by hunter-gatherers. “Formal ownership” is defined here as sets of rules and norms that define the who, when and where of territorial access. Ownership rules may be defined at the level of the individual or at the level of social groups or both levels simultaneously. The key is that individuals must act collectively to agree on, maintain and enforce such rules. Ownership rules in hunter-gatherer societies have also been viewed as a continuum in anthropological thought (Smith, 1988). On the far left of the continuum, territory is open access in which no formal rules restrict who can use a territory and when, but individuals may “ask permission” informally.

On the far right of the continuum individuals own private property or individually control who can access a territory.

Arguments for the adoption of agriculture have long postulated important feedbacks between the productivity of resources, forager population densities and the costs vs. benefits of individual foraging strategies (e.g., Binford, 2001, 1983; Bettinger, 1991; Dyson-Hudson and Smith, 1978; Hayden, 2003, 1981; Keeley, 1995, 1988; Kelly, 1995; Redding, 1988; Rosenberg, 1990, 1998; Smith, 1988; Winterhalder and Goland, 1993). However, only rather recently has the coevolutionary effects of the adoption of agriculture and territorial ownership on individual foragers become a topic of pressing research (e.g., Bettinger et al., 2009; Bowles and Choi, 2013; Freeman and Anderies, 2012; Kennett and Winterhalder, 2006; Smith, 2012; Zeder, 2012). The reason for the recent interest in the relationship between the adoption of agriculture and formal ownership institutions (either at the group or individual level) stems from two persistent and unexplained observations.

First, there is evidence that small-scale agriculture is less productive (in terms of energy return per person-hour) than hunting and gathering (Barker, 2011; Bowles, 2011). This evidence poses a conundrum: why would foragers give-up on more productive strategies for farming? Of course, one answer is that in some ecological-contexts small-scale agriculture is more productive than foraging (Barlow, 2006). Another potential answer is that agriculture and, in Bowles and Choi's (2013) terms, "private property" rights coevolve. In their formulation, where wild resources are dense and predictable (i.e., "rich"), the ownership of resources can provide an incentive for foragers to invest in agriculture because they can monopolize the gains, something that a mobile, foraging lifestyle severely constrains. As I discuss in chapter 2, Smith (2012) and Zeder (2012) make a similar argument.

Second, small-scale agriculture did not simply spread inexorably at the expense of hunting and gathering throughout the Holocene. In some places hunter-gatherer life-ways were remarkably persistent, even though foragers could have adopted agriculture (e.g., Bettinger

et al., 2009; Johnson and Hard, 2008; Zvelebil, 1996). For example, Texas is a relatively good place to grow maize, but prehistoric foragers over vast areas never adopted maize agriculture. Such examples of hunter-gatherers who persisted until very recently come from California, the Great Basin, Argentina and, of course, Australia. One reason for the persistence of Holocene hunter-gatherers may be that institutions of “ownership” compatible with farming were slow to evolve in these locations. Another possible reason is that foragers devised strategies of low-level food production (ecosystem management) and ways of organizing the ownership of foraging territories that were preferable to the adoption of agriculture.

Agriculture transforms the earth. From local patterns of erosion, to the eutrophication of lakes, to the composition of the atmosphere; the list of agriculture’s impacts on the bio-physical structure of the earth goes on and on. Ownership institutions set the “rules of the game” and coordinate who, when and where individuals can access resources. Such institutions can provide powerful incentives to conserve natural resources (Ostrom, 1990; Wilson et al., 1994). Such institutions, however, require individuals to potentially pay at least two costs. 1) Ownership institutions require individuals to cooperate and maintain trust in the rules of the game. 2) Ownership institutions provide a justification for inequality, in terms of access to resources and, thus, may severely constrain the ability of some individuals to secure critical resources. If we, as a global community, hope to reduce hunger, keep the bio-physical systems of the earth within a safe operating space for humanity and conserve biological diversity, then we need to understand the processes that led to the evolution of agriculture and formal institutions of ownership. Understanding such processes, I believe, is essential to understand how to navigate the complex dynamics of an earth with a population of over 7 billion people.

My second motivation is to contribute to a foundation of knowledge useful for understanding the prehistoric adoption of agriculture and territorial ownership. No one can

directly observe the past. This fact demands that practitioners of archaeology continually develop more robust theories and methods for using ethnographic observations to inform archaeological research. As Keeley (1995) pointed out almost two decades ago, controlled ethnographic comparisons provide an opportunity to identify the general processes that drive social and technological change in forager-resource systems. While archaeologists have long conducted controlled comparisons of ethnographic data to understand major changes in social-ecological systems, (e.g., Binford, 2001, 1990; Feinman and Neitzel, 1984; Keeley, 1995, 1988; Kelly, 1995; Pryor, 1986; Smith, 2001), these comparisons have largely been inductive and theoretically disjointed. The result is that the weight of the conclusions, although insightful, is somewhat diluted. In this dissertation, I develop formal and conceptual models from first principles of human behavior and use these models to develop explanations for investment in the low-level production of food and patterns of territorial ownership among hunter-gatherers. Rather than working from a primarily inductive frame of reference, I build on the work of hunter-gatherer scholars to i) model a forager-resource system and ii) develop and evaluate the relative merits of two explanations for the evolution of hunter-gatherer SES. My research contributes to a growing literature on the macroecology of human societies that uses large N cross-cultural data sets to evaluate the first principles of human-environment interactions and, subsequently, uses these analyses to ask questions about the archaeological record (e.g., Hamilton et al., 2009, 2007; Grove, 2010, 2009; Grove et al., 2012; Ullah, 2013; Johnson, 2013).

My final motivation is to contribute to the ever growing literature in archaeology that uses formal models (e.g., Anderies, 2006, 1998; Barton et al., 2010; Bowles and Choi, 2013; Bowles, 2009; Flannery, 1985; Freeman and Anderies, 2012; Kohler and van der Leeuw, 2007; Kohler and Gumerman, 2000; Janssen et al., 2003; Winterhalder and Lu, 1997; Winterhalder and Goland, 1993; Winterhalder et al., 1988, and many others), as well as conceptual models (e.g., Freeman, 2012b; Smith, 2012; Zeder, 2012) to understand the

coevolution of coupled social-ecological systems. This growing literature crystallizes the view that the evolution of individual decision making is inextricably linked to the evolution of the social, technological and biophysical environments that individuals must continually cope with. I believe that studying the coevolution of individual decisions, ecosystem structures, institutions and technology builds intellectual bridges between evolutionary ecology and resilience thinking (as well as other systems frameworks). These bridges, I am optimistic, are leading to advances in our understanding of cultural evolution. My motivation, however, is not simply to reinforce this point by building another model. I would like to contribute to a conversation on the epistemological status of models in archaeological research and on the costs vs. benefits of different kinds of modeling. Archaeologists have been quick to embrace so-called agent based models, but the use of formal systems of differential equations is trailing (Phillips, 2012). I argue that both kinds of modeling generate useful insights for archaeologists and are complementary. Somewhat against the grain, I use a very simple system of differential equations (simple as far as such models are concerned) to study the coevolution of foragers and resources.

Dynamic models in archaeological research

Dynamic models are indispensable tools for building explanations of prehistoric changes in social-ecological systems. By dynamic model I mean the formal representation of a system (in this case interacting humans and resources) and changes in the behavior of the system over time. At one level, the benefits of dynamic models are the same as those of models in general. Models help us evaluate the logic of our ideas (i.e., clarify our thinking); models often facilitate the development of quantitative predictions and, thus, help us discriminate between competing theories (Winterhalder, 2002). However, in addition to these benefits, dynamic models allow us to represent how a system changes over time and critically analyze how our assumptions lead to different trajectories of change. I argue that

this final benefit portends a deep epistemological reason that dynamic models are particularly important to investigate the research questions that archaeologists seek to answer. The reason stems directly from the epistemological challenge of archaeological research.

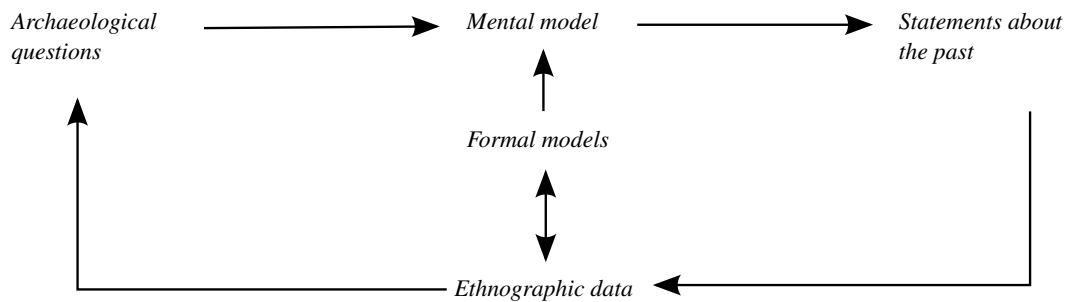


Figure 1.1: Process of archaeological research

As noted above, no one can directly observe processes that occurred 10,000 years ago. Thus, all statements that archaeologists make about the past are, ultimately, inferences. All archaeological inferences are statements about the past based on a mental model developed from our own intuition, ethnographic observations or experimental studies. This is true whether one is a positivist, post-positivist or a relativist. Figure 1.1 illustrates how I conceive the archaeological research process that my study is designed to help advance. This is a cyclical process of identifying archaeological patterns that need an explanation, building theories from actualistic studies (in this dissertation formal models and ethnographic data analysis) and evaluating the theories against archaeological data to make statements about the past. In turn, statements about the past inform the model building process and generate new questions about the archaeological record. The key part of this process that I contribute to here is the interplay between the construction of formal, dynamic models, ethnographic analysis and mental models. In the conception of archaeological research presented in Figure 1.1, the construction of formal, dynamic models is central to any attempt to understand patterns in the archaeological record. These formal models help clarify our thinking about

the mechanisms that generate change in SES and, thus, aid in our refinement of mental models.

Working from a scientific epistemology, once the centrality of model building to the process of building informed inferences is recognized, then the need to think carefully about the basis of models is apparent. For example, in studies of subsistence change, models are almost always based on ethnographic observations. Yet, ethnographic field studies occur at scales of space and time that are much smaller and faster than the scales of space and time over which major changes in human subsistence occur in the archaeological record. The result, archaeologists are forced to imagine how processes observed at scales of space and time appropriate to ethnographic studies play-out over longer time spans and larger geographic areas. This requires mental gymnastics that are difficult to manage using purely qualitative mental models. Moving across scales means dealing with increasingly complex evolutionary processes that are very hard to intuit.

If all social-ecological phenomena can be understood by scaling-up in space and time and, consequently, over levels of organization, then there is no problem. The idea that processes are scalable from one level of organization to higher levels of organization is known as the constructionist hypothesis (Anderson et al., 1972). However,

“The constructionist hypothesis breaks down when confronted with the twin difficulties of scale and complexity. The behavior of large and complex aggregates of elementary particles, it turns out, is not to be understood in terms of a simple extrapolation of the properties of a few particles. Instead, at each level of complexity entirely new properties appear, and the understanding of the new behaviors requires research which I think is as fundamental in its nature as any other” (Anderson et al., 1972:1).

This is a basic point that researchers who study biological systems have often made (Bak, 1996; Holland, 1995; Holling, 1992; Levin, 1999). In the language of complexity science, complex adaptive systems are more than the sum of the parts that compose a system. When cross-scale interactions between systems and agents operating at different scales of space and time lead to emergent social-ecological processes, then simply scaling-up in an additive way is incorrect. The constructionist hypothesis potentially obscures the feedback processes that affect evolutionary change. Formal, dynamic models are tools for playing with scales of space and time that help clarify our thinking, in particular, about how processes operating across levels of organization may lead to major changes in social-ecological systems. From an archaeological perspective, dynamic models help bridge archaeological questions and ethnographic data for which the scales of space, time and levels of organization are often poorly matched.

Research Questions

I believe that anthropology is in the throes of a major advance in our understanding of the general social-ecological processes that drive the evolution of SES. The major shift underway is the integration of evolutionary ecology and systems frameworks to understand the coevolution of social and ecological systems. In the parlance of modern anthropological theory, researchers are increasingly studying the reciprocal interactions of individual agents and the environmental structures that affect individual behaviors. This cross-level integration is not new; however, the intellectual development of interdisciplinary frameworks, like the complex adaptive systems framework, resilience thinking, and niche construction are creating a critical mass of researchers interested in coevolutionary processes. The study of coevolutionary processes

“require[s] a different way of thinking about evolution: one that no longer treats environments as context, that formally recognizes organisms as part

constructors of environmental states, and that views such construction and its legacy over time as evolutionary processes in their own right” (Laland, 2011:233-234).

A coevolutionary view of the processes that drive change in SES suggests that to explain the evolution of agricultural SES from hunter-gatherer SES and territorial ownership, *one must ask how the coevolutionary process works*. This requires understanding the structure and affects of feedbacks in SES on individuals. My research specifically explores how individual foraging strategies are potentially affected by changes in the attributes of feedbacks in forager-resource systems and how changes in the behavior of individuals impacts a forager-resource system. Two questions in particular, guide my research.

1. How do resource productivity and population density affect the robustness of foragers’ energy output in a forager-resource system to sets of potential shocks?
2. If there is an affect, how might the state of a forager-resource system, in turn, shape the costs and benefits of the foraging strategies selected by individuals?

These are critical questions because they center our attention on the long-term consequences of feedbacks between foragers and resources and the consequences of feedbacks on the costs vs. benefits of foraging strategies that individuals might adopt. The answers to these questions help illustrate the mechanisms that might cause individual foragers to change their strategies of resource exploitation and lead to the evolution of agriculture and territorial ownership.

The term ‘robust’ in the context of my work refers to the capability of a resource procurement strategy to reduce the likelihood that individual foragers experience a negative event, specifically, obtaining less food than desired. The difference between robustness and resilience in the context of my work is discussed more chapter 2. At this point, it is

sufficient to say here that resilience refers to how much change a system can cope with before the structure of feedbacks flips into a qualitatively new configuration. Robustness refers to the capacity of an individual to achieve a goal in a variable and uncertain environment. The two concepts are related here in that an increase or decrease in the resilience of a system may directly affect the ability of individuals to obtain their goal.

The importance of resilience and robustness: multiple system states

I would like to briefly illustrate why it is important to study the resilience of a human-resource system and the robustness of individual's goals to environmental change in a human-resource system. To illustrate the importance, I discuss the research questions that anthropologists have historically asked about the adoption of agriculture. There have been two major reformulations of the basic question that anthropologists ask about the adoption and spread of agriculture. I contribute to a third reformulation that has been poised to proliferate among researchers for at least two decades.

The human ecology of the adoption of agriculture starts first and foremost with the processes that cause hunter-gatherer SES to change. V. Gordon Childe (1928:46) stated the issue clearly in his explanation for the domestication of plants and animals:

“Faced with the gradual dessication consequent upon the redshift northward of the Atlantic cyclone belt as the European glaciers contracted, three alternatives were open to the hunting populations affected. They might move northward or southward with their prey, following the climatic belt to which they were accustomed; they might remain home eking out a miserable existence on such game as could withstand the droughts or they might, still without leaving their home-land, emancipate themselves from dependence on the whims of their environment by domesticating animals and taking to agriculture.”

In this argument, the environment provides a range of options that hunter-gatherers might choose to exploit. In response to climate change, the not so clever foragers “eek” out a miserable existence while the clever foragers either move or emancipate themselves from the constraints of a biophysical environment by adopting agriculture. Childe’s argument rests on the assumption that agriculture allows people to produce a surplus of food, settle in one place, relax and invent (Barker, 2011). This assumption is itself an outgrowth of a more fundamental assumption: a progressive view of cultural evolution. In the progressive view of cultural evolution, cultural evolution moves inexorably toward more complex forms as human social groups invent better technologies for producing food. Given these assumptions, there is really only one question to ask about the adoption of agriculture: why would foragers, once in possession of the knowledge to do so, not adopt agriculture? The answer to this question can only come from two sources: a) the mental deficiency of some groups or b) severe biophysical constraints, such as absolutely no water or lack of a growing season. Where mental capacity is lacking or water and solar energy are extremely scarce, agriculture is not an option and foragers end-up persisting, eking out an existence.

In the 1960’s the pioneering studies of anthropologists among hunter-gatherers in the Kalahari desert suggested that the hunter-gather economy was, in fact, not necessarily less advantageous than a farming economy (e.g., Lee, 1966). Many hunter-gatherer societies, including the !Kung, actually had more non-subsistence time than their farming neighbors (Sahlins, 1972). Given that hunting and gathering is not necessarily less advantageous than farming, many anthropologists reformulated the major research question. Instead of asking what limits farming, researchers began to ask: what processes *compel* foragers to give-up the foraging life-style for farming (e.g., Binford, 1968; Cohen, 1977; Flannery, 1968, 1973)? The proposed answers often drew on general systems theory and focused on structural triggers, like population growth or climate change that push a hunter-gatherer SES out of “equilibrium.” By structures, I mean the social and biophysical environments

that foragers live within (and create). Anthropologists have subsequently made many cogent criticisms of the application of systems theory to the study of hunter-gatherers (see Bettinger, 1991:53-59 for a summary from an archaeological perspective).

In my view, a misfortune of the application of systems theory in anthropology is the now pervasive idea that the concept of equilibrium is equivalent to a state of no change. This is not exactly the case. An equilibrium is a unique solution to a system of equations. As discussed in chapter 2, an equilibrium can have dynamic stability but this does not imply a state of no change (see Scheffer and Carpenter (2003:650) for a discussion in relationship to ecosystems). As I argue below, human behavioral ecology benefits from a theory of complex systems, such as that posited by resilience thinking, because feedback processes necessitate that forager-resource interactions are not scalable in an additive way. The resilience of a system state (collection of equilibria) allows us to understand how changes in the attributes of a system might affect the costs and benefits of individual foraging strategies in non-linear ways that are difficult to anticipate.

The second reformulation of research into the adoption and spread of agriculture has occurred in conjunction with the integration of theory from evolutionary ecology into anthropological research (e.g., Barlow, 2002; Bettinger and Baumhoff, 1982; Bettinger, 1991; Bird and OConnell, 2006; Keegan, 1986; Kelly, 1995; Kennett and Winterhalder, 2006; Layton et al., 1991; Redding, 1988; Winterhalder and Smith, 2000; Winterhalder and Goland, 1993; Wills, 1988). In general, evolutionary ecologists assume that individuals choose the behavioral strategy that best maximizes their reproductive success in any given environment. From this point of view, the adoption of domesticated plants by an individual forager may have either fitness costs or benefits, depending on the environment in which a forager resides. From an evolutionary perspective, then, the question becomes: when do the benefits of cultivating domesticated plants for food outweigh the potential costs of such behaviors for individual foragers? This is a well posed question. The strengths are numer-

ous. 1) The question avoids the essentialist assumption farming is “better” than foraging. 2) The question allows us to view foraging and farming as alternative strategies with fitness costs and benefits that are the outcome of forager-resource interactions. 3) The question suggests that researchers use specific foraging models to rigorously assess the costs vs. benefits of foraging and farming in different environments.

The cultivation of domesticates is the systematic control of growth, reproduction, competition and dispersal within assemblages of plants, along with the distribution of water and nutrients in space and time. The control of these basic ecosystem processes is not unique to human societies that produce domesticated plants for food. Rather, the control of basic ecosystems processes occurs in a wide range of hunter-gatherer societies to increase the productivity of wild plants and hunted game- which I call here the low-level food production of food from “wild” resources (Anderson, 2005; Gould, 1971; Keeley, 1995; Smith, 2001). Framed in this way, the cultivation of domesticated plants for food is really a specific instance of a more general class of behaviors that alter ecosystem structures and increase the productivity of food available to humans. This raises the more general question: in what contexts do the benefits of modifying ecosystem structures to augment the productivity of food in a given area outweigh the costs for individual foragers?

In the context of archaeological research, most studies guided by an evolutionary ecological framework use static models of optimal behavior developed in the field of microeconomics. By the term static model I mean that human foraging dynamics play out on a much faster time-scale than ecological dynamics; thus, the ecological system provides a “static” context in which foragers make choices. These models assume that for any given combination of environmental variables, there is a unique behavioral strategy that optimizes an individual’s fitness, and the behaviors of human actors evolve toward this unique strategy. Figure 1.2a is a representation of a static optimality model. There is a resource that foragers need to decide how to use. The resource is controlled by an external input, like

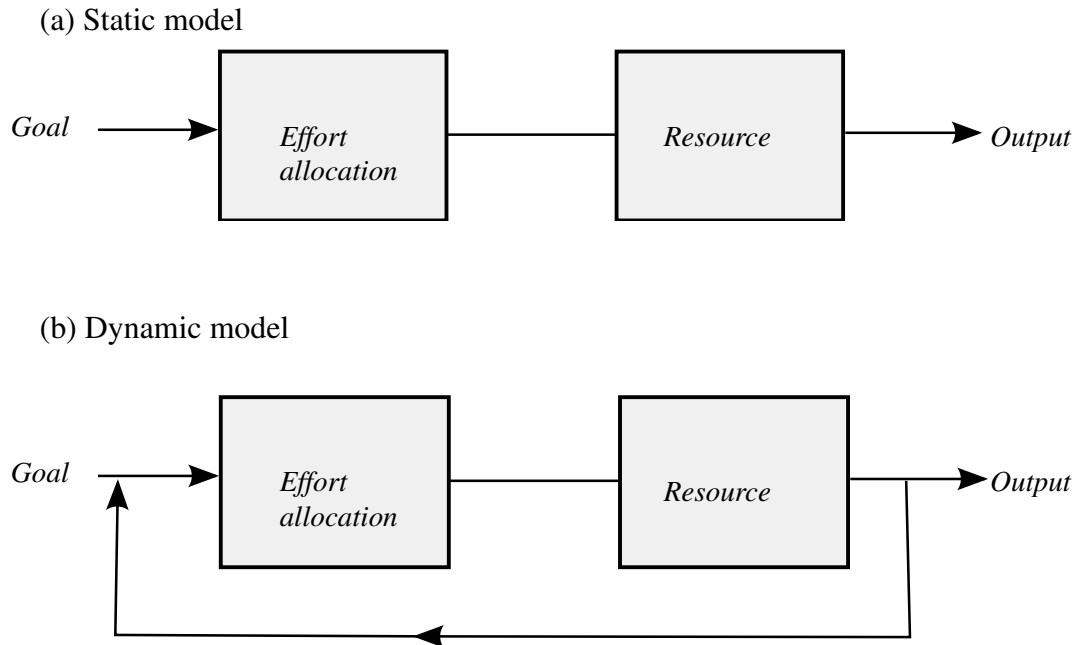


Figure 1.2: General stick figure representations of a human-resource system. Picture (a) is a “static” model and picture (b) is a dynamic model. In the dynamic model, the foraging decisions of humans and the resource base change at similar time-scales.

rainfall or sunlight. Given a static resource, individuals allocate effort to obtain an output, often energy. The output is compared to the assumed goal of a forager (e.g., maximize rate of energy gain). Variation in the resource creates a continuum of trade-offs between strategies for allocating effort (time) to meet a forager’s goal. Figures 1.3a & b illustrate how the equilibrium state (unique solution to a model) of a forager-resource system changes when there is a continuum of trade-offs between strategies for exploiting a resource. The blue dots represent the state of a forager-resource system at a given ecological parameter that determines the costs vs. benefits of individual behaviors. Though the state of the system may change rapidly (Figure 1.3b), there is always a smooth continuum of unique equilibrium states that a forager-resource system can occupy. In sum, the value of the ecological parameter determines the unique equilibrium state of the system and change is continuous, which implies that one can observe a smooth continuum of states in reality.

Let me give a very brief example to illustrate the kind of model that generates the dynamics described by Figures 1.3a or b. In one of the most sophisticated applications of a static foraging model to understand the adoption of maize by foragers, Barlow (2006) argues that the marginal rate of energy gain acquired from wild plants relative to the marginal rate of energy gain acquired from cultivating maize determines an individual's unique level of investment in the production of maize. For simplicity here, let's assume that the choice an individual has to make is whether to invest in cultivating maize or harvesting mesquite beans. Holding the time necessary to process mesquite beans constant, the primary determinant of the marginal rate of energy gain from mesquite is the density of the resource on a landscape. By analogy, the density of mesquite in an environment is the ecological parameter in Figure 1.3a or b. This implicitly assumes that the density of mesquite changes more slowly than decisions about the effort to invest in the production of maize. As the density of mesquite declines, selection pressures should favor increasing labor in the production of maize because an individual invests more labor in the production of maize whenever the marginal rate of energy gain from cultivating maize is higher than the marginal rate of gain from collecting mesquite. Given this dynamic, there is a continuum of unique investment levels in the production of maize.

Despite the strength and sophistication of static foraging models, such models have a potential weakness. In coupled SES, the coevolutionary dynamics of individual decision making and environmental structures may result in a special kind of nonlinear process, the emergence of multiple stable states of human-resource interaction (e.g., Anderies, 2006, 1998; Clark, 1976; Flannery, 1985; Freeman and Anderies, 2012; Janssen et al., 2003). Multiple stable states refers to the idea that there are discrete ways that social-ecological (or just ecological) systems could be organized under the same environmental conditions. Multiple stable states may be characteristic of many social and ecological systems from local scales to the global earth-climate system (Scheffer, 2009). The presence of multiple

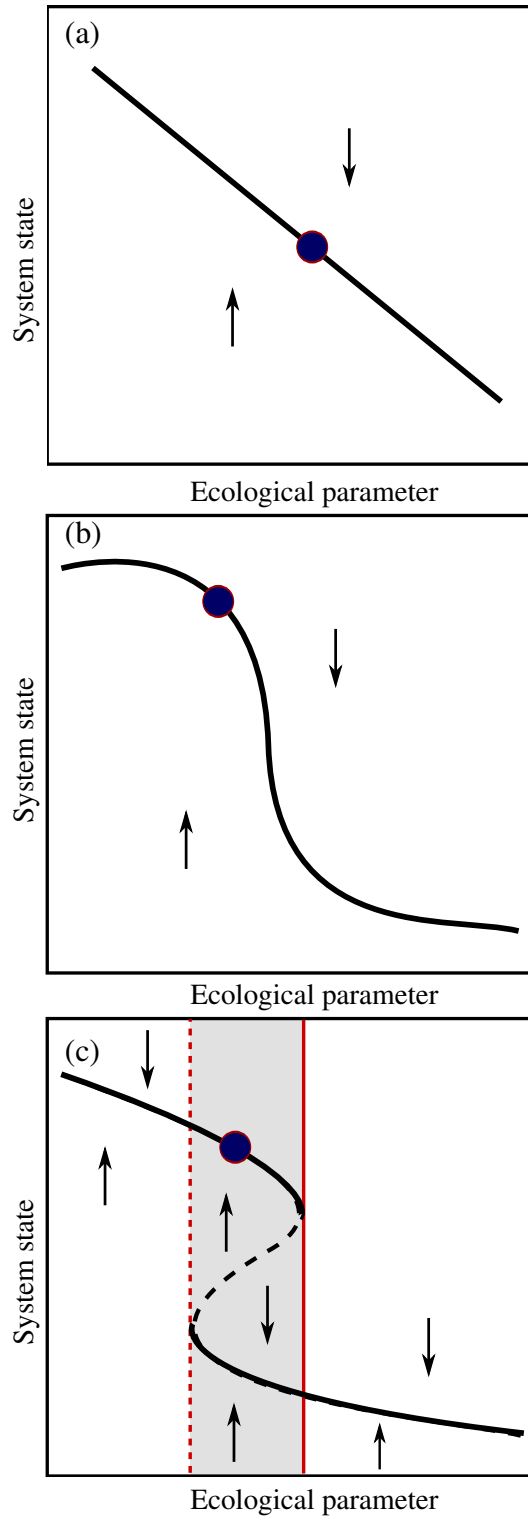


Figure 1.3: Different perspectives on the dynamics of change in social-ecological system (figures designed after Scheffer (2009)). The black curves represent all of the possible equilibrium states of a system for a given ecological parameter. The blue dots represent a unique equilibrium solution. The arrows indicate the direction that the system will move over time if it is not in equilibrium.

stable states in a system can 1) have an effect on the costs vs. benefits of individual strategies and/or 2) lead to transitions that are difficult to anticipate. The only way to investigate the potential presence and effects of multiple stable states is with dynamic models. Figure 1.2b illustrates a stick-figure dynamic model. In Figure 1.2b the allocation of effort now feeds back to affect the resource. This kind of feedback can lead to non-linearity, including the emergence of multiple stable states.

Figure 1.3c illustrates the view that there are two alternative stable states that a human-resource system might obtain represented by the two solid black curves. Again, changes in the ecological parameter cause changes in the equilibrium state of the system. However, in the gray shaded area there are two possible stable equilibrium states that the system might obtain for the exact same values of the ecological parameter. In addition, perturbations might cause an abrupt shift between the two possible states of the system. This is known as a variance induced critical transition (Scheffer, 2009).

Lets return to mesquite and maize to provide a concrete illustration of the kind of dynamics illustrated in Figure 1.3c. Flannery (1985) examines the potential trade-offs between clearing mesquite forests to plant maize and collecting mesquite from a systems perspective in the Valley of Oaxaca. Flannery (1985:505) 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 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 slow genetic changes in the population of plants managed by early Mesoamerican forager-

farmers. The equilibrium system state is the amount of area covered by mesquite, which determines how much mesquite is collected. If we analogize Flannery's argument to Figure 1.3c, then an increase in the productivity of maize causes a decrease in the level of effort devoted to the collection of mesquite because foragers 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 and high effort devoted to the production of maize. The dynamic that Flannery's argument is missing, however, is that when maize productivity hits the dashed red line, the system might become vulnerable to a variance induced critical transition.

In Flannery's argument, the whole reason the shift between equilibrium states occurs is because, at the red line, deforestation and seed consumption decrease the rate of mesquite reproduction past a critical threshold. Deforestation and consumption, however, are not the only process that might deplete mesquite. There are shocks that constantly hit a social or ecological system generated by dynamics such as atmospheric variation and pest cycles. For example, a disease outbreak could shock a mesquite forest and cause a decline in mesquite forest cover. In the gray shaded area of Figure 1.3c, this shock could stimulate forager-farmers to compensate by growing more maize despite the fact that productivity is, on average, below the 250 threshold. This behavior, in turn, might drive the rate of mesquite reproduction too low for a forest to recover and forager-farmers end up in an environment with a low density of mesquite trees and a high investment in the production of maize. The resilience of the high mesquite cover system state is defined by how big of a perturbation to the mesquite forest is required to push the system into the low mesquite cover, high maize production state.

The potential existence of multiple stable states due to non-linear feedbacks suggests a third reformulation of research into subsistence change in hunter-gatherer societies and the

adoption of domesticated plants. Rather than simply study the costs and benefits of cultivating domesticates relative to wild resources in different static environments, research questions must also focus on how the structure of a human-resource system feeds back on the costs and benefits of individual decisions. In the example above, once the high mesquite collection system state becomes vulnerable to variation, such as a pest outbreak, the robustness of individual's mesquite collecting goal may become uncertain. In such a situation, the costs vs. benefits of collecting mesquite vs. producing maize may change for individuals. Questions about the effects of feedbacks on the costs and benefits of individual strategies compliment the foraging models traditionally applied by archaeologists to understand changes in hunter-gatherer subsistence and the adoption of agriculture.

Let's Get it Started in Here

In the remainder of this dissertation, I review models of hunter-gatherer subsistence change that propose feedbacks between foragers and resources drive the evolution of hunter-gatherer SES. I use these models as a starting point to develop the first principles of forager-resource dynamics. In chapters 3 and 4, I use these first principles to frame a simple, dynamic forager-resource model. I use the model to develop two hypotheses that identify the social-ecological conditions that favor strategies of food production and ownership institutions. In chapter 5, I evaluate the consistency of these explanations with a large ethnographic data set. In chapter 6, I sketch out the implications of my analysis for understanding the prehistoric adoption of maize agriculture at the expense of hunting and gathering in the US Southwest. I also summarize the implications of my research for understanding the long-term evolution of forager-resource systems in general.

Chapter 2

INTELLECTUAL FOUNDATION: FEEDBACK PROCESSES IN HUMAN ECOLOGY

Anthropologists have long argued that a prerequisite to explain the adoption of domesticated plants by hunter-gatherers is a knowledge of the processes that cause hunter-gatherer social-ecological systems (SES) to change (e.g., Binford, 1983; Childe, 1928; Cohen, 1977; Flannery, 1985, 1973; Hassan, 1981; Hayden, 1981; Keeley, 1995; Pryor, 1986; Stiner et al., 1999; Winterhalder et al., 1988 and many others). In this chapter, I briefly describe the deep intellectual traditions in human ecology that inform models of subsistence change in hunter-gatherer societies. This review is necessarily selective. A comprehensive review could fill several volumes. I have two related goals. The first goal is to situate specific models of hunter-gatherer subsistence change within more general models of economic development. Models of economic development describe how feedback processes in SES might drive cultural evolution. The second goal is to propose a set of first principles that describe the dynamics of forager-resource interactions. These first principles provide a qualitative base upon which I model the coevolution of foragers and resources in chapters 3 and 4 and investigate the robustness of hunter-gatherer preferences to environmental change.

This chapter is divided into three sections. In the first section I briefly review models of economic development, in particular: the Malthusian, Weberian and Boserupian models. Models of economic development are intimately related to theories of cultural evolution, the main difference being the time-scale on which these processes play out (Richerson and Boyd, 1998), and these models have greatly influenced archaeological explanations of subsistence change. This review provides a general framework for describing the feedback structure of specific models that archaeologists propose to explain

subsistence change in hunter-gatherer SES. The second section reviews three models of subsistence change in hunter-gatherer SES proposed by archaeologists. The three models are the traveler-processor model (Bettinger, 1991), the packing model (Binford, 2001) and a modified version of the model of economic defensibility (Smith, 2012). These models provide the qualitative baseline that I begin from to quantitatively model the coevolution of foragers and resources in chapters 3 and 4. Finally, I describe a general framework to study the evolution of social-ecological systems. The framework achieves two aims. First, this general framework integrates aspects of the Malthusian, Weberian and Boserupian general models of economic development. Second, the general framework provides a set of overarching assumptions that guide my inquiry into the processes that cause the organization of forager-resource systems to change.

General Models of Economic Development

The history of human ecology is like one long dialog between competing models of economic development. Models of economic development are sets of statements about the processes that cause coupled social-ecological systems to change. Here, I describe three general models: The Malthusian, the Weberian and the Boserupian models. The primary differences between these general arguments is where researchers identify the locus of cause, that is, the environmental structure that induces change in SES and the structure of feedbacks that relate the elements of an SES. My comparison of these models provides an intellectual background for comparing specific models of subsistence change in hunter-gatherer SES.

The history of intellectual thought on subsistence change is closely tied to models of economic development because these models were devised to understand agricultural change and the development of capitalist markets. Each general model discussed here postulates the social or ecological conditions that cause the intensification of food production.

The concept of intensification is generally defined as the process whereby an individual or population extracts more food from a given unit of space (Binford, 2001; Richerson et al., 2001; Netting, 1993; Boserup, 1965). Scholars interested in the transition from hunting and gathering to agriculture have long sought to link the process of intensification with the adoption of agriculture by hunter-gatherers (e.g., Binford, 2001, 1983, 1968; Braidwood, 1960; Flannery, 1968; Hayden, 1981; Layton et al., 1991; Redding, 1988; Richerson et al., 2001; Smith, 2012; Wills, 1988; Zvelebil, 1996). This linkage is logical. The adoption of techniques that manage ecosystem processes and the dispersal of particular species facilitates the ability of individuals to augment the production of food from a given parcel of land (Hayden, 1981; Keeley, 1995). An extreme example of this process is the application of manure to agricultural plots. This behavior subsidizes the availability of nutrients that limit the rate at which plants can produce biomass on a given plot of land. Human foragers engage in similar kinds of ecosystem management to increase the availability of food, though often less labor intensive, such as the systematic burning of vegetation, re-planting tubers or dispersing the seeds of desired grasses-low-level food production (Bird et al., 2005; Keeley, 1995; Smith, 2001).

Boserup (1996) has developed an interdisciplinary framework for comparing models of economic development, and I have adopted her framework here. According to Boserup (1996), models of development are best characterized by the interaction of six environmental structures: culture (C), family organization (F), occupational structure (O), population (P), technology (T) and the biophysical environment (E). As Lemmen (2011) notes, these six organizational structures can be collapsed into four structures: population (P), the biophysical environment (E), culture (C) and technology (T). In this simplified framework, culture (C) represents the human capital (i.e., knowledge) possessed by individuals within social groups, as well as the social capital of a group the stems from the formation and maintenance of cooperative institutions. As such, culture is an aggregation of

Boserup (1996)'s culture (C) and family structure (F) categories. Technology is aggregated to include physical artifacts, as well as organizational forms like the "assembly line," and, as such, technology and occupational structure are aggregated into a single technological structure. In this four structure scheme, culture (C) and technology (T) are really a single "infrastructure" dimension, separated for analytical convenience, that mediates the interface of a human population with the biophysical environment (see Catton, 1987).

