

Disturbance, Complexity, Scale: New approaches to the study of human-environment interactions

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Keywords:

Human behavioral ecology, sustainability, ecosystem engineering, niche construction, complex adaptive systems

Abstract

New approaches to human resource interactions are beginning to move beyond a narrow focus on individuals and simple (patch-level) predatory or competitive interactions. These approaches link non-equilibrium theory from community and landscape ecology with theories of individual decision-making from behavioral ecology to explore new ways of approaching complex issues of diachronic change in behavior, subsistence and social institutions. I provide an overview of two such approaches, one to understand long-term hunting sustainability among mixed forager-horticulturalists in the wet tropics, the other to understand how foragers act as ecosystem engineers in a dry, perennial grassland in Australia. I conclude by describing the implications of these new approaches incorporating anthropogenic 'intermediate' disturbance (as an emergent property of human-environment interaction) for shaping environments through time and space and in so doing, patterning the sustainability of subsistence, how people share, what kinds of ownership norms develop, and even how gendered production is structured.

Introduction

Models of individual decision-making developed in behavioral ecology have proven remarkably robust at explaining the adaptive nature of human-resource interaction (Smith 2013, Smith & Wishnie 2000), especially when considering simple interactions: the decision of whether and when to take certain shellfish or pass them over (Bird & Bliege Bird 1997), which habitats to colonize first and whether to defend them (Winterhalder et al. 2010), or how far to transport items with low utility (Bettinger et al. 1997). Likewise, simple ecological models of predation and competition are utilized to explain how the environment is affected by human decision-making processes (Charnov et al. 1976, Nagaoka 2002). Such simple models have also proven useful in unveiling many of the dynamics that accompany a consideration of more complex phenomena, such as the interactive effects of environment on the development of social hierarchy and the colonization of continents (Kennett et al. 2006, 2009). However, for the most part, larger scale, dynamic social and ecological processes have proven more difficult to explain, as evidenced by the substantial debate over their applicability to the understanding of subsistence intensification and the transition from hunting and gathering to agriculture, (Gremillion et al. 2014, Smith 2007, 2011a,b; Zeder 2012).

The most common ecological approach to questions of human-environment interaction (such as the processes driving subsistence intensification) combines models of human-environmental response to different environmental conditions (central place foraging models, prey, patch, and habitat choice models, and territorial defense/marginal valuation models) with models of human impact on the environment, primarily predator-prey models. Such models are used to generate predictions about how

human populations cause resource depression, how this influences patterns of mobility and residence, and how population density and the colonization of less suitable habitat may result in declining residential mobility and increased socio-political stratification (Bird & O'Connell 2006, Kennett & Winterhalder 2006, Lupo 2007, Morgan 2014). As foragers spend proportionally more time handling lower ranked resources, and the costs of traveling elsewhere increase with higher human populations in neighboring habitats, the opportunity costs of investing in technology to reduce handling costs decline (Bettinger et al. 2006, Hawkes & O'Connell 1992), leading eventually to plant domestication and agricultural production.

Debates over the limitations of these models have highlighted two main problems. First, these models do not explain the origins of or variation in emergent social phenomena like the institutions that are a necessary part of such complex phenomena as the origins of agriculture. Co-evolutionary approaches such as that of Bowles & Choi (2013) address this limitation by proposing a sort of ratcheting up link between economic and social institutions. However, the absence of ecological dynamics and a lack of attention to individual decision-making processes in such models does not allow for the incorporation of adaptive processes other than group selection that change social institutions.

Second, these models are designed to explain ecological interactions at very local spatial and temporal scales and are not designed to explain population or community-level, dynamic interactions. They focus almost exclusively on dyadic relationships between species, negative interactions like competition and predation, and do not incorporate non-equilibrium, scale-sensitive approaches in which negative effects at one spatial scale can result in positive ones at the level of the landscape or community as a whole (Huston 1979). Given this, niche construction, or ecosystems engineering approaches such as those of Zeder (Zeder 2012) and Smith (Smith 2007, 2011a,b) propose that such complex phenomena as the origins of agriculture are best explained through the anthropogenic construction and management of ecosystems to improve subsistence productivity. However, as Eric Smith (2013) points out, while such models are good at calling our attention to dynamic and interactive effects of ecology and social structure, they provide no framework for developing hypotheses about individual decision-making with regard to resource use beyond a vague notion of intentionality in innovation, where actors intentionally modify habitats to gain via future, delayed payoffs. The solution to these issues is not to discard models of agency, nor to model social evolution in an ecological vacuum, but to generate new integrative models that can scale up from individual decision-making to the social and ecological causes and consequences of decision-making at the level of populations and ecological communities. As Layton put it, *"our best hope for reconciling Social and Evolutionary Theory lies in an ecological approach to social evolution that acknowledges the emergent properties of social interaction and their capacity to modify the environment to which individuals are adapting"* (Layton 2010):149).

