Fire mosaics and habitat choice in nomadic foragers

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In the mid-1950s Western Desert of Australia, Aboriginal populations were in decline as families left for ration depots, cattle stations, and mission settlements. In the context of reduced population density, an ideal free-distribution model predicts landscape use should contract to the most productive habitats, and people should avoid areas that show more signs of extensive prior use. However, ecological or social facilitation due to Allee effects (positive density dependence) would predict that the intensity of past habitat use should correlate positively with habitat use. We analyzed fire footprints and fire mosaics from the accumulation of several years of landscape use visible on a 35,300-km^2 mosaic of aerial photographs covering much of contemporary Indigenous Martu Native Title Lands imaged between May and August 1953. Structural equation modeling revealed that, consistent with an Allee ideal free distribution, there was a positive relationship between the extent of fire mosaics and the intensity of recent use, and this was consistent across habitats regardless of their quality. Fire mosaics build up in regions with low cost of access to water, high intrinsic food availability, and good access to trade opportunities; these mosaics (constrained by water access during the winter) then draw people back in subsequent years or seasons, largely independent of intrinsic habitat quality. Our results suggest that the positive feedback effects of landscape burning can substantially change the way people value landscapes, affecting mobility and settlement by increasing sedentism and local population density.

ideal free distribution | positive density dependence | niche construction | historical ecology | hunter-gatherer mobility

The ideal free distribution (IFD) is a game theoretic model commonly used to model habitat choice at landscape scales (1, 2). Increasingly applied to questions of human mobility and settlement systems, it has proven useful in explaining the patterns of Mormon land settlement (3), sustainability in an open-access pastoral system in Cameroon (4), dispersal and settlement in Arctic Alaska (5), the distribution of indigenous language groups in California (6), and the spread of populations in Oceania (7), California's Channel Islands (8, 9), and the West Indies (10). The logic behind the IFD is simple: Given two empty habitats that differ in quality, the richer one should be utilized first; then, as population density increases, resource competition causes patch quality to decline. Eventually, the payoffs to remaining in the highest quality habitat are equal to those of the next most suitable (but empty) habitat, at which point it should become attractive to new residents. At equilibrium, population density is proportional to resource availability. Once all habitats are filled—a condition known as habitat or population packing (11)—constraints on mobility and increases in resource competition are argued to lead to the conditions that favor more intensified economies (12, 13).

In most applications to human mobility decisions, the IFD is assumed to be structured by negative-density dependence, in which per capita fitness declines with population growth as more conspecifics compete for the same limited set of resources. In sparsely occupied landscapes, however, where individuals may have limited access to mates and there are benefits to cooperation that are facilitated through congregation, fitness may be influenced by Allee effects: the presence of positive-density dependence (14). Under positive-density dependence, individuals in small populations or who are living at low densities may actually have lower fitness, despite the release from resource competition, because they have lost some of the benefits conspecifics provide.

For dispersing, obligate cooperators like humans, Allee effects can be quite robust and significantly alter an IFD at low population densities (15–18). At higher population densities nearing the equilibrium condition, or under situations where individuals are spreading into unoccupied landscapes, predictions of the IFD with and without Allee effects are similar: The first arrivals should preferentially occupy the highest ranked habitats, and at equilibrium, population densities should correlate with resource availability. If Allee effects are strong, however, the population density at equilibrium might be higher than expected for a given habitat quality (19, 20). When populations are thinly distributed across a landscape—a circumstance that could arise during range expansions, colonization episodes, or recovery from stochastic population declines—Allee effects can change habitat choice decisions dramatically. Individuals may be drawn to lower-quality habitats if others are already present, ignoring unoccupied high-quality habitats in favor of those already occupied by conspecifics.

