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Niche construction and Dreaming logic: aboriginal patch mosaic burning and varanid lizards (Varanus gouldii) in Australia

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Anthropogenic fire is a form of ecosystem engineering that creates greater landscape patchiness at small spatial scales: such rescaling of patch diversity through mosaic burning has been argued to be a form of niche construction, the loss of which may have precipitated the decline and extinction of many endemic species in the Western Desert of Australia. We find evidence to support this hypothesis relative to one keystone species, the sand monitor lizard (Varanus gouldii). Paradoxically, V. gouldii populations are higher where Aboriginal hunting is most intense. This effect is driven by an increase in V. gouldii densities near successional edges, which is higher in landscapes that experience extensive human burning. Over time, the positive effects of patch mosaic burning while hunting overwhelm the negative effects of predation in recently burned areas to produce overall positive impacts on lizard populations. These results offer critical insights into the maintenance of animal communities in the desert, supporting the hypothesis that the current high rate of endemic species decline among small animals may be linked to the interaction between invasive species and mid-century removal of Aboriginal niche construction through hunting and patch mosaic burning.

1. Introduction

Despite the increasing attention to ecosystem engineering as an important constructive force in the ecology and evolution of biotic communities [1,2], humans are widely perceived primarily through their destructive effects on vulnerable prey communities. While there are many examples of negative effects, such as population depression, extinction and niche destruction [3,4]; positive effects, such as enhancing another species’ population growth or constructing new niches to support a wider range of other species, are difficult to find. Yet humans, particularly hunter–gatherers, do have the potential to be significant ‘ecosystem engineers’ [5]: organisms that physically modify the environment in ways that benefit other species as well as themselves [6–8]. When hunter–gatherers employ patch mosaic burning over large spatial extents, landscape heterogeneity is enhanced, which may stabilize species interactions [9–11] and provide rescaling and habitat protection effects for species that require a variety of habitats for both food and shelter [12–14]. When hunter–gatherers have broad-spectrum diets and hunt many different prey species at multiple trophic levels [15], food web stability might increase, allowing more species to persist with more stable populations than in the absence of such generalized predation [16].

Biotic communities characterized by substantial histories of such engineering should eventually become adapted to these niche-constructing activities, even dependent upon them. These kinds of evolutionary feedbacks are commonly observed through removal experiments, either natural or artificial: the
removal of a potent ecosystem engineer should have cascading
effects on many other species [17]. For example, sea otters
prevent urchins from denuding beds and promote the
return of sea grasses [18,19], providing habitat for many
species of fish and shellfish: in the absence of otters, vege-
tation disappears as well as the fish that depend on it.
Such effects have been demonstrated for a variety of other
species, but evidence for human niche construction has
been limited primarily to the introduction of novel species,
mainly through domestication [7].

Yet, plant domestication is not the only type of niche con-
struction: hunter—gatherers also have the potential to have
positive impacts on ecosystems, especially where their life
ways have persisted in situ for millennia. Australia is one con-
tinent where we are likely to find such evidence. In the arid
desert grasslands that cover much of the continent, human
foraging has been part of the landscape for at least the last
36 000 years or more [20,21], and in some places, still persists.
Desert foraging strategies (at least as documented ethnohis-
torically) have commonly incorporated the use of fire to
increase hunting returns. Hunting effort of both men and
women was focused around the acquisition of small-to-
medium-sized animals, both mammals and herpetofauna,
with the occasional larger prey (kangaroo, Macropus robustus
and Macropus rufus and emu, Dromaius novaehollandiae)
[22–24]. Throughout the desert, fires were used primarily
during the cool-dry season to clear areas of mature spinifex
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during the cool-dry season to clear areas of mature spinifex
(Triodia spp.) grassland in sandplain and dune country to
facilitate search for burrowed prey, especially sand monitor
(Varanus gouldii) and other herpetofauna, but also small
mammals, such as bilby (Macrotis lagotis, now rare), burrow-
ing bettong (Bettongia lesueur, extinct in the Australian
mainland) and rufous hare-wallaby (Lagorchestes hirsutus,
highly endangered). Spot fires for flushing prey were used
while hunting for larger monitors (Varanus giganteus and
Varanus panoptes), brushtail possum (Trichosurus vulpecula,
now rare in the desert) and the feral house-cat (Felis domesticus).
Plants found at high density only in recently burned areas
were dietary staples: Solanum diversiflorum and Solanum centrale,
and grass seeds, such as Engrodis and Panicum. Desert
foragers moved across an extensive landscape, concen-
trating their hunting and burning around reliable water, and
moving on to new camps when hunting returns declined.