Figure 2.1 compares the proposed dynamics of the Malthusian, Weberian and Boserupian models of economic development. The basic Malthusian model is characterized by a P-to-E-to-P (Figure 2.1a) feedback loop. According to Malthus, Population, when unchecked, increases at a geometrical ratio. Subsistence increases only in an arithmetical ratio. A slight acquaintance with numbers will show the immensity of the first power in comparison with the second (Malthus, 1888:4). In the Malthusian view, the world has a finite amount of agricultural land, thus population growth necessitates that farmers expend more labor on inferior land in an attempt to boost their supply of food. However, this strategy cannot keep pace with population growth and, eventually, a scarcity of food will cause population growth to cease and, potentially, decline. In this argument, it is the quality of the environment that ultimately limits the size of a population in a given area; long-term increases in population size only occur if some external force increases the quality of the environment. The Malthusian model, thus, proposes that the intensification of agricultural production is limited by the fact that population grows faster than farmers can increase their production of food. In my view, purely Malthusian arguments are very rare in the archaeological literature on subsistence change (although Bettinger (1991) and Zeder (2006) characterize Binford (1968) as a Malthusian argument).

Neo-Malthusian arguments, however, are more common. In the Neo-Malthusian view, technology (T) (or culture (C)) mediates the population-environment feedback loop, because technology partly determines the productive capacity of a biophysical environment.

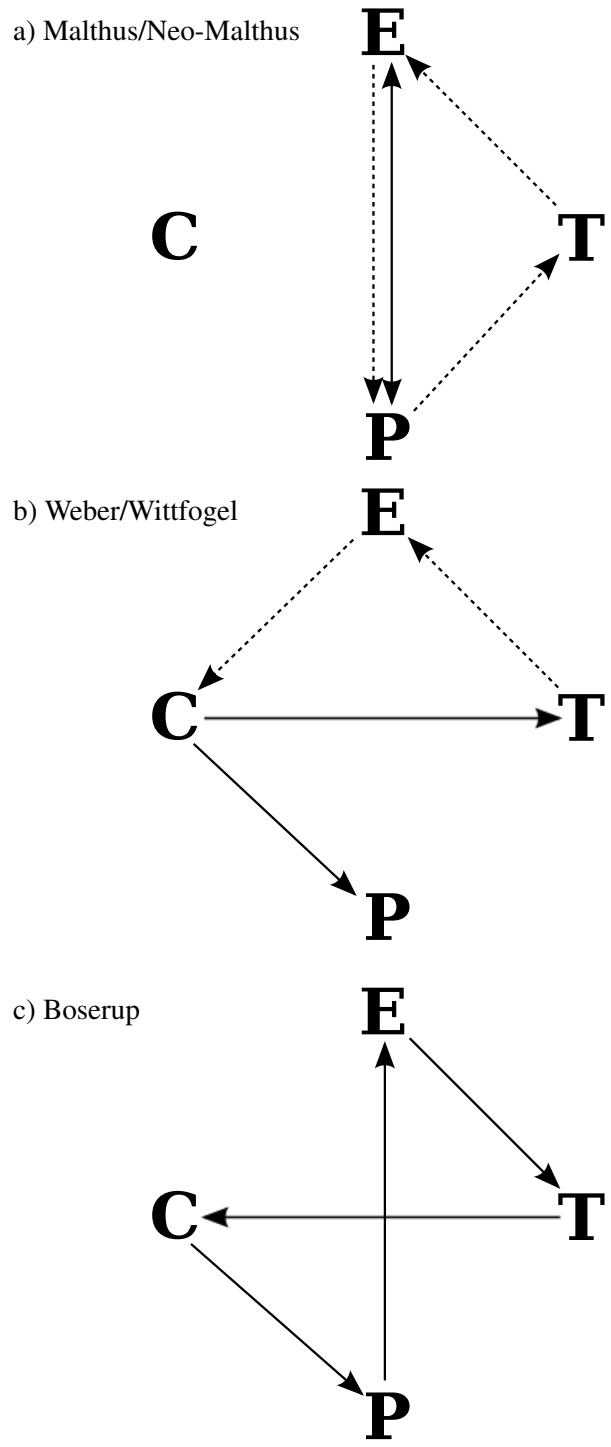


Figure 2.1: General models of economic development

For example, to explain the emergence of agriculture Richerson et al. (2001) argue that the amelioration of the Pleistocene climate set off a population-technological innovation positive feedback cycle. This positive feedback made agricultural production a compulsory economic outcome, over the long-run, during the Holocene. The dotted arrows on Figure 2.1a diagram the Neo-Malthusian model. In the Richerson et al. (2001) example, $E \rightarrow P$: improved climate leads to an increase in population growth. $P \rightarrow T$: population growth leads to higher innovation rates, including technologies that facilitate efficient, plant intensive subsistence strategies. $T \rightarrow E$: the innovation of technologies, new crops and/or forms of labor organization improves the quality of the environment. In turn, $E \rightarrow P$: the population size that a given environment can sustain increases and populations grow in size.

Figure 2.1b illustrates the Weberian model. Max Weber (1927)'s argument stemmed from an attempt to understand the development of capital markets and sustained economic growth. He argued that protestant institutions (C) promote hard work, honesty and trust. In turn, these institutions lead to smaller families (P) and, simultaneously, facilitate occupational specialization and exchange (T), fueling economic growth. Weber's central argument has been extended by economists and political scientists such as North (1990) and Fukuyama (1995) to explain the evolution of economic performance in general. Most important for the discussion here is the fact that changes in how individuals apply human capital and/or social capital are the primary drivers of the evolution of SES. For example, Wittfogel (1957) extended Weber's argument to explain agricultural change in his classic study of irrigation societies. The dotted arrowed lines on Figure 2.1b illustrate Wittfogel's extension of the Weberian causal format. For Wittfogel, agricultural change is an outcome of institutional innovators taking advantage of an opportunity presented by the intersection of technology and the biophysical environment. $C \rightarrow T$: institutional innovators cause changes in the technological organization of a society. $T \rightarrow E$: the technology of a society

determines the productive capacity of the biophysical environment. Finally, $E \rightarrow C$: the biophysical environment imposes constraints and provides new opportunities for institutional innovation. Wittfogel (1957:19) states this position succinctly in his discussion of the evolution of managerial institutions to coordinate irrigation systems:

“The pioneers of hydraulic agriculture, like the pioneers of rainfall farming, were unaware of the ultimate consequences of their choice. Pursuing recognized advantage, they initiated an institutional development which led far beyond the starting point. Their heirs and successors built colossal political and social structures; but they did so at the cost of many of those freedoms which conservative dissenters endeavored and, in part, were able to preserve.”

Note, in this context “conservative dissenters” refers to social groups who eschewed irrigation agriculture and maintained a rainfed agricultural system (see Wittfogel, 1957:15-19).

The Weberian argument in which culture (conceived of as knowledge and institutions) drives subsistence change is common in archaeology. In my view, there are two forms of Weberian argument developed by archaeologists. A social capital argument is exemplified by Hayden (2003) (see also Bender, 1978; Brookfield, 1984; Hayden, 1990, 1998; Sahlins, 1972). Hayden argues that humans have an innate desire to acquire power and prestige. Institutional innovators invest in the domestication of plants (and animals) to create a set of luxury goods that are produced at a minimum cost, in the short-run, to increase an individual’s prestige through social practices, such as feasting. This is a basic C-to-T structural relationship. However, the long-term effect is that domesticated plants become inexpensive and widely available due to genetic changes (Hayden, 2003). This population level change in domesticated species increases the productivity of an environment and allows all foragers to intensify their land use through the cheap manipulation of ecosystem structures ($T \rightarrow E$). In turn, institutional innovators must devise new ways to maximize their power and

prestige given the new properties of the biophysical environment ($E \rightarrow C$). In this Weberian argument, changes in population are dependent on the $T \rightarrow E \rightarrow C \rightarrow T$ feedback loop.

Alternatively, Braidwood (1960) makes a human capital argument for the adoption of agriculture. This argument relies on the application of knowledge to create a better fit with the environment, as opposed to institutional innovation per se. In this argument, knowledge of an ecosystem's processes (the human capital component of C) allows hunter-gatherers to recognize the benefits of domesticating plants and animals (T). As Braidwood (1960:134) states:

“[A]round 8000 B.C. the inhabitants of the hills around the fertile crescent had come to know their habitat so well that they were beginning to domesticate the plants and animals they had been collecting and hunting.”

Domestication allows foragers to extract more food from the environment (E) and improve their lives (the assumption being that farmers live “better” lives than foragers). In turn, changes in the biophysical environment set the new conditions in which individuals continue to learn how to most effectively exploit resources and improve their lives. This is a $C \rightarrow T \rightarrow E \rightarrow C$ feedback loop. Again, in this argument P is a dependent variable; population growth is an outcome of foragers getting better at exploiting resources.

Finally, the Boserupian model is depicted by Figure 2.1c. As Boserup (1981:5-6) sums-up her argument,

“A growing population gradually exhausts certain types of natural resources, such as timber, virgin land, game, and fresh water supplies, and is forced to reduce its numbers by emigration or change its traditional use of resources and way of life. Increasing populations must substitute resources such as labor for the natural resources which have become scarce. They must invest labor in creation of amenities or equipment for which there was no need so long

as population was smaller. Thus, the increase of population within an area provides an incentive to replace natural resources by labor and capital.”

The Boserupian model proposes a P-to-E-to-T-to-P feedback loop. P → E: population growth within a bounded area causes a degradation of the biophysical environment. In turn, E → T (or C): farmers face declining per capita production and are stimulated to adapt their technology and institutions to mitigate declines in productivity. T → P: where social or technological innovation is successful, population growth continues. The central feature of the Boserupian argument is that social-technological change occurs as individuals respond to the degradation of the biophysical environment.

Hunter-gatherer Subsistence Change

With a descriptive scheme in place for describing models of SES change, I would now like to examine three specific models of subsistence change and resource intensification in hunter-gatherer SES. These three models are all specific instantiations of the general theories of economic development described above and provide the inspiration form my formal investigation of the coevolution of foragers and resources in chapters 3 and 4. Each model provides insight into the evolution of hunter-gatherer SES. However, each model also raises questions that can only be answered by formally studying the feedback processes that affect the robustness of an individual’s energy goal to environmental change within coevolving forager-resource systems.

1. Traveler-processors

Bettinger and Baumhoff (1982) have proposed the traveler-processor model to explain subsistence change in hunter-gatherer societies. In general, the traveler-processor model is a Boserupian argument (Figure 2.2a). Specifically, the traveler-processor model qualitatively combines insights from the prey (also known as the “diet breadth model”) and patch

choice foraging models developed in evolutionary ecology (Charnov, 1976; MacArthur and Pianka, 1966; Stephens and Krebs, 1986). As was common in early optimal foraging models, the traveler-processor model assumes that individual foragers are rational actors and maximize the rate at which they obtain energy, which allows a forager to maximize her reproductive success. In the traveler-processor model, foragers position themselves on a landscape that is composed of many potential resource patches. Individuals can allocate their time to 1) travel between patches, 2) search for food within a patch, 3) peruse/harvest resources within a patch and 4) process resources post harvest. These categories, in the model, are mutually exclusive activities to which a forager can allocate her time. Further, following the prey choice model, a basic assumption of the traveler-processor model is that processing time is inversely related to the quality of prey that foragers harvest.

Given the assumptions described above, the traveler-processor model describes a continuum of behavioral strategies that foragers use to maximize their rate of energy gain. The population density of an environment determines the strategy that best minimizes the time that a forager invests in the acquisition of food and maximizes the time available for an individual forager to engage in other kinds of behaviors that maximize an individual's fitness (Bettinger, 1999:41-42; Winterhalder, 1983). Bettinger and Baumhoff (1982) argue that when population density is low, the optimal strategy for an individual to maximize her energy return rate (Kcals/time) is to minimize the time that she spends searching for resources within a patch and move frequently between patches within a habitat. Holding all other factors equal, as the population density of foragers in an environment increases, the availability of high quality prey within resource patches declines ($P \rightarrow E$) and, in response, foragers expand their diet breadth to include lower quality, more abundant resources ($E \rightarrow T$) (Bettinger, 1991). The increase in processing time associated with harvesting lower quality resources necessitates that foragers give-up time doing other activities, like traveling between patches. As population density increases, foragers are expected to spend

more and more time maximizing the quantity of energy obtained from any given patch because this strategy maximizes an individual's rate of energy gain better than spending time moving between patches in search of high quality prey.

An interesting feature of the traveler-processor model is that foragers maximize the quantity of energy taken from a patch to adapt to a context of resource depression caused by increases in population density relative to high quality prey. This adaptation Bettinger (1991:102) argues, creates a situation in which female labor is highly valued to maximize the returns gained from processing low-quality resources, and this leads to more population growth. "The most obvious avenue leading to this is that in which, as suggested, female infanticide is curtailed to make female labor available for resource processing" (Bettinger, 1991:102). This proposed process completes the feedback circuit: $(T \rightarrow C \rightarrow P)$.

2. Landscape "packing"

Binford (1999, 2001) has proposed the packing model, which also has theoretical underpinnings in ecology (e.g., MacArthur, 1972:64-65). In my view, the packing model is the basis of a Neo-Malthusian argument (Figure 2.2b). In this instance, it is important to recognize that C and T are artificially separated, both refer to infrastructure used to mediate human environment interactions. The basic idea is that hunter-gatherers aggregate into basal camp groups that display an average size. These camping groups primarily exploit a landscape by moving between foraging locations or resource zones. Population growth drives a process of group segmentation and an increase in the number of basal camp groups that occupy a landscape. Where all resource zones on a landscape have one camp group in residence at the most dispersed phase of an annual settlement cycle, the landscape is "packed" (Binford, 2001:238-239), and camp groups must either fight or cooperate to use resources beyond their own compressed territories ($P \rightarrow C$). Binford (1999:7-8) argues that the process of foraging territory compression to avoid conflict favors reductions in residen-

tial mobility, less reliance on animals of large body size and the targeting of food resources with high rates of productivity (Binford, 2001:365-370) (C → T).

Importantly, technology (resource selection) sets the “packing capacity” (as opposed to the carrying capacity) of a biophysical environment (T → E) because the resources that foragers target partly determines how much space a basal camp group needs to meet their subsistence needs (Binford, 2001:381). According to Binford (2001), foragers who primarily hunt for food become packed on a landscape at a density of approximately 1.5 people per 100 km^2 , while foragers who primarily harvest plants become packed at a population density of approximately 9 people per 100 km^2 . The dynamic scenario envisioned by Binford is one in which the technologically mediated biophysical environment determines the ability of basal camp groups to segment and reduce their territory without paying the costs to cooperate or fight for territory beyond their compressed own ranges (E → P). Binford states:

one [packing] threshold does not replace the other; rather, different constraints on groups size and subsistence strategy operate on groups whose diets are made up of resources from different trophic levels” (Binford, 2001:381) brackets mine.

The implication is clear. The technologically mediated biophysical environment sets the “packing capacity” of the environment, which constrains the ability of basal camp groups to segment in response to population growth.

As discussed below, both the packing and traveler-processor models postulate complete feedback circuits; all of the elements (P, C, T, & E) “co-influence” one another. The consequence is that making a clean distinction between the most general models of economic development is difficult. Indeed, this is a reason why dynamic modeling is needed.

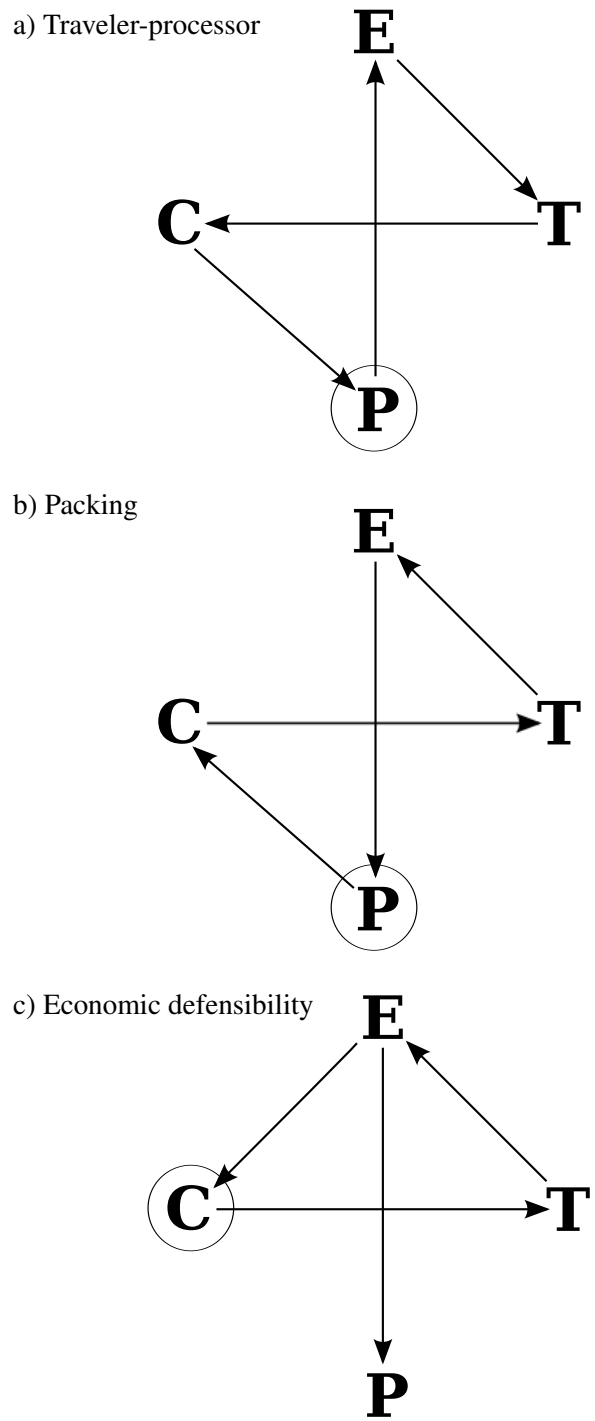


Figure 2.2: A comparison of three models of subsistence change in hunter-gatherer SES. The circles highlight the environmental structure identified as the causal locus of change in the text.

3. Economic Defensibility

Recently, Zeder (2012) and Smith (2012) have proposed a model that I call here the modified model of economic defensibility after Dyson-Hudson and Smith (1978). They argue that their model provides a foundation for understanding the use of space by hunter-gatherers and subsistence change. This modified model of economic defensibility is a specific example of the more general Weberian model (Figure 2.2c) and extends arguments made by Smith (1989), Rindos (1984) and Braidwood (1960).

The original model of economic defensibility is based on the evolutionary ecology of stationary, pair bonding non-human foragers (Brown, 1964). In the formulation presented by Dyson-Hudson and Smith (1978), the abundance and predictability of resources determine the costs and benefits, in terms of maximizing energy return rates of defending a territory for individuals. In the model of economic defensibility, where resources are abundant and predictable (relative to a given population density), territories are expected to shrink because an individual forager can maximize his net intake of energy by harvesting food from less territory (Dyson-Hudson and Smith, 1978). In turn, the size of a territory used by foragers decreases and, as a consequence, the costs of patrolling and defending a territory also decrease because there is less time and energy needed to monitor and locate intruders. Given the relationship between resource density, territory size and defense costs, foragers are expected to use less space, become less mobile and defend their territory as resources become more concentrated in space and time ($E \rightarrow C$) (Dyson-Hudson and Smith, 1978; Kelly, 1995; Smith, 1988; Zeder, 2012).

Smith (2012) and Zeder (2012) build on the logic of the model of economic defensibility to understand how the intensification of land use and the cultivation of domesticated plants might evolve in a forager-resource system. Drawing on the idea of symmetrical adaptation in which human foragers modify an environment to suit their needs, Smith (2012)

and Zeder (2012) propose a positive relationship between the modification of ecosystems by hunter-gatherers to produce food and an increase in the concentration of resources in an environment ($T \rightarrow E$). When this proposed relationship is combined with the model of economic defensibility, the behaviors that foragers use to modify ecosystem structures (like systematic burning, planting and weeding) augment the productivity of resources, and, in turn, the increased concentration of resources allows individuals to adopt strategies that exclude others from a territory because this strategy maximizes an individual's return rate. Given these relationships, Smith (2012:267) argues that systems of traditional ecological knowledge (TEK) are updated in a population of foragers to take advantage of the future opportunity that managing ecosystem productivity provides. When resources are abundant and predictable, foragers are expected to decrease the amount of territory that they use, become more territorial and invest in food production in a mutually reinforcing cycle ($C \rightarrow T \rightarrow E \rightarrow C$). According to Zeder (2012:253) the model of economic defensibility: “provides a framework for understanding how reduced mobility can come about within the context of resource abundance and predictability in the absence of population pressure.” Thus, population density is dependent upon the $C \rightarrow T \rightarrow E \rightarrow C$ feedback loop.

Feedbacks in hunter-gatherer SES

Figure 2.2 illustrates two important characteristics shared by each of the three models. First, although each specific model identifies an environmental structure that drives change, each model clearly presupposes feedback loops. This means that any of the environmental structures involved in the feedback loop might, in a simplistic sense, cause a hunter-gatherer SES to change. Second, due to the presence of feedback loops, all three models imply that system dynamics are important to consider. Certainly, it is individual foragers that select strategies for harvesting resources and create the interconnections between environmental structures. However, the presence of feedback loops introduces the possibility of non-

linearity and, as discussed in chapter 1, the possibility of multiple stable states. Non-linear changes in the structure of a system may affect the costs and benefits of the foraging strategies that individuals select in ways that are hard to predict or intuit. *We simply cannot know if multiple-stable states emerge from the presence of feedbacks and the subsequent effect of such a situation on the costs and benefits of foraging for individuals without the formal study of dynamic forager-resource systems.*

The primary difference between the three models discussed above is the structure of the feedback loops that link environmental structures. The traveler-processor and packing models both suggest a complete circuit in which P, C, T, and E are linked. In these models, there is no truly independent and dependent environmental structure. Conversely, the modified model of economic defensibility, discussed in more detail below, suggests that population is dependent on the quality of the biophysical environment, which depends on the C, T, E feedback loop.

The traveler-processor and packing models both describe a complete structural feedback loop (i.e., P, E, T & C are all linked). However, the form of the feedback loop in each model is slightly distinct. The main difference between these two models is the emphasis placed on the mechanism of direct vs. indirect competition. In the packing model, the formation of more basal camp groups on a landscape increases direct competition for resources; this competition “stresses” institutional rules, like kinship obligations to allow free access to a territory for relatives (P→C). In terms of economics, the number of basal camp groups in an environment partly determines the transaction costs of interaction between camp groups. Transaction costs, in this case, are those costs incurred, either in time or energy, to gain access to resources; or simply the costs of economic activity (North, 1990). The traveler-processor model places emphasis on indirect competition. An increase in population density degrades the availability of high quality prey and this increases the search and processing costs that individuals pay to obtain food (P→E).

My juxtaposition of the traveler-processor and packing models implies that increases in population density affect either the costs associated with exploiting the biophysical environment or the costs of interacting with other foragers. Of course, population density can affect both simultaneously, and, if so, we might expect that increases in population density have an increasing, non-linear affect on the costs associated with accessing resources.

Another subtle difference between the traveler-processor and packing models is the causal role of individuals and system level attributes. This difference captures a tension between systems explanations and individual level explanations in models of hunter-gatherer SES (e.g., Kelly, 1995:45-48; Winterhalder, 2002:221). Bettinger (1991) emphasizes the drive of individuals to maximize their fitness; natural selection favors the best fitness maximizing behavior over time. Changes in hunter-gatherer systems are, thus, the sum of changes in individual foraging behaviors. In Binford's view, packing is a continuous, deterministic process whereby the formation of new camp groups on a landscape causes camp groups to reduce their territory and sacrifice the collection of information (Binford, 1983:208-210) until a technologically determined threshold of camp group density is hit. When a landscape reaches the point where it is filled-up with basic camp groups, the landscape has reached a point of self-organized criticality (Binford, 1999). On a filled-up landscape, the formation of *just* one new camp group will send a cascade of unresolved competition through a hunter-gatherer SES (Binford, 2001). When this occurs, a break occurs where new hunter-gatherer systems must emerge. "The break in continuity and the new forms that appear directly after the packing threshold could not be anticipated, even if one had full knowledge of the systems extant prior to reaching the [packing] threshold" (Binford, 1999:9 brackets mine).

The dynamic model developed in chapters 3 is a tool that facilitates the study of how individual foraging decisions *scale-up* to effect the dynamics of resources at the system level, and, in turn, how resource dynamics feedback down to impact the costs and ben-

efits of individual foraging strategies. As discussed in chapter 1, when systems contain feedbacks, they might exhibit multiple stable states. In chapter 3 I begin to investigate how feedbacks between foragers and resources effect the long-term evolution of hunter-gatherer SES. I specifically investigate whether a dynamic model built on first principles of human behavior and resource dynamics can lead to multiple stable states. Given the presence of multiple stable states, I begin to investigate the mechanisms that might drive social and technological change in forager-resource systems.

This Weberian causal structure of the modified model of economic defensibility is quite different from the traveler-processor and packing models. This causal structure necessitates that population density is a dependent variable. Similar to the argument made by Braidwood (1960), Smith (2012:267), argues that where resources become more abundant and predictable, foragers are able to develop a detailed knowledge of ecosystems and manipulate ecosystems to boost the long-term productivity of food. This strategy “should be viewed as a purposeful activity that seeks to shape the environment in ways that directly and in the long-term promote the viability of groups that practice this behavior” (Zeder, 2012:258).

There is straight forward logic here. An increase in an individual or group’s knowledge of ecosystem dynamics facilitates increases in the productivity of the resources that foragers desire, which drives the relative benefits-to-costs of territoriality up for individuals. In turn,

“the concept of ownership and the growing commitment to maintaining a group’s investment in the territory serves as an additional incentive to engage in niche construction activities. In fact, increased investment in ecosystem engineering is another likely response, along with reduced mobility and territorial defense, to environments with abundant and predictable resources” (Zeder, 2012:259).

The catalyst, then, that accelerates the C, T, E feedback loop is the development of institutions of ownership that allow individuals to reap the gains of investments made to increase the long-term productivity of a resource base.

There are two unresolved questions associated with this argument. First, it makes no sense to defend a territory if there is no competition for resources. As Dyson-Hudson and Smith (1978:25) state “[i]f a resource is so abundant that its availability or rate of capture is not in any way limiting to a population, then there is no benefit to be gained by its defense and territoriality is not expected to occur.” Thus, by increasing the abundance and predictability of resources through low-level food production strategies, like systematically burning vegetation, foragers might reduce competition so much that there is no one to defend resources from. In this situation, we might expect small and stable territories, but no incentive to develop institutions of ownership and defense. However, as Rosenberg (1990) suggests, where resources are abundant and predictable, population growth and increases in population density should occur. This situation could, in turn, feed back through a forager-resource system and affect a food supply. Clearly, there is an implicit relationship between population density and the productivity of resources in the original model of economic defensibility. In chapter 4, I further develop an evolutionary argument for the development of food production following Smith (2012) and Zeder (2012). I formally consider the consequences of “free” strategies of low-level food production and the affects of such strategies on individual foragers.

Second, managing resources for the long-term would only makes sense if a social-ecological environment has a requisite amount of stability. When systems are characterized by feedback processes, the internal dynamics of a system can create instability or long-term uncertainties that make planning for the future difficult and/or costly. The modified model of economic defensibility raises a couple of interesting question. 1) In what social-ecological contexts does managing ecosystem structures to secure long-term bene-

fits actually allow individuals to accrue the future benefits? 2) Must foragers plan for the long-term, or might strategies that increase the long-term productivity of resources evolve even in some situations in which individuals place a low value on the future returns of resources? I take-up this second question in chapter 4.

The core dynamics of forager-resource interactions

My review of the three models above suggests two generalizations that characterize the dynamics of forager-resource systems.

1. The harvest strategies of foragers and resources coevolve. The resource harvest strategies of foragers modify the current state of a resource base. The current modification of the resource base determines the future state of the resource base (environmental inheritance), and, in turn, the future state of the resource base effects the strategies that foragers select in the future.
2. Competition, mediated by institutions, feeds back through a forager-resource system to affect both the costs associated with the transformation of food into energy (search and handling costs) and the social transaction costs associated with cooperating to access to resources.

The dynamic models presented in chapters 3 and 4 formalize these two core propositions into a system of differential equations. I use the models to build an understanding of the social-ecological processes that determine the robustness of foragers' supply of energy to environmental change.

A General framework to Study the Evolution of SES

A this point, I would like to transition from previous models of subsistence change and the evolution of hunter-gatherer SES to an explicit discussion of the assumptions and

concepts that underpin my study. Figure 2.3 describes my general approach to understanding the processes that drive the evolution of SES. The framework proposed in Figure 2.3 assumes that social-ecological systems are complex adaptive systems composed of agents that continually modify and adapt to their social-ecological environment. Social-ecological systems are artificially bounded for research purposes, but are always open systems through which energy, materials and information flux. Figure 2.3 identifies four internal components of an SES. The four components are: resource dynamics, resource users, infrastructure providers and the physical and social infrastructure that mediates forager-resource interactions. Anderies et al. (2004) originally proposed this framework to study the robustness of social-ecological systems to shocks in common pool resource settings. The shaded ovals place the components of the framework into the structural scheme proposed by Boserup (1996).

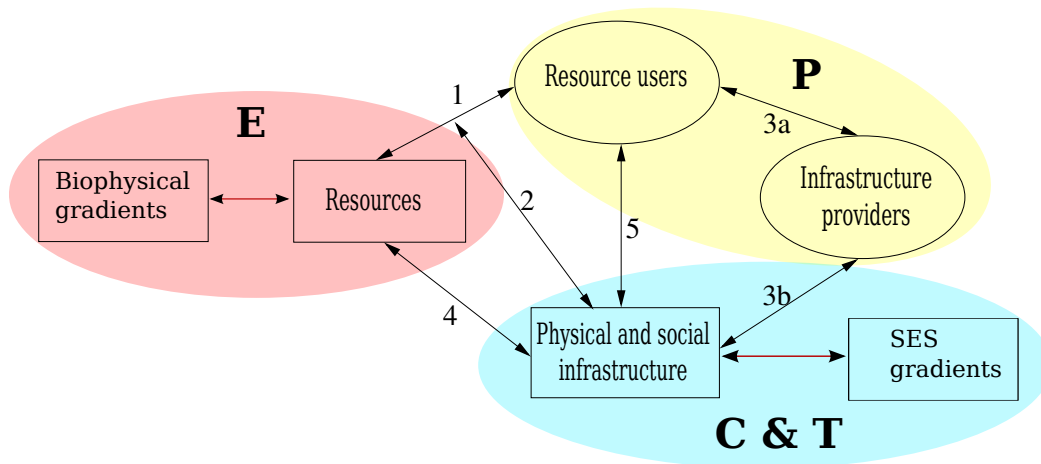


Figure 2.3: A general framework for the study of social-ecological systems. Figure adapted from Anderies et al. (2004).

Resource dynamics simply refer to key variables that characterize a resource base, for example, growth rate, tolerance to frost or carrying capacity. The resource users and infrastructure providers are positions within a SES that might be held by an individual or group. The resource users in this case are individual foragers. Variables such as population den-

sity characterize an aggregate attribute of the resource users in a system and preferences, such as minimizing harvest time, characterize individual foragers. Infrastructure providers refers to the individuals or groups in a position to construct physical infrastructure (a wall or fishing weir) and create social infrastructure (rules and norms about resource use). Physical infrastructure is the hard technology that facilitates the harvest and consumption of resources. Social infrastructure is the soft technology that partly determine the benefits and costs of cooperative and competitive behaviors (i.e., social transaction costs) in a system.

The links between the components of the system describe the potential effects of one component on other components. Link 1 is a feedback between resource users and the resource base. Link 2 denotes the effect of social and physical capital on the feedback dynamics of forager-resource interactions. In a generic hunter-gatherer SES, the resource users and infrastructure providers are generally the same individuals. Thus, links 3a and b denote the social sphere in which individuals adopt and negotiate physical and social infrastructure. Link 4 denotes the impact of social and physical capital on the density of a resource base. Finally, link 5 denotes the feedback between resource users and infrastructure. In this framework, all of the internal components of a forager-resource system are interrelated and mutually reinforcing due to the presence of feedbacks between the components.

In addition to the internal factors described above, a SES is perturbed by at least two external factors: biophysical gradients and other SES. Biophysical gradients are generated by variables such as mean annual temperature or rainfall that directly impact the characteristics of a resource base. The SES gradient refers to the matrix of SES systems with which individuals in the system under study interacts. The red arrows represent a dynamic feedback between the external and internal factors over long time scales. For example, I have argued that specialization in domesticated plants by one social group creates an opportunity for foragers who interact with this social group to adopt a method of agriculture

known as casual cultivation (Freeman, 2012a). The strategy of casual cultivation is one in which foragers spend very little effort in the production of domesticated plants and incur a high risk of total crop failure (Huckell et al., 2002). The availability of seeds or cuttings made possible by the specialized agriculturalists on a metaphorical SES landscape allows casually cultivating hunter-gatherers to replenish seeds and, again, take-up casual cultivation after an episode of crop loss. This is a long-term coevolutionary relationship that may result in a matrix of distinct types of foraging-farming SES on a landscape.

Basic Analytical Concepts from Dynamical Systems Theory

As Anderies et al. (2004:2) note, the framework presented above

“identifies a broad set of variables and their linkages. Within any particular framework, alternative theories are used to make broad predictions about the effect of changes in relevant variables, and multiple models operationalize theories using a variety of techniques.”

In this study I use the tools of dynamical systems to operationalize a forager-resource system and study the affects of factors such as population density, the productivity of resources and food production on the robustness of foragers’ supply of energy and time budget. In turn, I leverage my knowledge of the effects of such factors on the robustness of foragers’ supply of energy and time budget to environmental change to propose two theories of subsistence change in forager-resource systems.

In chapters 3 and 4 I model a general forager-resource system with two, coupled differential equations. Dynamical systems theory is the formal study of such systems and provides a foundation for understanding the behavior of systems characterized by coupled, non-linear differential equations. The models that I present are quite simple as far as such systems are concerned. Simple and general models always have the advantage that they

can be made more specific and/or complex to deal with any particular situation. To interpret the dynamics of the hunter-gatherer SES model presented in the following chapters, I present four analytical concepts drawn from dynamical system theory. These concepts provide a qualitative description of the processes and behaviors that occur in a model system. This is not a complete overview of dynamical systems theory. The purpose is to introduce concepts that are used to analyze the baseline hunter-gatherer SES presented in preceding chapters. Interested readers can consult Edelstein-Keshet (2005) and Tu (1994) for formal introductions to dynamical systems theory.

The first two concepts are attractor and repellor. An attractor is the set of equilibrium system states toward which a dynamical system tends as time tends to infinity. The simplest example of an attractor is a single stable equilibrium point, but attractors can be very complex and involve infinitely many points. A repellor is a set of equilibrium system states that a dynamical system tends to move away from as time tends to infinity. The simplest example of a repellor is, again, a single unstable equilibrium point. By studying the stability properties of equilibria, we can investigate how slow changes in parameters, like the growth rate of resources, affects the robustness of foragers' supply of food to perturbations. This knowledge, in turn, is useful for understanding the social-ecological contexts in which a forager-resource system is vulnerable to critical transitions from a desirable to an undesirable collection of system states. Such vulnerability can introduce uncertainty into a system and create an environment that favors the selection/copying of foraging strategies that reduce uncertainty and improves the robustness of individual foragers' supply of energy to environmental shocks.

Importantly, the concepts of attractor and repellor describe local behaviors of modeled forager-resource interactions as opposed to the global structure of a dynamical system. A stability landscape is a metaphor that helps illustrate the local dynamics of a system, as well as the global structure of a dynamical system. In Figure 2.4 the two valleys represent

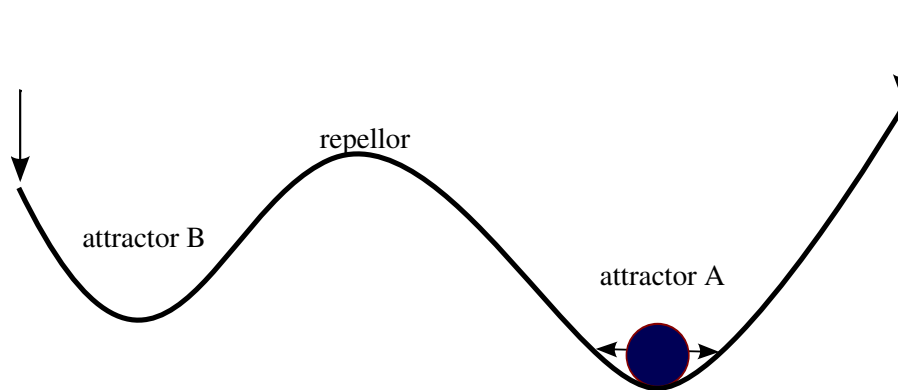


Figure 2.4: An example stability landscape. The global structure of the system consists of two attractors and one repellor. The ball represents a particular moment in time at which a system could exist. The ball in attractor A is “buzzing” as perturbations continually knock the system out of local equilibrium. The arrows pointing down on each end of the landscape are forces that can change the global structure of the system.

attractors and the peak a repellor. The global structure of this hypothetical system consists of two attractors separated by a repellor. On the valley bottoms and at the peak, 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 away by a shock. Notice that on the landscape represented by Figure 2.4, there are two attractors. If a perturbation that knocks attractor A out of equilibrium is too large, the system may not return to “A”, but, instead, get knocked into attractor B where the structure of feedbacks is different. This is an “attractor shift” also called a critical transition. There is always slow change in real systems and deviations from the long-run equilibrium state of a system. When I refer to real systems, I will, therefore use the term dynamic attractor or regime.

The final concepts that I would like to discuss in more detail are resilience and robustness. In the forager-resource systems that I operationalize in chapters 3 and 4, I study the resilience of forager-resource system states to draw conclusions about the robustness of foragers’ energy target and time budget to environmental change. As alluded to above, “A dynamical system is said to be structurally stable if small perturbations to the system itself result in a new dynamical system with qualitatively the same dynamics” (Jen, 2003:12).

