

# Disturbance, Complexity, Scale: New Approaches to the Study of Human–Environment Interactions\*

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## Keywords

human behavioral ecology, sustainability, ecosystem engineering, niche  
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## Abstract

New approaches to human–environment interactions are beginning to move beyond a narrow focus on individuals and simple (patch-level) predatory or competitive interactions. These approaches link nonequilibrium 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 and the other to understand how foragers act as ecosystem engineers in a dry perennial grassland in Australia. I conclude by describing the implications of new approaches that incorporate anthropogenic “intermediate” disturbance (an emergent property of human–environment interaction) as a force shaping environments through time and space, and in so doing patterning the sustainability of subsistence, ways of sharing, ownership norms, and even structures of gendered production.

## INTRODUCTION

Models of individual decision making developed in behavioral ecology have proven remarkably suitable for explaining the adaptive nature of human–environment 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 more complex phenomena, such as the interactive effects of the environment on the development of social hierarchy and the colonization of continents (Kennett et al. 2006, 2009). However, most 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 response to different environmental conditions (i.e., 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 sociopolitical stratification (Bird & O’Connell 2006, Kennett & Winterhalder 2006, Lupo 2007, Morgan 2014). The models predict that the costs of traveling elsewhere increase as more human populations occupy neighboring habitats, causing foragers to spend proportionally more time handling lower-ranked resources, and reducing the opportunity costs of investing in technology to reduce handling costs (Bettinger et al. 2006, Hawkes & O’Connell 1992). This leads eventually to plant domestication and greater investments in agricultural production.

Debates over the limitations of these models have highlighted two main problems. First, these models do not explain the origins of or variations in emergent social phenomena such as the institutions that accompany complex events such as the origins of agriculture. Coevolutionary 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, in these models the absence of ecological dynamics and of attention to individual decision making does not allow for the incorporation of adaptive processes other than group selection transforming social institutions.

Second, these models are designed to explain ecological interactions at very local spatial and temporal scales, and not population- or community-level dynamic interactions. They focus almost exclusively on dyadic relationships between species and on negative interactions such as competition and predation, and they do not incorporate nonequilibrium scale-sensitive approaches, which would allow one to capture how negative effects at one spatial scale can result in positive outcomes at the level of the landscape or the community as a whole (Huston 1979). Niche construction or ecosystems engineering approaches such as those of Zeder (2012) and Smith (2007, 2011a,b) propose that such complex phenomena as the origins of agriculture are best explained by the anthropogenic construction and management of ecosystems to improve subsistence productivity. However, as Smith (2013) points out, although such models succeed in calling our attention to the dynamic and interactive effects of ecology and social structure, they provide no framework

for understanding individual decision making with regard to resource use beyond a vague notion of intentionality in innovation, according to which actors intentionally modify habitats to gain 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 rather to generate new integrative models that can scale up from individual decision making to its social and ecological causes and consequences 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, p. 149).

I suggest that if behavioral ecology is to have any hope of generating better models of complex, dynamic social-environmental interactions, it must find ways of integrating individual decision making within ecological and evolutionary models that operate at broader spatial and temporal scales. This new approach should seamlessly integrate what are often perceived as theoretical divides between nature and culture, agency and adaptation, behavior and institutions, humans and other species, and individuals and communities. It should include humans as part of the fundamental structure and function of ecosystems; pay attention to the dynamic interactions among subsistence, social structure, social institutions, and the environment; and include considerations of different temporal and spatial scales, of variation, and of the complex ecological interactions between humans and other species. Finally, it should take a coevolutionary perspective to account for the interactive effects that take place 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 existing explanations of subsistence intensification by linking insights from research on 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. Although there is ample evidence of local population depression, evidence for the hypothesis that indigenous hunters completely exterminated species is quite limited and contentious (Meltzer 2015). 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 8,000 years (Jones et al. 2008). A narrow focus on the local-scale, dyadic interactions between humans and their prey overlooks 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 generally a source of disturbance to populations, and such disturbance, although negative at some temporal and spatial scales, can produce positive effects at others. Positive ecological interactions, often referred to as facilitation, include any direct or indirect force that positively affects the growth or reproduction of one or more organisms without negatively affecting other species (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; intermediate disturbances are 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 a higher density of Brazil nut trees where agouti are present (Asquith et al. 1999). Other interactions have negative direct effects on the species that are preyed on but positive effects on other species or the community as a whole. For example, 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; with the introduction of top carnivores, both plant populations and the small animals that rely on them rebound (Côté et al. 2004). Removing otters from nearshore environments causes a collapse of macroalgae and sea grasses as herbivores such as urchins and grazing snails increase (Estes & Palmisano 1974). Kelp forests in turn affect other species by increasing food availability for grazers and reducing wave height and current velocity. In otter-dominated kelp forests, barnacles and mussels grow three to four times faster (Duggins et al. 1989); rock greenling are roughly ten times more abundant (Reisewitz et al. 2006); 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 a 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 such as foxes and cats are more common, and populations of scrub-breeding birds decline (Crooks & Soulé 1999). Positive effects can also come about as a result of the engineering activities that are a side effect of some organism's foraging, housing, or predator evasion strategies. When such processes construct new niches or enhance existing ones, they are often referred to as ecosystem engineering (Jones et al. 1994). The classic example is beaver dam construction, which increases wetland areas and produces more environmental heterogeneity, supporting larger populations of a wider range of species at the 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 produce rescaling and habitat protection effects on habitat generalists, which are species that require a variety of habitats for 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, when they 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). Whereas individual populations may decline and become locally 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). The 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. 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.