Entangled within the practice of foraging is a body
of knowledge concerning the nature of the relationships between
humans and other species, and how those relationships were
maintained: the Dreaming, what Aboriginal people in the Wes-
tern Desert refer to as Jukurr. The Jukurrpa is described by
Aboriginal people variously as ‘Law’, ‘Business’ or ‘University’,
as cosmology, philosophy and natural history. It explains ‘not
just what animals do and where plants grow, but why they
live the way they do and how they are related to each other
and to the ancestral beings’ (P. Taylor 2003, personal communi-
cation). It contains information about the origins of life and the
mechanisms of its maintenance, including detailed information
about ecological interactions, down to the minutia of which
species of skink returns to the same location to defaecate and
which mouse prefers recently burnt spinifex. Critical to the per-
petuation of life is the proper adherence to Jukurrpa, which
frames the importance of fire within the notion that the country
must be used if life is to continue. As one elder puts it, to stop
hunting and to stop burning would mean ‘the end of the
world’ (P. Biljabu 2002, personal communication). Many
Aboriginal people believe that if they do not continue to re-
create the Jukurrpa through emulating the creative forces of the
ancestral beings across the landscape—hunting, collecting,
burning and caring for family—those plants and animals that
depend on their actions will cease to exist. This belief has
important material ecological expression.

Most of the last nomadic groups of desert foragers left the
desert regions between the late 1950s and early 1970s,
moving towards missions and pastoral stations around the
desert’s margins. During that time, somewhere between 10
and 20 native species went extinct, 43 more went into
sharp decline, and the landscape was dominated by extensive
lightening fires [25,26]. Analysis of aerial photography
and satellite imagery covering a large tract (241 210 ha) of
Western Desert grassland demonstrated significant shifts in
mean fire size, from 64 ha in 1953, when Aboriginal foragers
were present, to more than 52 000 ha in 1984 [26]. In 1984, a
group of Manyjiljarra, Kartujarra and Warmman-speaking
desert dwellers (Martu) returned to their traditional country
in the Little Sandy Desert after a 20-year absence and
immediately lamed the state of the land and especially
its perceived scarcity of edible foods (F. Walsh 2008, unpub-
lished data). They began to burn small fires near camps
and along tracks, paths and roads leading to hunting
locations and water sources. They adopted new technologies
(vehicles, rifles, etc.) to increase foraging efficiency in a
degraded landscape and imported supplemental food
sources (purchased goods). Since the 1980s, Aboriginal fires
in localized regions have restored a finer-grained, more
diverse successional mosaic, which prevents the spread of
large lightening fires and actually protects more mature
vegetation from burning. In regions without Aboriginal fires, far
from communities and hunting camps and tracks, lightening
is still the major source of fire ignition: fires are much larger,
farther apart and more habitat is burnt [27,28]. Because
Martu burn when they hunt small prey, hunting intensity is
correlated with the number and size of fires on the landscape,
leading to a finer-grained mosaic of patches in different
stages of regrowth (successional patch) compared with light-
ening-dominated mosaics (see the electronic supplementary
material). As use of a region by Martu hunters increases,
the mean number of successional patches increases, causing
successional patch diversity (Simpson’s Diversity Index),
edge density (the metres of contrast between two different
fire ages per square metre) and the amount of unburned
area to increase [27,28].