Allee effects can arise in a number of different ways: Some through passive facilitation, like the dilution effect of predator avoidance (21), the increased costs of finding mates in low-density populations (22), or increases in resource availability through habitat modification (23); others through active cooperation, such as reproductive enhancement through communal caretaking (24) and the sharing of information, food, or resource defense (25, 26). Allee effects can be present at the level of the group, or at the

Significance

Models of human habitat choice and landscape use assume that people have negative effects on resource availability, which causes them to avoid regions that are already occupied or that show signs of extensive past use in favor of regions of higher quality. We show that when people engage in activities that increase resource productivity, like burning, there is the potential for these improvements to change habitat preferences in favor of places that have been previously modified and occupied by people. This process changes the way we think about intensification (and the origins of broad-spectrum economies), which may arise not from the negative effects of people on resources, but from the positive (and often unintentional) feedbacks between people and their environments.

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population as a whole; they need not require individuals to live in social groups, only to live at higher density. Allee effects are commonly thought of mainly as a form of social facilitation, in which the benefits of communal caretaking or information sharing cause individuals to preferentially choose to join a group (increasing group size) regardless of the quality of the habitat associated with that group (27). However, one often overlooked type of Allee effect arises through ecological facilitation due to persistent niche construction, which may not affect the propensity of individuals to move into an area that is currently occupied, but rather may cause individuals to prefer habitats that have been previously occupied by other individuals. That is, Allee effects are felt at the level of the population. These modified habitats may increase the size of the residential group but they may also reduce the rate at which resources decline, causing land use to intensify by supporting longer residence times (greater sedentism), or more frequent visits (higher local population densities), as the marginal value theorem predicts (27, 28).

When niche construction dramatically improves habitat suitability in this way, it has the potential to create conditions of intense positive-density dependence leading to rapid increases in population density (29). Given that humans have the ability to modify environments in ways that might increase habitat quality, or affect its rate of depletion, it seems particularly important to consider the dynamic histories of these complex human ecological interactions and how past interactions shape the nature of choices in the present. Here, we are particularly interested in whether ecological facilitation through niche construction changes habitat choice decisions under conditions of low population density. Such conditions may be typical of those faced by immigrants to newly occupied regions, such as during the early phases of the peopling of North America and Australia; but they also characterize conditions of extreme population stress and high mortality, such as the Aboriginal out-migrations from the arid interior of Australia in the mid-20th century (30). For a 60-y period beginning about 1906 and ending in 1967, the Indigenous inhabitants of the Little Sandy and Great Sandy deserts of Australia (today known as Martu) migrated from the interior to settlements on the periphery (31). Our question is: At the low population densities typical of the later period of desert abandonment, were habitat choice decisions structured primarily by positive- or negative-density dependence?

The "De-Peopling" of the Western Desert

Migrations of people into and out of the sandy deserts of interior Australia have occurred many times since initial occupation, likely corresponding to the cycles of aridity and amelioration that typify the continent's climate (13, 32, 33). The most recent may have been influenced by the economic opportunities provided by two major development projects during the first decade of the 20th-century, the No. 1–3 Rabbit Proof Fence and the Canning Stock Route (CSR), which had important effects on movement, migration, and landscape use among Western Desert peoples (*SI Appendix*, Fig. S1). Nomadic Martu, whose homelands encompass much of the northwest regions of the Western Desert, began to engage in substantial trade with drovers along the CSR, with fencing crews housed at the Jigalong maintenance depot for the Rabbit Proof Fence, as well as with pastoral stations associated with the emerging cattle economy along the desert fringe, such as Balfour Downs and Ethel Creek (*SI Appendix*, Fig. S1). By the 1930s, emigration from the desert was in full swing as more and more individuals congregated at stations close to ration depots to obtain rations of flour, sugar, and tea, as well as for opportunities to obtain seasonal work in the pastoral industry. Of these fringe settlements, Jigalong—a telegraph depot on the Rabbit Proof Fence that became the site of an Apostolic Mission in 1945—quickly became the main destination for migrating nomads from this part of the Western Desert (31). Surveys undertaken by state and Commonwealth expeditions from 1954 to 1957 estimate that no more than 250 nomadic individuals remained in the region during this time, the majority of whom were observed along the CSR (34). Based on the proportion of surviving elders we interviewed who remained in the desert until the mid/late 1960s, when the final groups were cleared by government patrols in preparation for the Blue Streak intercontinental ballistic missile tests (30), we estimate that this represents less than half of the original occupants of the region (35). While economic "pull" factors undoubtedly played a large role in desert migration, "push" factors, negative affordances to remaining in the desert, may also have been important. Those who remained in the 1950s felt the impacts associated with the emptying desert so much so that they recall traveling long distances just to meet up with others, following the smoke of distant fires to come together in places where people were still living actively on the landscape. Many have suggested that life simply was not possible at such a low population density, and eventually, once population density fell below a certain threshold, those that remained were forced to follow their predecessors to have access to spouses of the appropriate age, sex, and kinship category (36).