Although charismatic nonhuman species take front and center in most ecological studies of facilitation, evidence of more complex and/or positive human–environment interactions is more slowly accumulating. One of the first ecological studies to suggest this was conducted by Castilla and colleagues (Castilla 1999, Castilla & Bustamante 1989). Through exclusion experiments

on the Chilean coast, they demonstrated 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 composed of mussels, algae, and barnacles. When humans were excluded, the predatory gastropods rapidly decimated the mussel beds, allowing barnacles to invade and therefore preventing mussels from reestablishing. Human exclusion also increased the size of keyhole limpets (as commonly observed archaeologically, human foragers preferentially choose larger individuals), but this had a devastating effect on algae because big keyhole limpets graze them down more effectively; the loss of algae also left more room for barnacles to invade. Whereas foraging strategies with wide diet breadths seem to actually improve coastal resources for human exploitation, narrow strategies focused on a single intertidal keystone species, such as the sea otter, cause trophic collapse, as commercial hunting did during the nineteenth century. Castilla (1999, p. 282) 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.” Castilla also implies that they may do so simply by virtue of their immediate subsistence strategies, and not necessarily through deliberate environmental modification designed to produce these community-level effects. 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 rain forest 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, it has been suggested that extensive forest-fallow horticultural systems would 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). Whereas some species of large game become depleted around indigenous settlements in the Amazon basin because of hunting (Alvard 1993), other species, particularly agouti, collared peccary, and deer, seem to be scarcely affected by it (Chacon 2012, Koster 2008, Smith 2005). Likewise, whereas some communities experience a decline in populations of preferred species over time, others, such as the Ache, show no effects (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); another hypothesis is that significant source-sink dynamics result in population influx from more remote regions (Hill & Padwe 2000). 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 found 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 forests, measured as catch per unit effort and catch per unit area (Dunn & Smith 2011, Parry et al. 2009).

But the reason for these effects may be not the presence of anthropogenic habitat per se, but rather 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 as well as agricultural landscapes with a diverse set of crops offering feeding opportunities for tapirs and other species. However, the positive effects of anthropogenic forest modification may peak at intermediate spatial extents: As agricultural production intensifies, landscape diversity decreases, and refuge habitat becomes more fragmented and dispersed, the potential for anthropogenic landscapes to support a wide range of animal species may decline. In southern Ghana, cocoa monocultures, which dominate the surrounding fragmented forest reserves, are highly depauperate and mainly support very small animals (Schulte-Herbrüggen et al. 2013).