The solution to the mystery of species extinctions in the
Western Desert may lie at least in part, in linking Dreamtime
logic to these ecological consequences. The belief that it is not
hunting that causes prey decline, but the lack of it, seems
paradoxical, and to some, evidence of a religiously mandated
mythology that has little to do with ecological reality [29].
Here, we propose one ecological hypothesis that is consistent
with (if not part of) Dreamtime logic: that the creation of
finer-grained habitat mosaics through the application of fire
(patch mosaic burning) in the course of hunting acts as a
type of ecosystem engineering that provides net positive
effects to some species, including humans themselves. Over
time, these ecosystem engineering effects change the avail-
ability of habitat niches, supporting a range of species that
would not otherwise persist in this desert region: such evol-
utionary consequences would turn ecosystem engineering
into a form of niche construction [17]. These positive effects
for some species could come about because finer-grained habitat mosaics increase returns for high-ranked resources through reducing search or pursuit costs, or reduce mortality rates from non-human predators (including invasive cats and foxes, which are now primary sources of mortality) by reducing distance between refuge and foraging locations. The fact that today, the landscape is segregated into areas of intense versus no human influence, provides a natural ‘removal’ experiment through which we can test for the ecosystem engineering effects on species distributions and human foraging returns.

Here, we investigate the interactive effects of patch mosaic burning and Martu hunting on sand monitor (V. gouldii) population density. The half-kilogram sand monitor is a generalist forager that pursues a wide variety of animal prey, especially smaller lizards, insects and arachnids [30]. Over 50% of contemporary Martu hunting foraging is devoted to hunting for V. gouldii. Foraging efficiency is constrained by visibility in spinifex-dominated sandplain, so foragers either target recently burned areas, or burn their own patches for immediate search. Herpetofauna enters a period of brumation during the cool-dry season (May to September) and most hunting fires are set during this time in habitat preferred for winter burrows. Hunters (more often women) work alone, or in small cooperative groups to burn an area of old-growth spinifex, search for fresh burrows, then probe with a long, narrow digging stick to search for the resting chamber, which usually lies 10–20 cm below the ground surface. Summer season hunts when varanids are more mobile target early successional habitat with good track visibility. While human hunting may provide direct negative effects on V. gouldii populations, it may also provide indirect positive effects either by increasing habitat suitability through patch burning or by removing other predators, such as giant perenties (V. giganteus), argus monitors (V. panoptes) and feral cats [31].

We tease out the linked effects of hunting and patch mosaic burning by examining landscapes at varying travel distances from Martu communities: given that Martu are central-place foragers, as travel distance increases, both use of fire and intensity of hunting on V. gouldii should decrease. However, hunting V. gouldii is linked to the immediate presence of fire: in heavy-use landscapes, burned patches are likely to be where Martu have removed prey. If there is a net positive effect of patch mosaic burning on V. gouldii, we should see an increase in prey density with landscape use (figure 1). Alternatively, if there is a net negative effect of hunting, we would expect to see a net decrease in prey density with use. However, it is likely that there are both positive and negative effects at different spatial scales and that the strength of the negative effect depends on whether a local area has been burnt and prey removed by human hunters. If so, we should see an overall increase in V. gouldii density with use in unburned patches (reflecting the positive effects of ecosystem engineering through patch mosaic burning), but depending on the balance of positive and negative forces, either a decline or an intermediate peak in density in burned patches, reflecting the negative effects of human hunting. Martu landscape use should show positive feedback effects to human hunters: here we measure such effects as % of harvests with no prey captured, harvest size (kcal of V. gouldii), and return rate (kcal V. gouldii per hour spent in search and pursuit). All of these metrics should increase consistently or show an intermediate peak with use if burning is a form of ecosystem engineering.