The difficulty of life in an emptying desert may have also been driven by a decline in the cumulative ecological effects of Martu subsistence activities. Martu employed many forms of niche construction, including changing local hydrology by digging wells and soaks, and dispersing seed and influencing plant distributions, but the most significant is undoubtedly the use of fire: The creation of pyrodiverse landscapes through large-scale patch mosaic burning (37–39). Fire is used because it immediately improves hunting returns for burrowed prey (lizards and small mammals) from 25 kcal/h in a long, unburned patch to 1,552 kcal/h in a fresh burn (40). Fire mosaics build up over several years of hunting in one region, creating a structurally heterogeneous landscape at a small spatial scale (Fig. 1). This heterogeneity (pyrodiversity) is driven by postfire successional dynamics: Plant species diversity declines with time-since-fire as pioneer species are gradually replaced by low-diversity stands of *Triodia* spp. hummock grasses and *Acacia* shrubs (41). Across most contemporary hunting intensities, the fire mosaics generated through hunting provide positive benefits for monitor lizards (*Varanus gouldii*) that often outweigh the negative effects of predation (40). Hill kangaroo (*Macropus robustus*) and dingo (*Canis dingo*) are more active in regions with greater pyrodiversity (42, 43). Fire mosaics not only improve hunting returns for some animal species, they also reduce the cost of acquiring some plant foods by rescaling the distance between patches, particularly seed grasses and the high-ranked fruits of *Solanum diversiflorum* and *Solanum centrale* (44, 45).

While the benefits of social grouping, trade, and landscape fire suggest positive-density dependence, there is also reason to suspect that resource competition might engender substantial negative-density dependence. One of these critical resources is water, which is particularly limited in this region. In the dry, cool winter months (May to August), Martu often traveled from water source to water source until they reached one of the few large, permanent waters that could sustain them over the upcoming dry season. During the following summer months (November to March), after the monsoon rains had fallen, there were initially large aggregations of people for ritual business, following which small groups would disperse across the landscape to claypans and smaller rockholes, no longer constrained by the availability of water. Food is also potentially limiting, especially in regions close to water. With greater hunting and foraging intensity, there is the potential for short-term resource depletion, especially among the larger animals and in limited patches of fruit. Martu recognize depletion as a function of use, but also the even more significant force of the "landscape of fear" (46) in heavily used regions, and how it affects the probability of hunting failure. After enduring