I suggest that if behavioral ecology is to have any hope of generating better models of complex, dynamic social-environmental interaction, it must find ways of integrating the power of individual decision-making with ecological and evolutionary theory designed to operate at the spatial and temporal scales of these broader phenomena. It needs to focus on how individual ecological and social processes and behaviors scale up to affect populations and communities. It should seamlessly integrate across what are often perceived as theoretical divides between nature and culture, agency and adaptation, behavior and institutions, humans and other species, individuals and communities. It should include humans as part of the fundamental structure and function of ecosystems, and pay attention to dynamic interactions between subsistence, social structure, social institutions and the environment, and include considerations of temporal and spatial scale, variation, and recognition of the complexity of ecological interactions occurring between humans and other species. It should take a co-evolutionary perspective to account for the interactive effects between things over time: between individuals (cooperation, conflict, cultural transmission), between species (mutualism, predation, competition, facilitation, niche construction /ecosystem engineering), and between scales of organization, from the individual to the population, to the community.

Here, I provide an example of such an approach, which reconsiders explanations for subsistence intensification by linking theory from community and landscape ecology with theories of individual decision-making from behavioral ecology.

A Theory of ecological interactions

Typical models of subsistence intensification usually assume that predation reduces populations of economically profitable species, causing shifts to lower-profitability resources. While there is ample evidence of local population depression, evidence for indigenous hunters completely exterminating species is quite limited and contentious (see Meltzer this volume). There is actually a long history of sustainable exploitation of most human prey: even the flightless duck in California, an easy mark for native hunters, coexisted with California coastal foragers for 8000 years (Jones et al. 2008). By focusing only on the local-scale, dyadic interactions between humans and their prey, we overlook the more complex effects of predation at larger scales and its indirect effects on other species that might be facilitating these sustainable interactions.

Predation is more generally a source of disturbance to populations, and such disturbance, while negative at some temporal and spatial scales, can paradoxically be a source of positive effects at others. Positive ecological interactions, often referred to as facilitation, include any direct or indirect forces positively affecting the growth or reproduction of one or more organisms without negatively affecting the others (Bertness & Leonard 1997). At the level of the community as a whole, positive effects are modeled as a function of the scale at which disturbance (mortality) occurs, with intermediate disturbances hypothesized to produce heterogeneous landscapes and source-sink dynamics that maximize the persistence of a wider range of coexisting species (Connell 1978, Huston 1979).

Positive effects have been documented for a wide range of predatory interactions. In some interactions, predation actually increases prey populations. Agouti (large rodents of the genus *Dasyprocta*) prey extensively on Brazil nuts, but they habitually bury seeds intact for later consumption, which increases seedling survival over unburied nuts and results in more Brazil nut trees where agouti are present (Asquith et al. 1999). Other predatory interactions have negative direct effects on the species in question, but positive effects to other species, or the community as a whole. In the absence of top carnivores, white-tailed deer suppress tree seedling recruitment and deplete many herbaceous plants, which reduces habitat for ground-nesting birds; introduce top carnivores and both plant populations and the small animals that rely on them rebound (Rooney et al. 2004). Removing otters from nearshore environments causes a collapse of macroalgae and sea grasses as herbivores like urchins and grazing snails increase (Estes & Palmisano 1974). Kelp forests in turn, affect other species through increasing food availability for grazers, and reducing wave height and current velocity. Barnacles and mussels grow three to four times faster in otter-dominated kelp forests (Duggins et al. 1989); rock greenling are roughly ten times more abundant (Reisewitz et al. 2005); glaucous winged gulls eat more fish (Irons et al. 1986); and bald eagles have a more diverse diet of fish, marine mammals, and seabirds (Anthony et al. 2008). In the absence of a disturbance such as storm or fire, pines or fir trees will gradually take over an oak woodland (Cocking et al. 2012) reducing overall plant diversity and abundance, especially on the forest floor, and increasing the risk of pathogen spread (Real & Biek 2007). The decline of a top predator, such as the coyote, releases smaller predators from competition, allowing their populations to surge and deplete prey populations: when coyotes are rare, smaller predators like foxes and cats are more common and populations of scrub breeding birds decline (Crooks & Soulé 1999). Positive effects can also come about through the engineering activities that are a side effect of some organism's foraging, housing, or predator evasion strategies. Such processes, when they construct new niches or enhance existing ones, are often referred to as ecosystem engineering (Jones et al. 1994). The classic example is of beaver dam construction, which increases wetlands areas and produces more environmental heterogeneity, supporting larger populations of a wider range of species at a landscape scale (Wright et al. 2002).