2. Material and methods

The study region includes more than 46 000 km² of the Great and Little Sandy Deserts bioregion of Western Australia (see the electronic supplementary material, figure S1). Within this area, there are four primary ecological communities: (i) spinifex (Triodia schinzeii and Triodia baseoaloeii) and Acacia (Acacia pachycarpa and Acacia ligulata, among others) dominated sandplains and dunes covering 85.6% of the total land area, (ii) lateric uplands and clay-dominated soils with mulga (Acacia aneura) woodland (2.4%) and Cassia shrubland (1.1%), (iii) Triodia-dominated but poorly vegetated rocky ranges (7.3%) and (iv) Eucalyptus (mainly Eucalyptus victrix and Eucalyptus microtheca)-dominated watercourse margins and floodplains (3.2%). This area includes a large portion of the Martu Aboriginal Native Title and Karlamilyi (Rudall River) National Park in which two Martu communities (Parnngurr and Punmu) are located.

Martu foraging data are available from 347 sample days and 4461 focal person-hours of search and pursuit in hunting and collecting (all seasons, June 2000–September 2010). The hunting returns used in the analysis below come from this dataset, in which on each sample day, we accompanied a foraging group from the community (Parnngurr or Punmu), usually in a vehicle, and recorded the location of the ‘dinner camp’, a centrally located cooking hearth which served as the temporary base for the foraging group and followed at least one hunter as they walked on foot from the dinner camp, which marked the beginning and end of each individual foraging bout. There were a total of 266 separate dinner camps for which spatial information and foraging data are complete. Each foraging bout ($n = 1811$ adult bouts, 104 different foragers) includes the number, type and weight of all resources acquired by each participant in the foraging party, total time each spent in search, pursuit and

![Flowchart illustrating the hypothetical process through which Martu hunting and burning affects sand monitor population density. Over the long term, human burning reduces mean fire size and increases diversity of regrowth patches across the landscape, increasing habitat edge density and providing positive feedbacks to V. gouldii populations. At the same time, human predation removes V. gouldii from recently burned areas (providing a negative feedback effect), but also removes V. gouldii predators (providing an indirectly positive effect).](https://rspb.royalsocietypublishing.org/lookup/fig/1)
processing of each resource type, as well as time spent in burning and the location of ignition points. In our sample, Martu harvested 0.83 V. gouldii per adult forager per day hunting occurred. This sums to 1754 V. gouldii over 315 foraging days (1882 person-days), captured in 705 hunts. Energetic returns are calculated as net energy gained per forager per hour in search and pursuit. Net energy calculations are estimated based on a standard value of 3 kcal min⁻¹, the cost of walking by a 60 kg individual at 3.2 km h⁻¹.

Martu are central-place foragers, and as such, the intensity with which any region is searched (forager-hours per square kilometre) should be, all else being equal, a function of travel costs from the central place. Prey depletion is thus more likely in regions that have lower (time) costs of travel. To determine how human activity and predation rates vary across the landscape, we mapped vehicle tracks used during foraging trips with a handheld GPS and used them to construct 12 separate buffer regions at varying distances from roads and communities. We then analysed the spatial distribution of the 266 foraging camps across each of the 12 buffers. Out of all foraging camps 50.2% were established within 20 km of the community (about 10–20 min one-way travel time) and less than 500 m from an established vehicle track: buffers within this distance were classified rank 4. A total of 38.4% of camps (rank 3) were located close to tracks between 20 and 50 km from a community, or close to the community but between 500 and 1500 m from a track. A total of 10.4% of all camps (rank 2) were within 20–50 km from a community and between 500 and 1500 m from a track, and more than 50 km and between 1500 and 5000 m from a track. The regions with the lowest human impact (rank 1, less than 1% of all camps) were those at all distances from communities that were more than 5000 m from a track. The intensity of use of each ranked region is calculated as forager-days per square kilometre observed in our sample (see electronic supplementary material, figure S1).