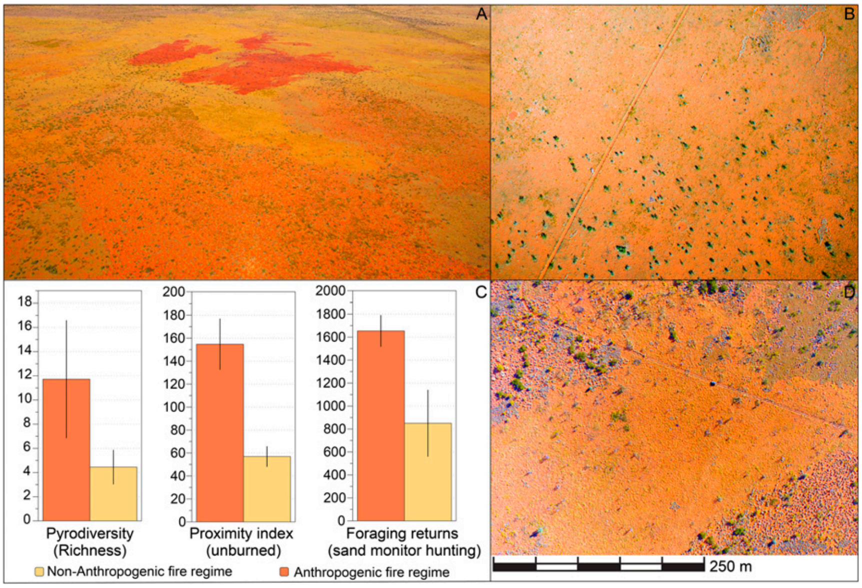

Fig. 1. Contemporary fire mosaics in the study area. (*A*) Typical hunting fires in July 2017 (the larger is 4 ha) surrounded by at least four different older fires. A faint vehicle track is visible in the lower left. (*B*) Spinifex sandplain in July of 2017 in a nonanthropogenic fire regime along the Talawana track. Two fires are visible, one burned last in 2011, the other in 2002. (*C*) Anthropogenic fire regimes increase landscape diversity (as measured by seral richness, the number of unique fire ages) and increase the proximity (reduce distance) between patches of unburned vegetation at smaller spatial scales (±SE across 695 lightning regime and 106 anthropogenic hexagonal regions of 23 km^2) (38). Foraging returns (kcal/h ± SE in search, pursuit and processing, $n = 750$ bouts) for spinifex sandplain resources like monitor lizards (*V. gouldii*) are also higher in anthropogenic regimes (40). (*D*) Spinifex sandplain in July of 2017 in an anthropogenic fire regime. At least five fires are visible: 2001, 2007, 2009, 2012, and 2016.

many unsuccessful pursuits by people over a period of time, most animals become "*ngurli-ngurli*," meaning they are more difficult to capture because they change their behavior to avoid being hunted by people, thereby increasing the risk of hunting failure. Martu note that kangaroos and emus that are *ngurli-ngurli* flee immediately upon sensing humans; they no longer stop, turn around, and watch the hunter from a distance after initially moving away. Monitor lizards that are *ngurli-ngurli* put their burrows closer to trees and shrubs where digging is more difficult among large roots. Hence, even without depletion, a landscape that is used can become a landscape where animals are more difficult to capture.

Because fires are set for hunting in ecological communities dominated by slowly growing *Triodia* grasses, the anthropogenic fire mosaics that build up over several years are an index of past use, and a potential marker either of regions that have been improved or regions that have been compromised or exhausted. If habitat choice is conditioned on a simple IFD with negative-density dependence, we would predict that dense and complex fire mosaics (as an index of past use) serve more as indicators of potential resource depletion, and thus people should be less likely to choose such regions for residential camps, or if they do camp, to spend less time there. Recent use should be positively correlated with habitat-specific (fire-independent) food availability and negatively correlated with the intensity of prior use. If habitat choice is predicted by an IFD with Allee effects, we would predict a positive relationship between fire mosaics and present use. As the mosaic builds, habitat preferences should be determined mainly by the benefits emerging from the existing mosaic and not by intrinsic food availability. Regardless of IFD type, both distance to water and the availability of trade opportunities should also shape habitat choice decisions, as neither is likely to change with prior use. To evaluate these hypotheses, we turn to a unique dataset of Martu movement and mobility patterns prior to settlement as revealed by fire footprints in mid-20th century aerial photography of the Western Desert of Australia.

Results

Spatial Patterning in Recent Fires and Fire Mosaics. Our analysis draws on a 35,300-km^2 aerial photo mosaic imaged between May and August of 1953, gridded into 100-km^2 landscape regions. The first step in our analysis was to determine how many recent fires there were relative to older fires, the likelihood that fires were anthropogenic, the time interval over which they accumulated, and their spatial patterning. We distinguish here between recent fires, those likely burning over a 6-mo period prior to the aerial imaging date, and the index of fire mosaic density, the approximate number of older fire scars visible in each of the 353 sample regions (see *Methods* for details).