The sum total of these facilitative ecological interactions affects the assembly of entire ecological communities. When ecosystem engineers affect landscape heterogeneity, this may stabilize species

interactions (Holt 1984, Roff 1974, Roxburgh et al. 2004), and provide rescaling and habitat protection effects for habitat generalists: species that require a variety of habitats for both food and shelter (Futuyma 1988, Marvier et al. 2004, Wiggins et al. 2006). When predators hunt many different prey species at multiple trophic levels, that is, have wide diet breadths (Beckerman et al. 2006, Redford & Robinson 1987), food web stability might increase, allowing more species to persist with more stable populations (Gross et al. 2009). While individual populations may decline and locally become extinct, the larger meta-population may be more likely to persist particularly if habitats are patchy and heterogeneous, and predators face lower costs of prey switching (Holt 1984, McCann et al. 2005, Rooney & McCann 2012). Those species providing more positive ecosystem effects may contribute to more stable ecological communities, minimizing destabilizing population fluctuations and allowing many more species to coexist over the long term. Organisms playing a key role in holding communities together are termed keystone species or sometimes, foundational facilitators. When these keystones are removed from the food webs they support, catastrophic species loss often follows that ripples down through the trophic levels of the web, from top consumers to herbivores, and even to the plants they consume.

While charismatic non-human species take front and center in most ecological studies of facilitation, evidence for more complex and/or positive human-environment interactions is more slowly accumulating. One of the first ecological studies to suggest this was Castilla and colleagues (Castilla 1999, Castilla & Bustamante 1989), who demonstrated through exclusion experiments on the Chilean coast that moderate levels of human predation (subsistence foraging) on a wide range of shellfish, including mussels (detritivores), limpets (herbivores) and gastropods (predators) increased species diversity and shifted the intertidal from one dominated by barnacles, to one evenly represented by mussels, algae and barnacles. When humans were excluded, the predatory gastropods rapidly decimated the mussel beds, allowing barnacles to invade, which then prevented mussels from re-establishing. Human exclusion also increased the size of keyhole limpets (a phenomenon commonly observed archaeologically: human foragers preferentially choose larger individuals) but this had a devastating effect on algae because big keyhole limpets graze it down more effectively; the loss of algae also left more room for barnacles to invade. While foraging strategies with wide diet breadths seem to actually improve coastal resources for human exploitation, narrow strategies focused on a single intertidal keystone species, like the sea otter, causes trophic collapse, as commercial hunting did during the 19th century. Castilla concludes that "humans affect the functioning of food webs by acting as an efficient and selective keystone predator. Humans can regulate predatory efficiency and/or selectivity, and thereby manage, enhance, reduce, conserve or reserve species or communities" and implies they may do so simply by virtue of their optimal foraging strategies (1999:282). In the following section, I pursue this hypothesis further with two case studies of very different ecosystems: the Neotropical rain forest, and the desert grasslands of Australia.

Case #1: Garden game in the Neotropical rain forest.