To survey V. gouldii populations, we conducted a series of ten 10 × 10 m linear pedestrian transects roughly perpendicular to vehicle tracks at varying distances from Parnngurr and Punnu communities during June and July of 2003. Each transect was subdivided into plots of 100 m² in which we enumerated all visible new burrows of V. gouldii and estimated the proportion of spinifex cover and successional stage. There were 368 plots in use-rank 4, 2921 in rank 3, 4282 in rank 2, and 607 in rank 1. Adjacent plots across transects exhibited no significant autocorrelation. Only fresh, likely burrow sites were counted (e.g. those with a loose mound of soil at the entrance): feeding holes (e.g. no or minimal soil mound at the entrance) were not enumerated. The criterion for burrow identification was developed by one of us, N.T., who is a Martu hunter herself. As this survey was conducted in the Austral winter, V. gouldii were brumating in their winter burrows. In this analysis, we use only plots falling entirely in spinifex sandplain and dunefield. Each plot fell entirely within a single successional stage: for this analysis, we collapse patch time since fire into two stages, approximately less than 5 years since fire (burned) and approximately more than 5 years since fire (unburned). This successional stage classification corresponds to the Martu distinction between ‘regrowing’ (waru-waru and nyankura) and ‘burnable’ (manguu and kunarla) vegetation. Analysis was conducted in JMP, v. 10, SAS Institute Inc.

3. Results

(a) Effects of use on lizard density
Paradoxically, lizards are denser where they are hunted most often. The mean percentage of plots with lizards present increases from 7.6 ± 1.8% (95% CI) in lowest use landscapes (use rank 1), to 9.9 ± 0.9 in rank 2, to 11.9 ± 1.1 in rank 3, to 13.0 ± 3.1% in landscapes under highest human hunting pressure (rank 4) (logistic regression, n = 8178, χ² = 16.10, p = 0.0011). Successional stage does not have a significant effect independently of use rank (χ² = 2.33, p = 0.1302). When we consider burned and unburned plots separately, use rank is a highly significant predictor of burrow presence in both (GLM binomial logit, maximum-likelihood estimation, burned: n = 6429, χ² = 14.22, p = 0.0026; unburned: n = 1748, χ² = 22.86, p < 0.0001). However, burned and unburned plots exhibit different responses to use rank (figure 2). Lizard densities peak under intermediate use in burned plots, with densities under high and low use not significantly different. However, there is no intermediate optimum for unburned plots: densities increase to a peak under highest use of a region. Differences between burned and unburned plots are significant only for the highest use rank. If V. gouldii are indeed at higher density in more diverse habitat, we should expect to see more burrows at the edges of patches, where lizards have easy access both to mature and early or mid-successional habitat. In the transect survey, there were 1748 late successional plots: 294 of these were within 20 m of an earlier burn. Controlling for the covarying effects of use rank, edge plots in late successional habitat were 1.51 times more likely to have burrows present compared with non-edge late successional plots (likelihood ratio test, χ² = 4.74, p = 0.0924). Use rank significantly predicts measures of fire patch size and landscape diversity (see electronic supplementary material, figure S2).

(b) Effects on Martu hunting returns
Landscape-level effects on lizard density have measurable impacts on Martu hunting return rates. Lizard hunting returns are poorer and more uncertain in landscapes unmodified by human activity. In comparison to use rank 1, a lizard hunter’s odds of harvest failure are 6.04 (p = 0.001), 6.23 (p = 0.001) and 5.42 (p = 0.003) times lower in use ranks 2, 3 and 4, respectively (logistic regression, controlling for sex, season,
Table 1. Least-squares mean net return rates for sand monitor hunting (s.e., 95% CIs) derived from LS mixed model with forager ID as random effect, controlling for rainfall, season and cooperation, n = 750 bouts; use rank effect F-ratio = 4.16, p = 0.0062. Values connected by the same letter are not significantly different (Student’s post-hoc t-test, p < 0.05).