Given this definition, I equate dynamic stability with Holling's (1973:14) concept of resilience "that is a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables." Hereafter, I use the term resilience when I discuss modeled forager-resource system states. Metaphorically, the resilience of an attractor is represented by the width and depth of a valley on a stability landscape.

As noted in chapter 1, I define robustness as the ability of some unit (an individual or a group) to obtain a performance measure when subject to unpredictable external shocks or uncertainty associated with internal design parameters (compare Anderies et al., 2004:1; Jen, 2003; Page, 2011:148-166). The difference between robustness and resilience is a pretty subtle epistemological divide. The two terms are related, and the resilience of a system can have enormous consequences for the robustness of a particular performance measure. For example, if foragers can meet their performance goal in attractor A but not in attractor B on Figure 2.4, then we can say that the performance goal of foragers is vulnerable and potentially uncertain due to perturbations that might generate a critical transition from "A" to "B."

Given the above definition of robustness, any analysis of robustness requires answering three questions: what is robust to what; robust for whom and robust for how long (Anderies et al., 2007; Carpenter et al., 2001; Freeman et al., 2014; Jen, 2003)? In this study, the what-to-what is the harvest output of foragers (chapter 3) and foragers' time budget (chapter ??) to both short-term shocks, generated by processes such as inter-annual deviation in rainfall, as well as long-term changes, such as a decline in the mean productivity of a resource base. The who is simply a modeled forager. The how long question in the theoretical work done here is a matter of hundreds of years (200 model time steps to be exact).

Conclusion

Now, the fun begins! In the following chapters, I present dynamic models of a forager-resource systems. The models build on and extend the ideas of Binford (2001), Bettinger (1991), Smith (2012) and Zeder (2012). The result of this effort is two hypotheses that state how the coevolution of foragers and resources cause the foraging strategies of individual foragers to change, including the adoption of food production and territorial ownership. These hypotheses provide a set of clear propositions that are evaluated through comparative ethnoarchaeological research. In turn, the comparative ethnoarchaeological analysis provides a more informed context for designing archaeological research.

Chapter 3

THE UNCERTAINTY REDUCTION HYPOTHESIS

As noted in chapter 1, no one can directly observe the past. This means that archaeological research is a process of constructing webs of inference to explain major changes in the archaeological record. All inferences are statements about what the world is like based on background knowledge that we assume is correct or at least useful. As a consequence, part of archaeological research should be the continual development *and* critical evaluation of the background knowledge upon which inferences about the dynamics of past social-ecological systems are built. This is not an easy task. Ethnographic studies are conducted at scales of space and time that are inappropriate for making inferences about long-term processes that play out across organizational scales and over large geographic regions. Thus, I argue that dynamic models are a core intellectual tool that aid in the quest to develop a corpus of background knowledge for making inferences. Dynamic models bridge analytical scales and help frame an analysis of large ethnographic data sets to identify basic principles of subsistence change that are testable against archaeological data.

My purpose over the next two chapters is to build and use formal and conceptual models to study feedback processes in hunter-gatherer SES and develop insight into how these processes might cause foraging strategies to evolve. The model that I specifically study in this chapter is a tool for understanding how individual foraging decisions scale-up to affect the robustness of food output in a forager-resource system to environmental change, and how the state of a system might feed back on the foraging strategies of individuals and drive the evolution of hunter-gatherer SES. The model presented here is a stylized, baseline hunter-gatherer SES originally developed by Freeman and Anderies (2012). This baseline model formalizes the core propositions identified in chapter 2: i) foraging strategies and

the state of a resource base coevolve and ii) competition affects the transformation and transaction costs of the acquisition of resources. I specifically ask, given the open-access nature of resources among hunters and gatherers, how do changes in the productivity of resources and population density affect the robustness of food output in a forager-resource system to potential shocks, and how might the state of a system effect the selection of foraging strategies by individuals?

In the remainder of this chapter, I present and analyze the hunter-gatherer SES developed by Freeman and Anderies (2012). Next, I re-scale the hunter-gatherer SES model to conceptually model the dynamics of forager-resource systems operating at multiple scales of space and time. The result of this exercise is what I call the Uncertainty Reduction Hypothesis (URH). This hypothesis proposes that when the resource productivity-to-population density ratio of a global forager-resource system is low, foragers can, in part, rely on natural capital (large scale ecosystem structures like forests) to modulate higher frequency variation in climate that might affect the availability of resources. However, once this ratio declines past a critical threshold, individual foragers begin to face a common pool resource dilemma at more local scales where natural capital has no modulating effect on higher frequency environmental variation. The consequence is a high degree of uncertainty about where to locate in space and time to harvest a sufficient level of food. In this situation, selection and copying pressure favors strategies that generate social and technological capital that reduce the uncertainty associated with planning where to locate in space and time to harvest resources.

A Baseline Hunter-gatherer SES

The Hunter-gatherer SES is a stylized model of consumer-resource dynamics developed by Freeman and Anderies (2012:Box 1). Consumer-resource models have a deep intellectual tradition in the study of non-human foragers in ecology and commercial fisheries

in economics (e.g., Clark, 1976; Noy-Meir, 1975; Scheffer, 2009). However, consumer-resource models have only been applied to understand to a handful of anthropological-archaeological questions (e.g., Anderies, 1998, 2006; Janssen et al., 2003; Lee and Tujapurkar, 2008; Lee et al., 2009; Puleston and Tujapurkar, 2008; Taylor and Brander, 1998), and such models are even more rare in the study of hunter-gatherers (e.g., Freeman and Anderies, 2012; Winterhalder and Lu, 1997; Winterhalder, 1993; Winterhalder and Goland, 1993; Winterhalder et al., 1988). The hunter-gatherer SES presented here links the behavior of individual forager units with the basic dynamics of a resource base to study the coevolution of individual decisions and the state of a resource base. The model is scaled to investigate the conditions that affect the robustness of food output in a forager-resource system within a single habitat embedded on a larger landscape of multiple habitats. This is important to note because there is a nested hierarchy of forager-resource systems in which individuals participate. The model is a story succinctly written as a set of coupled differential equations:

$$\dot{x} = G(x) - H(x, e) \quad (3.1)$$

$$\dot{e} = D(x, e). \quad (3.2)$$

Put into prose, the change in resource biomass (\dot{x}) is equal to the growth of resources, $G(x)$ less the total biomass harvested by a group of foragers, $H(x, e)$; \dot{e} is the change in harvest effort (workdays/day) that depends on a decision function, $D(x, e)$. The decision function stipulates how individual foragers allocate their time to the harvest of resources, given the different social and ecological conditions that they encounter. Please note that the equations are coupled. This means that the availability of resources depends on the decision function, and the decisions of foragers depend on the state of a resource base at time t , as well as how much effort is needed at time t . Interpreting the dynamics of this

story requires four assumptions stated by Freeman and Anderies (2012:423-424) that are expanded upon here.

State Variables	Definitions	Default Values
$x(t)$	The density of resources (biomass/area) at time t	varies
$e(t)$	The harvest effort (workdays/day) at time t	varies
Parameters	Definitions	Default Values
r	The mean intrinsic rate of resource growth (yr^{-1})	0.3
K	The mean carrying capacity for resources (biomass/area)	1
q	The harvest coefficient (biomass/effort/standing biomass)	0.2
p	The population density of foragers	0.7
γ	The energy target per forager	0.05
l	The baseline processing coefficient (Kcals/unit biomass/effort/forager)	1
m	Interference (Kcals/biomass/effort/forager)	0.7
c	Basal metabolic requirements (Kcals/time)	0.02
α	The biomass to energy conversion coefficient defined in the text	varies
α_1 and α_2	Relative weights given to harvest per unit effort and energy deficits	0.1 and 4
β	The sharpness of the transition between valuing energy deficits over harvest per unit effort	3

Table 3.1: Model state variables and parameters

First, the individual forager in the model is a “household” that exploits open access resources. This is a critical assumption because it means that foragers do not coordinate their access to resources via formal rules that define who, when and where resources may be accessed. Part of the reason this model is a “baseline” hunter-gatherer SES is because resources are, initially, treated as open access. However, the interference coefficient (m) can be used to simulate the potential effects of more restricted access to resources via formal rules that coordinate the harvest of resources within the system (Freeman and Anderies, 2012). Further, the resources that foragers exploit are stationary resources, such as grasses, nut bearing trees or jack rabbits that only have an annual range of 1 square kilometer (much smaller than the potential annual range of a human forager).

Second, the model implicitly holds space relatively constant at K , which is the carrying capacity of resources in terms of biomass/area. K or any other model parameter discussed, is not an absolute constant. The model structure allows one to systematically vary K . In the model, the value of K always defines the size of the habitat that foragers use to harvest resources. Practically, this means that the spatial scale described by the model is a choice made by the modeler. This choice is dictated by the scale of the question that one asks. In this case, I assume that foragers exploit a habitat embedded on a larger landscape that contains multiple habitats. A habitat is, metaphorically, the area that foragers cover from a central base camp in order to obtain food, thus modeled foragers are central place foragers (Kelly, 1995). Although not formally included in the model, I implicitly assume in the interpretation of the model's dynamics that a habitat contains a collection homogeneous resource patches that foragers might access on any given workday from a residential base camp. Further, I implicitly assume that foragers have complete information regarding the availability and location of resources within a habitat.

Third, the population density (p) of foragers is a parameter. Every potential variable that characterizes a social-ecological is dynamic. Real systems are *always* in a state of change. By making population density a parameter, as with K , I avoid the assumption that population density does not change. Rather, the assumption is that population density changes more slowly than the variables in the model that are dynamic (Freeman and Anderies, 2012:424). It is the judicious exploitation of time-scales by a researcher that, in part, gives dynamical systems their power to illuminate the dynamics of complex systems (see Scheffer (2009:82-83) for a very cogent discussion). In terms of interpretation, the assumption that population density is a parameter means that, again, foragers use a habitat that is embedded on a landscape of multiple habitats and a population of foragers. Individual foragers continuously flow through the various habitats on the landscape.

Finally, foraging effort (e) is the time spent to harvest resources (workdays/day). For example, it is assumed here that one workday is equivalent to eight hours, so $e(t) = 1 = 8$ hrs. worked per day. The decision function in the model assumes that foragers adjust their harvest time in an effort to achieve a harvest goal in a minimum amount of time. This is similar to assuming that foragers attempt to maximize their non-subsistence time, used to socialize, travel, sleep, *etcetera*. For example, foragers might use their non-subsistence time to perform an initiation ceremony . The above assumption, however, is contingent upon foragers achieving a rate of harvest that is sufficient to meet their basal metabolic needs (discussed below). Any formal model of a social-ecological system has to make an assumption about the behavior of humans. The assumptions made here are not viewed as universal, static preferences that motivate human behavior. A potentially powerful use of dynamic models is the ability to define the social-ecological contexts in which one might expect the preferences of individuals to change.

Given the above assumptions, the functions presented in equations (3.1) and (3.2) are now defined formally. $G(x)$ is defined by the logistical function $G(x) = rx(1 - \frac{x}{K})$, where r is the intrinsic growth rate of a resource base, and K is the carrying capacity of the resource base in units of biomass per unit area (the limiting effect of competition on resource growth). $H(x,e)$ is simply $ph(x,e)$, where p is population, and $h(x,e)$ is the biomass harvested by an individual forager household. The function $h(x,e) = qxe$, where q is a proportionally constant biomass capture coefficient (level of technological efficiency) in units of biomass captured per unit effort per unit of standing biomass. The variable $x(t)$ is biomass density at time t , and $e(t)$ is foraging effort at time t .

In order to determine time allocation, foragers must first convert the biomass that they harvest into energy. The biomass to energy conversion coefficient, α is defined as $\alpha = le^{(-mp)}$ (see Figure 3.1 for a graphic depiction); where l is a baseline processing coefficient in Kcals per unit biomass per unit effort per forager. The parameter l defines the

costs of handling resources (converting biomass into usable energy) absent any transaction costs in a system. The parameter m is an interference coefficient that defines the costs of interacting with other foragers, transaction costs, in terms of Kcals/biomass/time/forager, and e is the exponential. The interference coefficient is constrained by $0 < m < 1$. Thus, the energy obtained by a household is simply the energy conversion coefficient multiplied by the biomass harvested by a household, $\alpha h(x, e)$. The energy conversion coefficient is an aggregate measure of the effect of competition on how efficiently foragers convert biomass into energy (see Freeman and Anderies, 2012:425). The coefficient combines the effects of indirect competition and direct competition for resources.

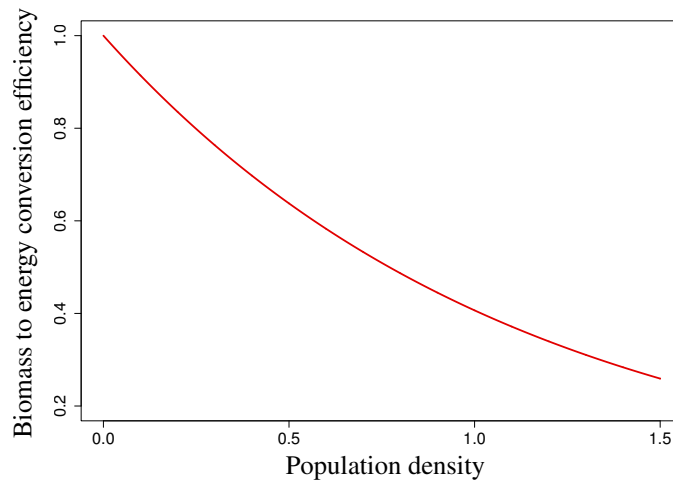


Figure 3.1: Biomass to energy conversion (α) dynamics are controlled by population density (p) and the interference coefficient (m). As population density increases, biomass is converted into energy less efficiently.

Time is allocated to the harvest of resources based on two energy targets. The target c defines the minimum rate of energy gain that foragers are willing to tolerate (basal metabolism), and the target γ defines the desired energy to maintain biological function, reproduce and maintain social relationships. Foragers allocate their harvest effort at each moment in time by evaluating if their harvest per unit of effort ($\alpha h(x, e)/e$) is less than or greater than their basal metabolic rate, c . If $\alpha h(x, e)/e \geq c$, then foragers harvest more food

when they are hungry and decrease their effort when they are satiated. This is formalized by the function: $\delta = \gamma - \alpha h(x, e)$, where δ is the energy deficit at time t . If $\alpha h(x, e)/e < c$, then foragers decrease the effort that they exert in a habitat no matter how hungry they are. If foragers cannot meet their basal metabolic need, the implication is that foragers leave and find a new place to set-up camp (as noted above). Together, these time allocation rules allow foragers to quickly find the allocation of effort that achieves γ in a minimum amount of time. Please note, the best time to leave a habitat is not addressed by this decision process. The decision process defines the allocation of time within a habitat, if the habitat appears of a suitable quality.

The decision dynamics are formalized by a rational function (Freeman and Anderies, 2012:Box 2),

$$D(x, e) = \frac{\alpha_1 \delta [\alpha h(x, e)/e]^\beta - \alpha_2 c^\beta}{[\alpha h(x, e)/e]^\beta + c^\beta} \quad (3.3)$$

where $\beta \gg 1$ is a parameter that scales the sharpness of the transition between the two time allocation behaviors. The parameters α_1 and α_2 measure how rapidly foragers adjust their effort based on the different resource conditions that they may encounter. Figure 3.3 graphically illustrates the decision process. At every moment in time, foragers evaluate which region of Figure 3.3 that they “occupy” and adjust the effort that they devote to the harvest of food accordingly.

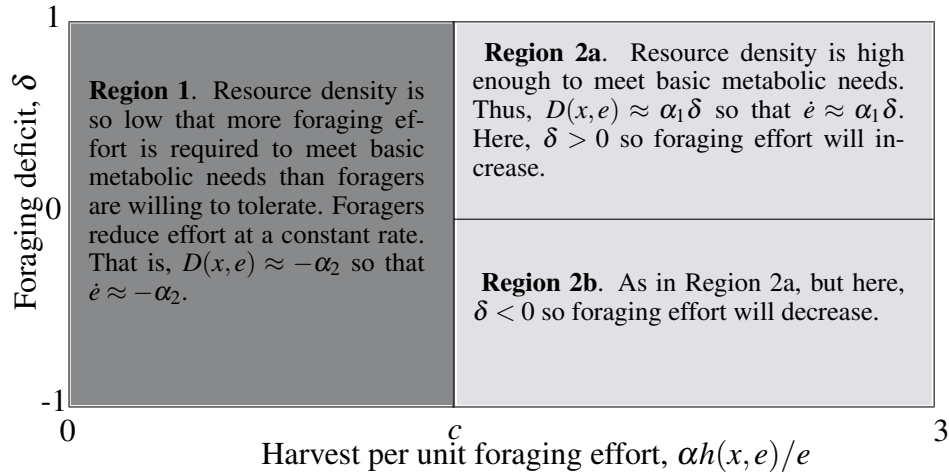


Figure 3.2: Foraging effort decision heuristic. The different regions in the daily energy deficit - daily energy harvest plane generates a decision heuristic that foragers use to allocate effort.

The Effects of Productivity and Population on Forager-resource System States

Figure 3.3 is a set of phase-plane diagrams that describe how systematically varying the productivity (growth rate) of resources (r) changes the global structure of the hunter-gatherer SES. The orange curve describes all of the points in the system for which foraging effort is at equilibrium ($\dot{e} = 0$) and the green curve all of the points at which resource density is at equilibrium ($\dot{x} = 0$). Where the two curves meet, an equilibrium emerges (i.e., $\dot{e} \& \dot{x} = 0$). All stable equilibria are marked by gray circles and the unstable equilibrium in Figure 3.3b by a square. Each phase-plane has a corresponding stability landscape that, metaphorically, represents the dynamics described by each respective phase-plane.

The black curves on each phase-plane represent individual model runs, and these illustrate how the system changes over time for a particular set of initial conditions. For example, the “1” on Figure 3.3a indicates an initial condition or starting point for a single model run. The arrows on the curve indicate how the model behaved over time. In this case, when the model run was initiated, foragers were in a depleted environment and spending

a significant amount of time in the harvest of food. Very quickly, foraging effort drops to zero (foragers realize that $\alpha h(x,e)/e < c$, so they decrease their effort). While foraging effort is at zero, the density of resources recovers. At approximately $x = 0.25$, foragers realize that $\alpha h(x,e)/e \geq c$ and begin to harvest resources (i.e., re-enter the habitat). Foraging effort and resource biomass increase over time until the orange curve is reached. At this point, foragers devote just enough time to the harvest of biomass to meet their energy target, γ . Resource density continues to increase because resource growth, $G(x)$ is faster than total harvest, $H(x,e)$. As resource density increases, foraging effort declines until a stable equilibrium is reached.

The global structure of the hunter-gatherer SES has a significant effect on the potential trajectory of any particular model run. In Figure 3.3a there is only one, globally resilient equilibrium. Thus, every potential model run will reach a system configuration that is productive (i.e., foragers, in the long-run, meet their energy target of γ in a minimum amount of time). Recall, the stable equilibrium reflects the position of the system, on average, over time-scales longer than the time-scale at which decision processes are made in the model. In this case, the long-term average is on a scale of successive years. The stable equilibrium does not reflect a condition of no change. Rather, in a real system, environmental variations, like population movement or droughts, would constantly shock forager-resource interactions out of the long-run equilibrium. Despite such shocks, in the environment described by Figure 3.3a, the ability of foragers to obtain their goal of γ is robust to environmental variation because the system is globally resilient and always characterized by a productive attractor.

However, if the mean intrinsic rate of resource growth declines too much, then the global structure of the system changes. In Figure 3.3b, r is equal to 0.3. In this environment, a second stable equilibrium, as well as an unstable equilibrium emerge. Initial conditions and environmental variation may now have a significant effect on the long-run

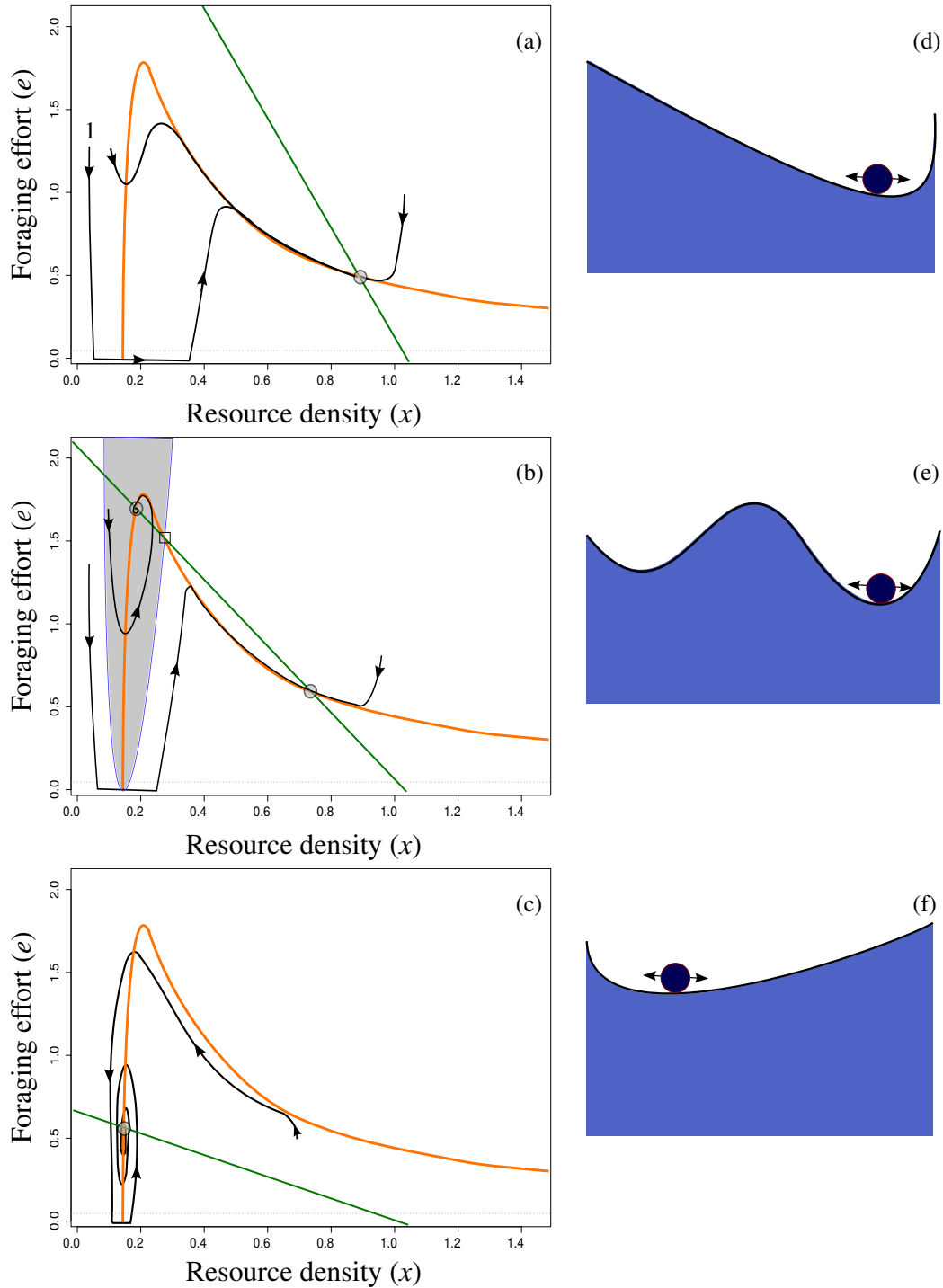


Figure 3.3: Phase plots of foraging effort against resource density. All parameters are held constant at default values except resource productivity (r). $a-r = 0.5$; $b-r = 0.3$; $c-r = 0.1$. The circles highlight stable attractors. The square in graph b highlights an unstable attractor. Each phase plot is paired with a stability landscape (a-d; b-e; c-f) that provides a metaphor for the dynamics portrayed in each phase plot.

configuration of the system. If the modeled foragers begin to harvest resources within the gray shaded area on Figure 3.3b, they get “caught” in a degraded attractor where resource density is positive, but foragers can only meet their basal metabolic needs. Further, due to the presence of a degraded attractor and a repeller (the unstable equilibrium), foragers are not sensitive to environmental variations that might knock the system too far out of equilibrium at the productive attractor. The distance between the equilibrium at the productive attractor and the unstable equilibrium at the repeller in Figure 3.3b determines how big of a shock the system can tolerate before flipping into the degraded attractor. It is important to recognize that foragers may never see a shock that drives their interaction with a resource base into the degraded attractor coming. In order to prevent such a possibility, *foragers would have to first recognize that a novel vulnerability had emerged in the system, then discover and remember the frequency, as well as intensity of shocks that might flip the system.* In contrast to the scenario depicted in Figure 3.3a, the system is vulnerable to a critical transition between the productive and degraded attractors and this means that the ability of foragers to achieve γ is potentially uncertain.

Finally, in Figure 3.3c r is equal to 0.1. In this environment the only stable equilibrium is a degraded state. Foragers can obtain food in a manner that is sustainable for the resources, but only enough food to meet their basal metabolic requirements. The system has been pushed over a “tipping point,” where the productive attractor is no longer an option. The degraded attractor is the only possible system state and the attractor is globally robust to perturbations. This means that the ability of foragers to obtain their basal metabolic requirement is globally robust, in the long-run, to environmental shocks, but it also means that foragers will not, in the long-run, achieve their energy goal of γ . In real systems, foragers are unlikely to ever tolerate such a situation for very long.

In general, the sequence of pictures shown in Figure 3.3a, b & c illustrates what is called a robustness-vulnerability trade-off for modeled foragers. As the intrinsic growth

of resources in the system declines, foragers work harder to achieve γ . Modeled foragers reallocate non-subsistence time to the harvest of resources to obtain their desired level of food, and this strategy makes individuals robust to declines in the productivity of the system (r). The strategy of working harder to obtain more food is effective. Working harder to make γ robust, however, decreases the resilience of the productive attractor and precipitates the emergence of the repeller and degraded attractor in Figure 3.3b. In turn, achieving γ becomes potentially uncertain for foragers because the the system is vulnerable to environmental shocks that can generate a critical transition from the productive to the degraded attractor. Importantly, this robustness-vulnerability trade-off is a consequence of subtle increases in foraging effort.

Beginning from Figure 3.3a, a decline in the net productivity of resources, initially, only has a small impact on how hard foragers work to achieve γ . The effort curve (orange curve) for which foraging effort is not changing in the hunter-gatherer SES is highly non-linear. Moving from right to left, the orange curve increases very slowly, then quickly until a threshold, at which point the curve declines sharply. Due to the form of this curve, the decline in resource productivity from Figure 3.3a to 3.3b is accommodated with only a slight increase in foraging effort, from 0.51 to 0.57. As noted above, $e(t) = 1$ is equivalent to one eight hour workday per day over the course of weeks to months of resource harvest. Thus, the change from $r = 0.5$ to $r = 0.3$ only causes foragers to spend about 28 minutes more per workday to harvest food at equilibrium in the productive attractor. This slight increase in work effort may have little effect of the harvest decisions of foragers. However, when every forager works just a bit harder, the aggregate effect is the depletion of resources just enough that the productive attractor becomes vulnerable to environmental variations that may “knock” the system into the degraded attractor. This situation is a stochastic common pool resource dilemma. When each forager works a bit harder to maintain their goal (γ), every forager in the system becomes vulnerable to a critical transition from the productive to

the degraded attractor induced by unpredictable environmental variation. When a negative critical transition is generated, not a single forager would achieve their energy goal.

Windows of vulnerability and common pool resource dilemmas

Figure 3.4 is a set of bifurcation diagrams that summarize the effects of the resource growth rate (r) and population density (p) on the global structure of the hunter-gatherer SES. A bifurcation diagram is a specialized tool. Such diagrams help illustrate critical changes in the global structure of a system.

Holding all other parameters constant at default values, the high productivity harvest branch in Figure 3.4a represents all of the values of r for which the productive attractor is present in the hunter-gatherer SES. The degraded harvest branch represents all of the values of r for which the degraded attractor is present and the dashed line all of the values of r for which the repeller is present. For example, viewing from right to left in Figure 3.4a, all of the values of $r > 0.337$ (right of the gray shaded area) result in a hunter-gatherer SES with only the globally resilient productive attractor (i.e., all values of r that result in the pictures shown by Figures 3.3a & d). All of the values of r inside of the gray shaded area result in a hunter-gatherer SES characterized by both the productive and degraded attractors, as well as the repeller (i.e., all values of r that result in pictures similar to Figures 3.3b & e). All of the values of r to the left of the gray shaded area result in a hunter-gatherer SES characterized by the globally resilient, degraded attractor. Similarly, the high productivity harvest branch in Figure 3.4b corresponds to all of the values of population density for which the productive attractor is present and so on.

The gray shading in Figures 3.4a & b highlights a “window of vulnerability” where environmental variation may shock the long-term state of the system back and forth between the productive harvest branch and the degraded harvest branch. In dynamical systems terminology, the movement back-and-forth between attractors is called hysteresis. In real

systems, environmental variation may have a positive or negative impact on an element in a system. To provide some intuition, inter-annual variation in rainfall may increase or decrease the growth rate of biomass useful as food in a real system. If we extend the window of vulnerability metaphor to describe the potential system states in a real hunter-gatherer SES, the effects of such positive and negative variations in rainfall may cause inter-annual shifts between a productive and degraded forager-resource regime (here I use the term regime instead of attractor because the reference is to a real rather than model system).

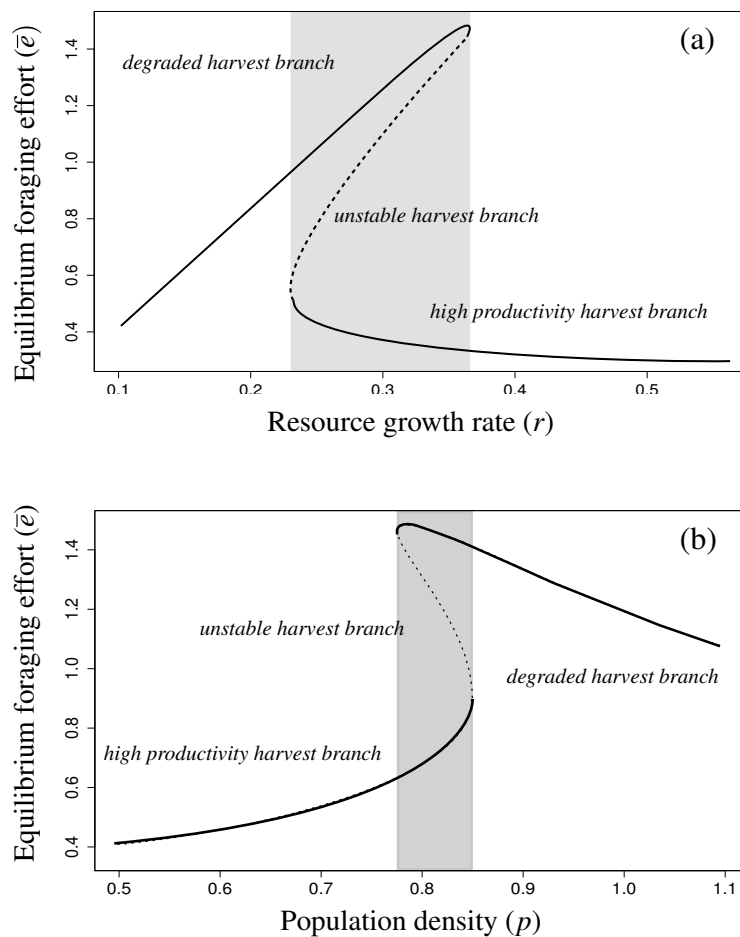


Figure 3.4: Summary of the long-run of harvest states in the hunter-gatherer SES. The lower solid line represents all of the productive harvest states as a function of resource growth rate (a) and population density (b); the dashed middle lines, all unstable equilibria, and the top solid lines all degraded states. The gray shaded areas indicate “windows of vulnerability” that define the parameter space for which environmental variation could generate a critical transition between the productive and degraded harvest branches.

In general, Figure 3.4 illustrates that as either the growth rate of resources declines or population density increases, in the model, foragers work harder to harvest resources at the productive attractor. Once a threshold of either $r = 0.337$ or $p = 0.775$ is hit, the system becomes vulnerable to a negative critical transition. When the system is vulnerable, a shock may generate a critical transition from the productive to the degraded attractor. These thresholds of $r = 0.337$ and $p = 0.775$ initiate “windows of vulnerability” in the hunter-gatherer SES. Within a window of vulnerability, if population density increases or the growth rate of resources declines, the productive attractor and repeller move closer together. If the productive attractor and repeller get pushed together, a fold bifurcation or deterministic critical transition occurs. Beyond this “tipping point,” the state of the forager-resource system is degraded and globally resilient, but foragers can only meet their basic metabolic needs (c).

In the window of vulnerability, modeled foragers face a stochastic common pool resource dilemma because each individual “selfishly” works to achieve γ , and this behavior makes the system vulnerable to a variance induced critical transition from the productive to the degraded attractor. Of course a negative critical transition would prevent every forager in the system from achieving γ . In this kind of social-ecological setting, some level of uncertainty associated with achieving γ is generated that depends on a) the predictability of external shocks that hit the system and b) the ability of foragers to accurately measure the amount of harvest effort that a resource base can handle. The question is whether or not foragers can realize that a common pool resource dilemma has emerged and adjust their strategies for producing resources before a system permanently flips into a degraded state? My argument is that foragers can detect the emergence of a common pool resource dilemma precisely because the dilemma generates uncertainty associated with achieving γ . How foragers adapt to this new social-ecological setting depends on their ability to process information over a nested hierarchy of forager-resource systems and discover the

risk of variance induced critical transitions in many localized forager-resource systems that compose a larger system.

Scaling-up: Localized Critical Transitions Drive the Evolution of Foraging Strategies

My analysis above focused on a forager-resource system scaled to a single habitat embedded on a landscape of multiple habitats. This single system is, conceptually, a local system that is simply a subsystem of a landscape scale forager-resource system (see Figure 3.5). Here, I conceptually rescale the hunter-gatherer SES to the landscape scale. This allows me to summarize the behavior of a forager-resource system aggregated across all of the habitats that comprise a landscape. Thus, equilibrium biomass and foraging effort ($\bar{x}(t)$ and $\bar{e}(t)$) now describe the level of biomass and foraging effort exerted on a landscape aggregated across all of the forager-resource systems that exist at the habitat scale.

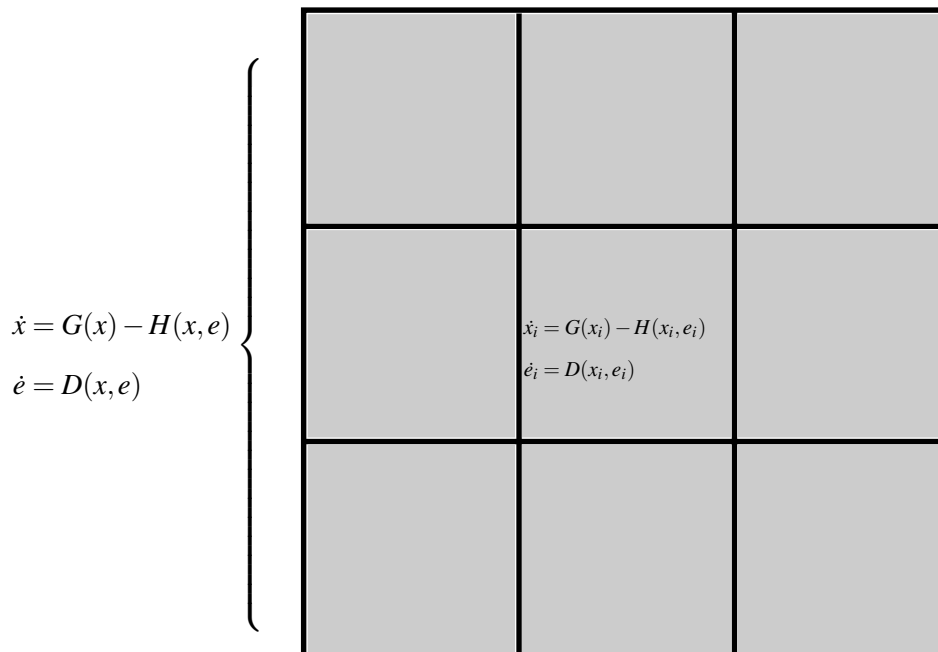


Figure 3.5: Idealized landscape composed of nine local forager-resource systems. The conceptual model is scaled to the size of the landscape, the global forager-resource system.

In a system at the landscape scale with many local forager-resource systems at the habitat scale, variation in characteristics of the local systems is important. On a landscape in which only one system at the habitat scale is ever vulnerable to a negative critical transition, the experience of a negative critical transition would simply stimulate foragers to relocate to a less vulnerable habitat. As long as there is a pool of forager-resource systems at the habitat scale on a landscape and most of these habitats are not vulnerable to a negative critical transition, then the experience of a negative critical transition is likely to only have a weak feed back on individual foragers. However, if a window of vulnerability is characteristic of many forager-resource systems, simultaneously, at the habitat scale, then simply moving around may not allow individual foragers to avoid negative critical transitions. In this setting, foragers must confront the fact that achieving γ is no longer a sure thing in any of the habitats in which individuals might create a forager-resource system.