The phenomenon of garden game in the neotropical rainforest is receiving increasing attention as researchers critically evaluate the differential effects of anthropogenic disturbance on animal communities. Disturbed forest tends to support a broader range of species than primary forest (Connell 1978); following this logic, extensive forest-fallow horticultural systems have been suggested to enhance biodiversity and augment populations of some species by improving access to food or new habitat niches (Fa et al. 2005, Linares 1976, Posey 1985, Smith 2005). While some species of large game become depleted with hunting around indigenous settlements in the Amazon basin (Alvard 1993), others seem to show very little effects of hunting, particularly agouti, collared peccary, and deer (Chacon 2012, Koster 2008, Smith 2005). Likewise, while some communities experience a decline in populations of preferred species over time, others, such as the Ache, show no effect (Hill & Padwe 2000, Hill et al. 2003). Some suggest that this is a function of population density and mobility, with seemingly sustainable offtakes expected where hunters are at low density or are highly mobile (e.g. Alvard 1998), or that significant source-sink dynamics result in population influx from more remote regions (Hill and Padwe 2001). But, there is also evidence that the increased food availability in anthropogenic environments may actually enhance populations of these species (Smith 2005). In one community in Western Panama, a majority of agoutis, armadillos, and collared peccaries were taken in the anthropogenically modified forests and

gardens surrounding the village (Smith 2005). Because hunting may be more predictable in anthropogenic habitats, returns may actually be higher: in at least two studies, hunters had higher returns in gardens and secondary forest, measured as catch per unit effort and catch per unit area (Dunn & Smith 2011, Parry et al. 2009).

But it may not be the presence of anthropogenic habitat per se, but the way that anthropogenic habitats are spatially patterned across a larger landscape. Dunn and colleagues (Dunn et al. 2012) suggested that sustainable hunting of Baird's tapir by Miskitu was possible because the landscape surrounding the Miskitu community was a diverse one, including extensive areas of primary forest experiencing low hunting pressure, and agricultural landscapes with a diverse set of crops offering increased feeding opportunities for tapirs and other species. However, the positive effects of anthropogenic forest modification may peak at more intermediate spatial extents: as agricultural production intensifies, landscape diversity decreases, and refuge habitat becomes more highly fragmented and dispersed, the potential for anthropogenic landscapes to support a wide range of animal species may decline. Cocoa monocultures in southern Ghana, which dominate the surrounding fragmented forest reserves, are highly depauperate and support mainly very small animals (Schulte-Herbrüggen et al. 2013).

While anthropogenic forest modification has been represented as an intentional forest management strategy (Posey 2003), there is no necessary reason that the large-scale landscape level effects of human disturbance needs to be intentional. Indeed, even processes as complex as plant domestication (and the patchiness and distribution of such plants across a landscape) may be the emergent outcome of the way people forage for wild plants, as (Rindos 1984) first hypothesized. In Central Africa, Baka wild yam harvesting and consumption at a central place facilitates the dispersal of yams, which do not colonize new regions very efficiently. Dense patches of wild yams and other secondary forest species colonize old habitation sites, and the activity of foraging alone is sufficient to generate enough patches of wild yams to support populations at their current densities (Yasuoka 2013).

Case #2: Lizards and kangaroos in the Australian Western Desert

Morton and colleagues (Morton et al. 2011) note that among some of the major drivers of plant and animal adaptation in Australia are longstanding feedback relationships between humans and environmental structure and function, mediated primarily via fire. Fire plays an especially prominent role in the summer-rainfall-dominated grasslands, savannahs and woodlands north of the Tropic of Capricorn. In the spinifex grasslands in this arid and semi-arid zone, anthropogenic fires are mainly lit during the early dry season, in the winter cold months, primarily to hunt burrowed sand monitor (*Varanus gouldii*). Martu hunters in this region are significant predators of sand monitor, which makes up more than 70% of all foraged foods acquired per foraging day. Sand monitor and hill kangaroo are the two major subsistence prey: hill kangaroo are limited to rocky hills and ranges, while sand monitor are most abundant in sandy substrates with extensive spinifex cover. During the colder winter months, sand monitor retreat to shallow burrows to live off extensive stores of abdominal fat, and it is at this time that hunters burn regions of mature spinifex hummocks to expose the burrows. During the summer months, monitors are tracked on the surface, and so hunts target recently burned patches where tracks can be followed more easily. Returns are highest within 6 months following fire, and decline as the patch revegetates, becoming almost negligible in grasslands more than 5-7 years since fire. Due high encounter rates and the high chances of pursuit success, sand monitor are a staple food resource, one in which harvests can be adjusted to need on a daily basis (Coddling et al. 2010). Variance discounting models show that although sand monitor hunting return rates have lower mean returns than kangaroo hunting, its lower variance and higher chances of success give it greater consumption utility than kangaroo hunting (Jones et al. 2013). In the context of a hybrid economy which includes some reliance on purchased goods, unlike kangaroo hunting, sand monitor hunting responds to economic scarcity: we have shown that more women hunt significantly more often when money is short (Scelza et al. 2014). As such, hunting monitor lizards is an important way that women, especially postmenopausal women, invest directly in their grandchildren and other dependents (Scelza 2009, Scelza & Bliege Bird 2008).