<table>
<thead>
<tr>
<th>use rank</th>
<th>LS mean (kcal d⁻¹)</th>
<th>s.e.</th>
<th>95% CI</th>
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<tr>
<td>1</td>
<td>850</td>
<td>288</td>
<td>283–1416</td>
</tr>
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</table>

Table 1 shows that the least-squares mean net return rates for sand monitor hunting are significantly different, with values decreasing from rank 4 to rank 1. Harvest sizes (per forager-day) in regions experiencing the lowest human predation intensity are halved compared with intermediate use ranks (table 1). This effect is driven by the rate at which foragers encounter successional patch diversity while hunting; an increase in diversity from 1 to 2 successional stages encountered per hour raises net foraging returns from 541 ± 827 to 1256 ± 675 kJ h⁻¹ (least-square (LS) mixed model (forager ID as random effect), model r² = 0.279, β = 727, model F ratio = 7.55, p = 0.0104, n = 31). The impetus to burn is owing to the impact of fire on foraging returns at the patch scale. Foragers gain their highest returns in the winter, when pursuits involve mainly burrow-spotting, by burning late successional vegetation: fire increases net foraging returns from 25 kcal h⁻¹ to 1552 (table 2). In the summer, when lizards are pursued by tracking, access to ground burned earlier in the season is critical: returns are lower with more plant cover as tracks become more difficult to see.

4. Discussion

Martu patch mosaic burning while hunting V. gouldii and other prey creates habitat patchiness that provides net positive benefits to lizard populations, feeding back to increase human hunting returns in regions of intermediate hunting intensity. Plots in unburned patches show an increase in V. gouldii density with use, whereas plots in burned patches show an intermediate optima. The difference between burned and unburned plots under heaviest human use reflects the extent to which hunting reduces local populations; the lack of a significant difference between burned plots under heavy use and burned plots under no human use suggest that the negative effects of hunting at the patch scale are balanced by the positive effects of human ecosystem engineering at the landscape scale. That this effect is owing to the rescaling of patch size through patch mosaic burning is indicated by the significant effect of edge contrasts on burrow presence. Burrows are more concentrated in patches of mature vegetation within a short distance of a previous burn. However, Martu patch mosaic burning is not designed to create more ideal habitat for V. gouldii; hunters burn primarily in the winter months when search and pursuit involves burrow-spotting because their net foraging returns increase more than 62 times. Sand monitor probably benefit because burning creates more diverse plant and animal communities across smaller scales on the landscape, increasing V. gouldii access to high-ranked prey [32,33].

Here, we have shown that at least one species is more abundant in anthropogenically modified environments, but there is at least circumstantial evidence to support the hypothesis that human ecosystem engineering has evolutionary consequences for a broader range of species. The fact that native mammal decline and extinction corresponded with an increase in invasive mesopredator populations and the departure of Martu and other linguistic groups from the desert between the 1930s and 1970s [25] suggests an even stronger argument for the niche construction aspects of Martu patch mosaic burning. The ecosystem engineering effects of burning that positively impact V. gouldii may also have supported a wide range of small mammals that also benefit from smaller fire mosaics. Rufous hare-wallabies (Lagerorchestes hirsutus, now highly endangered) are browsers that feed on plants in many different successional stages and require mature spinifex hummocks for nesting and predator protection. Prior to the 1950s, they were abundant and hunted frequently by Martu throughout the spinifex sand-plains, but their continued persistence may be dependent on patch mosaic burning to maintain access to early successional habitat adjacent to mature spinifex which provides refuge from predators [34–36]. Likewise, the brushtail possum (T. vulpecula) seems to have been able to persist in regions only where its habitat, riparian eucalyptus woodlands, is still protected from devastating fire through Aboriginal patch mosaic burning [37]. It was not human hunting of these small mammals that led to their extinction but the loss of human hunting. The loss of human hunting and burning may have led to an increase in predation (especially from invasive cats and foxes) and a reduction in the food supply that caused many of these animals adapted to smaller scale fire mosaics to go extinct or abandon the desert for more favourable regions.