Over the entire image mosaic, we observed 2,398 "recent" 1953 fires (ignited by an estimated population of 200 individuals) (Fig. 2). Most of these are likely to be anthropogenic in origin. Contemporary lightning-dominated fire regimes in this ecosystem average 0.28 summer fires and 0.01 winter fires per 100 km^2, while human-dominated regimes average 2.76 summer fires and 5.18 winter fires per 100 km^2 (ignited by a population of about 200 part-time hunters) (38). Of all fires annually, 96% are expected to be anthropogenic. Given our estimates of population density during the historic era, and the rate at which fire scars fade, the number of fire footprints is consistent with a mainly winter season ignition period. Based on our contemporary fire incidence rate, we would expect a total of 2 winter lightning fires and 1,832 winter hunting fires (for every 100 full-time hunters). This is consistent with recent fires accumulating over a 5- to 6-mo period between March and August of 1953, covering the end of the summer wet season (when lightning fires are more common) and the beginning of the winter dry season. The number of fire footprints is strongly correlated with cumulative forager hours spent winter monitor lizard hunting in our contemporary observations of landscape burning (39): Monitor lizards are a staple resource, comprising more than 40% of contemporary bush food harvest (47). Fire is used extensively during the winter season to reduce search costs for burrowed prey, and less extensively in the