Gaining high returns from sand monitor hunting is dependent not just on the immediate use of fire, but on the history of the cumulative effects of Martu subsistence activities on the structure of environmental variation. Sand monitor hunting is dependent upon an anthropogenic fire mosaic, which is built through the accumulation of about 10 years' worth of hunting fires. In two Martu communities, Parnngurr and Punmu, from 60 to 240 individuals set broadcast fires every 3-4 days, resulting in 360 hunting fires per year in an area of around 500,000 ha (Bliege Bird et al. 2012). Our analysis of ten years of satellite images covering 46,000 km² shows that landscapes emerging from hunting fires are very different from those dominated by lightning fires: hunting fires are much smaller and closer together than lightning fires (Bliege Bird et al. 2008b). Martu hunting fires are about 1 km apart, while lightning fires are nearly 9 km apart (Bliege Bird et al. 2012). The zone of Martu influence attenuates rapidly outside of hunting regions: the anthropogenic mosaic is tightly linked to the cost of travel from centralized places, with regions closer to roads, settlements, and frequent camping places more strongly affected by anthropogenic fire than regions farther away (Bliege Bird et al. 2008b).

Cumulatively, Martu burning radically rescales the temporal and spatial impact of fire disturbance across the region. Patches of regrowing vegetation are smaller, closer together, and the diversity of different types of patches regenerating after fire (successional or seral patch diversity) is greater at spatial scales typical of a human foraging range (Bliege Bird et al. 2008b). Martu fires also prevent more habitat from burning, protecting critical refuge for many small animals, increasing the number and evenness of such patches throughout the landscape (Bliege Bird et al. 2012). The effects of anthropogenic fire not only restructure the distribution of successional mosaics and attendant vegetation, but also the distribution of some animals. Sand monitor density is increased in regions where there is greater environmental heterogeneity: the higher the density of habitat edges—contrasts between new burns, regrowing vegetation, and old growth—the higher the density of monitor lizards (Bliege Bird et al. 2013). Mean returns in hunting sand monitor are 1.6 times higher in more heavily hunted regions than they are in regions that are rarely visited by Martu hunters and success rates are 6 times higher. Martu hunting fires also shape population distributions of hill kangaroo (Coddling et al. 2014). Hill kangaroo scat density is linked significantly to successional-stage heterogeneity: scat counts increase with the diversity of habitat edges created through sand monitor hunting fires. Fires also increase encounter rates with patches of seed grass, which grow mainly in early to mid-successional patches, suggesting a fundamental role for fire in the late Holocene proliferation of seed-grinding technologies here in the arid zone (Zeanah et al. nd).

Characteristics of many of the animal species that have recently disappeared or are in decline also suggest that they too may have been advantaged by Martu fire mosaics. In the mid-1960's, most of the last groups of desert nomads were cleared from or migrated out of the heart of the Western Desert, returning in the mid-1980's (Davenport et al. 2005). Their departure coincided with the local extinction of 21 species of native marsupial, and the decline of 43 more (Burbidge et al. 1988, Burrows et al. 2006, Finlayson 1961), including several common prey such as the rufous hare-wallaby and the brush-tail possum. In their place were feral housecats, camels, donkeys and foxes. Recent studies have suggested that the mammal decline here during the last 60 years may be fundamentally linked to the disruption of traditional hunting and land use practices.

Anthropogenic disturbance causes overall foraging returns (including searches for large animals, small animals, and plant resources) to peak in regions of intermediate anthropogenic activity, decline in the most heavily used regions, and to be lowest in remote regions barely touched by human activity (Bird et al. 2015). Small animals provide a greater proportion of the diet in anthropogenic regions. Daily variance between individuals foraging from the same central place hearth (dinner time camp, in Martu parlance) is lower in anthropogenic environments, mainly because more others are more successful at bringing in small game. Everyone in camp does equally well in an anthropogenic environment, while in a non-anthropogenic environment, there is more variation in returns across individuals: some do well, but most do not. Landscape modification thus, at least in the Martu case, seems to reduce the temporal and spatial variance in resource access across a camp, mainly by increasing access (ie. reducing cost or increasing productivity) to high ranked small game and plant foods.