The loss of Martu ecosystem engineering has had a negative impact on people as well. Facing an environment in which prey density is much lower than that in the past, foragers have adopted vehicles to reduce the costs of travelling between patches, and rely in part on imported foods. However, in doing so, Martu face new trade-offs. Using vehicles means that most hunting and burning is constrained to regions near tracks and roads, limiting the spatial extent that Martu can affect through fire, and creating vast landscapes interior to tracks where lightening fires burn unimpeded. The increased reliance on imported foods, which are expensive and of low quality has had damaging effects on indigenous health and well-being [38]. The logic of the Dreaming—that a healthy people and a healthy country are linked through fire and the use of resources—reflects a sophisticated ecological and evolutionary understanding of the ways that human activity functions as a keystone process in this desert climate. An environment that can support both healthy people and a wide range of now critically endangered species may now be linked to the continued presence and traditional hunting activities of Aboriginal people. Such effects are likely to be found in other environments in which indigenous patch mosaic burning and hunting provides a significant engineering effect.

Finding such effects requires recognizing the complexity of human–environment interactions: that there are both positive and negative feedbacks to humans and to other species, which are felt both directly, and indirectly via their effects on some other organism (e.g. removing a competitor), and
which are characterized by spatially varying degrees of intensity. This complexity is further enhanced by heterogeneity in species responses to human predation and landscape modification: some species, like the sand monitor lizard described here, with fast life histories and a generalized diet, may respond positively to anthropogenic landscapes; others, such as more specialized, slowly reproducing species, may not.

The extent to which humans do end up embedded within ecosystems as a keystone species is likely to be a function of a long history of coevolutionary interaction between cultural practice and particular ecological communities, where eco-evolutionary feedbacks to human decision-making processes are the main force of cultural evolutionary change. This would be more likely where cultural evolutionary change is not complicated by the flow of practices and technologies between individuals living in widely varying environments, where individuals cannot simply move away to a new region or new environment when things get bad locally, and where populations can make it through the initial instability caused by practices that are not sustainable. There are certainly many examples of populations moving into new environments (for example, small oceanic islands) and importing practices that cause ecosystems to collapse, with subsequent negative effects on the human populations themselves. However, given enough time and given that human effects are spatially variable, we should see a cultural practice which is highly fine-tuned to local environments, where activities that produce net negative feedbacks to humans result in a decline in population, whereas those that produce net positive feedbacks increase populations. Beliefs such as the Jukurr are the institutionalization of such histories of ecological practice.

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2. Kikvidze Z, Callaway RM. 2009 Ecological facilitation and the many examples of populations moving into new environments caused by practices that are not sustainable. There are certainly many examples of populations moving into new environments (for example, small oceanic islands) and importing practices that cause ecosystems to collapse, with subsequent negative effects on the human populations themselves. However, given enough time and given that human effects are spatially variable, we should see a cultural practice which is highly fine-tuned to local environments, where activities that produce net negative feedbacks to humans result in a decline in population, whereas those that produce net positive feedbacks increase populations. Beliefs such as the Jukurr are the institutionalization of such histories of ecological practice.

Table 2. LS mean net return rates by habitat type and season. LS means derived from LS regression mixed nested model (forager random effect) n = 170 patches, model r^2 = 0.217, PursuitType (nested within successional stage) effect test, F-ratio = 2.40, p = 0.0706, successional stage effect test F-ratio = 5.70, p = 0.0010. Values connected by the same letter are not significantly different (post-hoc Student’s t-test, p < 0.05).

<table>
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<th>type of pursuit</th>
<th>successional stage</th>
<th>LS mean (kcal h⁻¹)</th>
<th>s.e.</th>
<th>95% CI</th>
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<td>late</td>
<td>76^3</td>
<td>711</td>
<td>1339 to 1492</td>
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<td>early</td>
<td>13^4</td>
<td>616</td>
<td>1224 to 1252</td>
</tr>
<tr>
<td>winter</td>
<td>mid</td>
<td>403^5</td>
<td>380</td>
<td>551 to 1358</td>
</tr>
<tr>
<td></td>
<td>late</td>
<td>25^6</td>
<td>407</td>
<td>929 to 981</td>
</tr>
<tr>
<td></td>
<td>burn late</td>
<td>1532^7</td>
<td>326</td>
<td>634 – 2469</td>
</tr>
</tbody>
</table>

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Data accessibility. All data referenced here are in the possession of the primary author and can be obtained upon request.