Uncertainty in the ability to achieve γ arises from two potential sources. The first is assessment error. As illustrated in Figure 3.3b, harvesting resources at a rate that is initially too high can drive a system into the degraded harvest state. So, when every habitat scale system is vulnerable, the ability to discover and measure the harvest effort that a habitat can handle and still converge to the productive attractor is critical for meeting a forager's energy target. Second, environmental variations that depress the availability of biomass, like an immigration event or a drought, can cause habitat level systems to transition from the productive to the degraded attractor and generate uncertainty in the ability of individuals to schedule their movements between habitats to obtain γ . In both cases uncertainty is a consequence of the fact that foragers "selfishly" work to meet their energy target and generate a resource commons and associated stochastic commons dilemma. Although both sources of uncertainty are potentially important, in the conceptual model that follows, I investigate how environmental variation and the r/p ratio of a system at the landscape scale interact to drive the evolution of foraging strategies. I argue that in settings where most

forager-resource systems at the habitat scale are vulnerable to a negative critical transition, the uncertainty associated with locating in space and time to obtain food increases and this is a signal that generates selective pressures on individual foragers.

Conceptual forager-resource systems

To interpret the dynamics of my conceptual model, I would like to precisely define three terms: risk, uncertainty and information processing. Risk refers to a decision maker's perception of the probability distribution that a set of outcomes will occur (Knight, 1921; Winterhalder et al., 1999); uncertainty is incomplete information about the possibility that a set of outcomes will occur. As Knight (1921:233) makes the distinction,

“The principle difference between the two categories, risk and uncertainty, is that in the former the distribution of the outcome in a group of instances is known (either through calculation *a priori* or from statistics of past experience), while in the case of uncertainty, this is not true, the reason being in general that it is impossible to form a group of instances, because the situation dealt with is in a high degree unique.”

For example, when the productive and degraded attractors are both potential long-run states of a system at the habitat scale, modeled foragers risk experiencing a negative critical transition every time they participate in a habitat level system. If critical transitions occur in a highly patterned space-time context, then foragers might discover through experience and cultural transmission the probability of a critical transition in any given system at the habitat scale. This knowledge can then be used to estimate the risk of a negative critical transition in the future. Uncertainty is the gap between foragers' estimated risk of a negative critical transition in a local system and the actual rate at which variance induced critical transitions

actually occur. This gap is what Heiner (1983) refers to as the competence-difficulty gap (C-D gap).

Information is, strictly speaking, a sequence of cues or symbols that can be interpreted as a message. The message is informative because it resolves some degree uncertainty about the state of a system. I assume here that foragers update and transmit messages by observing cues within their social and ecological environments. These messages are encoded by symbols that represent the state of some aspect of a forager-resource system. Information processing occurs anytime that foragers update their representation of the current state of a system *and* infer the likely future state of the system. Information processing is an inherent dynamic of the knowledge base (collection of messages used to represent a social-ecological system's possible states) known as traditional ecological knowledge (TEK). The information processing capacity of populations connected by a shared body of TEK is described by Menzies and Butler (2006:7):

“TEK is rooted in, and informed by, a traditional or customary lifestyle, but it adapts to change and incorporates contemporary information and technology. New information is continually added and old information deleted, as the environment is transformed, as weather patterns shift, or as species are wiped out or introduced.”

In this view, human foragers are Bayesian decision makers. A body of culturally transmitted TEK forms a forager's prior beliefs about the probable state of a social-ecological system, and foragers process information to update their expectations about the probable future state/s of a social-ecological system.

Given these definitions, I would like to compare three forager-resource systems scaled to the level of a landscape and composed of nine “local” forager-resource systems or habitat

level systems (Figures 3.6a-c). I assume that each system at the landscape scale is occupied by one forager group and this group distributes harvest effort evenly among the nine systems at the habitat scale in a given year. This assumption holds population density constant and means that the only decision a forager has to make is where to locate in space and time and, thus, the sequence in which harvest effort is devoted to each habitat level system. In traditional anthropological terms this sequencing process is called scheduling (Flannery, 1968; Jochim, 1976). I assume that all other potential parameters in each system at the landscape scale are constant as well, except productivity (r). The landscape level system in Figure 3.6a has a high value of r , 3.6b a moderate value and 3.6c a low value of r . Each landscape is composed of pictures that illustrate how the probable system states of forager-resource systems at the habitat scale vary as the net productivity-to-population ratio (r/p) of the landscape changes. Each figure contains four elements. These elements and associated assumptions are:

1. A hypothetical time series graph that illustrates the change in the aggregated r/p ratio of the landscape (the dashed black line), for an average year (an interval of 52 weeks). Holding population density constant, the gray shading around the dashed line represents the inter-annual coefficient of variation around the mean aggregated r/p ratio over a time interval of 50 years. I assume that the aggregate r/p ratio changes intra-annually based on external divers, like seasonal changes in temperature and inter-annually due to atmospheric dynamics.
2. Each time series graph contains a solid red line and a dashed red line. The solid red line denotes the aggregate r/p ratio on the landscape at which every forager-resource system at the habitat scale is vulnerable to a critical transition. That is, when the dashed black line is below the red line, all nine forager-resource systems at the habitat scale are characterized by two potential stable states, the productive and degraded

attractors. The dashed red line marks the r/p value at which all nine forager-resource systems at the habitat scale are characterized by the globally resilient, degraded attractor.

3. Each time series graph is paired with a set of four snap shots of the landscape at four short segments of time.
4. The pie charts visually represent the vulnerability of each of the nine systems at the habitat scale to a variance induced critical transition. The black indicates the probability $p(e_i)$ that a system will experience a negative critical transition if hit by a shock of some kind; $p(e_i)$ is the average of all potential shocks that might hit a system, again, assuming an equal distribution of harvest effort.

Figure 3.6a illustrates a with a very low degree of uncertainty. In this system, it really does not matter how the forager sequences their allocation of effort to each system at the habitat scale because each local system is globally resilient and will always converge on a productive attractor. Please note, as the dashed black line in the time series graph approaches the solid red line, forager-resource systems at the habitat scale might become vulnerable to a negative critical transition. In Figure 3.6a, this does not occur, on average. However, in years where the r/p ratio is below the mean, a few of the nine systems at the habitat scale may become vulnerable to a negative critical transition. In general, then, this landscape is characterized by the globally resilient, productive attractor (analogous to Figure 3.3a). In terms of real hunter-gatherer SES, another way to conceptualize Figure 3.6a is in terms of the TEK that foragers draw on to locate in space and time to access and harvest resources; TEK is sufficient for choosing where and when to expend foraging effort in virtually any sequence that foragers would like. It is unnecessary for a forager to process information and update their TEK to discover and estimate the future vulnerability

of systems at the habitat scale to a negative critical transition because all nine systems are globally resilient.

Figure 3.6b illustrates a landscape in which meeting γ is more uncertain and this requires foragers to find a strategy for sequencing their distribution of foraging effort that reduces uncertainty. On this landscape, each system at the habitat scale is susceptible to a negative critical transition during a well defined annual interval. The susceptibility of each localized system to a negative critical transition varies with the intrinsic rate of resource growth (r_i) in each habitat. The probability $p(e_i)$ that a shock will generate a negative critical transition into the degraded attractor is, thus, heterogeneous across systems at the habitat scale. On the landscape summarized by Figure 3.6b, there are now good and poor strategies that foragers might choose to secure γ and avoid localized negative critical transitions. To develop the best possible strategy, foragers must discover from an assessment of the state of the system and past experience of potential shocks, the $p(e_i)$ associated with each forager-resource system at the habitat scale. In short, the benefit of processing information on the probable future states of forager-resource systems at the habitat scale increases from Figure 3.6a to 3.6b, but processing information also costs time.

Foragers must invest time in collecting and processing information to make accurate estimates about the risk of experiencing a negative critical transition in any of the nine forager-resource systems at the habitat scale. Holding population density constant at 1 forager, the ability to make accurate predictions, should depend on the predictability of the r/p ratio from year-to-year driven by inter-annual changes in moisture and temperature. As the coefficient of variation from the mean r/p ratio increases, foragers would have to spend more time attempting to measure the current state of the systems at the habitat scale to make inferences about the probable future states of these local systems. This would stress the updating capacity of foragers' TEK because the higher the coefficient of variation, the more random actual critical transitions would appear from year-to-year. On the simplified

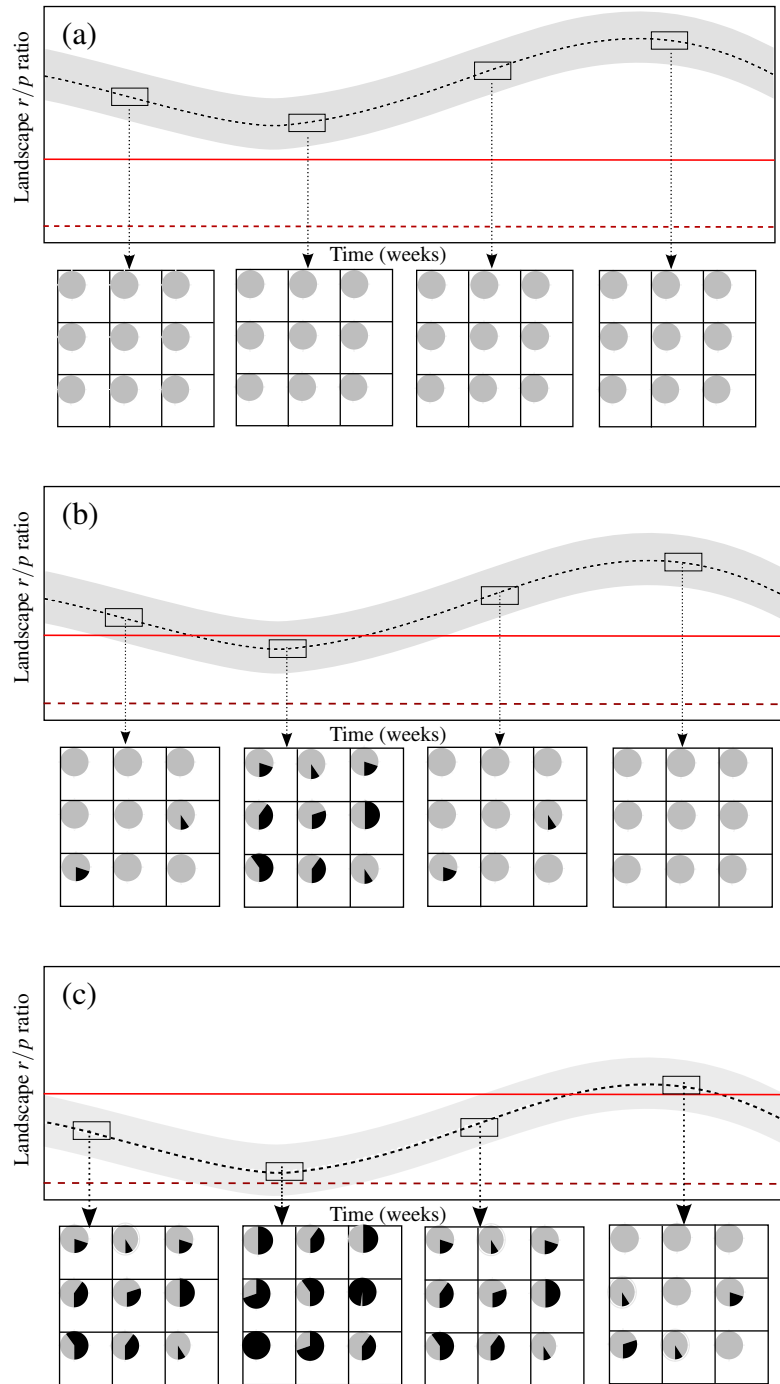


Figure 3.6: Conceptualize forager-resource systems at the landscape scale. Each landscape is composed of nine forager-resource systems at the habitat scale. In all three pictures: the top graph illustrates the r/p ratio over time on the landscape. The black shading indicates the probability of a negative critical transition, $p(e_i)$ for each system at the habitat scale. No black shading is equivalent to $p(e_i) = 0$.

landscape described by Figure 3.6b, when the red line is crossed, the C-D gap of foragers is controlled by external inputs (like inter-annual variation in rainfall). The higher the coefficient of variation, the greater the C-D gap because the difficulty of estimating $p(e_i)$ from year-to-year also increases.

Again, in terms of TEK in real hunter-gatherer SES, Figure 3.6b represents a landscape in which there are periods of time during an average year that TEK is potentially insufficient to locate in space and time to harvest resources. But, if these periods are predictable, then foragers can plan ahead. For example, if the spatial location of the most and least vulnerable systems at the habitat scale are always the same from year-to-year, foragers could monitor the biophysical conditions of the environment and plan ahead to serially move from the most to least susceptible systems, using the least susceptible systems as “fall back” habitats (Gould, 1991). Again, however, this strategy depends on the ability of individuals to discover and accurately predict the spatial distribution of $p(e_i)$ from year-to-year.

Figure 3.6c illustrates a landscape where r/p is, on average, consistently below the red line. As above, if the spatial distribution of $p(e_i)$ is constant, then foragers may experience localized critical transitions over time and discover the spatial distribution of $p(e_i)$ for an average year. However, this depends on the coefficient of variation associated with the mean r/p ratio. If the coefficient of variation gets too high, the temporal distribution of $p(e_i)$ will start to appear more random. With a higher coefficient of variation, in some years many systems at the habitat scale will have a 100 % probability of flipping into the degraded attractor; in other years, almost none of the systems would even be vulnerable to a negative critical transition.

The critical point is the inability of an individual to know, *from accumulated and transmitted experiences*, which attractor is likely to characterize a given forager-resource system at the habitat scale at any given time. As the coefficient of variation goes up, previous ex-

periences used to establish the “prior probabilities” that any of the nine systems at the scale of the habitat will experience a negative critical transition become meaningless.

In sum, Figures 3.6a to 3.6c illustrate two points. First, as the r/p ratio of a landscape declines past the red line threshold, foragers must process more information on the current state of forager-resource systems at the habitat scale to compute the probable future states of habitats. Second, as the r/p ratio of a landscape declines past the red line threshold, the prior knowledge (i.e., already accumulated body of TEK) becomes more irrelevant as the coefficient of variation from the mean r/p ratio of a landscape increases. An increase in the coefficient of variation will increase the likelihood that foragers poorly estimate $p(e_i)$ and end up, temporarily, harvesting food in a system at the habitat scale that appears to have a low likelihood of a negative critical transition but ends up in the degraded attractor. As noted, these dynamics occur holding population density and the distribution of harvest effort among habitats constant on a landscape. The only decision process that foragers have to make is the sequence of locating in space and time to distribute harvest effort. Even with these simplifying assumptions, the information processing load and the potential to incorrectly assess the risk of a negative critical transition are very sensitive to environmental variation once the r/p ratio of a landscape crosses the red line. The complexity of devising harvest schedules increases even more dramatically if we add more foragers to the landscape.

At this point, let’s reconsider Figure 3.6c. Now imagine that there are two foragers on the landscape (adjust the net productivity of the landscape up so that the mean r/p ratio remains the same). Now with two foragers, the spatial distribution of $p(e_i)$ has the potential to vary considerably from year-to-year. As long as the foragers closely coordinate the spatial location of their harvest action, the spatial distribution will remain consistent. The maintenance of coordinated movement requires time and effort, however. If movements between systems at the habitat scale are not coordinated by agreed upon rules, then each

forager will have to monitor the other to estimate the spatial distribution of $p(e_i)$. Adding population density, even if the mean r/p is the same, requires individuals to increase their investment in processing information to estimate the spatial distribution of $p(e_i)$, unless individual foragers engage in collective action to coordinate movement, which also costs time.

Let me end this discussion by providing a concrete example of the kind of processes described above. In their study of the role of information in Kua foraging strategies, Hitchcock and Ebert (2006:146-147) state:

“prior to the seasonal breakup of hunter-gatherer groups, the localities to be occupied by various family units were surveyed. The resources available in the area to which people might move were assessed carefully, as were the current states of occupancy, use and sentiments about resource sharing among groups that had rights to that area. Once this process was complete, the relative advantages and disadvantages of the alternative places were exhaustively discussed prior to reaching a consensus on what options should be perused.”

This passage illustrates the central importance of information processing to plan out a sequence of movements in space and time to gain access to resources. The argument that I use Figure 3.6 to demonstrate is that once the r/p ratio of a landscape crosses the red line, this scout, discuss and move strategy is stressed. The emergence of multiple stable states in many habitats both makes the time necessary to scout and discuss where to move next longer *and*, depending on how unpredictable shocks are that hit a resource base, makes this process of decision making less effective. People make a decision about which habitat it is best to move into, but end up in the degraded attractor. This occurrence at the scale of habitats is a signal that drives foragers to adopt strategies for reducing this possibility.

The Uncertainty Reduction Hypothesis

The uncertainty Reduction Hypothesis (URH) has two parts. First, the evolution of foraging strategies in hunter-gatherer SES occurs when foragers attempt to reduce the uncertainty associated with finding a sufficient level of food on a landscape. The uncertainty is controlled by the r/p ratio of a forager-resource system and the scale of a landscape composed of many systems at the habitat scale. Once this ratio passes a critical threshold, all of the forager-resource systems at the habitat scale in which individuals might participate are susceptible to a negative critical transition. In this social-ecological context, local negative critical transitions occur at some rate determined by the distribution of people on the landscape and variation in the climate drivers of net productivity, like temperature and rainfall. The development of a critical transition rate in systems at the habitat scale acts as a kind of “signal” to individual foragers that their body of TEK used to schedule where to locate in space and time is “out of whack.” The risk of a critical transition between a productive and degraded attractor may stimulate punctuated adaptation on the part of individual foragers; this adaptation, in turn, would create a new SES with novel feedback loops that condition the future coevolution of individuals and resources. In sum, localized commons dilemmas are generated when the r/p ratio of a landscape approaches and crosses a threshold. This situation creates an environment in which foragers try out strategies for reducing the uncertainty associated with experiencing localized negative critical transitions and the winnowing processes of selection and/or copying lead to a reorganization of human-environment relationships or the abandonment of a landscape (i.e., emigration or extinction on said landscape).

The second part of the URH builds on two additional generalizations. 1) Forager-resource systems form a nested hierarchy in space and time (Figure 3.7) because ecosystem structures form a nested hierarchy (Odum and Barrett, 2002; Holling, 1992; Peterson et al.,

1998) in space and time. Due to the hierarchical structure of ecosystems, human foragers face a decision hierarchy regarding how to allocate effort (Orians, 1980). At the smallest and fastest scale is the individual resource and food choice, next is the patch and patch choice, then the habitat and habitat choice and so on. There are two important consequences of this hierarchy.

First, as a forager moves up the decision hierarchy, the greater the number of ecological and social dynamics that individuals must deal with to make decisions thus, the greater the information processing load for an individual to make decisions. The logic behind this statement is quite intuitive. If you are in a patch of raspberry bushes, all you need to decide is which raspberries are ripe and which are not. However, at the habitat scale, you must know what patches of food (raspberries, wild onions, etc) comprise each habitat, when those patches are in season, and who else might want those resources. Second, as Holling (1992) describes, as one moves up the hierarchy, one encounters larger ecosystem structures. A patch is clump of raspberry bushes and associated organisms. A landscape encompasses a whole forest and is a mosaic of habitats. The point here that disturbance dynamics, like fires, or dry periods, occur faster than the dynamics of change in ecosystem structures (Holling, 1992:478; Peterson et al., 1998). This is important because large ecosystems modulate variation in fast disturbance dynamics and “make their own weather” (e.g., Hare and Ritchie, 1972; Zeng et al., 1999). If foragers use enough space (i.e., have a pool of potential forager-resource systems at the landscape scale), they gain the benefit that ecosystem structures modulate variation in fast disturbance dynamics, but individuals have to process more information to take advantage of this benefit. This information load trade-off, in part, is why Holling (1992) expects non-human foragers to use rule’s of thumb high up on the hierarchy and make more optimal decisions lower on the hierarchy.

2) As illustrated in Figure 3.6, when the r/p ratio of a landscape crosses a critical threshold, many forager-resource systems at the habitat scale become vulnerable to shocks

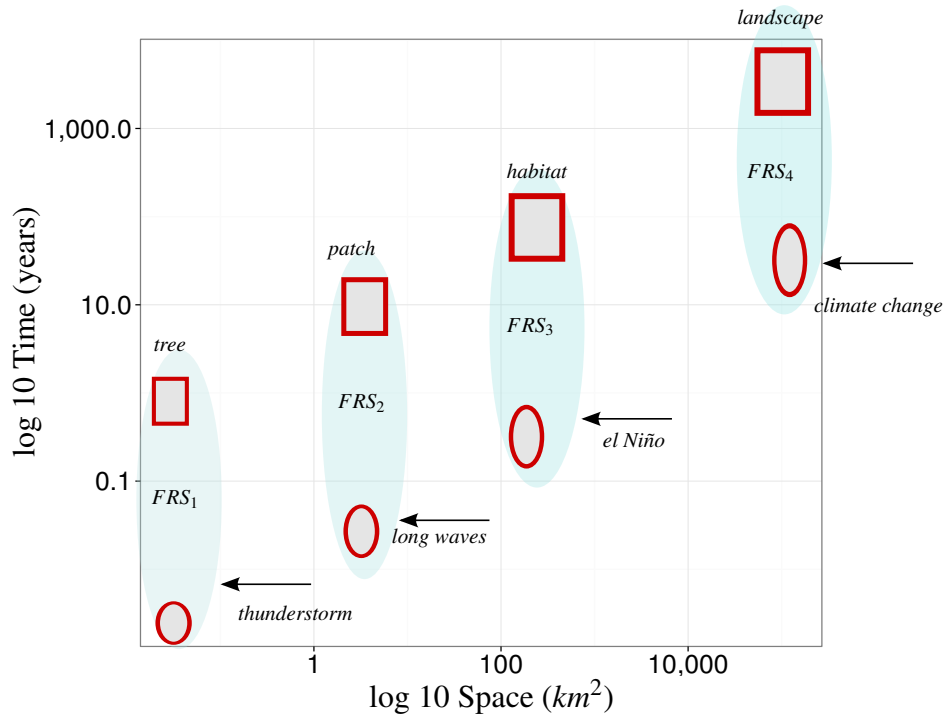


Figure 3.7: Nested hierarchy of ecosystems, decisions and forager-resource systems after Peterson et al. (1998). The rectangles are ecosystem structures. The circles are decisions associated with each ecosystem structure. The blue shaded ovals represent forager-resource systems (FRS) operating at different scales of space and time. The arrows illustrate the kinds of disturbances that hit a FRS.

(e.g., temperature or rainfall extremes) that can generate a negative critical transitions. As a consequence, large scale ecosystems no longer modulate environmental variation in any meaningful way and processing information on the vulnerability of habitat level systems is potentially costly and fruitless. The signal that this situation has arisen is the experience of localized negative critical transitions. The more unpredictable the variation in physical inputs and population movements on a landscape, the more difficult it is for foragers to estimate the risk of negative critical transitions in systems at the habitat scale, and, thus, uncertainty associated with establishing a productive foraging regime increases. As uncertainty increases, foragers have two options: a) migrate to a new landscape or b) reduce the scale of space and time at which they use a landscape. Option b) has the benefit of reducing the amount of information that foragers must process to make decisions about where and

when to locate to harvest food, but also has the cost of concentrating harvest effort on a few habitats, which might further decrease the resilience of the productive foraging regime in those systems.

I propose that when migration is not an option, selection and copying pressures favor strategies that simultaneously reduce the scales of space-time over which decisions are made to locate in space and time (i.e., decrease an individual's information processing load) and dampen the susceptibility of systems at the habitat scale. This means strategies that reduce the chances that variation in productivity caused by fluctuations in temperature, rainfall, and/or population movements are favored. There are two important strategies that fit this bill: the production of food to increase r and ownership institutions that decrease the costs of interference defined in the hunter-gatherer SES model by m . The configuration of these different means for constructing a niche should result from the sum of selection and copying pressures that act on a population of hunter-gatherers in specific environments.

Expectations

Based on the logic of the URH, I expect the following general empirical patterns to manifest in actual hunter-gatherer SES. First, the selection of land ownership" rules that formally define who, when and where resources are accessed is favored in environments where hunter-gatherer SES cross a critical r/p ratio and variation in the climate drivers of productivity is relatively predictable. In human social groups the costs associated with a owning a territory are potentially determined by the costs necessary to coordinate the harvest of resources and defend territories from intruders (i.e., social transaction costs) (Willems et al., 2013). The recognition of ownership by individuals likely creates benefits for individuals that outweigh the costs when many habitat level systems on a landscape are vulnerable to a negative critical transition. Ownership rules should mitigate the need for individuals to invest time to monitor where and when other foragers harvest resources on a landscape,

which is costly when many habitats on a landscape are characterized by multiple stable states. Further, by regulating the amount of foraging effort that can be applied in systems at the habitat scale, individuals cooperating in groups to regulate the movement of people should obtain a more predictable supply of resources. I should note, however, that developing rules and norms of ownership requires some individuals to incur potentially significant costs, like ceding control of a productive location to an owner or incurring bodily injury in defense activities. Based on the URH, I expect that the benefits of collective action necessary to develop ownership institutions outweigh the costs when foragers need to reduce the uncertainty generated by the uncoordinated movement of population in and out of forager-resource systems.

Second, the selection of strategies that modify ecosystems to produce food is favored in environments where hunter-gatherer SES cross a critical r/p ratio and variation in factors like rainfall or temperature, unpredictably shock the productivity of forager-resource systems and generate negative critical transitions. In effect, food production raises the average r/p ratio of the systems at the habitat scale. In turn, this would have the effect of decreasing the susceptibility the forager-resource systems at the habitat scale to negative critical transitions. For example, in the ethnographic record, some foragers are known to plant wild” species of plants and systematically burn vegetation (Anderson, 2005; Gould, 1971; Keeley, 1995; Mills, 1986). Both of these behaviors are different ways of modifying an ecosystem that can increase the productivity of food. For example Shipek (1981:298) describes how Kumeyaay foragers managed “wild” plants to increase the productivity of desired species,

“Burning was followed by broadcasting seeds for next year’s crop.... In addition to seed, families ‘planted gardens’ of annual and extending grass areas by broadcasting perennial greens, seeds, roots, and cactus cuttings in clearings made near their homes.”

The key process is the management that individuals exert over the dynamics of vegetative communities. This, in turn, may decrease the vulnerability of foragers to unpredictable environmental variation that can generate a negative critical transition. The secondary adoption of staple domesticated plants by foragers is a potential alternative for producing food when foragers face the risk of resource shortfalls generated by the presence of multiple stable states across multiple scales of forager-resources systems.

In chapter 5, I challenge the expectations listed above with large ethnographic and environmental data sets. As developed in chapter 1, the whole point of the modeling exercise undertaken in this chapter has been to begin to understand how feedbacks between foragers and resources across different scales and levels of organization might generate evolutionary change in hunter-gatherer SES. This exercise provides a more informed context for conducting large scale ethnographic comparisons and identifying general principles of subsistence change.

Conclusion

I began this chapter by asking: given the open-access nature of resources among hunters and gatherers, (1) how do changes in the productivity of resources and population density affect the robustness of food output in a forager-resource system to potential shocks, and (2) how might the global structure of the system determine the selection of foraging strategies by individuals? The answer to question (1) is really important because it suggests that feedbacks between individuals and resources lead to non-linear dynamics in a highly general forager-resource system. Given the assumptions of the model, either medium-term declines in the productivity of resources (r) or increases in population density (p) result in the emergence of alternative stable states. One of the stable states is productive in that modeled foragers can meet their energy goal of γ in a minimum amount of time; the other stable state is degraded in that foragers can only meet their basal metabolism c . The pres-

ence of multiple stable states precipitated by crossing critical thresholds of productivity and/or population density makes question (2) quite interesting. When the productive and degraded attractors are simultaneously potential long-run stable states, the global structure of the system dictates that foragers face a stochastic common pool resource dilemma. The aggregate effect of individual foragers working to achieve their energy goal opens every forager up to the risk of not achieving their energy goal due to a negative critical transition from the productive to the degraded attractor.

Of course the potential common pool resource dilemma is of little consequence if foragers can simply move around to alternative forager-resource systems where the risk of a negative critical transition is irrelevant. However, in a large scale forager-resource system composed of multiple smaller scale forager-resource subsystems in which foragers risk a negative critical transition, the resilience of the productive attractor, I propose, affects the robustness of the strategies that individuals use to secure food in a variable environment. Figure 3.8 illustrates the general feedback dynamics that I propose drive the evolution of foraging strategies in hunter-gatherer SES. Variation in factors such as rainfall and temperature perturb the resource base from which foragers harvest food. Foragers harvest resources and obtain an energy output and compare the output with their underlying preference/goal. Based on the energy output, foragers update their TEK, which they use to make decision about how to secure food in the future. Critically, when many forager-resource systems at a habitat scale nested on a landscape are vulnerable to a negative critical transition, foragers face uncertainty associated with their ability to secure resources. The uncertainty is a function of the external climate variation that affects the productivity of systems at the habitat scale and the movement of foragers between systems because harvest effort makes local systems more vulnerable. Foragers may be able to reduce uncertainty by processing information and discovering the strength and frequency of variations that cause negative critical transitions in systems at the habitat scale. However, as climate variation and for-

ager movements become more unpredictable, such information processing becomes more costly and potentially fruitless.

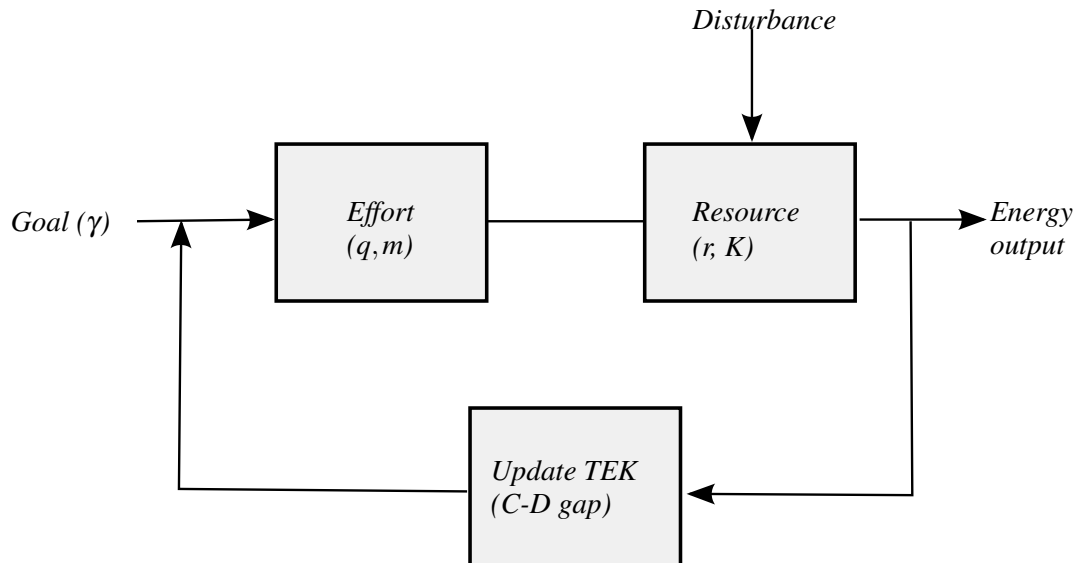


Figure 3.8: System diagram of the hunter-gatherer SES that illustrates feedback processes.

In terms of the model, there are two strategic options that foragers might select to make their energy target more robust to climate variation and population movements when every local system is vulnerable: (1) invest effort or adopt resources that increase the productivity of a resource base or (2) invest in collective action that regulates the distribution of foraging effort across local systems. I have argued above that option (1) is adopted when climate variation that determines inter-annual changes in the productivity of resources is too unpredictable. When variation becomes too unpredictable, the best strategy is to alter ecosystems and attempt to boost the mean productivity of resources. This should reduce the vulnerability of systems to shocks and increase the robustness of the food output of individuals to shocks. I argue that option (2) is selected when variation in climate is relatively predictable. Of course both options may be selected simultaneously.

An archaeological implication

Frequently, archaeologists turn static foraging models into dynamic models by qualitatively assuming feedbacks between foragers and resources (e.g., Bettinger, 1991; Stiner et al., 1999). This is a good thing. This intellectual strategy recognizes that archaeological data are often organized to study change over time and dynamic models are needed to study change over time. The recognition of feedbacks between, in the language of chapter 2, environmental structures implicitly recognizes that foragers operate in a forager-resource system. The fact that feedbacks may cross-cut levels of organization introduces the possibility that non-linear dynamics characterize forager-resource systems. If this is indeed the case, archaeology needs the intellectual tools of systems thinking and the mathematical tools of dynamical systems theory to understand the foraging ecology of individuals. This is not a new revelation per se, but the application of dynamical systems to archaeological problems really remains in its infancy. We have much to learn about the coevolution of individual decision making and the structure of social-ecological systems.

A clear next step in the modeling that I have presented in this chapter is to formalize the conceptual model developed in conjunction with Figure 3.6. For anyone familiar with agent based models, I think the potential to transform the baseline hunter-gatherer SES into an agent based model is relatively obvious, and there are potentially good reasons for doing so. The point that I would like to make here, however, is somewhat different. In general, the application of dynamical systems to archaeological questions is sorely lagging the application of computational models or agent based models. There are no doubt a number of reasons for this, but one potential reason is the argument made that agent based models are epistemologically superior to dynamical systems of differential equations for archaeological research because they are bottom up rather than top down representations of SES (Kohler and Gumerman, 2000). There are intellectual trade-offs associated with

each type of modeling. Agent based models have the potential to capture more realism but are difficult to analyze and the results are applicable to a more narrow array of settings. The analysis of formal models is more robust to analytical uncertainty and generate results that are useful for making generalizations across many social-ecological contexts, but the results of such models may be so general that they boarder on trivial. These trade-offs are why model building is as much an art as a science. Our challenge is to balance the costs and benefits of the use of these tools. This balance facilitates our ability to understand the dynamics of very complex processes and make statements about the processes that drive the evolution of SES (see for example Barton et al., 2011).

Onward

The challenge ahead in this dissertation is to evaluate the URH with ethnographic data. As I discussed in chapter 1, the model analysis and URH facilitates the deductive analysis of cross-cultural data. However, simply evaluating the fit of the URH with data is not enough. Almost every hypothesis purported to explain the dynamics of complex systems garners some modicum of support in actual data sets. Does this mean that the hypothesis is correct? Of course not. To most productively make use of broad-scale ethnographic comparisons, I suggest that ethnographic data should be used to evaluate the relative merit of multiple competing hypotheses. The next step is to develop an alternative hypothesis to the URH. This is what chapter 4 is all about.

Chapter 4

THE SOCIAL OPPORTUNITY HYPOTHESIS

One of the goals of this dissertation is to help build a corpus of knowledge useful for understanding the processes that cause hunter-gatherer SES to change, with specific emphasis on the social-ecological contexts that favor the adoption of food production. The approach that I advocate is the use of dynamic models to develop hypotheses that explain variation in the foraging strategies documented among ethnographically recorded societies. In turn, the analysis of large ethnographic and environmental data sets to evaluate these hypotheses generates a set of first principles useful for explaining major transitions in hunter-gatherer subsistence documented in the archaeological record. This strategy, however, depends on multiple competing hypotheses (Chamberlin, 1931). Simply creating one hypothesis is not enough. Almost any reasonable hypothesis will find a modicum of support in data sets that describe the attributes of complex systems (Johnson and Omland, 2004). The idea of evaluating multiple competing hypotheses is basic scientific epistemology, but, in practice, most of us tend to evaluate one model, find support and then stop (Keeley, 1995). The point of this chapter is to build an alternative, though not necessarily mutually exclusive, hypothesis to the URH.

In this chapter, I modify the baseline hunter-gatherer SES so that, as a byproduct of foraging effort, the productivity (r) of a forager-resource system increases. This modification formalizes the idea that the harvest strategies of foragers actually increase rather than deplete the abundance of food in a system. The chapter is divided into three sections. First, I describe how the augmentation of resources is incorporated into the baseline hunter-gatherer SES model. Second, I investigate the effect of foraging strategies that augment the abundance of food on the resilience of forager-resource system states and the robustness

of foragers' non-subsistence time budgets to climatic and demographic shocks. Finally, I leverage the knowledge gained from my analysis of the modified hunter-gatherer SES model to build a multi-level selection argument for the coevolution of foraging strategies and a resource base. This argument builds on the modified model of economic defensibility proposed by Smith (2012) and Zeder (2012). As discussed in chapter 2, my work buttresses the potential short-comings of Smith (2012) and Zeder's (2012) argument by i) integrating the affect of population density on foraging strategies and ii) eliminating the need to assume that foragers make decisions based on expected gains in the long-term. A final insight that emerges from my work is that individual foragers might be more sensitive to variation in their non-subsistence time budgets than variability in their ability to achieve a desired level of energy per se. This illustrates how our assumptions about the preferences of individuals fundamentally alters how we explain coevolutionary processes. Understanding the contexts in which one preference or another forms the basis of decision making is an important direction for future research to which archaeologists should begin to contribute.

Incorporating the Augmentation of Biomass into the Hunter-gatherer SES Model

The basic dynamics of the baseline hunter-gatherer SES are described by a set of coupled differential equations:

$$\dot{x} = G(x) - H(x, e) \quad (4.1)$$

$$\dot{e} = D(x, e). \quad (4.2)$$

This story simply states that a change in the biomass of resources is the growth of resources less the total harvest of resources by foragers. The effort invested in the harvest of resources depends on a decision function, which depends on the level of biomass and effort at time t . One of the basic assumptions that underlies the behavior of this system is

that foragers attempt to satisfy a sufficient level of energy, γ in a minimum amount of time. This assumption is critical to consider if foragers augment the production of biomass on a landscape.