While these processes have long been referred to as 'firestick farming' (cf Jones 1969), the terminology unfortunately implies that burning by individuals is designed to produce optimally diverse landscapes, and the adaptive maintenance of burning is via the long-term benefits derived from the increased foraging returns possible in such landscapes. Rather, what seems clear is that burning is designed only relative to immediate hunting returns, and the long-term benefits are emergent properties of a complex adaptive system in which Martu play an integral role in sustaining a diverse and richly structured food web in this arid and hypervariable environment.

Feedbacks to social institutions and social organization

At the landscape scale, disturbance, or mortality (on both plants and animals), when applied over certain temporal and spatial dimensions, can have positive effects on the stability and diversity of species interactions and may actually favor populations of some species. These positive effects are not accomplished through conservation, management, or foraging restraint, but through the emergent properties of foraging decisions. The next step in this theory of human-environment interaction is to consider not just the impacts of subsistence on ecological structure and function, but also the structure and function of both individual decision-making and the properties of social groups living on these landscapes. The impact of human subsistence on populations, communities, and landscapes should feed back to influence human social organization and social institutions via links to foraging decisions, mobility, sharing, the gender division of labor, and resource defense. In the following section, I explore one way of accomplishing this by considering how the emergent properties of disturbance caused by human subsistence activities affect social phenomena.

In both case studies presented here, disturbance seems to have similar effects: increased landscape-level heterogeneity and a reduction in the variance associated with hunting. Central place subsistence activities produce spatial variation in human disturbance (predation and ecosystem engineering) across the landscape, focusing the strongest effects at the core regions close to communities, and diminishing outward as travel cost increases. Spatially varying engineering activities create greater patch diversity at more intermediate spatial scales in regions close to communities. One common effect of this seems to be a shift in the structure of animal communities: different types of disturbance seem to favor different types of animal communities, with smaller animals possibly favored over larger ones in more heterogeneous landscapes. Smaller animals with generalized foraging strategies seem to do very well in anthropogenic environments, such that in some cases the benefits supplied by habitat modification may even outweigh the costs of increased predation by human hunters. Theoretically, a patchy, heterogeneous environment would reduce the cost of prey switching, allowing a generalist forager to encounter more high ranked prey animals with lower travel cost between encounters (MacArthur & Pianka 1966). While very little is known about how human landscapes affect animal communities, some species seem to thrive in more heterogeneous environments: deer, which are habitat generalists, have smaller home ranges where disturbance creates greater landscape heterogeneity at smaller spatial scales (Saïd & Servanty 2005), and a number of species reproduce at higher rates in more heterogeneous landscapes, including meadow voles (Bowers & Dooley 1999), and raccoons (Dijak & Thompson III 2000); but many birds experience higher rates of predation due to increased mesopredator activity in such landscapes (Kurki et al. 2000), as diverse landscapes tend to increase the proportion of a community composed of generalists, especially generalist predators (Marvier et al. 2004). Increased levels of disturbance and fragmentation may act as an evolutionary force to favor medium-sized generalists over very small or very large bodied animals: over 175 years of increasing habitat fragmentation, very small Danish animals got larger, large animals got smaller, and medium sized ones did not change (Schmidt & Jensen 2003, 2005).

Archaeologists are beginning to recognize the long history of human and medium-sized animal coexistence, providing some support for the notion that species more likely to thrive in anthropogenic environments tend to flourish over time, coming to dominate species assemblages (Schollmeyer & Driver 2012). Schollmeyer and Driver review 159 assemblages from 129 sites across western North America and

57 assemblages from 23 sites on the Iberian peninsula and conclude that most assemblages show an increased emphasis on smaller terrestrial animals over large ones, and that this is not just a shift in hunting focus, but an actual increase in populations of smaller relative to larger animals as foragers modify environments through their foraging activities. At some sites, source-sink dynamics in heterogeneous landscapes keep large game populations high relative to small (or some large species are advantaged by the kinds of environmental modification humans engage in, like tapirs or kangaroos), and at others, smaller animals may actually increase due to habitat improvements offered by human activity (Schollmeyer & Driver 2013).