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In this supplement, we describe the link between use rank and fire size, which affects the diversity and size of successional patches on the landscape. Such analyses are also available (using different metrics for use, such as total foraging time and distance from community) in previous publications [1,2]. To construct the fire history of the study region, we used a time series of 21 30 m resolution Landsat 7 TM+ (1999-2002) and Landsat 5 TM (2003-2010) two-image mosaics taken at roughly six month intervals from November 1999 to April 2010. Fire scars were classified by hand on each image using a ratio of bands 7 and 4, which increased the reflectivity of recent burns. The rate at which vegetation regrows is a function of rainfall, but on average, an area reaches a late-successional phase characterized by a dominance of perennial hummock grasses (Triodia spp) and shrubs, within about 7-10 years following fire. Each fire footprint was hand-digitized in ENVI by comparing the current image with the previous time-step, with November 1999 serving as the base image. The minimum size of detectable fires was 0.09 hectares (2 pixels). Ground-truthing of the fire boundaries of the classified map was completed in May 2011. 50 randomly selected points (constrained to be within 500 meters of a road or track) were subject to visual ground checks. 45 out of the 50 points, or 90%, were classified correctly. The firescar map was analyzed at the scale of a human foraging range to determine the relationship between intensity of use and habitat structure. This analysis examines successional patch diversity and scale at the end of the time series, in March 2010. This map merges and overlays the fires from each time-step. The resulting merged raster image classifies the successional age of each patch on the landscape in roughly six month intervals. We used a 3 km radius hexagonal grid of 1244 hexagons (each 23.38 km²) to clip the raster map. Hexagons were generated within each of the 12 buffer regions and not allowed to cross boundaries. There were 997 hexes in use-rank 1 regions, 120 in use-rank 2, 106 in use-rank 3, and 21 in use-rank 4 (see Figure 1). All landscape statistics were generated using Fragstats v4 [3].

Hunting intensity, because of its correlation with mosaic burning, has a significant effect on most patch and landscape metrics (Fig. 2). As use of a region (forager-days per km²) increases, the mean number of successional patches (patches at different times since fire) increases, causing successional patch diversity (Shannon's Diversity Index) to increase. Because the anthropogenic mosaic buffers against very large and intense wildfires, the number of unburned patches also increases with hunting intensity, leading to a greater percentage of total area remaining long unburned, and a higher density of patch edges, contrasts between burned and unburned patches.

Figure 2. Use effects on successional diversity, habitat structure, and scale across 1244 sample hexes of 2338 ha each across landscapes characterized by the intensity of human use (rank increases with use, forager-hrs per ha). Panel A: effects of rank on the mean number of patch types per ha (successional patch density), where patch type is categorized by the six month interval between 1999 and 2010 in which it burned. Patches which did not burn in that interval were categorized as "long unburnt". Panel B: Mean Shannon's Diversity Index by use rank. The Shannon Index is calculated by adding for each patch type, the proportion of area covered, multiplied by the natural log of the proportion. Shannon's Diversity Index increases as the number of different patch types increases and/or the proportional distribution of the area among patch types becomes more even. Panel C: Use rank effects on edge density, or the density of contrasts (measured in meters per ha) between burned (< 5 years since fire) and unburned (>5 years since fire) patches. Panel D: Use rank and the mean percentage of the landscape long unburned (>10 years since fire).
References


Figure 1. Map of the study area showing transect locations and use-rank categories. Use rank buffers 1-3 surround vehicle tracks (both graded and ungraded). Fire scars are visible in the Landsat satellite image background in use rank 1 as lighter grey patches.