Although anthropogenic forest modification has been characterized as an intentional forest management strategy (Posey 2003), the large-scale landscape level effects of human disturbance do not need to be intentional. Indeed, even processes as complex as plant domestication (and the patchiness and distribution of 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, the fact that Baka harvest and consume wild yam 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 et al. (2011) note that among the major drivers of plant and animal adaptation in Australia are long-standing 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 semiarid zone, anthropogenic fires are mainly lit during the early dry season, in the winter cold months, primarily to hunt burrowed sand monitor lizards (*Varanus gouldii*). Martu hunters in this region are significant predators of sand monitors, which make up more than 70% of all foraged foods acquired per foraging day. Sand monitor and hill kangaroo are the two major subsistence prey: Hill kangaroos are limited to rocky hills and ranges, whereas sand monitors are most abundant in sandy substrates with extensive spinifex cover. During the colder winter months, sand monitors retreat to shallow burrows to live off extensive stores of abdominal fat, and at this time hunters burn regions of mature spinifex hummocks to expose the burrows. During the summer months, monitors are tracked on the surface, and so hunters 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 after the fire. Due to high encounter rates and the high chances of pursuit success, sand monitors are a staple food resource, the harvest of which can be adjusted to need on a daily basis (Coddington et al. 2010). Variance discounting models show that although sand monitor hunting has lower mean returns than kangaroo hunting, its lower variance and higher chances of success make it more useful for consumption than kangaroo hunting (Jones et al. 2013). In the context of a hybrid economy that includes some reliance on purchased goods, sand monitor hunting, unlike kangaroo hunting, responds to economic scarcity: It has been shown that more women hunt significantly more often when money is short (Scelza et al. 2014). As such, hunting sand monitor lizards is an important way that women, especially postmenopausal ones, provide for their grandchildren and other dependents (Scelza 2009, Scelza & Bliege Bird 2008).



The high returns from sand monitor hunting depend not only on the immediate use of fire, but also on the history of cumulative effects of Martu subsistence activities on the structure of environmental variation. Sand monitor hunting is dependent on an anthropogenic fire mosaic built through the accumulation of approximately 10 years' worth of hunting fires. In two Martu communities, Parnngurr and Punmu, between 60 and 240 individuals set broadcast fires every 3–4 days, resulting in 360 hunting fires per year in an area of approximately 500,000 ha (Bliege Bird et al. 2012). Our analysis of 10 years of satellite images covering 46,000 km<sup>2</sup> shows that the 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. 2008). Martu hunting fires are about 1 km apart, whereas 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, and regions closer to roads, settlements, and frequent camping places are more strongly affected by anthropogenic fire than regions farther away (Bliege Bird et al. 2008).

Cumulatively, Martu burning radically rescales the temporal and spatial impact of fire disturbance across the region. Patches of regrowing vegetation are smaller and closer together, and the diversity of the types of patches regenerating after fire (successional or seral patch diversity) is greater at spatial scales that are typical of a human foraging range (Bliege Bird et al. 2008). Martu fires also prevent more habitat from burning, protecting critical refuge for many small animals and increasing the number and evenness of such patches throughout the landscape (Bliege Bird et al. 2012). The effects of anthropogenic fire restructure the distribution not only of successional mosaics and the attendant vegetation, but also 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 sand monitor lizards (Bliege Bird et al. 2013). Mean returns in hunting sand monitor are 1.6 times higher in more heavily hunted regions than 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 (Coddington 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 that fire played a fundamental role in the late Holocene proliferation of seed-grinding technologies in the arid zone (Zeanah et al. 2015).

The 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-1960s, 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-1980s (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 in this area during the past 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, to 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

(dinnertime camp, in Martu parlance) is lower in anthropogenic environments, mainly because more individuals are successful at bringing in small game. Everyone in the camp does equally well in an anthropogenic environment, whereas in a nonanthropogenic 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 to high-ranked small game and plant foods (by reducing foraging cost or increasing its productivity).

These processes have long been referred to as “fire-stick farming” (cf. Jones 1969), which unfortunately implies that burning by individuals is designed to produce optimally diverse landscapes and that the adaptive maintenance of burning is a consequence of the long-term benefits derived from the increased foraging returns that are possible in such landscapes. To the contrary, what seems clear is that burning is only relative to immediate hunting returns and that 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 an arid and hypervariable environment.