If human disturbance tends to increase patchiness and predictability of prey animals, as well as increasing encounter rates with medium-sized prey species, it is likely to reduce the costs of travel and reduce stochasticity in returns for human foragers. Larger animals tend to be encountered less frequently than smaller animals, and larger animals have higher escape velocities (up to around 150 kg body size, Morin 2012), and as such, both on-encounter returns and daily trip returns (including search and travel time to and from the foraging locale) tend to be more variable: there is a higher risk of complete harvest failure, a higher chance of coming home empty-handed, but also a higher chance of a harvest bonanza (see Bliege Bird et al. 2008a). While larger animals may provide big bonanzas on average, when such bonanzas are discounted by the variance in reward, they may actually provide less utility than a lower mean, but less variable prey (Jones et al. 2013). In general, foraging portfolios dominated by smaller or less mobile types of prey tend to be associated with less intra and inter-individual variance than those dominated by larger prey.

Sharing and social structure

Patchiness and predictability in turn have a suite of ramifying effects on social structure via their impacts on mobility and the costs and benefits of ownership and sharing. Both the marginal valuation of resource defense at the scale of the individual harvest (Blurton Jones 1987, Winterhalder 1996), and the marginal valuation of defense at the scale of the patch or landscape (Dyson-Hudson & Smith 1978) is predicted to affect the benefits of defending claims to exclusive use rights over a resource. Individuals are predicted to share more and defend less when there is high inter-temporal variation in foraging success (stochasticity), when package size and perishability is high, and when the degree of inter-forager correlation in harvest success is low (Winterhalder 1986). Empirical observations of sharing among hunter-gatherers and experimental work on the links between sharing norms and unpredictable rewards among Japanese and American participants tends to support these predictions about how people share (what benefits they receive from sharing is another matter). More synchronously and predictably acquired resources, like small game, tend to be characterized by a greater percentage kept for the consumption of the acquirer and his/her family (Gurven 2004), while high variance foods are associated with less kept by the producer (Hiwi: Gurven et al. 2000, Ache: Gurven et al. 2002). Independently of variance, foods that come in large packages are either shared to more others or in larger amounts than food in small packages (Kaplan and Hill 1985, Gurven et al. 2001, Gurven et al. 2002). Low variance resources (e.g. cultivated or collected foods) may be shared more contingently, while high variance resources (e.g. stochastic income such as large animals) show evidence of long-term one-way flows (free-riding) and lack of discrimination between recipients. Among the Ache in the forest (see Gurven et al. 2001, Gurven et al. 2002) women worked harder to acquire large harvests of low variance foods like fruit, palm heart, and palm starch, keeping a consistent portion for themselves and giving away the remainder, usually in the form of cooked food. But they seemed to be more choosy about recipients: they gave shares to fewer other families, and such giving was more contingent (more was given to those with whom one had received more), compared to higher variance resources like meat, which were given away without contingency to twice as many recipients, with hunters often relinquishing control over distribution (Hill and Gurven 2004. Hill, K., & Gurven, M. (2004). Similarly, Altman and Peterson (Altman & Peterson 1988) noted that among the Kuninjku (Gunwinggu), individual producers were expected to exert stronger claims to ownership (ie keep more within their own families) for small game, but not larger game; the key feature, they suggest, is synchronicity: even cash, when acquired asynchronously and unequally across the community, is widely

shared, while when it is simultaneously and equitably provided, is more likely to be kept for personal use. In industrialized society as well (Japan and the US), the links between expectations about sharing vs. keeping can be manipulated by providing resources that are associated with an unpredictable link between labor and reward: windfall (stochastic) resources (as high variance animals) are commonly shared more widely than resources with strong links between labor and production (Kameda et al. 2002), suggesting a common mechanism behind such norm development.

Shifts to lower-variance resources thus are likely to bring about shifts in community-level patterning of ownership and sharing. Those who have more low variance resources have surplus because they worked longer hours to get it: this sets up an association between resources and work effort that tends to result in things being recognized as belonging to those who worked to produce it. Thus, when everyone has access to economically defensible resources, and these resources are predictable in space and time and densely distributed such that the benefits of sole consumption outweigh the costs of defense, and where the amount of time invested predicts harvest size, ownership may be likely to emerge and spread in a population. Norms of ownership and sharing can thus emerge from the spatially explicit disturbance effects that human subsistence has on landscapes.