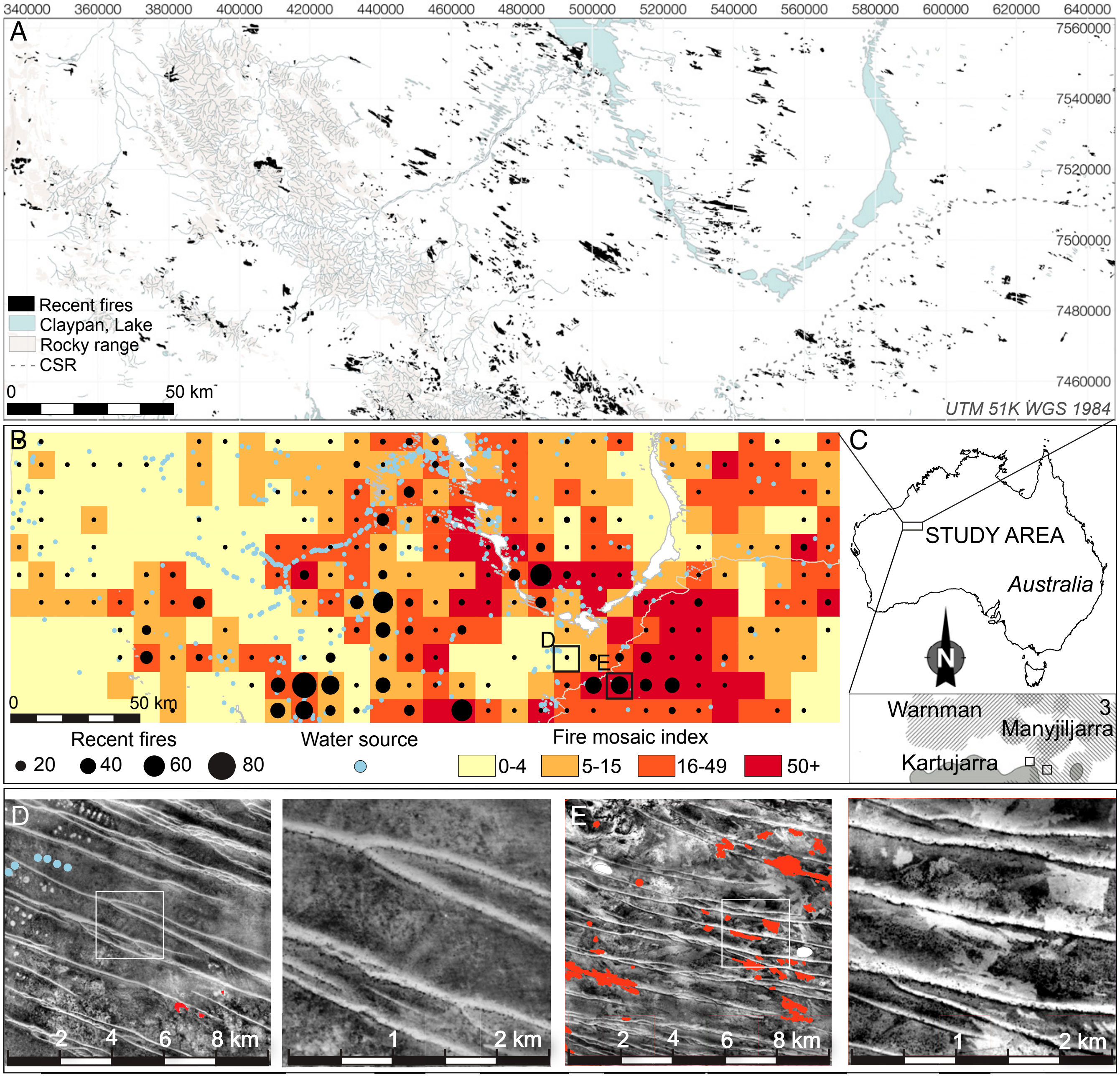

Fig. 2. Map of the study area. (*A*) Recent fires visible on the 1953 photo mosaic across the entire 343,000-km^2 study region. (*B*) Spatial variation in the fire mosaic index and number of recent fires, indicated by circle size, across the entire study region by habitat grid cell (100 km^2). (*C*) Location of the study area and major linguistic groupings across the study region. Shaded areas represent the approximate core area of each linguistic group as a density map of named water sources. Location of *D* and *E Insets* indicated by the window squares. Overlap indicates that more than one linguistic group has a name for that source. (*D* and *E*) *Inset* of aerial photo imagery over two 100-km^2 habitat regions near the CSR. Scars classified as recent fires are indicated in red. *D* illustrates one region with no visible fire mosaic and few recent fires, with the *Inset* (*Right*) showing a more detailed view at the 2.5-km scale. In comparison, *E* (and *Inset*, *Right*) shows one of the densest fire mosaics with many recent fires. Fires with straight-edge ignition lines are clearly visible in *E* (*Right Inset*).

summer, to drive or push mobile prey in particular directions to reduce pursuit costs. Fire size is also consistent with an anthropogenic origin. Contemporary winter hunting fires observed between March 2000 to October 2010 average 109 ± 41 ha (SE, n = 2,514) with a median of 3.3 ha; observed 1953 fires average 16 ± 1.2 ha with a median of 2.6 ha. Lightning fires are much larger, averaging between 2,000 and 6,000 ha depending on the season (38). The 1953 fires also exhibit nonrandom spatial clustering, also consistent with anthropogenic origin. A nearest-neighbor analysis of the center-points of each fire scar shows that they are highly clustered in space ($Z = -57.6$, $P < 0.0001$), and more likely to be found in regions closer to water, with a high percentage of spinifex sandplain habitat (Fig. 3). Fire mosaics also exhibit nonrandom spatial patterning; they are more likely to be present in resource-rich habitats closer to water and farther from habitat edges (Fig. 3 and *SI Appendix*, Fig. S2).

We are thus confident that the number of recent fires is a good index of the intensity of Martu use of the winter 1953 landscape,