The augmentation of biomass production requires effort (i.e., time) and may entail a trade-off between the time spent to augment the productivity of resources and the actual harvest of resources. To modify the model, the most basic assumption possible is made. This assumption is that resource augmentation occurs as a byproduct of the harvest strategy of foragers. For example, in their pursuit of sand lizards, Martu foragers of the Australian western desert burn off vegetation, mainly economically unimportant spinifex grasses, to locate and collect lizards. This burning has the consequence of reallocating nutrients and sunlight to plant species that recolonize the burned area and increases the quality of available habitat for lizards; this, in turn, increases the density of lizards in foraging areas harvested by the Martu (Bird et al., 2005, 2008). Under the assumption that augmentation occurs as a byproduct of time spent in the harvest of resources, effort invested to augment the productivity of resources does not require a trade-off in time allocation. However, the elaboration of strategies of food production, like weeding or water control, likely would require trade-offs in time investments.

In the baseline hunter-gatherer SES model, the growth or resource biomass, $G(x)$ is defined by the logistic function,

$$G(x) = rx\left(1 - \frac{x}{K}\right) \quad (4.3)$$

where r is the intrinsic rate of biomass growth and K is the growth limiting effect of competition (carrying capacity) on the resource base. To augment the production of resource biomass foragers can either manage ecosystems to increase r , K or both parameters simultaneously. Management is a matter of manipulating disturbance-succession dynamics

to reallocate flows of nutrients, solar energy and water from undesired to desired species (from a human forager's perspective) and/or the dispersal of species within an ecosystem.

State Variables	Definitions	Default Values
$x(t)$	The density of resources (biomass/area) at time t	varies
$e(t)$	The harvest effort (workdays/day) at time t	varies
Parameters	Definitions	Default Values
r	The mean intrinsic rate of resource growth (yr^{-1})	0.3
r_{max}	The maximum intrinsic rate of resource growth for a given harvest regime (yr^{-1})	0.5
K	The mean carrying capacity for resources (biomass/area)	1
q	The harvest coefficient (biomass/effort/standing biomass)	0.2
p	The population density of foragers	0.7
γ	The energy target per forager	0.05
l	The baseline processing coefficient (Kcals/unit biomass/effort/forager)	1
m	Interference (Kcals/biomass/effort/forager)	0.7
c	Basal metabolic requirements (Kcals/time)	0.02
α	The biomass to energy conversion coefficient	varies
α_1 and α_2	Relative weights given to harvest per unit effort and energy deficits	0.1 and 4
β	The sharpness of the transition between valuing energy deficits over harvest per unit effort	3
\bar{E}	The upper limit of total effort at which harvest activities impact the growth of resource biomass	2.5
\underline{E}	The minimum level of total effort required for harvest activity to impact the growth of resource biomass	0.1
z	The coefficient of resource augmentation	0
a	The proportion of foragers that adopt resource augmenting strategies	0

Table 4.1: Model state variables and parameters with resource augmentation

To capture the effect of resource augmentation, I assume that foraging activities, such as burning off vegetation, increase the growth rate of a resource base (r). As noted above, the augmentation of r is modeled as a byproduct of the effort put into the harvest of resources; therefore, foragers in the model do not face time allocation trade-offs between time invested in food production vs. the harvest of resources. The primary variable, then, that determines the degree of resource augmentation is the total harvest effort exerted by foragers. Total

effort, E is simply $E = pe$; where p is population density and e is the effort exerted per forager at time t . Equation 4.4 describes the augmentation of a resource base's growth rate as a function of total effort:

$$A(r) = \begin{cases} r & E \leq \underline{E} \\ r + az(E - \underline{E}) & \underline{E} < E \leq \overline{E} \\ r_{max} & E > \overline{E}. \end{cases} \quad (4.4)$$

Where \underline{E} and \overline{E} are critical total effort thresholds that determine whether or not harvest activity has an affect on the growth rate of resources. The parameter z describes human modification of the environment. This coefficient defines how effectively the harvest strategies of foragers enhance the flow of resources in a system. It is important to recognize that z is a function of the strategies that foragers use to harvest resources. For example, in the case of sand lizards mentioned above, burning is not a requirement of catching sand lizards; the harvest of lizards could be done without burning. In the case of non-burning, the simple search and find strategy would not augment r as effectively as the strategy of burn, search and find. The parameter a is the proportion of foragers within a population that adopt harvest strategies that augment the productivity of resources. The parameter a is constrained by $0 \leq a \leq 1$. When $a = 1$, every forager in a system engages in harvest strategies that augment r .

Equation 4.4 simply states that below a minimum total effort threshold, the harvest activities of human foragers have no impact on the growth rate of a resource base. This means that when population density is extremely low, harvest activities, like burning, have no measurable impact, on average, on the growth rate of useful resources. Once a minimum threshold of total effort has been crossed, the augmented growth rate of a resource base increases as a linear function of total effort up to the maximum effort threshold, \overline{E} . At the maximum effort threshold, a landscape has been so transformed, at a given level of

technology, that harvest effort no longer increase the growth rate of resources. This is r_{max} for a given resource augmentation regime. Thus, the growth of resources in the hunter-gatherer SES model is now simply

$$G(x) = A(r)x\left(1 - \frac{x}{K}\right). \quad (4.5)$$

The Effect of Biomass Augmentation on Forager-resource System States

Figure 4.1 illustrates phase-planes of resource biomass (x) plotted against foraging effort (e). Each plot illustrates a phase-plane in which population density is held equal at 0.8 for three different values of z , while all other parameters are held equal at the default values specified in Table 4.1. As discussed in chapter 3, for the default parameter values, a population density of 0.8 results in the simultaneous presence of the productive and degraded attractors. When these two attractors characterize the global structure of the hunter-gatherer SES, foragers face the risk of not achieving the resource flow that they desire (γ). As with Figure 3.3 in chapter 3, the orange curve describes all of the points in the system for which foraging effort is at equilibrium ($\dot{e} = 0$) and the green curve all of the points at which resource density is at equilibrium ($\dot{x} = 0$). Where the two curves meet, the system is at equilibrium (i.e., \dot{e} & $\dot{x} = 0$). All stable equilibria are marked by gray circles and unstable equilibria by squares.

Two observations are revealed by Figure 4.1. First, as the effectiveness or resource augmentation increases (z), the growth rate of biomass increases and foragers spend less time in the harvest of resources at the productive attractor compared with foragers who do not augment the production of biomass. For example, in Figure 4.1a where $z = 0$, equilibrium foraging effort (\bar{e}) is equal to 0.68 at the productive attractor, while $\bar{e} = 0.67$ at the productive attractor in Figure 4.1b and $\bar{e} = 0.65$ at the productive attractor in Figure 4.1c. Second, the parameter space (i.e., the window of vulnerability) in which two attractors are present

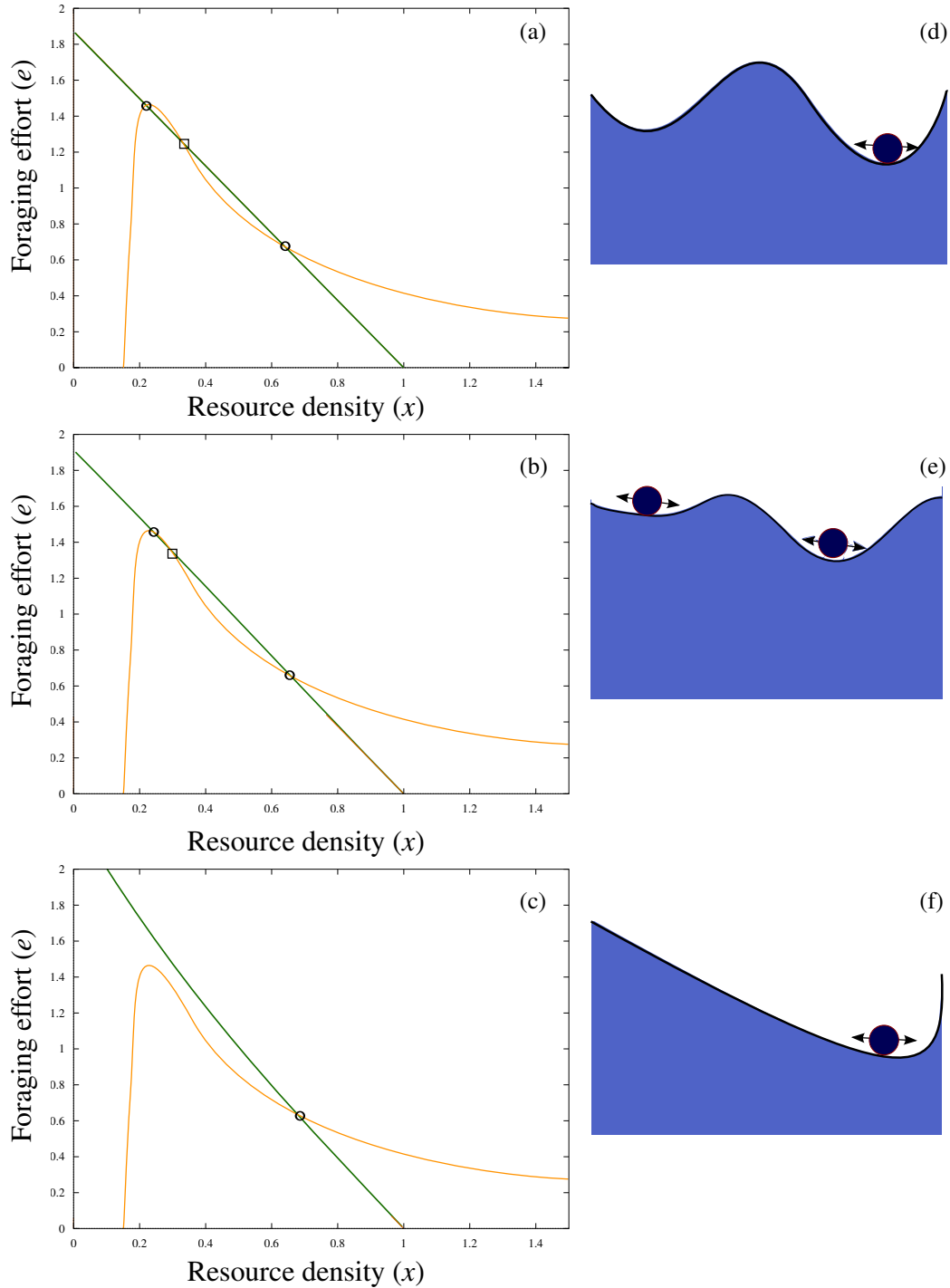


Figure 4.1: Phase plots of foraging effort against resource density. All parameters are held constant at default values except the ecosystem input reallocation coefficient (z). a- $z = 0$; b- $z = 0.01$; c- $z = 0.04$. The circles highlight stable attractors. The squares highlight unstable attractors. Each phase plot is paired with a stability landscape (a-d; b-e; c-f) that provides a metaphor for the stability of the attractors portrayed in each phase plot.

and foragers face the risk of a negative critical transition is potentially eliminated by the augmentation of biomass. For the parameters specified in Figure 4.1, once the coefficient of resource augmentation (z) crosses a threshold of approximately 0.03, the productive attractor is the only possible long-run system state in the model.

Overall, Figure 4.1 demonstrates that an increase in the effectiveness of biomass augmentation (z) 1) increases the time available for individuals to engage in non-subsistence activities (holding all else constant) and 2) reduces or even eliminates the possibility that environmental variations generate a negative critical transition. Even though the overall decrease in equilibrium foraging effort (\bar{e}) is relatively slight, even very small changes in z can have a qualitative effect on the global structure of the system. The augmentation of resources increases the resilience of the productive attractor and, as a byproduct, increases the robustness of γ to potential shocks that could decrease the availability of biomass and generate a negative critical transition into the degraded attractor.

Return time and variance in non-subsistence time

The URH (chapter 3) relies on the premise that non-subsistence time is a resource that foragers use to accommodate declines in the r/p ratio of a system. This implicitly assumes that foragers are willing to give-up non-subsistence time to achieve their energy target of γ . However, this assumption may not be correct. . The dynamics of the modified hunter-gatherer SES that includes augmentation suggests an alternative preference that we might consider as a fundamental preference of individuals in a generic, baseline hunter-gatherer SES.

Figure 4.2 illustrates the effects of population density and the augmentation of resources on the resilience of the productive attractor. The resilience of the productive attractor is estimated here by the return time of the system near the equilibrium. Return time refers to how fast a system returns to an equilibrium if perturbed. Following Pimm (1984), I quantify

return time as $\frac{1}{|\lambda|}$, where λ is the dominant eigenvalue of the equilibrium at the productive attractor. Please recall, in the real world, a system is constantly perturbed. Return time measures how quickly the interaction between foragers and resources will return to the long-run equilibrium after a system is hit by a shock. The longer it takes a system to return to equilibrium, the more variance that foragers would experience in their harvest of resources and foraging effort over time-scales shorter than the long-run equilibrium.

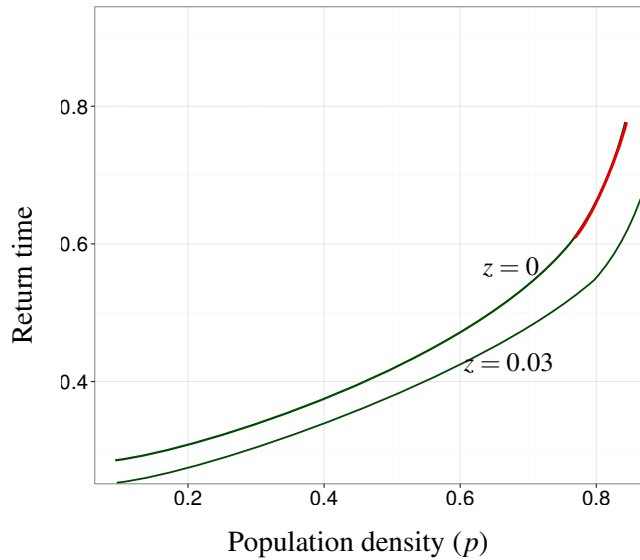


Figure 4.2: The effects of population density (p) and the coefficient of augmentation (z) on the return time of the productive attractor. The red portion of the $z = 0$ curve indicates the values of p where the system is vulnerable to a negative critical transition. All other model parameters are held equal at default values.

Figure 4.2 demonstrates that as population density increases the resilience of the productive attractor decreases and, thus, return time increases. This is an increasing non-linear relationship. An increase in z has the effect of decreasing return time per unit of population density. A subtle effect of increasing how well foragers augment a resource base, then, is that foragers are less sensitive to shocks that cause, at the scale of the model, variance in their harvest effort. Consequently, as z increases (holding all else constant) foragers would also experience less variation in their budget of non-subsistence time and might be able to convert this situation into future fitness gains because they can more easily plan ahead and

efficiently use time to find food and engage in non-subsistence activities. Foragers may, in fact, have a specific tolerance level of variance in non-subsistence time that they are willing to accept. Thus, foragers might have a fundamental preference for foraging strategies that minimize variance in their budget of non-subsistence time. This preference may lead to a different set of evolutionary dynamics than those described by the URH.

The Coevolution of Food Production, the Productivity of Resources and Territoriality

In this section, I use my understanding of the hunter-gatherer SES model to identify the social-ecological contexts that might favor the coevolution of food production, territoriality and increases in the productivity of resources. To do this, I make three basic assumptions. 1) Foragers have an underlying preference for minimizing variance in their budget of non-subsistence time. The basis of this assumption is that individuals with a predictable budget of non-subsistence time can convert time into fitness gains better than foragers with less predictable budgets of non-subsistence time. 2) Time is a finite resource, thus if an individual works harder to obtain γ , she necessarily gives up time that could be invested in non-subsistence activities (see Dunbar et al., 2009). 3) Foragers make decisions in a hierarchical matrix of ecosystem structures that scale in space and time. The patch is a homogeneous area of resources; a habitat is a larger area with multiple patches and a landscape is an area composed of many habitats. Each level of the hierarchy is described by a forager-resource system, with systems at each higher level aggregating many local systems from the next lowest level. Given these assumptions, the dynamics of hierarchically organized forager-resource systems can generate directional, multi-level copying/selection pressure for increasing investment in food production, territoriality and increasing resource productivity.

Figure 4.3 describes my multi-level selection argument. From left to right, Figure 4.3 describes how cross-level dynamics bridge the patch-habitat-landscape hierarchy to gener-

ate directional copying and transmission of foraging strategies that coevolve with resources. The fast dynamics of disturbances constantly shock a resource base at the lowest level of the hierarchy (most acutely at the patch). In response to these shocks, following Flannery (1985), I propose that foragers experiment with harvest strategies and discover the strategies that augment productivity and reduce negative deviations in the availability of biomass. For instance, burning off vegetation to look for small game increases the productivity of the game more than a simple search and kill strategy. In this example, individuals who systematically burn in foraging patches, increase the density of resources (x) within that patch, which increases the resilience of the patch level forager-resource system. As noted in the previous section, when z is free, an increase in the resilience of a forager-resource system at the productive attractor *also* reduces time spent foraging and variance in the non-subsistence time budget of individuals (e). I argue that at the patch level individuals who find harvest strategies that reduce variance in their budget of non-subsistence time are copied by other individuals (which increases a) because, as assumed above, individuals preference strategies that reduce variance in their non-subsistence time budget. This process is the $az \rightarrow x \rightarrow e$ feedback loop at the patch level illustrated in Figure 4.3.

The habitat level forager-resource system is an aggregate of many patch level forager-resource systems. Thus, an increase in the augmentation of resources in many patch level systems should scale-up and create an increase in the aggregate density of resources at the habitat level ($x_p \rightarrow x_h$). Following Smith (2012) and Zeder (2012), this increase in the density of resources should provide an incentive for individual to “own” and defend habitats from intruders because individuals need less space to find food and the costs of defense decline. This assumes that incentives to cooperate in the ownership of territory linearly scale-up from an individual to a social group. The consequence of the adoption of ownership, at first glance, may not be obvious. However, the dynamics of the hunter-gatherer SES suggest that institutions of ownership actually amplify the increase in resource density

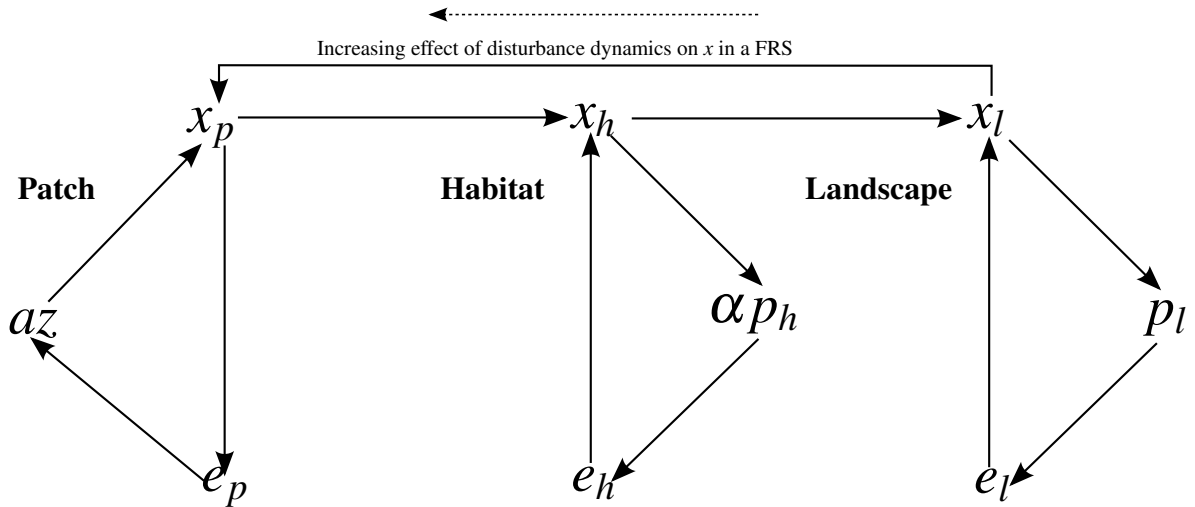


Figure 4.3: A schematic of the multilevel selection argument made in the text. Fast disturbance dynamics (e.g., inter-annual variation in rainfall) have a greater effect on x at lower levels in the forager-resource system (FRS) hierarchy.

cause by the adoption of strategies that increase z at the patch level ($x_h \rightarrow \alpha p_h$). One of the main components of the hunter-gatherer SES discussed in chapter 3 is α . This parameter defines competition for resources as $\alpha = e^{-mp}$, where e is the exponential; m is an interference coefficient that defines the cost of social interactions; and p is population density. A reduction in the interference coefficient of m reduces competition for resources and harvest pressure. The result is that the density of resources available per unit of population density actually increases as interference decreases (Freeman and Anderies, 2012). In short, ownership institutions should allow groups of foragers at the habitat level to increase the predictability of their non-subsistence time budget because ownership institutions increase the resilience of the forager-resource system at the habitat level ($\alpha p \rightarrow e \rightarrow x_h$) above and beyond increases cause by an increase in z .

Finally, the landscape level forager-resource system is a collection of many habitats, thus an increase in the resource density of habitat level systems should scale-up to increase the density of resources at the landscape level ($x_h \rightarrow x_l$). Again, the increase in resource density should make the productive attractor in the landscape scale forager-resource system

more resilient. And the consequence of more resilience is that the energy supply of foragers is more robust to potential perturbations and a consistent surplus of energy for individuals. This fact results in population growth and an expansion of forager population density in the landscape scale system, $(x_l \rightarrow p_l)$. In this way, landscape scale systems with many foragers who adopt strategies that augment resources at the patch level are more robust at the landscape level to shocks and should out compete landscape level systems with few foragers who adopt strategies that augment resources at the patch level. As noted in my description of model assumptions, however, resource augmenting strategies have an r_{max} where foraging effort, for a given strategy, no longer augments the productivity of resources. At this point, forager-resource systems across the hierarchy are “reset,” and z is no longer “free.” This means that beyond the critical threshold of \bar{E} , any additional increase in population density would necessitate that individuals reallocate time from non-subsistence activities to harvest resources, and this can deplete the resource base $(p_l \rightarrow e_l \rightarrow x_l)$, which feeds back down to the patch level $(x_l \rightarrow x_p)$.

There are two points that I would like to make here. First, this multi-level selection scenario takes time to unfold. Second, in the above scenario, food production coevolves with territoriality and increases the productivity of resources because it does not take time to augment a resource base (i.e, z is a byproduct of harvest effort). However, once r_{max} has been hit, the only way to improve z is for foragers to invest in food production strategies that have a cost in terms of time. Once the coevolutionary process has taken hold, the incentive is for individuals to invest in more elaborate forms of food production. This is because the combination of territoriality and increases in population density make abandoning food production very costly. Once population density gets high enough and groups have stable, owned territories, these conditions create an incentive to respond to decreases in the r/p ratio of a system at the landscape scale by investing in more elaborate forms of food production. Simple, the alternative of migrating somewhere else would only work if

empty landscapes were available. In short, once territoriality and low-level food production have coevolved, in part, because foragers preference maintaining a predictable budget of non-subsistence time, a kind of lock-in takes place where foragers are on path dependent trajectory of increasing investment the production of food.

Comparing landscape level systems: The Goldilocks zone

There are three caveats to the argument made above. First, if there are diminishing returns to the fitness benefit gained from a predictable budget of non-subsistence time, foragers may never experience meaningful increases in the variance of their non-subsistence time. As a consequence, individuals would have little incentive to copy other foragers who experiment with foraging strategies that boost z because those strategies would not affect variance in their budget of non-subsistence time. Second, if the r/p ratio of a hierarchy of forager-resource systems is incredibly low, foragers might, again, gain no benefit from adopting strategies that increase z . The reason is that the effect of biomass augmentation is not strong enough to increase the robustness of foragers' supply of energy by reducing the chances foragers end up in a degraded state. Finally, if the r/p ratio is too variable on a decade-to-century time scale due to climate variation, there likely would not be enough time for the multilevel selection/copying processes to generate a self perpetuating selective pressures for food production and territoriality. The reason for this is that drastic shifts between biophysical environments may generate a situation in which strategies that augment the production of food in one environment do not work when the environment shifts or even begin to have a negative impact. Below, I explore these caveats by comparing three conceptual landscape scale forager-resource systems.

Figure 4.4 is analogous to Figure 3.6 in chapter 3. In each figure I hold population density constant at two foragers and vary the intrinsic rate of productivity (r) from high in 4.4a to medium in 4.4b and low in Figure 4.4c. The dashed line is the mean resource-to-

population (r/p) ratio of a landscape level forager-resource system at the habitat level and the gray shading indicates inter-annual deviations around this mean for a 50 year interval. The red line is the critical r/p ratio at which every local forager-resource system becomes vulnerable to a negative critical transition. The dashed red line is the critical r/p ratio where every local system transitions into the degraded basin of attraction.

Figure 4.4a illustrates a forager-resource system at the landscape level where the intrinsic productivity is high relative to population density, thus none of the nine habitat level systems are vulnerable to a negative critical transition. On this landscape, inter-annual deviations in the r/p ratio are present, and foragers might adopt harvest strategies that increase the z of patch level systems. However, it is not clear that this will necessarily occur. The intrinsic productivity of the landscape in Figure 4.4a is so high that foragers will not necessarily gain a fitness benefit from strategies that augment a resource base and decrease variance in non-subsistence time (due to diminishing returns). In systems where r is naturally very high, holding population density constant, non-subsistence time may be so predictable that there is little to no pressure on individuals to experiment, discover and copy foraging strategies that augment z because shocks do not ever increase variance in an individual's non-subsistence time budget above a tolerance threshold.

Figure 4.4b illustrates a landscape in which every habitat level system is vulnerable to a negative critical transition. Further, each individual forager must work harder, relative to Figure 4.4a, to obtain food. On this landscape, there is an incentive for individuals to experiment and copy strategies that increase the z of patch level systems because the effect is to make patches and habitats more productive, which increases the resilience of the productive attractor and makes an individual's budget of non-subsistence time less variable. In the social-ecological context described by Figure 4.4b, the immediate benefits of a predictable budget of non-subsistence time favor the directional copying of strategies that increase the productivity of a resource base (z) at the patch level. This copying scales the effects of food

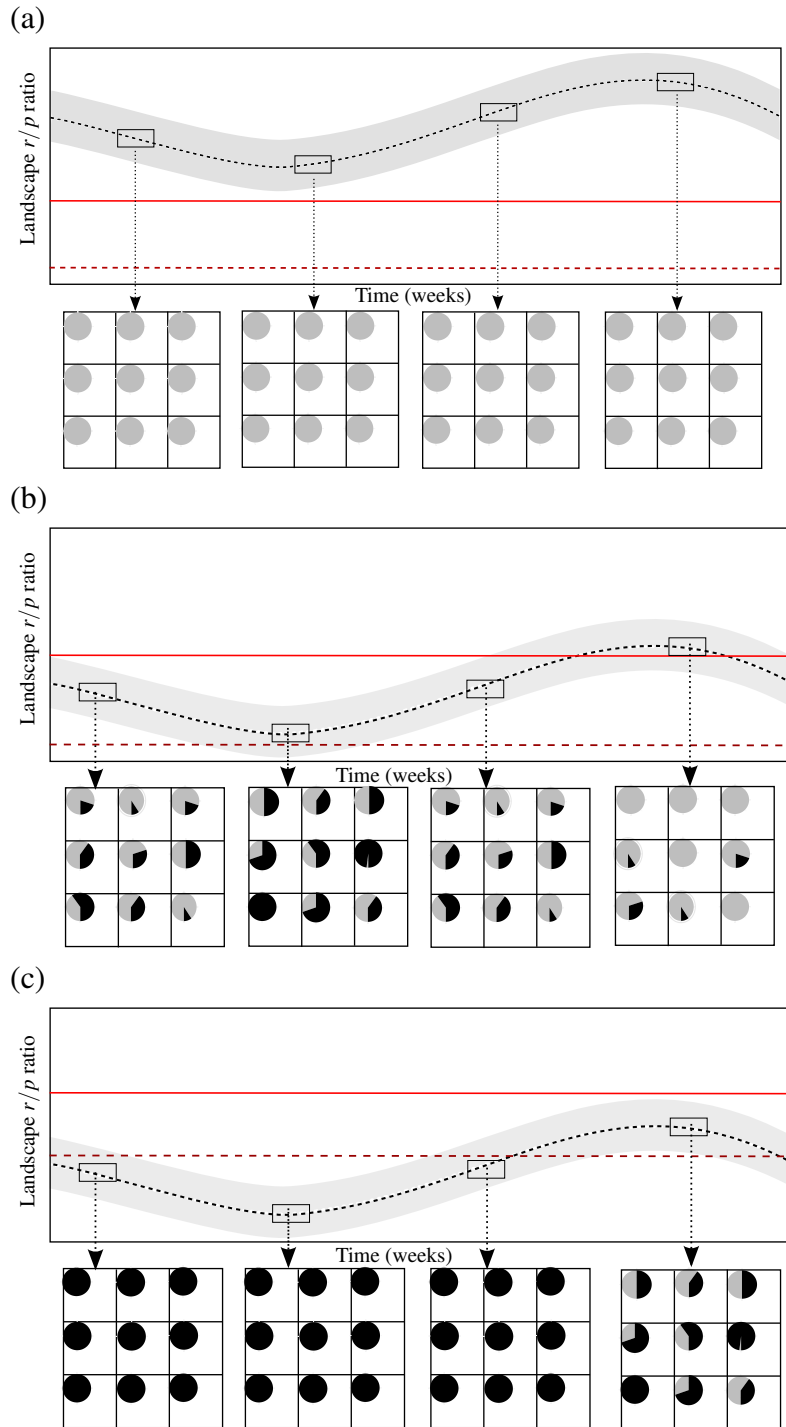


Figure 4.4: Three forager-resource systems at the landscape scale composed of nine forager-resource systems at the habitat scale. In all three pictures: the top graph illustrates change in the landscape's r/p over an average 52 week period. Each time series graph is paired with four snapshots of the nine forager-resource systems at the habitat scale. The black on the pie charts indicates the probability ($p(e_i)$) of a negative critical transition in a habitat.

production strategies up to the habitat level where foraging populations have an incentive to adopt ownership institutions. Ownership institutions allow foragers to more efficiently achieve their energy target and this compounds the effect of an increase in z on the density of biomass at the landscape level. At the landscape level, the r/p ratio, initially, increases and so does the robustness of foragers' supply of food to potential shocks. Over decades to centuries, landscape level systems where the food supply is robust to shocks have higher rates of population growth and expand at the expense of less robust systems. However, population growth eventually pushes a system to the r_{max} associated with a particular foraging strategy and the dynamics of depletion again threaten the ability of foragers to maintain a predictable budget of non-subsistence time and this feeds back to the patch level and favors the elaboration of strategies that increase z .

My postulate is that there is a zone of r/p ratios bounded by the landscape level systems described in Figure 4.4a and 4.4b. I call this the Goldilocks zone. In the Goldilocks zone the ecological conditions are just right for the coevolution of food production, territoriality and increasing productivity of resources. The lower bound of the Goldilocks zone described by Figure 4.4b is likely sensitive to inter-annual changes in the climate drivers that shock the productivity of resources. This is because this variation occurs faster than the net effect of augmentation scales-up, which, at minimum, likely takes years to increase the density of resources in habitats and decades on landscapes. If the coefficient of variation in Figure 4.4b gets too high, then negative critical transitions are going to occur both more unpredictably and frequently. Under these conditions, the coevolutionary cycle cannot become self-perpetuating because frequent, habitat level negative critical transitions cause foragers to abandon habitats. Following the model of economic defensibility, this ecological context should favor foraging strategies that are territorially extensive and resources are treated as common property.

Figure 4.4c illustrates a landscape in which the intrinsic productivity of resources is very low. In this system, each habitat level system may have foragers who adopt the augmentation of resources. But, in environments so low in productivity that landscape wide flips into the degraded attractor are the norm, the proportion of foragers that adopt food production may never boost resource growth rates high enough to sufficiently improve the robustness of forager's food supply to shocks and facilitate population growth. There would, therefore, be no potential gain in the predictability of non-subsistence time and fitness benefit for individuals in systems with high proportions of adopters. Some foragers within hunter-gatherer SES may adopt strategies that augment resources in this environment, but a positive feedback cycle that causes these strategies to proliferate can not get started because the productivity of forager-resource systems across the hierarchy are not transformed enough to meaningfully increase the robustness of individual's food supply to shocks. The ability to achieve γ is just not a possibility in landscape level systems characterized by Figure 4.4c.

A final point is that climate variation occurring at decade-to-centennial scales of time may limit the coevolution of food production, territoriality and the productivity of resources. In general, the Pleistocene witnessed much higher amplitude variations at this time scale than is characteristic of the Holocene. Holding population density constant, such high amplitude variation could move forager-resource systems in and out the Goldilocks zone defined above on the time scale of decades. This means that food production strategies that augment the productivity of resources in one decade may not do so in the following decade. In this scenario, there likely would not be enough time for the multilevel selection/copying processes to generate a self perpetuating cycle (Bowles and Choi, 2013; Richerson et al., 2001). Given enough stability at the centennial scale, the Goldilocks zone should lead to systems where individuals are primed to improve z . And adopting the cultivation of domesticated plants is a very powerful way to do so when the institutions are in place to protect

resources from competition. Of course, the adoption of domesticated plants would have long-term consequences that totally transform a forager-resource system and might change individual's preferences for non-subsistence time.

The Social Opportunity Hypothesis

I propose that there is a Goldilocks zone where investments in the augmentation of resource biomass provides individual foragers with a relatively short-term fitness benefit derived from a predictable budget of non-subsistence time. The budget of non-subsistence time is more predictable because the augmentation of resources makes a forager-resource system, at the productive attractor, less sensitive to shocks that might depress the availability of food. In this Goldilocks zone, the fitness benefits of non-subsistence time favor the directional copying of strategies that increase the productivity of a resource base. This copying scales the effects of food production strategies up from the patch to the habitat level where foraging populations have an incentive to adopt ownership institutions. Ownership institutions allow foragers to more efficiently achieve their energy needs and this compounds the effect of an increase in z on the density of biomass at the landscape level. At the landscape level, the r/p ratio increases and so does the robustness of foragers' supply of food to potential shocks. Global systems where the food supply is robust to shocks have higher rates of population growth and expand at the expense of less stable global systems. However, population growth eventually pushes a system to the r_{max} associated with a particular foraging strategy and the dynamics of depletion again threaten the ability of foragers to maintain a predictable budget of non-subsistence time and this feeds back to the patch level and favors the elaboration of strategies that increase z . In this way, the very strategies that foragers use to obtain food transform the social and biophysical environment and drive the future evolution of a hunter-gatherer SES. Going farther afield, I speculate that when this process gets started, foragers who have the opportunity to adopt domesti-

cated plants are very likely to do so, but this act will have long-term consequences, fueling the growth of institutions, inequality and labor demands to manage more intensive food production (a la Hayden, 2003).

Based on the logic of the social opportunity hypothesis, I develop three basic quantitative expectations for the social-ecological relationships that characterize variation in hunter-gatherer SES.

1. Hunter-gatherers who invest in food production strategies live at higher population densities than hunter-gatherers who do not. This expectation follows from the positive feedback proposed between increasing investment in the production of food and increases in population density. With increasing fidelity of food production making possible increases in population density and increases in population density, in turn, creating contexts in which investment in the production of food is needed to maintain a predictable budget of non-subsistence time.
2. The adoption of food production increases the likelihood that hunter-gatherers recognize territorial ownership. This follows from the argument that by increasing z , foragers decrease the amount of territory necessary per forager to collect food. This increases the net benefit of territorial ownership.
3. Finally, territorial ownership favors a continued investment in the production of food by hunter-gatherers. As territorial ownership develops within a region composed of multiple hunter-gatherer SES, territorial boundaries should become less permeable and limit the ability of foragers to expand their range in response to population growth or a decline in the intrinsic productivity of resources in an environment. This situation, in turn, should favor hunter-gatherer SES with high proportions of foragers who invest in food production and increase the overall productivity of their

territory because this increases a system's resilience and reduces variation in the non-subsistence time budgets of individuals.

Conclusion

In this chapter, I modified the hunter-gatherer SES model developed in chapter 3 to study the effects of foraging strategies that augment rather than deplete a resource base. In general, strategies that augment the productivity of a resource base, as a byproduct of foraging effort, increase the resilience of the productive attractor in the hunter-gatherer SES model. This means that foragers spend less time harvesting food and experience an increase in the robustness of their food supply to shocks. Importantly, an increase in the resilience of the productive attractor also decreases variation in how much foraging effort individuals devote to the collection of food and, as a consequence, variation in an individual's budget of non-subsistence time also declines. Given these results, I have conceptually proposed a set of processes that link hierarchical levels of forager-resource systems together to drive the coevolution of food production, territoriality and the productivity of a resource base. The SOH provides a highly general explanation for the evolution of food production and territorial ownership.

The SOH builds on a set of ideas that, ultimately, trace back to Braidwood (1960) and Rindos (1980, 1984) and Smith (1989) and are developed more fully by Zeder (2012) and Smith (2012). In chapter 2, I discussed the modified model of economic defensibility that Zeder (2012) and Smith (2012) propose to explain changes in resource use among hunter-gatherers. This model has a compelling logic, but there are two fundamental short-comings. The first is that population density is treated as a completely dependent variable. The second is that the model relies on the premise that individual foragers make decisions based on gains expected in the long-term. Individuals certainly plan ahead, but making decisions that increase the benefits of foraging in the future is a process fraught with uncer-

tainty. In fact, human foragers seem to discount the future at a very high rate, meaning that individuals value immediate gains over the possibility of future gains (Tucker, 2001). So, of course, understanding why discount rates change for individuals is important. I believe that the SOH buttresses both of these short-comings associated with the modified model of economic defensibility.