Social inequality and gender-based divisions of labor

With ownership comes the potential for despotism and increasing social hierarchy and inequality, and this may be more likely where there is spatial variation in how ecosystems respond to anthropogenic influence. If anthropogenic activity has little positive effect on resource distributions, despotism and social inequalities may develop over time as only those who gain access to 'naturally' rich patches can enjoy the benefits of owning them. On the California coast, Kennett et al. 2009 and (Winterhalder et al. 2010) use an ideal free distribution model to document the increase in despotism over time in the Channel Islands. Initial occupation dominated regions of dense, predictable resources. Infilling of habitats with dispersed or more unpredictable resource bases occupied subsequently resulted in increasing differentiation in the population between the haves and the have nots as dominance relations developed that excluded later arrivals from resource ownership (Kennett et al. 2010).

Environmental shifts in resource variance caused by increasing landscape heterogeneity might also be expected to affect the gender division of labor by affecting resource acquisition variance. Men and women tend to respond to resource variance differently, where variance is defined as the unpredictable risk of harvest failure, and in the unpredictable range of harvest values. Both men and women include in their subsistence repertoires a suite of activities or resource types with a variety of variances, but they differ in the relative proportions of time spent on high and low variance activities. While men forage for some low-variance resources, they also include many more high-variance resources than do women. The extent to which men include such high variance resources predicts the degree to which women are highly significant producers of the subsistence economy (Bliege Bird et al. 2009, Codding et al. 2011), and where women produce more, they may have more autonomy and engage more in cooperative intergenerational partnerships with other women. If anthropogenic landscapes reduce inter-forager variance, increase encounter rates with some prey and thus increase success predictability, and foster a greater reliance on low-variance prey relative to high-variance prey, women's economic production is likely to become equal, if not greater than men's.

Conclusions

While there have been calls to incorporate niche construction as an alternative to models of human-environment interaction which typically consider only the way humans respond to environmental conditions (behavioral ecology), the two approaches can be integrated by drawing on complex adaptive systems theory, in which human environmental interactions at larger spatial and temporal scales are best viewed as an emergent property of a co-evolved social-ecological system maintained by the short-term benefits to individual agents (Lansing 2003, Lansing & Fox 2011, Lansing et al. 1998). The putative

weaknesses of behavioral ecology in explaining complex phenomena like subsistence intensification are then dissolved by an approach that integrates across spatial scales and considers the dynamic feedbacks between subsistence, ecological structure, and social organization. Rather than assuming that environmental modification was an intentional attempt to increase environmental productivity, as niche construction models suggest, the emergent properties of disturbance may be a fundamental component of human subsistence whose effects shape social norms of sharing via the way disturbance changes the nature of resource patchiness, defensibility and inter- and intra-individual variance in returns.

The approach I've outline here shows how to incorporate issues of spatial and temporal scale, and links patterns of individual behavior, explained through decision theory, with large scale landscape and group level outcomes that in turn, feed back over time to influence individual behavior. Integrating human behavioral ecology with landscape and community ecology, demonstrates how social norms may emerge from the fundamental properties of human disturbance. This approach considers humans as integral components to ecosystems, upon which may depend a host of other networked species supported by the emergent properties of human landscape interaction. It does not require that ecosystem engineering be 'intentional' and thus dissolves the perennial debate over whether foragers are intentional conservationists or destructive predators. As Bird et al. (Bird et al. 2015) conclude, disturbance processes may lie at the heart of many complex social-environmental phenomena, such as subsistence intensifications and diet breadth shifts in prehistory.

Acknowledgements

I am grateful for the support of friends and family in Parnngurr community in conducting the research described here. Douglas Bird and Brian Coddling contributed to the development of many of the ideas in this paper. The Martu research project has been funded by grants from the National Science Foundation BCS-0850664, BCS-0314406, SBR-0211265, BCS-0127681, BCS-0075289; The Leakey Foundation, The Christensen Fund, The University of Maine, Stanford University Office of Teaching and Learning, The Lang Fund for Environmental Anthropology, Stanford Institute for Research in the Social Sciences, and the Woods Institute Environmental Venture Program.

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