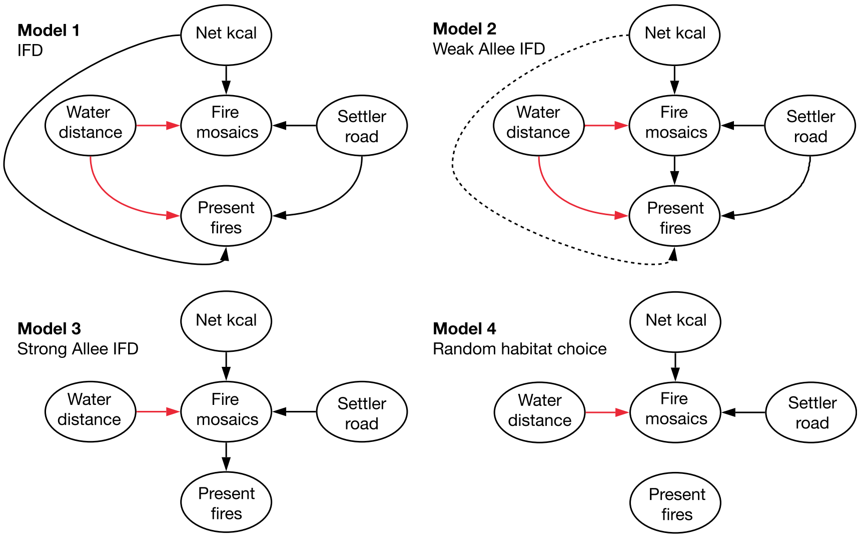

Fig. 3. A priori conceptual models of the drivers of past and present land use. Model 1 assumes a simple IFD under the constraints of water availability: That patterns in past and recent land use (i.e., the mosaic index and the use index) are due only to resource availability. Therefore, both the mosaic index and the use index will be a function of distance to water, net calories available, and the presence of a settler road (indicating the opportunity for trade). Model 2 assumes weak Allee effects on the IFD, suggesting that while fire mosaics will be related to resource availability, recent use intensity will be related to a combination of resource availability and past land use, as might occur where constructed resources do not entirely compensate for resource competition. Note: The path between recent fires and total calories is dashed because it was excluded from the SEM to avoid fitting a saturated model (see *Methods*). Model 3 assumes strong Allee effects on the IFD: It predicts that patterns in the mosaic index are due to food, water, and trade opportunities (as mosaics will only initially build up in higher-quality habitats), but recent land use intensity will be predicted only by the mosaic index due to the strong habitat improvementeffect of the construction of fire mosaics. We might expect strong Allee effects if people are drawn to places where prior use is an indicator of other important (constructed) resources that outweigh intrinsic food/water availability, such as shelters, tools, or wells, or where the fire mosaic itself enhances food availability so much that it swamps the effects of resource competition. Model 4 is a null model of random habitat choice that assumes that while the fire mosaic is related to resource availability, more recent land use is random with respect to both resource availability and fire mosaics.

and fire mosaics are built up through several months to years of prior anthropogenic fire activity.

Structural Equation Modeling. Our analysis draws on piecewise structural equation modeling (SEM) (48) to analyze the interrelationships among drivers of past and present landscape use. We built four a priori piecewise SEMs that described the relationships among the fire mosaic index, the use index, average distance to water, the presence/absence of a settler road or track, and the total net energy availability within each landscape. All a priori models contain two "nodes" or response variables: 1) the mosaic index and 2) the number of new fires (Fig. 4). Under a simple IFD, we expected a negative relationship between the fire mosaic index and recent fire presence, which may diminish in the highest-quality habitats as they can support a higher intensity of use. Under the Allee effect IFD, we expected to see the

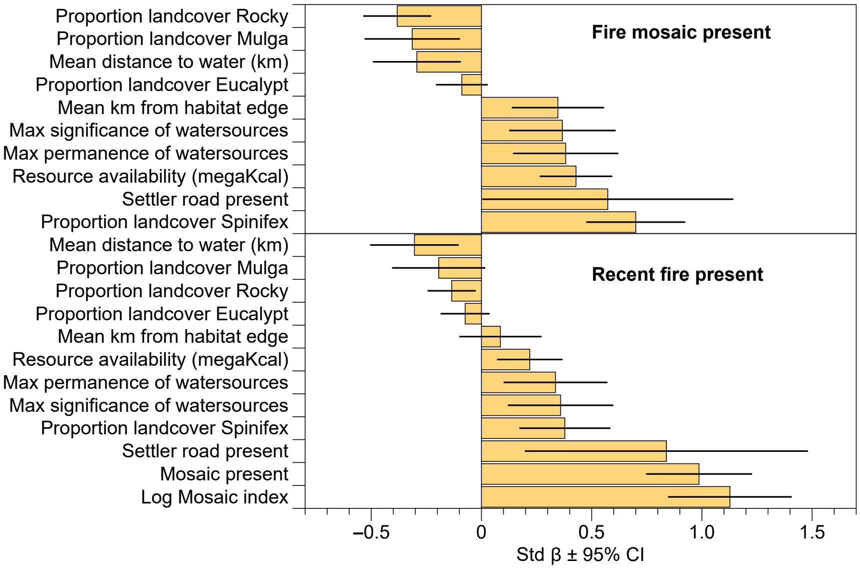

Fig. 4. Predictors of recent fire presence and the presence of fire mosaics. All parameter estimates are calculated from standardized variables in separate univariate GLMs (binomial, logit). Confidence intervals that include 0 are not significant.