## FEEDBACKS INTO SOCIAL INSTITUTIONS AND SOCIAL ORGANIZATION

Disturbances of 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 only the impact 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 into human social organization and social institutions via foraging decisions, mobility, sharing, gender-based division of labor, and resource defense. In this section, I explore one method 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 on 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, so that in some cases the benefits of 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 and to sustain lower travel costs between encounters (MacArthur & Pianka 1966). Although 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). At the same time, however, many birds experience higher rates of predation due to increased mesopredator activity (Kurki et al. 2000), as diverse landscapes tend to increase the proportion of a community that is 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 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). These authors 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. They argue that this is not just a shift in hunting focus, but an actual increase in populations of smaller animals relative to larger ones as foragers modify environments through their activities. At some sites, source-sink dynamics in heterogeneous landscapes keep large game populations high relative to small game (or some large species are advantaged by the kinds of environmental modification humans engage in, such as tapirs or kangaroos); at other sites, smaller animals may actually increase due to the habitat improvements offered by human activity (Schollmeyer & Driver 2013).

If human disturbance tends to increase patchiness and the predictability of prey animals, as well as encounter rates with medium-sized prey species, it is likely to decrease the costs of travel and reduce stochasticity in returns for human foragers. Larger animals (cf. Morin 2012) tend to be encountered less frequently than smaller animals, and they run faster. Therefore, 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 and a higher chance of coming home empty-handed, but also a higher chance of a harvest bonanza (see Bliege Bird & Bird 2008). Whereas larger animals may provide big bonanzas on average, when the variance in reward is taken into account, such bonanzas may actually provide less utility than a lower mean return on 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 lower intra- and interindividual 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 on the costs and benefits of ownership and sharing. The marginal valuation of resource defense both at the scale of individual harvest (Blurton Jones 1987, Winterhalder 1996) and 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 tend to share more and defend less when there is high intertemporal variation in foraging success (stochasticity), when package size and perishability is high, and when the degree of interforager 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 tend to support these predictions about the way people share (what benefits they receive from sharing is another matter). Resources acquired more synchronously and predictably, like small game, tend to be kept in larger amounts for the consumption of the acquirer and his/her family (Gurven 2004b), whereas high-variance foods are retained less by the producer (Hiwi: Gurven et al. 2000, Ache: Gurven et al. 2002). Independently of variance, foods that come in large packages are shared with more people or in larger amounts than food in small packages (Gurven et al. 2001, 2002; Kaplan & Hill 1985). Low-variance resources (e.g., cultivated or collected foods) may be shared more contingently, whereas 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, 2002), women worked hard to acquire large harvests of low-variance foods such as 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 choosy about recipients: They gave shares to fewer other families, and such giving was more contingent (more was given to those from whom one had received more) compared to the sharing of higher-variance resources such as meat, which were given away without contingency to twice as many recipients, with hunters often relinquishing control over distribution (Gurven 2004a). Similarly, Altman & Peterson (1988) noted that among the Kuninjku (Gunwinggu), individual producers were expected to exert stronger claims to ownership (i.e., to keep more within their own families) for small game than for larger game. The key feature, they suggest, is synchronicity: Even cash, when acquired asynchronously and unequally across the community, is widely shared, whereas it is more likely to be kept for personal use when it is simultaneously and equitably provided. In industrialized societies as well (e.g., Japan and the United States), the expectations about sharing versus keeping can be manipulated by providing resources associated with an unpredictable link between labor and reward: Windfall (stochastic) resources (such as high-variance animals) are commonly shared more widely than resources with strong links between labor and production (Kameda et al. 2002), which suggests a common mechanism behind such norm development.

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

## 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 distribution, despotism and social inequalities may develop over time as only those who gain access to “naturally” rich patches enjoy the benefits of owning them. Kennett et al. (2009) and Winterhalder et al. (2010) use an ideal free distribution model to document the increase in despotism over time on the Channel Islands off the California coast. Initial occupation was concentrated in regions of dense, predictable resources. Subsequent occupation of habitats with