As argued in conjunction with Figure 4.4, population density plays an integral role in creating the context in which food production, territoriality and resource density can co-evolve. This is due to cross-level interactions that link the hierarchy of forager-resource systems that hunter-gatherers create. If the resource-to-population density (r/p) ratio of a landscape level system is too high, the positive coevolutionary feedback cycle is unlikely to get started because each individual already has a sufficiently predictable budget of non-subsistence time to get all the fitness gains that they can. Similarly, if the r/p ratio of a landscape level system is too low, then the degraded attractor is almost a permanent foraging context. In this setting, foragers are likely to abandon a landscape, if at all possible, rather than invest in the production of food (provided more productive areas are available). So, there is a Goldilocks zone where “population pressure” is just right (i.e., the r/p ratio of hierarchically organized forager-resource systems) to foment the coevolution of food production and territoriality.

The SOH does not rely on the assumption that foragers make decisions meant to increase future benefits. Rather, I assume that foragers preference strategies that best reduce short-term variation in their budget of non-subsistence time. I assume that foragers can increase their fitness when they have a more predictable budget of non-subsistence time because they can maximize their opportunities to socialize, find mates, and carry out the proper rituals. Recall, in the Goldilocks zone, the augmentation of resources increases the resilience of forager-resource systems and decreases variation in the time budgets of individuals. Given my assumption about the benefits of a predictable budget of non-subsistence

time, this dynamic creates a situation in which copying might favor the proliferation of strategies that augment a resource base's productivity. Forager's do not need to plan for the long-term to initiate a multilevel selection feedback process that favors the production of food, territoriality and increases in the productivity of resources.

Questions for future research

A fundamental question raised by the SOH is whether foragers are willing to give-up non-subsistence time to harvest food or are more sensitive to variations in their budget of non-subsistence time. Further, what is the tolerance level of variation in non-subsistence time? If the tolerance for variation is high, then the dynamics proposed by the URH are potentially more likely to characterize the evolution of forager-resource systems. If the tolerance is low, then the dynamics proposed by the SOH are more likely to characterize evolutionary processes in forager-resource systems. The only way to answer these questions is by conducting controlled behavioral experiments with real humans, either in the field or in the lab. This is not an area of research in which archaeologists typically participate. But basic assumptions about preferences and the ecological contexts in which individuals have different preferences are critical to the construction of models of coevolutionary processes. This is especially true of models that attempt to work from first principles of human behavior. No one is going to study these issues in small-scale societies for archaeologists, and I believe this is an area in which we need to expand and broaden our conception of "ethnoarchaeology" to include contextualized behavioral experiments.

Onward

The next step is to evaluate the merits of the URH and SOH against ethnographic data. This analysis provides a more informed body of knowledge for understanding patterns of subsistence change in the archaeological record.

Chapter 5

A CROSS-CULTURAL ANALYSIS OF FOOD PRODUCTION AND TERRITORIAL OWNERSHIP

In chapter 1 I argued that dynamic models help clarify our thinking about complex processes that operate across scales of space, time and levels of organization. In turn, the models are useful tools that aid in our development of explanations for social and technological change in SES. Two of the most fundamental evolutionary changes that occurred prehistorically in hunter-gatherer societies are the adoption of food production and the adoption of territorial ownership by social groups. The coevolutionary relationship between institutions of ownership and the adoption of food production is a critical debate that we need to resolve to understand the evolution of subsistence economies based on agriculture (Bettinger et al., 2009; Bowles and Choi, 2013; Hayden, 1995; Rosenberg, 1998, 1990; Smith, 2012). In this chapter, I work back and forth between the Uncertainty Reduction Hypothesis (URH), the Social Opportunity Hypothesis (SOH) and cross-cultural patterns to help clarify the underlying relationships between investment in the production of food and territorial ownership.

One of the primary differences between the URH and the SOH is how each hypothesis logically links the formal ownership of territory and the practice of food production. In the URH, the ownership of territory and food production are alternative strategies for reducing the information processing costs associated with making robust land use choices when a forager-resource system is characterized by multiple stable states. In the SOH, the ownership of territory and food production are linked in a mutually reinforcing relationship. Food production increases the incentive for individuals to own territories. In turn, the ownership of territories increases the incentive for individuals to invest in more elaborate

forms of food production. The central question that I address in this chapter is whether or not food production and territorial ownership are necessarily co-occurring strategies or are potentially alternatives strategies adapting to distinct ecological contexts that generate uncertainty associated with land use. The chapter is divided into four sections. In the first section I describe the data and methods used to evaluate the consistency of the data with each respective hypothesis. In the second section I evaluate the ability of each hypothesis to explain the presence and absence of low-level food production strategies among hunter-gatherers (e.g., burning vegetation, planting). In the third section I evaluate the ability of the hypotheses to anticipate the presence and absence of territorial ownership among ethnographically documented hunter-gatherers. In the fourth section I reflect back on the URH and SOH to identify important questions for future research. In the end, the data are more consistent with the URH than the SOH. The implication is that the adoption of food production and the subsequent evolution of agriculture is driven by systems dynamics that generate uncertainty in the ability of foragers to make robust land use choices.

Preliminaries: Data and Methods

The ethnographic data used here were compiled from three sources, Keeley (1995) and Binford (2001) and my own data collection efforts to increase the sample of societies studied by Keeley (1995). The Keeley data set plus the cases I have added from ethnographic sources is a sample of 110 societies. This data set records the presence and absence of low-level food production strategies such as burning vegetation and planting select species. These strategies may augment the productivity of terrestrial resources. A critical point is that the data collected by Keeley and Binford were done independently of the theory developed in chapters 3 & 4. By independent, I mean that I did not go through the ethnographic sources and select data to support one hypothesis or the other.

In general, the Keeley data set constitutes a sub-set of the data reported by Binford. Both authors report population densities and the observations are consistent between the two authors. The observations made on each society were collected from primary sources written by ethnographers working independently and at different times and places. The data, therefore, approximate an independent and unbiased sample of observations made on hunter-gatherer societies (Hamilton et al., 2007). No data are perfect, and the data used here are no different. However, the large sample sizes provided by Binford (2001) and Keeley's (1995) data allow researchers to check the consistency of competing hypotheses with data, even if the falsification of a hypothesis is not realistic due to the potentially poor quality of some ethnographic observations. These data have been used productively in a similar manner by various authors (e.g., Fenner, 2005; Freeman and Anderies, 2012; Grove, 2009, 2010; Grove et al., 2012; Hamilton et al., 2007, 2009).

Keeley (1995:247-248) has recorded and published the presence and absence of four activities that he originally termed protoagriculture. These are strategies of low-level food production that hunter-gatherers use to influence the productivity of ecosystems, either on purpose or as a fortuitous byproduct. 1) The systematic burning of vegetation to enhance the availability of game (16/96 societies); 2) the systematic burning of vegetation to enhance the availability of plants useful as food (29/96 societies); 3) the cultivation (planting/seeding) of non-food plants (24/96 societies); and 4) the cultivation of plants for food (9/96 societies). All four of these behaviors stimulate the productivity of resources within a hunter-gatherer group's territory. If a group practiced any one of these strategies as recorded by Keeley (1995), they have been assigned a value of 1: the production of food present. If the above strategies were not recorded by Keeley, I assigned a value of 0: the production of food absent. I have supplemented these data with 14 additional hunter-gatherer groups. I chose the added groups to develop a more complete coverage of the continent of Australia and to try and increase the sample size of groups living in tropical settings (data reported

in Appendix A). Of course, more work can be done and should be done in the future to document as fully as possible the strategies that hunter-gatherers use to modify ecosystems via low-level food production.

Data on territorial ownership were obtained from a sample of 339 ethnographically recorded hunter-gatherer societies (Binford, 2001). To assess territorial ownership, the variable recoded by Binford (2001:384) called *OWNERS* is used. This variable is a categorical description of hunter-gatherer territorial ownership.

- 1 None reported, but all groups have identity and practical links to both land and resources. There may be strong attachments in the form of persons seen as stewards of both land and lore. There are, however, no personnel of local group claims on the area in general. One's interests and association are acknowledged by others asking permission for economic use or camping privileges.
- 2 The local group definitely claims exclusive use rights, over resource locations, residential sites, and the home range, in general. There may be a further set of claims among the households within the local group— special trees, shell beds, etc. There may be a kind of endogamous inheritance of stewardship roles with respect to landmarks or special places.
- 3 Local group claims hunting areas, dominant animals, fishing sites, and animal drive locations. Administration is by a group leader. Some resources may be said to be “clan or lineage” owned. The system is characterized by differentiated and nested ownership. The basic family, the descent unit, and the larger settlement group may each claim land and resources at different scales of inclusiveness.
- 4 Elite ownership of land and resources. In addition, there may be family claims to particular resource locations. Resource patches may be “owned” by a family and can

Table 5.1: Variables and definitions

Variable	Definition	Reference
<i>Enhancement</i>	The production of resources	Keeley, 1995
<i>Ownership</i>	The ownership of territory	Binford, 2001
<i>Density</i>	Population density	Binford, 2001
<i>Fishing</i>	The percent of diet obtained from aquatic resources	Binford, 2001
<i>Hunting</i>	The percent of diet obtained from hunting large bodied animals	Binford, 2001
<i>NPP</i>	Net primary productivity (the growth rate of biomass in <i>grams/m²/year</i>)	Grieser et al., 2006
<i>CV Rainfall</i>	The coefficient of variation of inter-annual rainfall	Beck et al., 2004

be given away, inherited or disposed of within the group. This may include house sites as well. Not uncommonly, such “owned” resource locations are marked and first fruit contributions may be expected by the elite from productive units within the society.

This variable is collapsed here into a binary indicator variable for the presence of territorial ownership, *Ownership*. Category 1 above is indicative that territories are open access and ownership is “absent” (a new code of 0), even though permission may be asked to use particular resources. Categories 2-4 indicate that territories are owned by social groups at various levels of organization from households to larger settlement groups (a new code of 1).

five additional variables are used to evaluate the consistency of the URH and SOH with ethnographic data (see Table 5.1). 1) Population density, 2) the percent of diet obtained from fishing, 3) the percent of diet obtained from hunting large animals 4) the net primary productivity in a hunter-gatherer group’s territory and 5) the coefficient of variation in rainfall in a group’s territory.

Net primary productivity is used to estimate the mean intrinsic productivity (r in the hunter-gatherer SES model) of an environment occupied by hunter-gatherer groups. Net primary productivity is a rate of biomass growth (see Odum and Barrett, 2002; Porter and Marlowe, 2007). I assume that the higher the rate of biomass growth in an environment, the higher the rate of growth for biomass that is useful as food. Of course, the relationship between the growth of biomass and biomass useful as food may be more complex. Understanding the relationship between the rate of biomass growth and the growth of biomass useful as food is an important direction for (collaborative) research in comparative hunter-gatherer studies. I use the coefficient of variation in rainfall to estimate the predictability and intensity of variation in the availability of water that plants in an ecosystem need to produce biomass. The higher the coefficient of variation in rainfall, the more unpredictably the

productivity of terrestrial biomass varies from year-to-year. The coefficient of inter-annual variation in rainfall was calculated from global, gridded precipitation means calculated between 1950 and 2000 at a one decimal degree scale (Beck et al., 2004). The grid cell nearest to the center of each group's territory was used to estimate the coefficient of variation in inter-annual rainfall experienced by each society.

Methods

I use an information theoretic approach to evaluate the consistency of each explanatory hypothesis with the data (Burnham and Anderson, 2002). Multiple, binary logistic regression is used to develop statistical models that determine the joint probability, given a set of explanatory variables, that a response variable is present or absent. In the two analyses conducted here, food production (*Enhancement*) and the ownership of territory (*Ownership*) are the response variables. Binary logistic regression is a general linear model that is useful for statistically modeling qualitative differences between two potentially distinct groups in a population (Dielman, 2001). I use the logistic function to relate the joint probability that *Enhancement* or *Ownership* is either absent or present in a given society. For example

$$P(\text{Enhancement} = 1 | x_1, \dots, x_i) = \frac{1}{(1 + e^{-(\alpha + \sum_i b_i x_i)})} \quad (5.1)$$

where x_1, \dots, x_i refers to a given set of explanatory variables, α is a constant and b_i is a coefficient associated with each variable. Equation 5.1 can be transformed into a general linear model using the so-called logit link function, such that

$$\ln\left(\frac{\hat{p}}{1 - \hat{p}}\right) = \alpha + \sum_i b_i x_i \quad (5.2)$$

where \hat{p} is the joint probability that a hunter-gatherer group Enhances the productivity of resources, given a set of explanatory variables.

The coefficients (b_i) in equation 5.2 describe the effect that a change in an explanatory variable has on the log-odds that a hunter-gatherer group either practices the production of food or owns territory. I assume here that groups of hunter-gatherer societies are, *a priori*, independent of model parameters and are equally likely to engage or not to engage in the production of food or the ownership of territory. Thus, groups who are predicted to engage in food production or territorial ownership with a probability greater than or equal to 0.5 are predicted to produce food or own territory and groups predicted with a probability of less than 0.5 are predicted not to produce food or own a territory.

Model selection methods are used to evaluate the sign and relative importance of the explanatory variables considered in this analysis. Model selection methods are useful for comparing competing explanatory hypotheses, especially when the evaluation of these hypotheses relies on observational data drawn from complex systems (Johnson and Omland, 2004). The analysis of the relative importance of the explanatory variables is based on the Akaike Information Criterion (AIC). AIC is a measure of the fit and complexity of a statistical model. The analytical procedure for estimating the sign and relative importance of each explanatory variable was conducted using the R computing environment (R Development Core Team, 2008) as follows.

1. The MurMin R package is used to calculate all potential binary logistic regression models for the set of explanatory variables on the response variable. For example, to analyze the presence and absence of food production (*enhancement*) in the subsample of societies ($n=110$), there are five potential explanatory variables (population density, the percent of diet obtained from fishing, the presence/absence of ownership, net primary productivity, and the coefficient of variation in rainfall). Thus, this procedure results in 32 candidate logistical regression models, including a “null” model that only includes an intercept.

2. Each model is ranked according to its AIC value from lowest to highest AIC. The best model is the statistical model with the lowest AIC (i.e., the model that best balances fit and complexity) This ranking allows one to calculate the change in AIC, Δ_i , as $AIC_i - \min AIC$, where AIC_i is the AIC of a candidate model under consideration and $\min AIC$ is the AIC of the model that best balances fit and complexity.

3. Standardized Akaike weights, w_i are calculated for each candidate model. Akaike weights summarize the likelihood that a given model is the best approximate fit, given the data. The Akaike weight is calculated by first determining the likelihood that a model is the best approximation to the data, which conveniently is: $L(\text{model}|\text{data}) \propto e^{0.5\Delta_i}$. Next, the the sum of the likelihoods of all regression models is calculated. Then, the Akaike weight is simply $w_i = \frac{e^{0.5\Delta_i}}{\sum_{r=1}^R e^{0.5\Delta_r}}$. The Akaike weight is used here to define a 95% confidence set of models; that is, the set of models that is likely to contain the regression model that is the best fit to the data.

4. The mean regression coefficient and standard error of each explanatory variable included in the 95% confidence set of regression models is calculated. The relative importance of each explanatory variable present in at least one regression model of the 95% confidence set is also calculated. The relative importance of an explanatory variable is simply the sum of the Akaike weights of each model in which a variable is present. To illustrate, please consider the following hypothetical example. If the 95% confidence set of regression models analyzed to predict the production of food contains three candidate regression models, each model with an Akaike weight of 0.40, 0.30 and 0.25, and population density is an explanatory variable in the top two weighted models, then the relative importance of population density is 0.70 (0.40+0.30). If the percent of diet obtained from fishing were present in all three models, its importance measure would be 0.95 (0.40+0.30+0.25). The importance

measures describe the relative likelihood that an explanatory variable is included in the best regression model (i.e., the model closest to truly representing the data). In this hypothetical example, fishing is 1.37 times more likely than population density to have a true effect on the likelihood that foragers produce food. The closer a variable's importance measure is to 1, the more likely the variable is to have an effect on the response variable, given the data and candidate set of regression models.

Finally, I combine the formal information theoretic approach described above with exploratory data analysis (EDA) to identify and illustrate important patterns in the data. Now that these preliminaries are out of the way, let's analyze some data!

The Social-ecological Contexts of Food Production

The two explanatory hypotheses outlined in chapters 3 & 4 specify the social-ecological contexts that should partly determine the benefits and costs of food production for hunter-gatherers. Below, I develop expectations reasoned from the logic of these alternative hypotheses. My goal is to identify expectations that are mutually exclusive to each explanatory hypothesis. This is a strategy for determining the relative consistency of each hypothesis with the data.

Predictions

First, both the URH and SOH suggest that population density has a positive effect on the likelihood that hunter-gatherers engage in the production of resources (P_{em1}). The mechanisms that cause this predicted relationship simply differ. In the URH, foragers begin to produce food because a decrease in the r/p ratio in a large scale forager-resource system generates localized common pool resource dilemmas. In this situation, forager-resource systems at the level of habitats are vulnerable to environmental shocks that can precipitate a negative critical transition to the degraded attractor. An increase in population density

should, therefore, create ecological conditions where foragers are more likely to produce food to buffer against the risk of getting shocked into a degraded basin of attraction. In the SOH, the positive effect should result from the process of population growth in a forager-resource system at the landscape scale with high proportions of foragers who adopt the production of food. The population growth, in turn, should contribute to the establishment of a social-ecological context that favors the continued elaboration of food production to boost the productivity of resources.

Second, an implicit assumption of both the URH and SOH is that foragers primarily target terrestrial species for food. This is because the hunter-gatherer SES model that the hypotheses are based upon makes this simplifying assumption (see chapter 3). Human foragers clearly eat a wide variety of fresh and marine water resources (fish and shellfish). It is not at all clear that managing the disturbance-succession dynamics of terrestrial ecosystems would affect the productivity of aquatic resources. I assume here that as hunter-gatherers become more dependent on aquatic resources for food, they are less likely to engage in the production of food from terrestrial ecosystems (Keeley, 1995). This process occurs because, as foragers invest more in aquatic resources, time is more likely invested in strategies that affect the productivity of aquatic resources rather than terrestrial ecosystems (P_{em2}). Thus, to evaluate the URH and SOH as explanations for the adoption of food production, we must control for the amount of food obtained from fishing.

Third, holding population density constant, the URH suggests that the intrinsic rate at which biomass regenerates in an environment has an inverse effect on the likelihood that foragers produce food (P_{em3a}). In the URH, it is the r/p ratio that determines whether or not a forager-resource system is vulnerable to a negative critical transition from the productive to the degraded attractor. Per the dynamics of the hunter-gatherer SES model in chapter 3, as the growth rate of resources declines, foragers are more likely to enter a window of vulnerability. And when a system is in the window of vulnerability, individuals

face the risk that systems will transition to a degraded state before they can meet their desired level of energy. The production of food is one way that foragers might adapt to commons dilemmas generated by multiple stable states and the uncertainty associated with planning how move among habitats on a landscape.

The SOH suggests a slightly more complex relationship between the intrinsic productivity of resources and the likelihood that foragers produce food. Holding population density constant, prediction 3_{emb} is a set of three statements: i) above a threshold of extraordinarily high productivity, hunter-gatherers are less likely to produce food; ii) as productivity declines below this upper threshold, hunter-gatherers are more likely to produce food until a lower productivity threshold is reached; iii) below this lower threshold, hunter-gatherers are less likely to engage in the production of food. It is probably rare for hunter-gatherers to live in terrestrial environments that are so productive, relative to population density, that variation in non-subsistence time would not decrease in a meaningful way if the productivity of resources was increased. I, therefore, predict that the productivity of resources has a positive effect on the likelihood of food production (P_{em3b}). I explore this relationship further in the section called “Ecological thresholds” below.

Fourth, the SOH posits a positive feedback between the production of food, the size of hunter-gatherer territories and the costs of owning territory for hunter-gatherer groups. In particular, the costs associated with owning a territory decline due to the increase in the density of resources generated by the production of food. The ownership of territory, in turn, partly catalyzes a positive feedback that favors the elaboration of strategies for managing ecosystems to produce food. Thus, it is a basic prediction of the SOH that the ownership of territories has a positive effect on the likelihood that foragers produce food (P_{em4a}), because the two strategies co-occur in a mutual feedback relationship.

In contrast, the URH postulates that ownership and the production of food are alternative, though not mutually exclusive strategies. As argued in chapter 3, in forager-resource

systems where the risk of a negative critical transition in is more predictable in space and time, the ownership of territory may be sufficient to reduce the uncertainty associated with land use choices, particularly the uncertainty associated with choosing how much effort to exert various habitats by regulating who and when individuals can access habitats. As the risk of a negative critical transition becomes harder to estimate from experience and transmission, due to the impact of unpredictable environmental variation, the production of food is a more useful strategy. As alternative strategies that are adopted in different social-ecological contexts, the URH suggests that there is no discernible effect of territorial ownership on the likelihood that hunter-gatherers produce food (P_{em4b}) because the two strategies are not linked in a direct feedback loop. The two strategies are equally likely to occur separately as to co-occur, controlling for all other explanatory factors.

Fifth, in the URH, the r/p ratio merely controls a threshold that, once crossed, exposes foragers to the consequences of potentially negative environmental variations, like droughts. In this hypothesis, the predictability and intensity of environmental variation is a critical determinant of how foragers respond to the emergence of habitat level common pool resource dilemmas. The more unpredictable inter-annual changes in resources are, the URH suggests, the more likely foragers are to adopt the production of food. Thus, the URH suggests that the unpredictability of inter-annual variation in the productivity of resources has a positive effect on the likelihood that hunter-gatherers produce food (P_{em5a}) and, this variable is more important than population density and/or the intrinsic productivity of resources. Inter-annual variation in, for example, rainfall, is more important precisely because it is this variation that generates negative critical transitions that serve as a “signal” that a system is “out of whack”. The negative critical transitions create uncertainty associated with where to locate in space and time to harvest food and, thus, a social-ecological context in which the benefits of food production outweigh the costs for individuals because food production decreases the likelihood of negative critical transitions.

Table 5.2: The predicted direction of the effect of explanatory variables on the likelihood that hunter-gatherers produce food. SOH is the social opportunity hypothesis; URH is the uncertainty reduction hypothesis.

Hypotheses	Explanatory variables				
	Density	Fishing	NPP	Ownership	CV Rainfall
SOH	+	-	+	+	-
URH	+	-	-	no effect	+

Finally, the SOH suggests that the predictability of inter-annual variation in the productivity of resources has a negative effect on the likelihood of food production (P_{em5b}). As argued in chapter 4, in the Goldilocks zone there is a positive feedback between food production, ownership and population growth. Whether or not this feedback process gets started is sensitive to the predictability and intensity of inter-annual deviations in the productivity of resources. If the coefficient of variation associated with a system's productivity gets too high, this drives the costs of territorial ownership up and generates a higher likelihood that habitat level systems will experience a negative critical transition. If variation gets too unpredictable, there just is not enough time for the coevolutionary, cross-level feedback cycle to get going.

Table 5.2 summarizes the expected effects of explanatory variables on the likelihood that hunter-gatherers produce food through burning and planting. There are two analytical questions that I answer regarding the predictions in 5.2: 1) what is the direction of the effect of each explanatory variable, and 2) how likely is an explanatory variable to have an effect on the production of food relative to the other variables in the data set? To have confidence in either the URH or the SOH, a hypothesis needs to correctly predict the sign of the effect of an explanatory variable and said explanatory variables should, in all likelihood, have an effect on food production, given the data set and models analyzed.

Results

The main result of my analysis is that the URH is more consistent with the data than the SOH and, thus, we should have more confidence in the processes prosed by the URH than the SOH to explain the adoption of food production. In the data set analyzed here, the coefficient of variation in rainfall and population density both have positive effects on the likelihood that hunter-gatherers produce food and these two variables are far more likely to have an effect than the percent of diet obtained from fishing, net primary productivity and the ownership of territories. In sum, we can have a high degree of confidence that three of the URH's predictions are consistent with the data (P_{em1} , 4b & 5a) while we can only have a high degree of confidence that one of the SOH's predictions is consistent with the data (P_{em1}).

Table 5.3 presents the 95 percent confidence set of models that best explain the presence and absence of food production among hunter-gatherer societies. The best model includes two variables, the coefficient of variation in rainfall and population density. The first regression model is approximately 1.73 times more likely to fit the data than the second best regression model (0.33/0.19), which includes the following variables: the coefficient of variation in rainfall, population density and the percent of diet obtained from fishing. The second best model is 1.58 times more likely to fit the data than the third best model (0.19/0.12), which includes the following variables: the coefficient of variation in rainfall, population density and net primary productivity. Overall, the coefficient of variation in rainfall is an explanatory variable in all 9 regression models in the 95 % confidence set, while population density is an explanatory variable in 8/9 regression models. This fact reveals the overwhelming importance of the coefficient of variation in rainfall and population density for estimating the likelihood that hunter-gatherers produce food relative to the other variables.

Table 5.3: The 95 percent confidence set of logistic regression models. 1=*CV Rainfall*, 2=*Density*, 3=*Fishing*, 4=*Ownership* & 5=*NPP*

Explanatory Variables	Residual Deviance	AIC	Δ_i	w_i
1,2	94.88	100.90	–	0.33
1,2,3	94.00	102.00	1.12	0.19
1,2,5	94.87	102.90	1.99	0.12
1,2,4	94.88	102.90	2.00	0.12
1,2,3,4	93.91	103.90	3.03	0.07
1,2,3,5	93.98	104.00	3.10	0.07
1,2,4,5	94.87	104.87	3.99	0.04
1	101.9	105.90	5.02	0.03
1,2,3,4,5	93.91	105.91	5.03	0.03

Table 5.4: Means, standard errors and relative importance ($\sum w_i$ for each variable) of the explanatory variables in the 95 percent confidence set of models (n=110).

Explanatory Variable	Coefficient (<i>b</i>)	Standard Error	Importance
<i>Intercept</i>	-4.04	1.02	–
<i>CV Rainfall</i>	20.06	4.45	1.00
<i>Density</i>	2.15	0.93	0.97
<i>Fishing</i>	-0.01	0.01	0.36
<i>Ownership</i>	0.04	0.57	0.26
<i>NPP</i>	0.0001	0.004	0.26

Table 5.4 displays the mean coefficients for each explanatory variable in the 95 percent confidence set of regression models. The two most important variables with importance weights of 1.00 and 0.97 are the coefficient of variation in rainfall and population density. The positive effect of population density on the likelihood that hunter-gatherers produce food is consistent with the predictions of both explanatory hypotheses (P_{em1}). However, the positive effect of the coefficient of variation in rainfall on the likelihood of food production is only consistent with URH (compare P_{em6a} & $6b$). Moreover, the coefficient of variation in rainfall is a slightly more important than population density, as the URH implies. In general, however, both variables are very likely to have an effect on the likelihood that foragers produce food.

Consistent with the idea that investment in aquatic resources decreases the likelihood that foragers produce food, the percent of diet obtained from fishing has a negative effect

on the likelihood that hunter-gatherers produce food (P_{em2}). However, the percent of diet obtained from fishing is 2.77 times less likely to have an effect on the production of food than the coefficient of variation in rainfall and 2.69 times less likely than population density. In sum, we can only have a low degree of confidence that fishing has a true effect on the likelihood of food production, relative to the predictability of rainfall and population density.

The negative effect of net primary productivity on the likelihood of food production is consistent with the URH (P_{em3a}) and inconsistent with the SOH (P_{em3b}). However, net primary productivity is 3.84 times less likely than the coefficient of variation in rainfall to effect the likelihood of food production and 3.73 times less likely than population density. This all indicates that we should have a very low degree of confidence that net primary productivity has an effect on the likelihood that hunter-gatherers produce food, in this data set, relative to population density and the coefficient of variation in rainfall.

Finally, the ownership of territory has a positive effect on the likelihood that hunter-gatherers produce food. This is consistent with the SOH (P_{em4a}). However, there is a very low likelihood that the ownership of territory has an effect on the likelihood that hunter-gatherers produce food, relative to the other variables in the data set. This observation is potentially consistent with the URH's prediction that ownership does not necessarily co-occur with the production of food by foragers (P_{em4b}).

Ecological thresholds

Figure 5.1a presents evidence of a threshold near a coefficient of variation in rainfall value of 0.21. This threshold distinguishes hunter-gatherers who produce food by managing ecosystems from those who do not. When the coefficient of variation in rainfall is greater than approximately 0.21, all but 5 hunter-gatherer societies produce food, even in settings where the net primary productivity-to-population density (r/p) ratio is high! Further, 5.1a

illustrates that there is not an upper and lower threshold of productivity-to-population density that distinguishes societies who produce food from those who do not with, as the SOH would suggest. The five hunter-gatherer groups who are not recorded to produce food, even though the coefficient of variation in rainfall is greater than 0.21 are the Gunwinggu, Mamu, Taramuit, Karankawa and Seri. Interestingly, a normalized individual in three of these groups is recorded to get more than 1/3 of their diet from aquatic resources (Binford, 2001:Table 5.01). These exceptions raise the interesting possibility that if the data set were expanded, the effect of fishing on the likelihood of food production might increase. Other factors not controlled for here, such as the quality or detail of ethnographic sources is something to also consider for future empirical analyses.

Figure 5.1b illustrates the importance of the coefficient of variation in rainfall where hunter-gatherer specialize in terrestrial resources. The vertical reference line at 33 percent of the diet obtained from fishing on Figure 5.1b marks the point at which hunter-gatherers obtain 2/3 of their diet from terrestrial resources (plants + animals). To the left of this vertical line, there is a striking differentiation between hunter-gatherers who produce food and hunter-gatherers who do not. In this region of the graph (the left half), all but two societies that live in settings where the coefficient of variation in rainfall is greater than 0.21 produce food. In short, hunter-gatherers who primarily exploit terrestrial resources and live in predictable environments do not produce food; conversely, hunter-gatherers that primarily depend on terrestrial resources and live in environments characterized by unpredictable inter-annual deviations in rainfall, and, presumably, biomass growth, produce food.

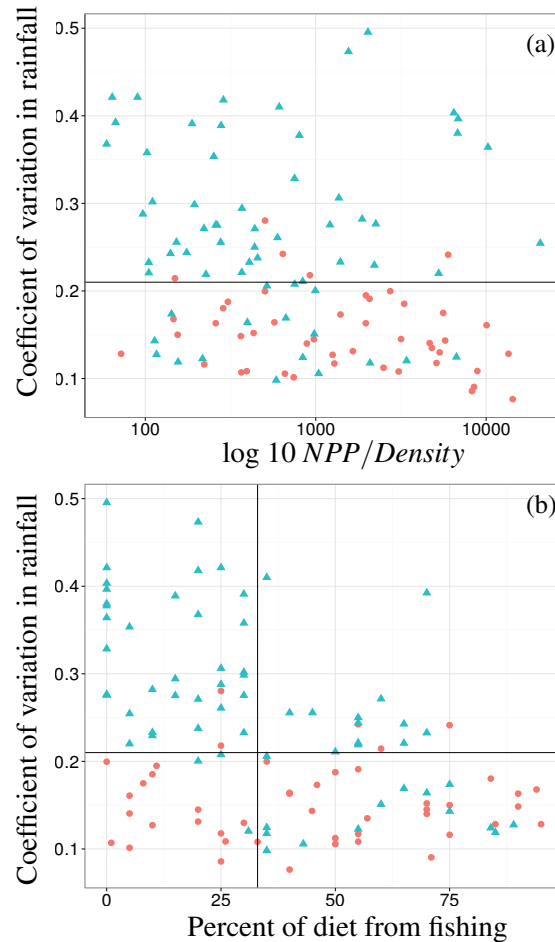


Figure 5.1: (a)-The Relationship between the estimated productivity-to-population density ratio r/p and the coefficient of variation in rainfall . NPP is in units of $g/m^2/yr^{-1}$ and Density is in units of $people/km^2$. (b)-The percent of diet from fishing and the coefficient of variation in rainfall. In both graphs, triangles = groups who produce food; circles= groups who do not produce food.

The Social-ecological Contexts of Territorial Ownership

Given the recent proliferation of arguments that institutions of resource ownership are a necessary condition for foragers to adopt domesticated plants for food (e.g., Bettinger et al., 2009; Bowles and Choi, 2013; Smith, 2012; Zeder, 2012, as well as chapter 4), it behooves us to evaluate the processes that drive the evolution of territorial ownership. In my analysis above, there is little evidence that ownership effects the likelihood that foragers produce food through strategies such as burning and planting favored food species. The production

of food may have an effect on the likelihood that foragers own territories, however. In this section, I continue to evaluate the relative ability of the URH and SOH to explain the presence and absence of territorial ownership. I study both the “full” data set (n=339) reported by Binford (2001) and the subsample of 110 societies studied above.

SOH predictions

As stated in chapter 4, the SOH predicts that the adoption of food production positively effects the likelihood that foragers adopt formal institutions of territorial ownership. This prediction is based on the underlying assumptions of the model of economic defensibility. This model states, in general, that foragers are territorial and defend ownership claims when resource density is high and predictable, and foragers forgo the defense of resources as the predictability and/or density of resources declines (Baker, 2003; Dyson-Hudson and Smith, 1978). Stated within the framework of SOH, where resources are abundant and predictable relative to a population, territories are expected to shrink because an individual forager needs less time and territory, (assuming a proportional link between time needed to harvest food and territory size) to satisfy their desired level of energy. In turn, the costs of patrolling and defending a territory also decrease as the size of a forager’s territory declines. Given these relationships, several predictions for hunter-gatherer ownership follow from the SOH.

First, we should expect that population density and the concentration of resources are positively linked. As resources become more concentrated in space-time, populations grow, density increases and, indirectly, population density has a positive effect on the likelihood of territorial ownership (P_01).

Second, as the density of resources in an environment increases, the likelihood that hunter-gatherers own territories should also increase. In hunter-gatherer societies, the density of exploited resources is a function of diet (i.e., the foods that foragers primarily target) and the growth rate (biomass growth per area per unit time) of resources. In terms of diet,

large bodied mammals are less dense than plant resources and fish or shell-fish. Thus, we should expect that groups who primarily hunt are less likely to own territories than groups who primarily gather plants or fish for food (P_o2a). Similarly, as biomass accumulates at a faster rate, resource density should increase and the likelihood that hunter-gatherers own territories should also increase (P_o2b).

Third, the predictability of resources is also a function of diet and intrinsic variation in the basic physical inputs that determine the productivity of resources, such as temperature and rainfall. It is expected here that as the inter-annual coefficient of variation associated with the productivity of resources increases, terrestrial resources become less predictable in space and time and the likelihood that hunter-gatherers own territories declines because the costs of staying put to defend resources increase and the benefits decline as resources becomes less predictable (P_o3a). Further, large bodied game are mobile and less predictable in terms of harvest than stationary resources (Coddington et al., 2011); therefore, I expected that the likelihood of ownership increases as diet shifts from mobile to stationary resources (P_o3b).

Finally, the proposed positive feedback, coevolutionary cycle between the production of food and ownership (see chapter 4) suggests a positive effect of food production on the likelihood of ownership. I expect that the likelihood of territorial ownership in hunter-gatherers societies increases in contexts where foragers produce food (P_o4).

URH predictions

As stated in chapter 3, the URH suggests that the selection of rules that formally define when and where resources are accessed (ownership) is favored in contexts where hunter-gatherer SES cross a critical net productivity-to-population density (r/p) threshold. The consequences of crossing such a threshold are discussed in chapter 3 and above. The key point is that forager-resource systems are characterized by a common pool resource

dilemma when this threshold is crossed and may transition, unpredictably, from a productive to a degraded attractor. Given this dynamic, the URH suggests that as population density increases, foragers are more likely to own territories (P_05). As population density increases, tracking and predicting the consequences of other foragers' movements on a landscape gets more and more complex. It is the information processing costs associated with determining the risk of negative critical transitions in multiple habitat level systems that provides an incentive for individuals to cooperate and use well defined rules to regulate each others movements. Thus, as population density increases and depletion creates a commons dilemma, foragers may cooperate to manage the risk of getting flipped into a degraded harvest attractor (see also Charnov et al., 1976).

In contrast to the SOH, the URH suggests that as the productivity of resources declines, the likelihood that hunter-gatherer societies own territories increases (P_06a). This prediction follows from the same argument made for the effect of increases in population density on the likelihood of ownership. A decrease in productivity too far pushes the r/p ratio past a critical threshold, and this results in the emergence of localized commons dilemmas and associated increases in the costs of processing information. Further, holding population density constant, foragers who produce food are less likely to own territories than foragers who do not (P_06b). If foragers produce food, they will dampen the effects of depletion and mitigate the emergence of localized commons dilemmas. This should result in less territorial ownership behavior, at least in the medium-term.

Finally, the URH suggests, holding the r/p ratio constant, that as inter-annual variation in the productivity of biomass increases, foragers are less likely to own resource locations (P_07). In predictable environments, individuals can discover the likelihood that external shocks, in a given year, will flip a system into a degraded basin of attraction. Thus, foragers can regulate the use of forager-resource systems on a landscape through formal rules that reduce the need to collect information on where and when foragers are harvesting

Table 5.5: The predicted direction of the effect of explanatory variables on the likelihood that hunter-gatherers own territories.