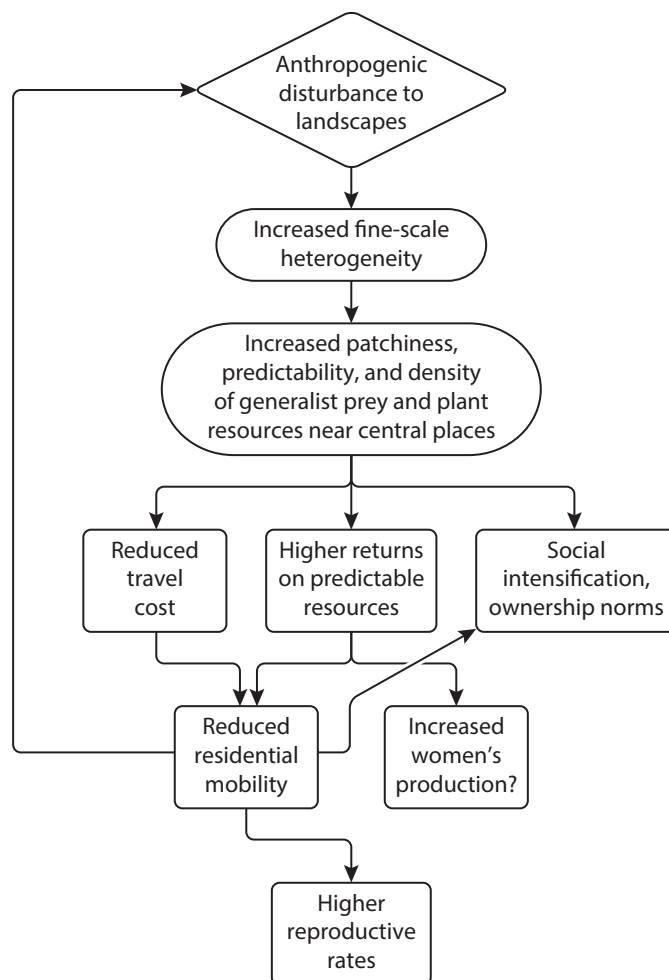
dispersed or more unpredictable resource bases resulted in increasing differentiation in the population between the haves and the have-nots, as the development of dominance relations excluded later arrivals from resource ownership (Winterhalder et al. 2010).

Environmental shifts in resource variance caused by increasing landscape heterogeneity can also be expected to influence the gender division of labor by affecting resource acquisition variance. Here variance is defined as the unpredictable risk of harvest failure and is observed in the unpredictable range of harvest values. Men and women tend to respond to resource variance differently: Both men and women include in their subsistence repertoires a suite of activities or resource types that show a variety of variances, but they differ in the relative proportions of time spent on high- and low-variance activities. Whereas men do forage for some low-variance resources, they 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 significant producers in the subsistence economy (Bliege Bird et al. 2009, Coddling et al. 2011): Where women produce more, they may have more autonomy and engage more in cooperative intergenerational partnerships with other women. If anthropogenic landscapes reduce interforager variance, increase encounter rates with some prey and thus augment 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 to men's, if not greater.

## CONCLUSIONS

Despite calls to incorporate niche construction as an alternative to models of human–environment interaction that 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 where human–environment interactions at larger spatial and temporal scales are an emergent property of a coevolved social-ecological system maintained by 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 such as subsistence intensification can be overcome by an approach that integrates across spatial scales and considers the dynamic feedbacks among subsistence, ecological structure, and social organization. Rather than seeing environmental modification as the result of an intentional attempt to increase environmental productivity, as niche construction models suggest, this approach views the emergent properties of disturbance as a fundamental component of human subsistence, whose effects shape social norms of sharing through the way disturbance changes the nature of resource patchiness, defensibility, and inter- and intraindividual variance in returns (see **Figure 1**).

The approach I have outlined 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 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 of the ecosystem upon which depend a host of other networked species supported by the emergent properties of human–environment interaction. This perspective 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. (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.



**Figure 1**

Conceptual model for the positive human–environment feedbacks described in the text.

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# Contents

## Perspective

- Some Things I Hope You Will Find Useful Even if Statistics  
Isn't Your Thing  
*George L. Cowgill* ..... 1

## Archaeology

- Pleistocene Overkill and North American Mammalian Extinctions  
*David J. Meltzer* ..... 33
- The Archaeology of Ritual  
*Edward Swenson* ..... 329
- Recent Developments in High-Density Survey and Measurement  
(HDSM) for Archaeology: Implications for Practice and Theory  
*Rachel Opitz and W. Fred Limp* ..... 347

## Biological Anthropology

- The Evolution of Difficult Childbirth and Helpless Hominin Infants  
*Holly Dunsworth and Leah Eccleston* ..... 55
- Health of Indigenous Peoples  
*Claudia R. Valeggia and J. Josh Snodgrass* ..... 117
- Energy Expenditure in Humans and Other Primates: A New Synthesis  
*Herman Pontzer* ..... 169
- An Evolutionary and Life-History Perspective on Osteoporosis  
*Felicia C. Madimenos* ..... 189
- Disturbance, Complexity, Scale: New Approaches to the Study of  
Human–Environment Interactions  
*Rebecca Bliege Bird* ..... 241
- Fallback Foods, Optimal Diets, and Nutritional Targets: Primate  
Responses to Varying Food Availability and Quality  
*Joanna E. Lambert and Jessica M. Rothman* ..... 493

Resource Transfers and Human Life-History Evolution <i>James Holland Jones</i> .....	513
An Evolutionary Anthropological Perspective on Modern Human Origins <i>Curtis W. Marean</i> .....	533
<b>Anthropology of Language and Communicative Practices</b>	
How Postindustrial Families Talk <i>Elinor Ochs and Tamar Kremer-Sadlik</i> .....	87
Chronotopes, Scales, and Complexity in the Study of Language in Society <i>Jan Blommaert</i> .....	105
Linguistic Relativity from Reference to Agency <i>N. J. Enfield</i> .....	207
Politics of Translation <i>Susan Gal</i> .....	225
Breached Initiations: Sociopolitical Resources and Conflicts in Emergent Adulthood <i>Norma Mendoza-Denton and Aomar Boum</i> .....	295
Embodiment in Human Communication <i>Jürgen Streeck</i> .....	419
The Pragmatics of Qualia in Practice <i>Nicholas Harkness</i> .....	573
<b>Sociocultural Anthropology</b>	
Virtuality <i>Bonnie Nardi</i> .....	15
Anthropology and Heritage Regimes <i>Haidy Geismar</i> .....	71
Urban Political Ecology <i>Anne Rademacher</i> .....	137
Environmental Anthropology: Systemic Perspectives <i>Yancey Orr, J. Stephen Lansing, and Michael R. Dove</i> .....	153
The Anthropology of Life After AIDS: Epistemological Continuities in the Age of Antiretroviral Treatment <i>Eileen Moyer</i> .....	259
Anthropology of Aging and Care <i>Elana D. Buch</i> .....	277

Anthropology of Ontologies <i>Eduardo Kohn</i> .....	311
Oil and Anthropology <i>Douglas Rogers</i> .....	365
The Post–Cold War Anthropology of Central America <i>Jennifer L. Burrell and Ellen Moodie</i> .....	381
Risks of Citizenship and Fault Lines of Survival <i>Adriana Petryna and Karolina Follis</i> .....	401
Siberia <i>Piers Vitebsky and Anatoly Alekseyev</i> .....	439
Of What Does Self-Knowing Consist? Perspectives from Bangladesh and Pakistan <i>Naveeda Khan</i> .....	457
Addiction in the Making <i>William Garriott and Eugene Raikbel</i> .....	477
Waste and Waste Management <i>Joshua Reno</i> .....	557
<b>Theme: Resources</b>	
Virtuality <i>Bonnie Nardi</i> .....	15
Pleistocene Overkill and North American Mammalian Extinctions <i>David J. Meltzer</i> .....	33
Urban Political Ecology <i>Anne Rademacher</i> .....	137
Environmental Anthropology: Systemic Perspectives <i>Yancey Orr, J. Stephen Lansing, and Michael R. Dove</i> .....	153
Energy Expenditure in Humans and Other Primates: A New Synthesis <i>Herman Pontzer</i> .....	169
Disturbance, Complexity, Scale: New Approaches to the Study of Human–Environment Interactions <i>Rebecca Bliege Bird</i> .....	241
Anthropology of Aging and Care <i>Elana D. Buch</i> .....	277
Breached Initiations: Sociopolitical Resources and Conflicts in Emergent Adulthood <i>Norma Mendoza-Denton and Aomar Boum</i> .....	295



Recent Developments in High-Density Survey and Measurement  
(HDSM) for Archaeology: Implications for Practice and Theory  
*Rachel Opitz and W. Fred Limp* ..... 347

Oil and Anthropology  
*Douglas Rogers* ..... 365

Resource Transfers and Human Life-History Evolution  
*James Holland Jones* ..... 513

Waste and Waste Management  
*Joshua Reno* ..... 557

**Indexes**

Cumulative Index of Contributing Authors, Volumes 35–44 ..... 591

Cumulative Index of Chapter Titles, Volumes 35–44 ..... 595

**Errata**

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