Hypotheses	Explanatory variables				
	<i>Density</i>	<i>Hunting</i>	<i>NPP</i>	<i>Enhancement</i>	<i>CV Rain fall</i>
SOH	+	-	+	+	-
URH	+	Na	-	-	-

resources. However, when productivity is too variable from year-to-year due to external drivers (climate as opposed to population density), the URH suggests that foragers invest in the production of food rather than ownership. However, the two adaptations are not necessarily mutually exclusive.

Table 5.5 summarizes the expected effects of the explanatory variables on the likelihood that territorial ownership is practiced in hunter-gatherer societies. To determine the consistency of each model with the data, I, again, focus the analysis on the direction of the effect of each explanatory variable and the relative importance of each explanatory variable for predicting the likelihood of ownership.

Results

My analysis indicates that the URH is more consistent with the data than the SOH. We should, therefore, have more confidence in the processes proposed by the URH to explain the adoption of territorial ownership than the processes proposed by the SOH. In general, we can have a high degree of confidence that 3/4 of the URH's predictions are consistent with the data (*P*_o5, 6a & 7), and we can have a high degree of confidence that 2/5 of the SOH's predictions are consistent with the data (*P*_o1 & 4). Critically, the expected effects of net primary productivity and food production on the likelihood of ownership are consistent with the URH but not the SOH. This is critical because the URH and SOH suggest mutually exclusive predictions for the effects of these two variables on the likelihood of ownership.

Table 5.6 illustrates the 95 percent confidence set of models for the analysis of the full data set (n=339). The best model includes three explanatory variables: population density, net primary productivity and the coefficient of variation in rainfall. The second best model includes all four explanatory variables. The weighting factor, w indicates that the best model is about 1.02 times more likely to fit the data, given this set of models, than the second best model that includes the percent of diet obtained from hunting. While the top two models are equally likely to provide the best fit to the data, the relative importance of individual explanatory variables tells a more interesting story.

Table 5.6: The 95 percent confidence set of models: 1=CV Rainfall 2=Density, 3=Hunting & 4=NPP

Explanatory Variables	Residual Deviance	AIC	Δ_i	w
1,2,4	407.6	415.62	–	0.44
1,2,3,4	405.7	415.69	0.07	0.43
2,4	418.11	404.61	2.48	0.13

Table 5.7 illustrates the mean coefficient and relative importance of each explanatory variable included in the 95 percent confidence set of regression models. First, population density has a positive effect on the likelihood that hunter-gatherer groups own territories, and this observation is consistent with both hypotheses (P_o1 & P_o5). Second, net primary productivity has a negative effect on the likelihood that hunter-gatherers own territories. This observation is inconsistent with the SOH (P_o2a) but consistent with the URH (P_o6a). Third, the coefficient of variation in rainfall has a negative effect on the likelihood that hunter-gatherers own territories, and this is consistent with both explanatory hypotheses (P_o3a & P_o7). Finally, the percent of diet obtained from hunting has a negative effect on the likelihood of ownership, and this is consistent with the SOH (P_o2 & P_o3b).

Although the effect of hunting is negative, the importance measure indicates that hunting is the least likely variable to have a true effect on the likelihood of ownership in the data set. The percent of diet obtained from hunting is 2.32 times less likely to have an

Table 5.7: Means, standard errors and relative importance ($\sum w$ for each variable) of the explanatory variables included in the 95 % confidence set of models for the full data set (n=339).

Explanatory Variable	Coefficient (<i>b</i>)	Standard Error	Importance
<i>Intercept</i>	0.66	0.64	–
<i>Density</i>	0.04	0.007	1.00
<i>NPP</i>	-0.007	0.002	1.00
<i>CV Rainfall</i>	-3.07	1.44	0.87
<i>Hunting</i>	-0.01	0.007	0.43

effect on ownership than population density and net primary productivity. The percent of diet obtained from hunting is 2.02 times less likely to have an effect on ownership than the coefficient of variation in rainfall. In total, the effect of hunting on the likelihood of ownership is much more uncertain than the effects of populating density, net primary productivity and the coefficient of variation in rainfall on ownership, in the full data set.

Table 5.8 examines the consequences of food production on the likelihood of ownership in the reduced sample of societies (n=110). The best model in this analysis includes population density, net primary productivity and the coefficient of variation in rainfall. The second best model includes population density, net primary productivity and the food production variable. The best model is 1.86 times more likely to fit the data than the second best model.

Table 5.9 reports the coefficients and importance of the explanatory variables for the 95 percent confidence set of regression models in the reduced sample. Consistent with the analysis of the full data set, population density has a positive effect on the likelihood of ownership and net primary productivity has a negative effect on the likelihood of ownership. Moreover, population density has a summed Akaike weight (importance) of 1, which suggests that this variable is likely to have a true effect on ownership, given the data. Net primary productivity has the second highest Akaike weight of 0.81. In contrast to the analysis of the full data set, the coefficient of variation in rainfall is a less important explanatory

Table 5.8: The 95% confidence set of models for the reduced sample of 110 societies. 1=*CV Rainfall*, 2=*Density*, 3=*Hunting*, 4=*NPP* & 5=*Enhancement*

Explanatory Variables	Residual Deviance	AIC	Δ_i	w
1,2,4	123.6	131.55	–	0.24
2,4,5	124.8	132.77	1.22	0.13
2,4	127.0	133.01	1.45	0.12
1,2,4,5	123.3	133.29	1.74	0.10
1,2,3,4	123.4	133.40	1.85	0.09
2	130.3	134.27	2.72	0.06
1,2,	128.6	134.59	3.04	0.05
2,5	128.7	134.72	3.17	0.05
2,3,4,5	124.8	134.77	3.21	0.05
2,3,4	126.9	134.92	3.27	0.04
1,2,3,4,5	123.1	135.11	3.56	0.04
2,3	130.0	136.04	4.49	0.03

Table 5.9: Means, standard errors and relative importance ($\sum w$ for each variable) of the explanatory variables included in the 95 percent confidence set of models for the reduced sample of societies (n=110).

Explanatory Variable	Coefficient (b)	Standard Error	Importance
<i>Intercept</i>	0.60	0.90	–
<i>Density</i>	4.36	1.40	1.00
<i>NPP</i>	-0.007	0.0003	0.81
<i>CV Rainfall</i>	-3.27	2.72	0.42
<i>Enhancement</i>	-0.50	0.52	0.37
<i>Hunting</i>	-0.002	0.015	0.25

variable in the reduced data set. Population density is 2.38 times more likely and net primary productivity 1.92 times more likely to have an effect on the likelihood of ownership than the coefficient of variation in rainfall. This result is very likely the consequence of reduced sample size, though it is an indication that the effect of the predictability of rainfall on the likelihood of ownership is much weaker than the effects of population density and net primary productivity.

A critical observation illustrated in Table 5.9 is that the production of food by hunter-gatherers has a negative effect on the likelihood of ownership. This observation is inconsistent with the SOH (P_o4), but is consistent with the URH (P_o6b). As with variation in inter-annual rainfall, however, the relative importance of food production is quite low.

Population density and net primary productivity are 2.70 and 2.18 times more likely to affect the likelihood of ownership, respectively, than food production. In sum, it is highly uncertain whether food production has an effect on the likelihood of ownership, relative to population density and net primary productivity.

Finally, in the reduced data set, the percent of diet obtained from hunting is the least important explanatory variable. The effect of hunting on the likelihood that hunter-gatherers own territory is consistent with the SOH (*P_o2a & 3b*). In this reduced data set, however, hunting is the least likely variable to have an effect on the likelihood of ownership.

Reflection & Conclusion

Ethnographic observations have a fundamental role in the development of explanations for archaeological phenomena; this is commonly recognized (e.g., Skibo, 2009). There are two competing views on the role of ethnographic observations in archaeological research. The first view is that ethnographic observations provide a store house of analogies that archaeologists can draw upon to interpret the archaeological record (Watson, 1980). A second view is that ethnographic observations are best studied from a comparative perspective to identify the general principles that underlie variation in human societies (Binford, 2001, 1990). In turn, patterns in the archaeological record, in conjunction with other data sets, are used to evaluate the relevance of general principles identified from ethnographic comparisons. In this chapter, I contribute to the identification of general principles that operate across hierarchical levels in social-ecological systems to drive the coevolution of foraging strategies and a resource base.

In chapters 3 and 4 I took on the challenge of defining two explanations for social and technological change hunter-gatherer SES. I developed the URH and SOH, in particular, to explain the evolution of territorial ownership and the adoption of food production in hunter-gatherer SES. My purpose in this chapter has been to evaluate the relative merits of

Table 5.10: A summary of the predicted effects of explanatory variables on food production and territorial ownership. Predictions highlighted in bold were supported by the data, predictions with a strike were not supported, and predictions in plain text were supported, but with a very low degree of confidence relative to the predictions in bold.

<i>Food production</i>		Explanatory variables			
Hypotheses	<i>Density</i>	<i>Fishing</i>	<i>NPP</i>	<i>Ownership</i>	<i>CV Rainfall</i>
SOH	+	-	+	+	+
URH	+	-	-	no effect	+

<i>Ownership</i>		Explanatory variables			
Hypotheses	<i>Density</i>	<i>Hunting</i>	<i>NPP</i>	<i>Enhancement</i>	<i>CV Rainfall</i>
SOH	+	-	+	+	-
URH	+	Na	-	-	-

these two hypotheses. I have used large ethnographic and ecological data sets to evaluate the consistency of ten predictions reasoned from the logic of each hypothesis with the data (see Table 5.10). The URH is, in a sense more consistent with the data than the SOH. While not a single prediction of the URH was inconsistent with the data, we can only have a low degree of confidence in the effects of the percent of diet obtained from fishing on food production and food production on ownership. In contrast, 4/10 predictions reasoned from the SOH are inconsistent with the data. The most important are: 1) hunter-gatherers are less likely to own territories and less likely to as the growth rate of biomass increases (*NPP*); 2) hunter-gatherers are less likely to own territory, controlling for all other variables, when they also engage in the production of food. 3) Finally, hunter-gatherers are more likely to produce food the the net primary productivity of an environment declines.

A prediction unique to the SOH was the positive effect of territorial ownership on the likelihood that hunter-gatherers produce food. This prediction follows from the supposition that the ownership of territory and food production are directly related in a positive feedback loop. In chapter 4, it was illustrated that the augmentation of resource biomass in a hunter-gatherer SES results in an increase of non-subsistence time because, if adopted by a sufficient number of foragers, food production increases the availability of biomass to

foragers and decreases the amount of time necessary to harvest resources. Following Smith (2012), food production would have the effect of decreasing the territory size of foragers and reducing the costs of territorial defense/ownership. This is where the positive feedback loop is expected to emerge. The production of food creates a context in which the benefits of territorial ownership outweigh the costs, and ownership rules and norms evolve. These rules and norms, in turn, provide an incentive to invest more in the production of food and manage the productivity of resources. This is a clean argument; however, it is not process that seems occur in the ethnographic data analyzed in this chapter. On average, the ownership of resources has a negative effect on the likelihood of food production, but there is a great deal of uncertainty associated with this coefficient (Table 5.9). Of all of the variables analyzed, the ownership of territory is the least important (i.e., least likely variable to have an effect on the likelihood of food production in the data set).

Even more intriguing is the fact that the production of food by hunter-gatherers actually has a negative effect on the likelihood that hunter-gatherers own territories (see Table 5.9). This observation, combined with the irrelevance of territorial ownership for predicting the production of food, suggests that the adoption of food production and ownership are not related in a positive feedback cycle, at least as far as synchronic ethnographic comparisons are able to reveal. In retrospect, this is perhaps not all that surprising. The SOH makes the assumption that as the density of resources in space and time increases, foragers use less territory to meet their energetic desires and the costs of “owning” a territory decline while the benefits simultaneously increase. This assumption applies to individuals and the costs vs. benefits for one individual do not necessarily scale-up in an additive way to a social group. The ownership of territory by a social group requires collective action to agree upon rules that govern who, when and where resources may be accessed. Such an agreement requires individuals to undertake costly behaviors, such as: perform rituals that reaffirm the rules, monitor and defend territories, as well as sanction individuals who violate the

rules (e.g., Fehr and Fischbacher, 2004; Ostrom, 1990; Sigmund et al., 2010). The costs of these behaviors may not simply add up to the costs experienced by each individual, while the benefit accrues to the social group rather than each individual directly per se. In fact, ownership rules may relegate some individuals to inferior territories.

This raises the intriguing question of why individuals would agree to rules that are costly and the benefits are potentially unequally distributed? The logic of the URH suggests an answer. Individuals cooperate to institute ownership rules when shirking the rules means that everyone has to deal with more uncertainty in their ability to make robust land use choices. Based on the URH, we can surmise that one social-ecological context in which the benefits of collective action to own territories outweigh the costs for individuals is when localized commons dilemmas emerge in a larger forager-resource system. I argued in chapter 3 that once a critical, landscape specific r/p ratio is hit, every local forager-resource system on a landscape is vulnerable to a negative critical transition. Two sources of environmental variation might generate a negative critical transition. One is external drivers of the availability of biomass, like inter-annual variations in rainfall. The other is the actual harvest behavior of foragers that locally depletes biomass on a landscape. Local harvest rates vary as individuals and groups move between habitats on a landscape. Both of these sources of variation might perturb local forager-resource systems and vary predictably or extremely unpredictably in space and time.

If foragers live in environments where uncertainty in the ability to estimate the risk of local critical transitions is only driven by external variations, like variations around climate means, then foragers cannot adapt by simply cooperating to regulate who, where and when local systems are accessed on a landscape. This is because it is very difficult to process enough information to know from year-to-year the systems that are most and least likely to transition into a degraded attractor. In this context, the best option is to increase the growth rate of resources in an environment, and mitigate the chances of local attractor shifts by

increasing the r/p ratio of habitat level systems. This is, in fact, evidenced in Figure 5.1a where foragers produce food in environments where the inter-annual coefficient of variation in rainfall is greater than 0.21.

In contrast, if the harvest activity of other foragers is the primary source of variation that can depress the availability of biomass, then uncertainty in the ability to estimate the risk of a negative critical transition is primarily a function of population density. An increase in population density (which creates a decrease in the r/p ratio) means that there are more foragers to keep track of and the potential that foragers incorrectly estimate how much harvest effort systems at the habitat level can cope with without generating a negative critical transition. This, again, creates a highly non-linear increase in the amount of information that foragers must process and, I suggest, creates a context in which the benefits of collective action for individuals outweigh the costs. In this case, cooperating to define who, when and where habitats are accessed will regulate the distribution of harvest effort on a landscape, and reduce the uncertainty associated with planning where to locate in space and time to harvest food.

Onward

How does all this translate into an understanding of archaeological data? This is the issue taken up in the final chapter. At this point, suffice it to say that the URH implies that the adoption of food production and territorial ownership are alternative strategies for reducing the uncertainty associated with planning where to locate in space and time to harvest food. The strategies may or may not co-occur. Co-occurrence will depend on the interaction of the r/p ratio of a landscape, variation in the movement of populations and variation in ecosystem inputs (like rainfall). I now turn my attention to describing how the knowledge gained in chapters 3-5 can be used to guide archaeological research.

Chapter 6

CONCLUSION

“The hardest thing of all is to find a black cat in a dark room, especially if there is no cat.

According to Stuart Firestein (2012), science, as a process of learning, is a lot like searching for a black cat in a dark room. Science is the process of searching for answers in a dark room that may contain no answers at all. Chapters 3-5 have been the search for a black cat in a dark room. The black cats, if you will allow, are the evolutionary processes that lead to the adoption of food production and territorial ownership by hunter-gatherers. This search, I believe, has shown a glimmer of light into *one* of the dark rooms that might shroud the evolution of hunter-gatherer SES into agricultural SES in a veil of ignorance. The challenge ahead is to decipher if the room even contains a cat. In this final chapter I have two aims. First, I revisit the Uncertainty Reduction Hypothesis (URH). Second, I sketch out how the URH can guide archaeological research into the evolution of agricultural SES at the expense of hunting and gathering SES. This final chapter is not about answers. It is about questions. The questions are a result of the processes revealed by my study of simple, dynamic models and the analysis of ethnographic data. Our understanding of how feedback processes generate evolutionary change in small-scale societies, however, is (from the viewpoint of anthropology) still in its infancy. I am optimistic that the integration of data and theory, as well as a commitment to evaluating multiple arguments with a diversity of methods will radically change this situation in the coming years.

The Uncertainty Reduction Hypothesis Revisited

In chapter 1 I made the argument that evolutionary ecology needs theory from dynamical systems and concepts from resilience thinking to understand some of the major evolutionary transitions in human-resource systems. The reason is quite simple. When systems are characterized by feedback processes, then the dynamics of the system are not simply an additive result of the behaviors of individuals that make-up the system. This idea is succinctly captured by the well turned phrase that “the whole is more than the sum of its parts” (Bak, 1996; Holland, 1995). When the whole is more than the sum of its parts, the non-linear dynamics of a system can generate selective pressures on individuals to modify their strategies for using resources. In turn, this modification at the level of the individual transforms a human-resource system. This is no doubt old news in evolutionary ecology (e.g., Clark and Mangel, 1986; Stephens et al., 2007), but the field of human behavioral ecology has been slow to adopt and use the tools of dynamical systems (but see Anderies, 2006, 1996; Brander and Taylor, 1998; Freeman and Anderies, 2012; Janssen et al., 2003; Phillips, 2012; Winterhalder et al., 1988; Winterhalder and Lu, 1997). In this dissertation, I have used formal and conceptual models to study the effects of feedback processes in forager-resource systems on the potential costs and benefits of foraging strategies for individuals. In particular, I sought to understand how feedback processes might affect the costs and benefits of food production and territorial ownership for individual foragers. I asked two general questions about a generic forager-resource system (chapter 3):

1. How do changes in the productivity of resources and population density affect the robustness of foragers’ energy output and time budget in a forager-resource system to sets of potential shocks?
2. If there is an effect, how might the state of a forager-resource system shape the costs and benefits of the strategies that foragers could select to manage resources?

My investigation of these questions led to the construction of two alternative hypotheses, the URH and the Social Opportunity Hypothesis (SOH). The SOH deserves and will receive further consideration. However, cross-cultural analysis of hunter-gatherers suggests that the dynamics proposed by the URH are more relevant for understanding food production and ownership documented ethnographically than the SOH (Table 5.10).

There are two basic generalizations that ground the URH. First, hunter-gatherer SES are characterized by a nested hierarchy of forager-resource systems. The dynamics in each forager-resource system play out at different scales of space and time (See Figure 3.7 in chapter 3). Thus, individuals face a decision hierarchy that scales in space with the forager-resource hierarchy (Orians, 1980). However, decisions about how to position within the forager-resource system hierarchy occur faster than the processes that perturb resource systems (i.e., ecosystems) as one moves up the forager-resource hierarchy (Holling, 1992; Peterson et al., 1998). Second, in general, moving up the forager-resource system hierarchy means that the dynamics of forager-resource systems get more costly to track for an individual forager simply because there are more dynamics operating in space and time.

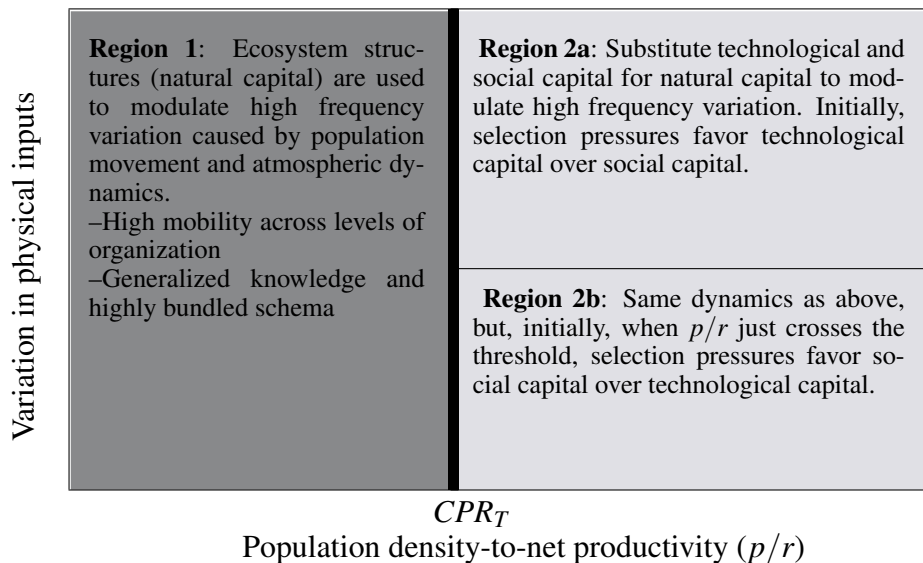


Figure 6.1: Summary of the uncertainty reduction hypothesis.

Given these two generalizations, I have used my knowledge of the dynamics in the baseline hunter-gatherer SES (presented in chapter 3) to generate insight into the social-ecological conditions that effect the costs vs. benefits of territorial ownership and the adoption of food production. Figure 6.1 summarizes the URH. The primary variables that control the dynamics of a forager-resource system are the population density of foragers and the net productivity (growth rate) of a resource base. In any given system, when the p/r ratio is really low (Region 1 on figure 6.1), foragers can obtain their desired level of energy in a minimum amount of time and their ability to achieve their energy goals is completely robust to high frequency environmental perturbations. I propose that in real SES, this type of robustness is derived from landscape scale ecosystem structures. At the landscape scale, ecosystems serve as a storage bank of natural capital that modulates the effects of higher frequency disturbances that affect resources at more local scales. For example, a fire might wipe out several stand of oak trees that foragers use for food within a habitat scale system, but at the landscape scale, the forest has many habitats with stand of oak trees. To take advantage of this, however, individual foragers must keep track of processes that operate at many scales of space and time, which increases their high information processing load.

I propose that when forager-resource systems operating at the upper two levels of the forager-resource hierarchy are simultaneously in Region 1 of Figure 6.1, selection and copying pressures favor: (1) high mobility across levels of ecosystem structures (i.e, the use of many patches, habitats and landscapes at different scales of time (Binford, 1983) and 2) ecological knowledge that sacrifices detail for generality. I expect (1) because it is frequent movement across all scales that allows foragers to minimize the time expended to get food and preserve their budget of non-subsistence time that can be converted into fitness gains. I expect (2) because individuals need to minimize the information processing cost (time) necessary to keep track of dynamics across many levels of forager-resource systems. Highly generalized knowledge allows an individual to quickly categorize the state of a

forager-resource system and efficiently plan how to sequence their movements in space and time.

As the p/r ratio increases at the upper level of the forager-resource system hierarchy (i.e., on landscapes), foragers can maintain the robustness of their energy supply by working a little harder. I expect that this leads to slight increases in residential stability. From the perspective of an individual forager, working harder may not even be all that noticeable. In chapter 3, I demonstrated that an increase in the p/r ratio (by decreasing r from 0.5 to 0.3) results in a mere increase of 28 minutes per workday over the course of months-to-a couple of years to harvest food (holding all other parameters constant). The insight is that simply working a bit harder may appear satisfactory for maintaining a robust supply of energy to an individual, but the aggregate effect of all individuals doing this creates a stochastic common pool resource dilemma. In short, by working harder, individuals make achieving their harvest goal robust to slow changes in population density or the mean resource growth rate of a system, but the forager-resource system becomes vulnerable to a critical transition into a degraded attractor caused by environmental variations (like negative deviations from the mean in rainfall). In the degraded attractor, no forager can achieve a desired level of resource harvest.

The p/r ratio labeled CPR_T in Figure 6.1 marks the threshold at which every forager-resource system at the habitat level in a forager-resource hierarchy is vulnerable to a negative critical transition. Although working harder may not seem onerous for an individual, once the CPR_T threshold is hit in a system, some habitats will experience variance induced flips from a productive to a degraded attractor. This will not cause anyone to starve (unless every habitat permanently flips simultaneously), but it will create increasing variance in the ability of individuals to obtain their desired level of food over successive years. I argue that it is this variance that creates a context in which selection favors foraging strategies that substitute technological and social capital for natural capital to increase the robustness

of individuals' food output. Individuals who find successful strategies are more likely to be copied than those who are unsuccessful, leading to the spread of such strategies in a population.

In chapter 3 (Figure 3.6), I argued that the primary consequence of a landscape level forager-resource system crossing the CPR_T threshold is that it becomes computationally messy for individual foragers to discover and transmit the best sequence of moves between habitat level systems to distribute their foraging effort. Two sources of variation generate uncertainty and stress the information updating capacity of foragers. 1) Fluctuation in the physical inputs that disturb a resource base (rainfall and solar energy), and 2) population movements that change the distribution of foraging effort among systems. I argue that the production of food at lower-levels of the forager-resource hierarchy is selected by foragers in response to unpredictable variation in the physical inputs that shock a resource base. Where physical inputs are more predictable, foragers use rules of territorial ownership to regulate the movement of individuals among habitat level systems. These arguments are summarized by Region 2a and b on Figure 6.1. Both of these strategies would reduce the need to collect information over many habitat scale systems for individuals and reduce or hold steady the susceptibility of habitat scale systems to a negative critical transition by decreasing or stabilizing the p/r ratio of habitat level systems.

Although I argue that food production and ownership rules are alternative strategies for gaining robustness to variation in population movements and physical inputs, I expect that if the p/r ratio increases too far, selective pressures do necessitate that foragers adopt both strategies simultaneously. Once a system crosses into Region 2, selection pressures also favor less movement at the habitat level and increasingly detailed knowledge of the resources nested with the habitats that foragers use. In Region 2a, I expect that selection favors strategies that allow foragers to maintain access to different landscapes through the formation of social capital. This way, if a forager's landscape gets hit by a physical shock

that causes every habitat system to temporarily undergo a negative critical transition, a forager can access alternative landscapes via social connections. This, of course, depends on alternative landscapes experiencing anti-correlated shocks (e.g., Anderies et al., 2008; Cashdan, 1983; Kelly, 1995; Winterhalder, 1990). In settings with predictable physical inputs into ecosystems, I expect more spatially constricted social networks that are not as likely to cross-cut many landscape level systems.

Some final thresholds

To conclude my discussion of the URH, I would like to illustrate several empirical thresholds highlighted by Figure 6.2a. Figure 6.2a displays the strategies of hunter-gatherer groups in the reduced sample studied in chapter 5. The graph is divided into four quadrants. In the lower left quadrant, 16/19 “generic” hunter-gatherer groups are recorded. These groups neither own territory nor produce food, and most of these cases cluster at a very low p/r ratio. The lower left quadrant also contains 24/27 groups who own territory but do not produce food. Thus, groups who simply own territory are biased toward environments with predictable rainfall. These groups also tend to live at a p/r ratio greater than “generic” hunter-gatherer groups. The upper left quadrant of the graph contains 21/26 groups who just produce food. Finally, in the right two quadrants of the graph, 12/13 societies practice ownership and produce food, regardless of the predictability of rainfall. These patterns suggest that foragers select strategies that elaborate their technological and social capital as the p/r ratio of a system increases in an effort to reduce uncertainty in the maintenance of a sufficient flow of resources. The long-term consequences, I speculate, are increasing population growth, inequality and increases in per capita energy use (Tainter, 2011). Different Boserupian “fixes” to Malthusian constraints.

Figure 6.2b adds agricultural societies to the mix (see Freeman (2012a) for data). There is a clear threshold at approximately $\log_{10} p/r = 0.018$ where hunter-gatherer societies

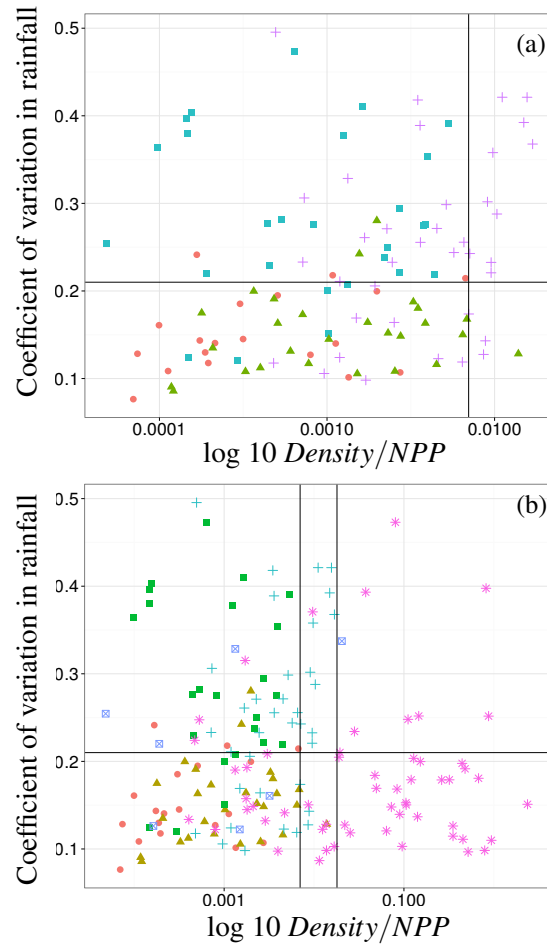


Figure 6.2: Both graphs illustrate the log 10 of the ratio of population density (people/ km^2) to net primary productivity (grams/ $m^2/year^{-1}$) on the x-axis and the coefficient of variation in rainfall on the y-axis. Threshold lines are placed at a coefficient of variation of 0.21 and a population density-to-resource growth ratio of -4. Circles=generic hunter-gatherers; squares=hunter-gatherers produce food; triangles=hunter-gatherers own territories, plus sign=hunter-gatherers both produce food and own territories; box with x=ancillary cultivating hunter-gatherers; stars= agriculturalists ($\geq 30\%$ of their diet from agriculture after Freeman (2012a).

end and agricultural societies dominate. However, agricultural societies also “overlap” with hunter-gatherer societies, especially in settings with predictable rainfall. I suspect that the secondary adoption of domesticated plants by hunter-gatherers is an alternative way to decrease the uncertainty associated with maintaining a flow of resources when commons dilemmas are a threat in multiple habitats on a landscape (Freeman and Anderies, 2012). I strongly suspect that, in some environments, the adoption of domesticated plants allows

individuals to maintain a greater autonomy over their access to resources than elaborating rules of ownership might allow. If this is so, a counter intuitive expectation arises. In predictable environments where foragers share the same p/r ratio as forager-farmers, the forager-farmers are less territorial and wild resources are more freely accessed relative to hunter-gatherer groups who recognize territorial ownership.

Moving on...

One motivation of this dissertation has been to investigate, in general, how feedback dynamics between foragers and resources drive the evolution of hunter-gatherer SES. At a deeper level, my motivation has been to identify the general evolutionary processes that cause agriculture SES to evolve at the expense of hunter-gatherer SES. My basic, though implicit, assumption is that highly general arguments provide a necessary compliment to local studies that focus on historically contingent sequences and processes. Consider the statement made by Zeder (2006:114-115) on the emergence of agriculture:

[r]ather than a single forcing mechanism, it seems more likely that the trajectory of plant and animal domestication in the Near East and the emergence of agriculture was shaped by various broad-scale factors, such as climate change, economic goals, and social opportunities and constraints, interacting with highly local, contingent factors, such as the density and diversity of available resources, the history of human occupation, and the agency of individuals coping with their environment, each other, and their universe...Attempts at explanation that champion any one of these factors and deny the importance of others will not, in the long run, contribute to understanding agricultural origins either as a general process or as it played out in particular instances.

Certainly, Zeder's (2006) assertion is sound; every phenomenon, whether it is a society, person, animal or daisy results from a unique confluence of processes. But, are the processes that lead to the evolution of agricultural SES so contingent that every possible variable is equally important in the construction of an explanation? I argue, no. By formally studying feedbacks in a modeled and highly general forager-resource system, the power of generalization is unleashed. Generalizations are tools for learning that illuminate the contingent variables that are important in any particular place and time. The URH is a highly general argument that applies to any system in any place or time. However, the above thresholds suggest that to continue building our understanding of the processes that cause agricultural systems to evolve at the expense of hunting and gathering, we have to leverage the URH to ask questions about the more specific attributes that affect the stability of forager-resource interactions in specific regional contexts. The URH provides a set of general dynamics that serve as a guide for designing archaeological research to do just that.

Using the URH to Guide Archaeological Research

As Binford (2001:epilogue) has optimistically noted, the primary constraint on our ability to understand the archaeological record is our imagination, which implies that we can explain almost any archaeological phenomenon, as long as we develop the tools to expand imagination. The URH provides a more informed position to imagine why agricultural systems evolved in human societies at the expense of hunting and gathering. In this section I would like to provide a brief illustration of how the URH might be used to guide archaeological research. Specifically, I illustrate how the URH can guide archaeological research into the evolution of economies based on agriculture at the expense of hunting and gathering.

The processes that might lead to the initial adoption of domesticated plants are intensively studied by archaeologists (e.g., Barker, 2006; Bellwood, 2005; Binford, 2001,

1968; Childe, 1928; Flannery, 1985, 1973; Hayden, 1990, 1998; Huckell, 1995; Kennett and Winterhalder, 2006; MacNeish, 1992; Piperno and Pearsall, 1998; Rindos, 1984, 1980; Smith, 1995; Wills, 1988; Winterhalder and Goland, 1993, this dissertation). The long standing justification for this intensity of research is that the adoption and spread of domesticated plants fundamentally altered human-environment interactions, eventually leading to dramatic changes in settlement, land use and social equality (e.g., Harris, 1996; Hayden, 1990; MacNeish, 1992:3; Smith, 1995:3; Wills, 1988:1). However, a change in settlement, land use or social equality is not always correlated with the adoption of domesticated plants per se (as argued above), but is often coincident with the specialization of production on domesticated plants (Bender, 1978; Flannery, 1968; Hayden, 1990; Hunter-Anderson, 1986; Nichols, 1987). Prehistoric human-environment interactions changed profoundly when prehistoric societies began to specialize by disproportionately allocating their time to the production of domesticated plants at the expense of time previously devoted to hunting and gathering. Thus, a fundamental question is: *Once domesticated plants became part of the subsistence base, why did people in some archaeological regions increase their time invested in farming at the expense of hunting and gathering while in other regions people engaged in persistent mixed foraging and farming* (Bettinger et al., 2009; Doleman, 2005; Freeman, 2012a; Harris, 1996; Hard, 1986; Hunter-Anderson, 1986; Phillips Jr, 2009; Smith, 2001; Vierra, 2005; Zvelebil, 1996)?

The URH suggests a set of dynamics that can help generate analyses to answer this question in archaeological contexts. Figure 6.3 summarizes the feedback dynamics that should determine the resilience of a productive attractor in a forager-resource system and, as a consequence, the robustness of individuals' supply of wild resources to climate variation and population movements (variation in harvest effort). At base, the URH suggests that where forager-farmer's supply of wild food is more robust to population and climate shocks, the evolution of agricultural systems is slow. Where forager-farmer's supply of

food is less robust to climate and population variation, individuals specialize on domesticated plants more quickly at the expense of hunting and gathering. My basic postulate is: *the more effectively feedback processes identified in Figure 6.3 modulate variation in climate and population movement, the more resilient the productive attractor of a forager-resource system. In turn, the wild resource food supply of individuals' is more robust and uncertainty is less likely to stimulate forager-farmers to substitute domesticated plants for wild resources.*

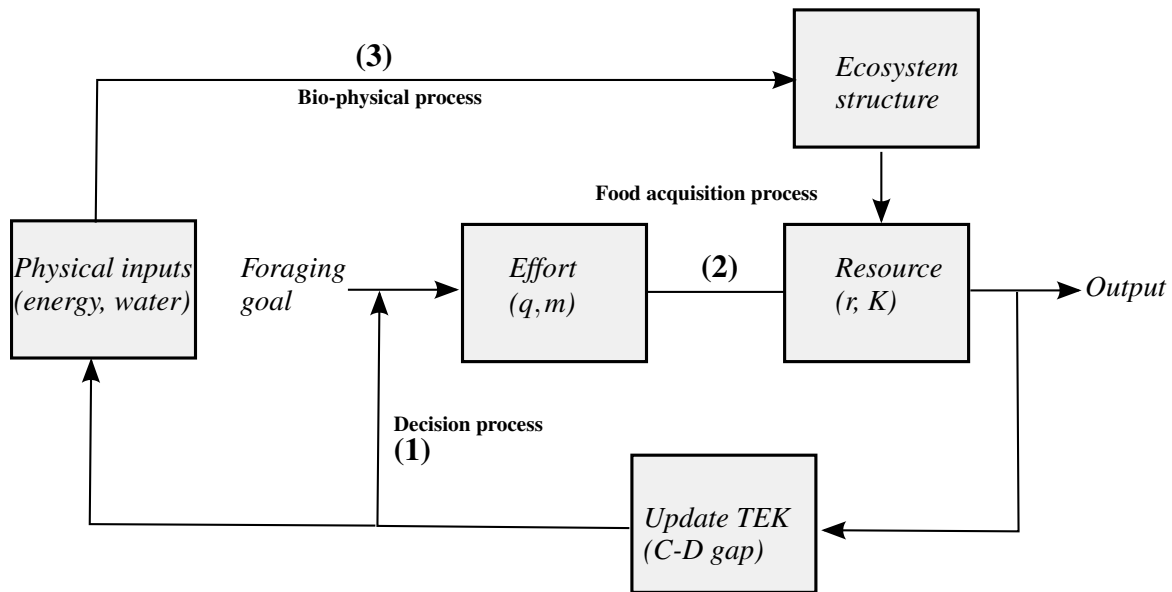


Figure 6.3: Final proposed feedback structures that affect the robustness of foragers' supply of energy to population movements and climate variation.

Figure 6.3 has two feedback loops. The outer loop links the physical inputs, like water and energy, that determine the productivity of an ecosystem with the structure of an ecosystem (e.g., the composition of species) and, finally, the resource base. This outer loop simply states that variation in the growth rate (r) and carrying capacity (K) of a resource base is determined by variation in the physical inputs that hit the resource base. Variation in r and K , in turn, is modulated by the composition of the community of organisms that make-up and ecosystem. This is simply to say that, due to variation in the structure of ecosystems,

a 10 % change in rainfall will not affect all ecosystems the same. The inner loop links the goal of the foragers in a system with the resource base and body of cultural knowledge that foragers use to make decisions about where, when and how to harvest resources.

The decision process (1) links the knowledge system of foragers with the rules, norms and technology that foragers draw on to allocate effort to the acquisition of food. The decision process primarily modulates variation in the distribution of harvest effort. Institutions set the rules of the game (Ostrom, 2005) that individuals follow to make decisions about where and when to harvest resources. Variation in the effectiveness of rules that coordinate the use of forager-resource systems within a hierarchy should affect how unpredictable the distribution of harvest effort is on a landscape. More formal rules that reward collective action should yield less unpredictability and less formal rules should yield more unpredictability (given that the CPR_T threshold for a “pure” foraging system has been crossed).

The food acquisition process (2) links the foraging decisions of foragers and the resource base to produce an output of food. The food acquisition process for a given technological regime can either increase or deplete the future availability of food in a forager-resource system. This process modulates the susceptibility of a forager-resource system to climate and population shocks. Holding population density constant, a negative effect of harvest effort on resource density will make a system more susceptible to shocks while a positive effect will make a system less susceptible (see chapter 4). The effect of harvest effort on resource density is a function of harvest strategy (e.g., burning to find prey) and the reproductive characteristics of the resources in question. For example, flowers with underground storage organs that reproduce vegetatively (which many mammals eat) may actually increase in density due to harvest pressure rather than deplete (Anderson and Rowney, 1999). This is a result of the reproductive strategy of the plants. In situations where foragers adopt domesticated plants for food, if the net effect of harvest effort on wild resources increases the density of those resources, I expect that the wild resource sys-

tem is more resilient and a mixed forager-farmer strategy persists. In situations where the net effect is negative, I expect that the wild resource component of the diet is more sensitive to environmental variations and forager-farmers compensate for uncertainty in the wild resource domain by specializing more quickly on domesticated plants.

Finally, the bio-physical process (3) links atmospheric dynamics that create patterns of rainfall and energy availability with the structure of ecosystems. This process describes the modulating effects of ecosystem structures on variation in the productivity of an ecosystem caused by “disturbance,” in this case, variation in the physical inputs that flow into an ecosystem. As I argued above and in chapter 3, ecosystem structures modulate the effects of variation in physical inputs on the productivity of an ecosystem. Structures refer to the attributes of communities of organisms interacting at either the patch, habitat or landscape scale of an ecosystem hierarchy.

Recent work in community ecology has demonstrated the overwhelming importance of two attributes of ecosystems for modulating variation in the productivity of an ecosystem: functional redundancy and response diversity (e.g., Elmqvist et al., 2003; Norberg et al., 2001; Norberg, 2004; Tilman et al., 1996; Walker et al., 1999). Functional redundancy refers to the role of an organism in an ecosystem (e.g., a nitrogen fixer), and the number of species in an ecosystem that perform the same function. Response diversity refers to the variability in how species tolerate and come back from a disturbance. For instance, consider an assemblage of 5 fruiting species of plants. If all five plants stop producing fruits if subject to a light frost, this assemblage is has no response diversity (every species responds by shutting down the production of fruit). On the other hand, if only one of five species stop producing fruit when hit by the frost and the other four each have an alternative response (possibly including no response), the assemblage has a high response diversity.

Norberg et al. (2001) elegantly demonstrate that ecosystems composed of species with diverse tolerances of climate conditions are more productive and less variable over long

time-scales than ecosystems composed of species with a more limited number of tolerances and functional redundancies. The increase in long-term productivity results from the modulating effect of response diversity on short-term boom and busts in productivity generated by environmental variation. In terms of the resilience of forager-wild resource systems, we should expect a productive forager-resource regime to be more resilient as the response diversity of the food resources in an ecosystem increases. As the response diversity of resources increases, we should expect that variation in the availability of food caused by climate shocks is reduced. As the response diversity of food resources decreases, we should expect greater variation in the availability of wild food driven by disturbance processes.

Table 6.1 summarizes the general dynamics of the URH, the expected effects of these dynamics on how quickly forager-farmers specialize in the production of domesticated plants and data that might be used to assess the expected effects. Table 6.1 provides a set of expectations for archaeological research into the persistence of low-level food production. To end this dissertation, I would like to briefly illustrate how we might start to use these expectations to investigate questions about archaeological data.

A brief illustration from the US Southwest

The deserts of the southwestern United States provide an interesting case study to briefly illustrate how the dynamics of the URH might start to be evaluated in an archaeological context. The pace at which the specialized production of maize farming developed prehistorically across the Eastern Jornada, Western Jornada Mogollon and Southern Arizona/Tucson Basin archaeological regions of the American Southwest differs markedly (Figure 6.4). Archaeological data, in general, suggests that specialization toward maize farming was most rapid in Southern Arizona while specialization in the farming of maize was the least rapid in the Eastern Jornada (Abbott et al., 1996; Diehl, 2005, 1996; Doleman, 2005; Hard, 1986; Hard and Roney, 2005; Hard et al., 1996; Huckell, 1995; Mabry, 2008;

Table 6.1: Expected effects of feedback processes on the pace of specialization on domesticated plants for food at the expense of hunting and gathering.

Feedback process	URH dynamic	Expected effect	Relevant data
Bio-physical process	Increasing response diversity of food species to disturbance in a FRS	Reduce rate of specialization	Catalog of edible species in archaeological region, tolerances of species to physical inputs
Food production process	Positive effect of harvest behavior on the density of wild resources	Reduce rate of specialization	Catalog of edible species, reproductive traits of edible species, pollen data for evidence of fire, site density or radio carbon date frequencies to estimate population density
Decision process	Ownership institutions regulate population movement and reduce uncertainty	Reduce rate of specialization	Site density or radio carbon date frequencies to estimate population density, distance of ceramic or obsidian movement territory boundedness, bone isotopes to estimate territory size or movement, rock art consistent with territorial demarcation

Mauldin, 1996; Phillips Jr, 2009; Roth, 1992).

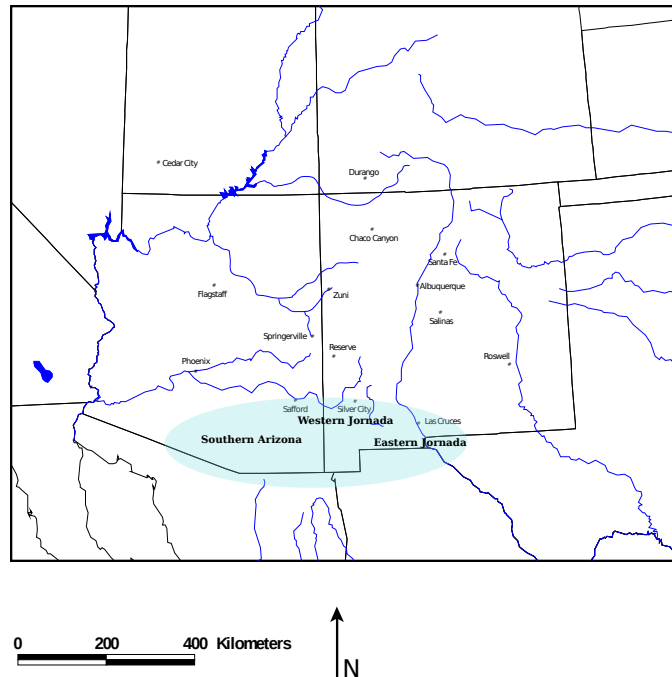


Figure 6.4: Map of the Southwest United States and Northern Mexico. Archaeological case studies are highlighted by a blue oval.

All three regions are located in the basin and range zone of the American Southwest, and were initially colonized by Paleoindian populations by 12000 BP (Abbott et al., 1996; Huckell, 1996; Mauldin, 1995). By 3000 BP prehistoric inhabitants in all three regions had adopted the production of maize (Abbott et al., 1996; Diehl, 1996; Hard, 1986; Huckell, 1996, 1995; Mabry, 2008; Mauldin, 1995). However, after the initial adoption of maize in Southern Arizona, specialization occurred relatively quickly with investments in irrigation infrastructure, storage and significant residential stability by 2500 BP, a trend of increasing specialization that was fully manifest prior to 1000 BP (Huckell, 1996, 1995; Mabry, 2008, 2002; Roth, 1996; Wills and Huckell, 1994). In the western Jornada, maize specialization occurred more slowly after the initial introduction of the crop; however, by 1500 BP populations in the region were rapidly specializing in maize production (Diehl, 1996) and investments in irrigation and significant residential stability are evident by 1000 BP

(Diehl and LeBlanc, 2001). In the Eastern Jornada, maize use remained relatively minor between 3000 and 900 BP (Hard et al., 1996; Mauldin, 1996; Whalen, 1994). Populations maintained a relatively stable mixed forager-farmer subsistence strategy for roughly 2100 years, with specialization occurring rapidly after 900 BP (Abbott et al., 1996; Hard et al., 1996).

The response diversity of species to temperature extremes in the southern US Southwest

What explains the apparent persistence of a mixed forager-farmer adaptation in the Eastern Jornada and more rapid specialization in the production of maize at the expense of hunting and gathering in the Western Jornada and Southern Arizona? Based on the URH, one possibility is that the wild food species that foragers had access to in the Eastern Jornada had a greater level of response diversity than did the food species in the Western Jornada and Southern Arizona/Tucson Basin. If this were the case, once foragers in all three regions had adopted domesticated plants, I would expect that foragers in the Eastern Jornada experienced less variance in their ability to gather wild resources and less pressure to reduce their information processing over a forager-resource system hierarchy by specializing in the production of maize. Differential rates of population growth, the effectiveness of institutions of ownership and the net effects of harvest pressure also may be important. Here, I simply treat these variables as constants. This is a simplification dictated by purpose: to illustrate the potential of the URH to guide archaeological research not to fully resolve why specialization was slower in the Eastern Jornada.

I focus here on the tolerances of assemblages of edible plants in the southern US Southwest to cold extremes. I assume the greater the response diversity of an assemblage of food species is to cold, the better able that assemblage dampens variation in a food supply that might be caused by a cold extreme of a given intensity. The range of plant tolerances in

an assemblage dictates the most intense cold extreme that an assemblage can take and is likely to still contain species that produce food. The methods for estimating the number of edible plant species (n=741 species) and the tolerance of each species to cold is detailed in Appendix A. As I stated above, the point of this data exercise is to illustrate how the URH can guide analyses and help us investigate prehistoric human-environment interactions.

Figure 6.5a illustrates the estimated number of edible species in a vegetation zone across the southern US Southwest. The study regions are highlighted by the dashed box. Figure 6.5a illustrates that in the western portion of the focal study area, there is fine grained variation in the number of edible species across the landscape. This is to say that the distance between a vegetation zone with many edible species and a zone with a few edible species is very short. In the eastern portion of the study area there are large vegetation swaths full of many edible species and larger swaths that have fewer species. This overall pattern might be related to how elevation gradients change from east-to-west and may affect how hunter-gatherers use a landscape (Doleman, 2005). Please note, my analysis here is simply illustrative. More work is required to rigorously quantify at various spatial scales the number of edible species across the study region, using tools like moving window analysis.

Figure 6.5b illustrates the mean tolerance of an assemblage of food species. This map provides a very different picture of the landscape than Figure 6.5a. Although the western portion of the study area tends to have more edible species than the eastern portion of the study area, the mean tolerance of vegetation communities to cold is very homogeneous in the west. The eastern portion of the study area is more heterogeneous, though there are big patches of tolerant and intolerant communities.

Figure 6.5c illustrates the relative mean tolerance of an assemblage of plants to cold. Positive values indicate that food species are less tolerant of cold than non-food species in a vegetation zone and negative values that an assemblage of food species is more tolerant

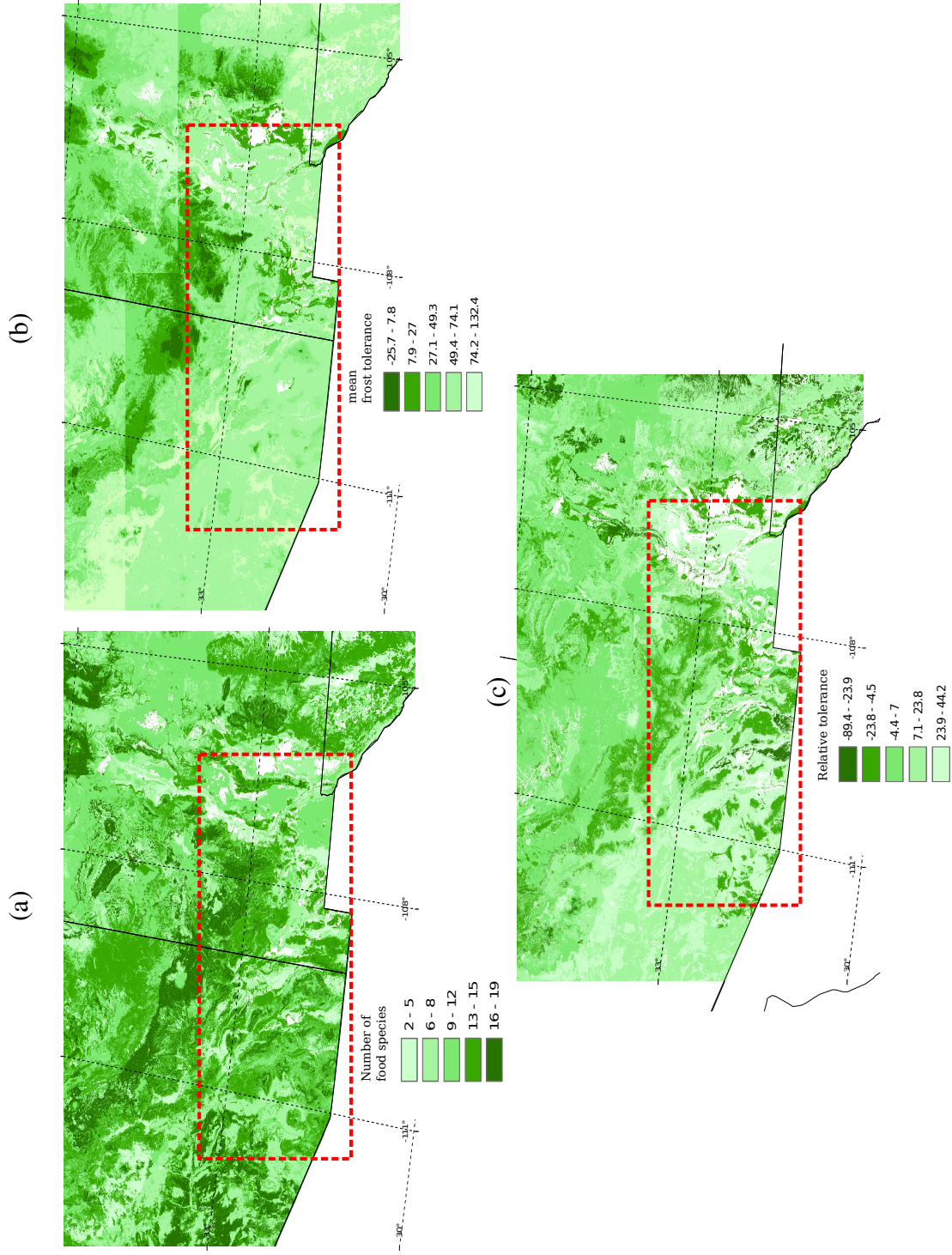


Figure 6.5: Maps of vegetation zones. Map (a) describes the number of edible species in each zone; map (b) the mean frost tolerance of edible plants; map (c) the tolerance edible plants relative to all plants in a vegetation zone (see Appendix A for details). The dashed boxes highlight the study areas. Temperature units in map (b) are in degrees C times 10.

of cold than the full assemblage. This measure provides an estimate of the relative intensity of cold that would be required to shock the productivity of food species. In general, food plants in the eastern portion of the study area have a greater relative mean tolerance of cold extremes. Again, however, the western portion of the study area shows more fine grained variation. There are many small vegetation zones where food plants are tolerant of cold and many small vegetation zones where food plants are, on average, very intolerant of cold.

Obviously, much more work is needed. There are multiple disturbance dynamics that affect vegetation communities, like rainfall and fire. So understanding the tolerance diversity of vegetation communities to these processes will begin to more fully illustrate how well assemblages of food might tolerate the kinds of external inputs that shock ecosystems in the US Southwest. My point here is simply that by using the URH to structure archaeological analysis, we can raise interesting questions. For instance, there is not a simple gradient of less tolerance to more tolerance of cold from west to east. What we do see is very different scales of patchiness in the vulnerability of plant assemblages to cold. How might different scales of patchiness in the assemblages of plant foods that are potentially more resilient to cold snaps impact the strategies of prehistoric forager-farmers? Perhaps where vegetation zones clump in very low and very high tolerance patches that are large in spatial extent, it may take less information processing to discover and accurately predict the vulnerability of habitat level forager-resource systems to cold shocks. Conversely, with more fine grained variation, it may take more information processing to discover and accurately predict the vulnerability of habitat scale forager-resource systems to cold shocks. Based on the logic of the URH, this would suggest that fine grained environments are more costly to learn about in terms of time. This is speculation that suggests further avenues of research between the spatial grain of potential forager-resource systems and the costs of information processing for individuals. Regardless, my point is that the URH is useful for structuring more nuanced analyses of how climate variation and resources interact and

might effect the evolution of agricultural SES from hunter-gatherer SES in specific regional contexts.

Conclusion

This dissertation has used dynamic and conceptual models to study feedback processes across multiple scales of space and time in a general forager-resource system. The models were used to construct two competing hypotheses that explain the adoption of foraging strategies that manage the productivity of ecosystems and territorial ownership: the uncertainty reduction and social opportunity hypotheses. The relative merits of these two competing hypotheses were evaluated against each other using large ethnographic and environmental data sets. The ethnographic and environmental data were more consistent with the uncertainty reduction hypothesis. The ethnographic analysis provides an ethnoarchaeological foundation for understanding the evolution of social-ecological systems based on agriculture at the expense of hunter-gatherer social-ecological systems.

Overall, my work illustrates the potential importance of systems dynamics in human behavioral ecology. I have illustrated how feedback processes in a forager-resource system create environmental legacies that effect the costs and benefits of the foraging strategies that individuals might adopt to secure resources. An important direction of future research in the human behavioral ecology of the archaeological record is to develop a more sophisticated understanding of the consequences of feedback processes in human-resource systems on the fitness of individuals. I argue that to understand major transitions in human-resource systems, studies grounded in human behavioral ecology are enhanced by the study of feedback processes with the tools of dynamical systems theory and concepts drawn from resilience thinking.

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1996. The agricultural frontier and the transition to farming in the Circum-Baltic. In *The Origins and Spread of Agriculture and Pastoralism in Eurasia*, D. R. Harris, ed., Pp. 323–345. Washington DC: Smithsonian Institution Press.

APPENDIX A
REPORTS OF HUNTER-GATHERER FOOD PRODUCTION

This appendix reports on the 14 ethnographic groups that I added to the data set developed by Keeley (1995). For a description of why these groups were added see chapter 5.

Name: G/Wi

References:

Tanaka, Jiro. 1980. *The San Hunter-gatherers of the Kalahari: A study in ecological anthropology*. Tokyo: University of Tokyo Press.

Observations of Burning:

1) “During the dry season, the brush all over the withered veld is burned off to facilitate the sighting of game and to improve the next year’s plant growth. On one occasion, driven by the wind, one such fire meandered slowly for eight days until it reached a campsite some 15 km away” (Tanaka 1980:112).

Observations of planting and tending:

1) “Again, some G//ana cultivate the tsama melon, *n//an* (*Citrullus lanatus*), but this in no way replaces the gathering of wild tsama melons and does not alter the overall San food pattern. These habits of civilization were picked up by the G//ana from the Kgallagadi and are not seen at all among the *g/wi* of the =/ Kade area” (Tanaka 1980:14-15).

Name: Tiwi

References:

Hart, C. W. M., Pilling, A. 1960. *The Tiwi of North Australia*. Holt, Rinehart and Winston: New York.

Observations of Burning:

1) “At the appointed time the hunters assembled, perhaps ten or fifteen adult men, with younger ones doing the actual hunting and the older ones supervising. The woman and children acted as beaters; the grass was set on fire over a big area, and the kangaroos rounded up and killed while dazed by the smoke and the noise....”

2) “This sudden glut of meat was not, however, the main object of the burning, but a dividend. Even though few kangaroos were caught in the smoke and confusion, the burned-over area would provide good visibility for kangaroo hunting during the rest of the dry season, since the new tender shoots that sprang from the burned-over grass were a favorite food of the kangaroo and served to lure them out of the denser scrub areas and the mangrove swamps where hunting them was always difficult” (Hart and Pilling 1965:42).

Observations of planting and tending:

Not reported in the consulted source.

Name: Kaurareg

References:

Moore, David r. 1979. Islanders and Aboriginies at Cape York. Humanities Press Inc.: New Jersey, USA.

Observations of Burning:

Not reported in the consulted source.

Observations of planting and tending:

1)“she makes it clear that the Kaurareg did plant sugarcane, in the form of slips brought over by the Kulkalaig, and elsewhere she says that until 1849 there was only one garden in the Prince of Wales group, on Horn Island, owned by a small group of men and their wives (Brierly 1849:162-163).....Barbara Thomson mentions that they would not take up the koti planted in the garricup in the current season, but would keep them as a standby in case the wild ones 'should get scanty in the rocks', so obviously this was considered a possibility (Brierly 1849:178-179)” (Moore 1979: 278-279).

Name: Anbara

References:

Meehan, B. 1982. Shell bed to shell midden. Canberra : Australian Institute of Aboriginal Studies ; Atlantic Highlands, N.J. : Distributed by Humanities Press.

Observations of Burning:

1) “During the wet season grass growing up to 2 m in height covers the whole site, as it does at Ngalidjibama, only to die or be burnt off during the height of the dry season. [site refers to large campsite called Kopanga. [No indication of economic benefit of burning, information below indicates it is to help with mosquito problems] These measures [to deter mosquitos] include the thoughtful locatoin of camps and designs of houses, burning off grass, making smoky fires,... ”(Meehan 1982:152-155).

Observations of planting and tending:

Not reported in the consulted source.

Name: Gunwinggu

References:

Altman, J. C. 1987. Hunter-gatherers Today: An aboriginal economy in North Australia. Australian Institute of Aboriginal Studies, Canberra.

Observations of Burning:

Not reported in the consulted source.

Observations of planting and tending:

Not reported in the consulted source.

Name: Worora

References:

Blundell, V. J. 1975. Aboriginal Adaptation in Northwest Australia. PhD Thesis, University of Wisconsin, Madison.

Observations of Burning:

1) "A group of men congregate and set the dry grass ablaze so that animals are driven a head of the flames to a point where waiting hunters kill them with spears and clubs. This practice of burning off the vegetation also serves to kill smaller marsupials and reptiles which are also collected. It further brings about the quick regeneration of the vegetation with the ensuing first rains, which attracts marsupials and the larger birds into cleared areas where they are stalked by individual hunters"(Blundell 1975:467).

Observations of planting and tending:

Not reported in the consulted source.

Name: Mamu

References:

Harris, D. R. 1982. Aboriginal Subsistence in a Tropical Rainforest Environment: Food procurement, cannibalism and population regulation. In Food and Evolution: toward a theory of human food habits, M Harris and E. B. Ross (eds.) pp. 357-385. Temple University Press: Philadelphia.

Harris, D. R. 1978. Adaptation to a tropical rain-forest environment: Aboriginal subsistence in Northeastern Queensland. In Human Behavior and Adaptation, N. Blurton Jones and V. Reynolds (eds.) pp. 113-134. Taylor and Francis Ltd.: New York.

Observations of Burning:

Not reported in the consulted source.

Observations of planting and tending:

Not reported in the consulted source.

Name: Ngatajara

References:

Gould, R. 1971. Uses and Effects of Fire among the Western Desert Aborigines of Australia. *Mankind* 8:14-24.

Observations of Burning:

1) “There is evidence that in certain areas large fires were set to drive game....Ngatatjara Aborigines residing today at Warburn say that in earlier times (i.e. during the first few years after the founding of the Warburton Ranges Mission) they used fires to drive game over cliffs or up onto rock outcrops where the animals, mainly kangaroos and wallabies, could be surrounded and easily killed..”

2) “In anticipation of the possibility of these rains, numerous instances were noted where men would set fire to areas of spinifex with the idea that the green grass-shoots which spring up shortly after a rain would attract kangaroos and other macropods into the area.....”

3) “From an aboriginal subsistence point of view, spinifex and the few small trees and shrubs associated with spinifex climax (mainly species of Acacia) are not particularly attractive, whereas, in contrast, an area of spinifex which has burned and contains a wide variety of plants during the regeneration process may be much better. For among these plants there are likely to be important staple species (like the ngaru observed 40 miles south of Warburton) ” (Gould 1971:19,22).

Observations of planting and tending:

Not reported in the consulted source.

Name:Mardudjara

References:

Tonkinson, R. 1978. The Mardudjara aborigines: living the dream in Australia’s desert. New York : Holt, Rinehart and Winston.

Observations of Burning:

“The firing of vegetation flushes out small game such as marsupial rats, snakes, mice, lizards, and such, which can then be easily tracked and caught. Also, the burning of spinifex, in particular, promotes the growth of grasses, herbs, and bush tomatoes that are more useful as food resources, since spinifex seeds only for a short time and is laborious to

harvest” (Tonkinson 1978:39).

Observations of planting and tending:

Not reported in the consulted source.

Name: Kuku-Yalanji

References:

Hill, R., Baird, A., Buchana, D. 1999. Aborigines and Fire in the Wet Tropics of Queensland, Australia: Ecosystem Management Across Cultures. *Society & Natural Resources: An International Journal* 12:205-223.

Observations of Burning:

“For subsistence purposes, Kuku-Yalanji people lit fires throughout the year from the time the grass would first burn at the end of the wet season, to jarramali time, the hot dry time of the year. This created a mosaic of patches at different stages of regrowth. Some food plants are easier to gather after ngalku, as they sprout first. Others have their productivity enhanced, notably *Cycas media*, previously the most important carbohydrate food source” (Hill et al. 1999:211-212).

Observations of planting and tending:

Not reported in the consulted source.

Name: Kwakiutl

References:

Boas, F. 1921. *The Kwakiutl of Vancouver Island*. AMS Press: New York.

Turner, N C and Bell, M A M. 1973. The Ethnobotany of the southern Kwakiutl Indians of British Columbia. *Economic Botany* 27: 257-310.

Observations of Burning:

1)“Although the Kwakiutl did not actually cultivate plants, they did attempt to improve yields by periodically burning over berry patches and by clearing the clover and cinquefoil ‘gardens’ of sticks and large rocks”(Turner and Bell 1973: 293).

Observations of planting and tending:

1)“They collected only the larger roots, leaving the smaller ones to grow for the next harvest (Boas 1921, 1934).”

Name: Digueno

References:

Shipek, F. C. 1981. A Native American Adaptation to Drought: The Kumeyaay as Seen in the San Diego Mission Records 1770-1798. *Ethnohistory* 28, 295-312.

Observations of Burning:

1)“Finally, fire was used to promote natural food crop succession on chaparral slopes by the use of a three to five, or more, year burning sequence, depending upon the plants desired in each locality” (Shipek 1981:298)

Observations of planting and tending:

1) “This grass was harvested by cutting and gathering stalks into sheaves. After harvest, the stubble was burned,a section at a time as it dried. Burning was followed by broadcasting seeds for next year’s crop.....”

2) “In addition seed, families planted”gardens”of annual and extending grass areas by broadcasting perennial greens, seeds, roots, and cactus cuttings in clearings made near their homes. Corn, beans, and squash were also planted in selected locations in mountain valleys, below running springs, and on the desert, including the Colorado River delta distributory system” (Shipek 1981:298).

Name: Shompen

References:

Arora, D. 2010. Sustainable management of tropical forest through indigenous knowledge: A case study of Shompens of Great Nicobar Island. *Indian Journal of Traditional Knowledge* 9:551-561.

Observations of Burning:

Not reported in the consulted source.

Observations of planting and tending:

“They clear a small patch of forest, say 10-15 m long and 10-15 m wide for their temporary camps. The trees are felled by cutting the trunk using the iron machete. The trunks are cut not at base or ground level but at a fairly high level of about 5-6 m above the ground. This is an ingenious action as the trees in the forest of Great Nicobar have wide wing like basal trunk growths called buttress. If the tree is to be cut at base, it would take more time and efforts as girth at that level is many times more than the actual girth of trunk. It also provides a chance to the jungle to grow again.... They are also said to possess gardens enclosed in zigzag fences, where they cultivate bananas, yams, and other tubers” (Arora

2010:559).

Name: Yuqui

References:

Stearman, A. M. 1989. Yuqui: Forest Nomads in a Changing World. Holt, Rinhart and Winston, New York.

Observations of Burning:

Not reported in the consulted source.

Observations of planting and tending:

Not reported in the consulted source.

APPENDIX B
ESTIMATING RESPONSE DIVERSITY

In this document I focus strictly on the plant resources that may have composed the wild resource portion of mixed forager-farmer diets in the southern Southwest US. To estimate the plants available for food, I used McLaughlin's (1986) floristic inventory of the Southwest US to gain an inventory of the plants that occur in the southern Southwest US. This yielded a sample of 2394 species or a little less than 1/2 of the total number of species that McLaughlin (1986) inventoried for the entire Southwest. I then used the North American Ethnobotany Database to check for the use of each plant as a food by groups recorded ethnographically. This yielded a sample of 394 species used as food ethnographically. In addition, I cross referenced the McLaughlin database of species with the database of species that the USGS uses to calculate vegetation cover in the United States (Geological Survey 2010). This cross-reference results in a list of 741 species of plant that were used as food by ethnographically recorded societies in North America. I use the data set as an estimate of the species that were potentially available to prehistoric inhabitants of the southern Basin and Range province of the US Southwest.

The detailed methods for calculating the response (tolerance) diversity of assemblages of species is detailed in Butterfield (2014). This work was done as part of an interdisciplinary team funded by a Coupled Human Natural Systems Grant provided by the National Science Foundation (Nelson et al., 2010). In brief, species tolerances of cold extremes were estimated by plotting the spatial distribution of each species over mean annual temperature climate layers in GIS. The spatial distribution of all species were acquired from the Southwest Environmental Information Network (SEINet; www.swbiodiversity.org/portal), a data access portal to digital records from herbaria across the Southwest USA. Only georeferenced records after 1900 were included and duplicate observations were removed. Climate data used to estimate each species' tolerance to cold were acquired from WorldClim (Hijmans et al., 2005). This data set provides 1 km² resolution rasters of interpolated monthly mean minimum temperature. WorldClim is a slightly coarser data set than the well known PRISM climate data calculated for the lower 48 United States, but provides the ability to estimate the tolerances of species whose distributions extend into Mexico, as many of the species considered here are recorded in Mexico, as well as the US.

After the the spatial distribution of each species was plotted over the mean annual temperature raster, these values were extracted to the location of each species record. This was done for both species used as food in the ethnobotanical record and species not used as food. For instance, Figure B.1 illustrates the spatial distribution of *Larrea tridentata* and the mean annual temperature gradient in the US Southwest and Northern Mexico. At each location where *Larrea tridentata* has been observed, the raster value for mean annual temperature was assigned to that individual species record. In this case, there are 955 species records, so we have 955 estimates of the minimum mean monthly temperature where the species lives. This allows one to calculate a climate distribution (Figure B.2) for *Larrea tridentata*. It is assumed that the climate distribution reflects the constraints of temperature on the niche space of a species. Beyond the tails of the distribution, the climate variable acts as an environmental filter, restricting the dispersal or post dispersal establishment of the species.

The 5th percentile is used as an estimate of the species tolerance of cold. This same procedure was carried-out for every species. It is assumed that if a plant experiences conditions colder than this value, in any given year, it is likely to die or not produce edible parts due to cold stress. This is an initial simplification. Some plant parts, like bark, can obviously be used as starvation food even if a tree is hit by a really cold snap. It is important to

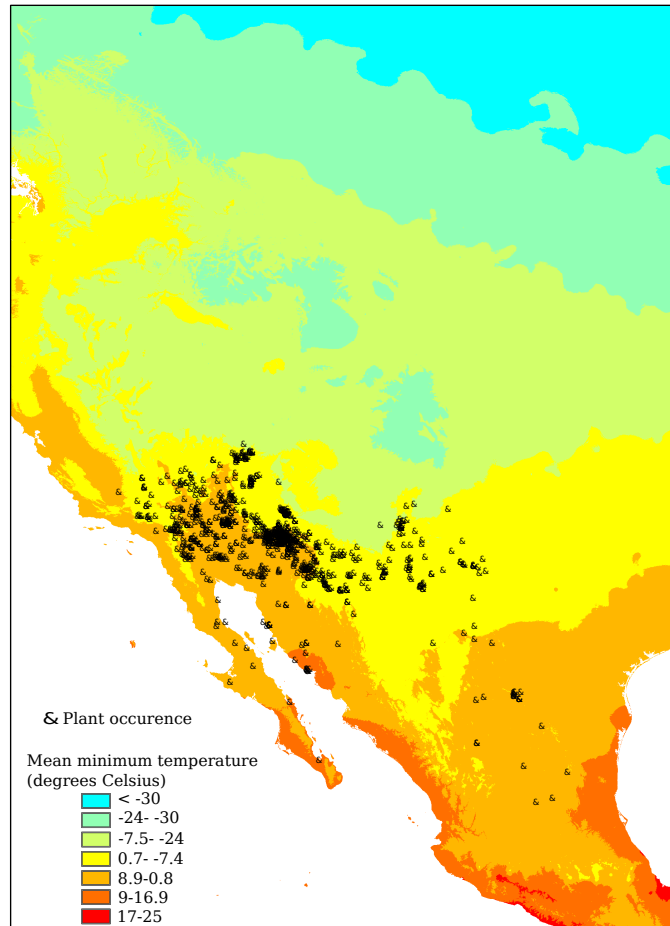


Figure B.1: Map of mean minimum monthly temperature and the spatial distribution of *Larrea tridentata*.

remember that the data analysis done here is an illustration meant to forward more detailed studies. In any assemblage of species then, the response diversity of an assemblage to cold is the collection of 5th percentiles from each species' climate distribution. The assumption is that if a plant experiences a time period colder than this 5th percentile, the plant is stressed and is less likely to produce edible biomass for humans. A diverse assemblage is one with many different individual tolerances to cold. An assemblage that lacks response diversity is one in which each species has the same tolerance of cold.

Each species was assigned an Ecological System, which are meso-scale vegetation classifications representing vegetation types that recur consistently across similar physical habitats. These vegetation communities can be reliably mapped through remotely sensed and topographic data (Comer et al. 2003), and are the predominant vegetation classes in the 30m-resolution LANDFIRE Existing Vegetation Map of the United States (Geological Survey 2010; <http://landfire.cr.usgs.gov/viewer/>). 93 vegetation zones are present in the study area and these zones are the scale at which the measures presented in Figure 6.5 are calculated.

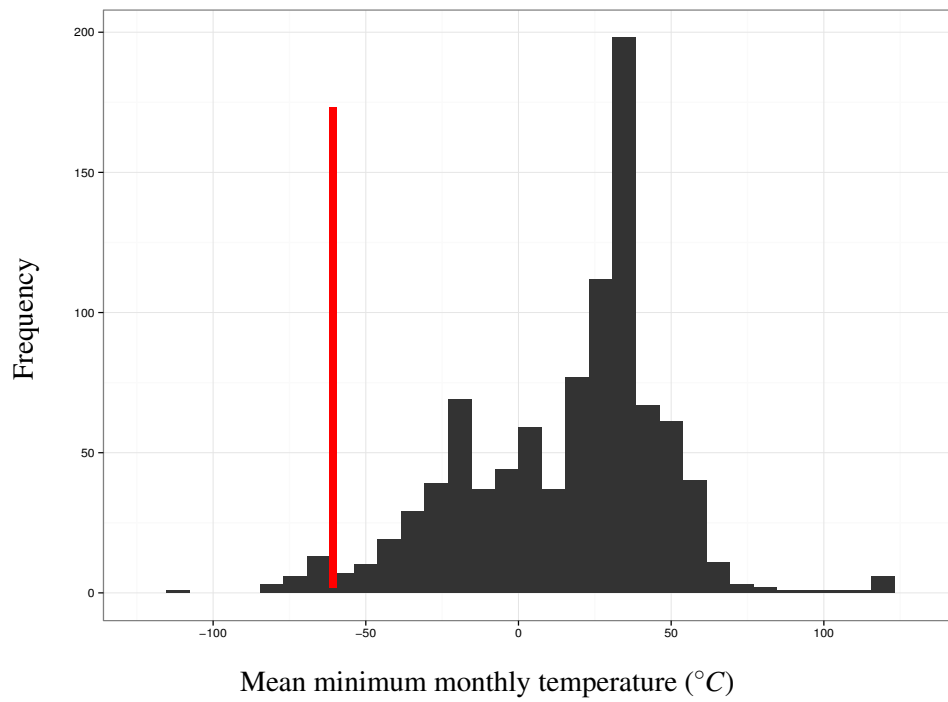


Figure B.2: Climate distribution of *Larrea tridentata*. The red line marks the 5th percentile of the distribution.