Table 1. Model selection of structural equation models explaining past and recent land use

Model	AIC	Δ(AIC)	w_i
Weak Allee IFD	21.088	0.000	0.980
Strong Allee IFD	28.863	7.775	0.020
Random habitat choice	68.823	47.735	0.000
Simple IFD	74.823	53.735	0.000

Italicized values were not supported.

opposite, a positive relationship that may become less positive in the highest-quality habitats as prior fire becomes a smaller component of overall habitat quality. Model selection revealed strong support for a version of the weak form of the IFD with Allee effects: This was the only model with Δ_i values < 2 and had an Akaike weight (w_i) > 0.9 (Table 1), indicating it was clearly the best model in the candidate set. The directed separation (d-sep) test (*Methods*) confirmed the independence claim that recent fires are independent of total calories (Fisher's $C = 0.278$, $P = 0.87$), and that, therefore, the hypothesized relationships are consistent with the data and there is no missing link in the weak Allee IFD model between total calories and recent fires. Parameter estimates from the piecewise SEM corresponded largely with the *a priori* conceptual model; all relationships had the expected direction (i.e., positive or negative).

As predicted, our index of fire mosaic density was higher in landscapes closer to water sources that had higher food availability and more immediate road access. Food availability was the strongest driver of fire mosaics (as measured using relevant range coefficients), followed by distance to water and road presence. All predictors of fire mosaics were significant (i.e., $P < 0.05$) (Table 2). Our index of present use (number of recent fires) was lower in areas distant from water, and higher in landscapes with a higher fire mosaic index (Table 2). The fire mosaic index was the strongest predictor of present use (i.e., had the largest effect size), followed by distance to water and road presence (Fig. 5), but the latter did not have significant relationships with recent use intensity (i.e., $P > 0.05$). Model fit was moderate for both variables (Table 2).

Discussion

Habitat choice by Western Desert Indigenous peoples in the mid-20th century is not predicted well by an IFD model assuming negative density dependence, in which resource competition leads to the avoidance of regions already populated or heavily utilized by others. Rather, we find there are more recent fires in regions with more evidence of past use, represented by fire mosaic density, and that the number of recent fires is predicted by water access but not the availability of food. Our results provide support for a model of landscape use structured by positive-density dependence emerging through the ecological facilitation that arises from the way that past fires improve the predictability of resources and habitat suitability, the firestick farming hypothesis (see refs. 39 and 49). This may help explain why, despite attempts by small numbers of Indigenous Martu to retain a nomadic lifestyle, the desert became depopulated in the mid-20th century.

That there are more recent fires in regions with more older fires, but not necessarily in regions with high intrinsic food availability, suggests that people may be more inclined to visit and remain in an area (or the region is able to support more people at any one time) because past fires have increased the availability of resources or reduced the rate at which they decline. Through our observations of the contemporary relationship between fire and resource availability, we know that fire mosaics greatly increase the probability of monitor lizard presence (per 100-m^2 plot) in unburned patches from 0.08 in unmodified landscapes to 0.25 in heavily hunted regions (40). Kangaroo prefer recently burned patches, and are more than twice as active (as measured by scat counts) in mid-successional patches compared to mature habitat, and scat counts triple in habitats with high successional patch diversity, an effect that appears to balance the pressure of hunting in the most heavily used regions (42). Fire mosaics may also have an effect on foraging returns from plant-based resources, as many of the highly ranked plant foods are limited to early and mid-successional patches regenerating following fire. Anthropogenic fire mosaics rescale this pyrodiversity, which may reduce the costs of collecting fire-dependent resources, such as grass seeds and *Solanum* fruit (44). In landscapes subject to Aboriginal burning, diets shift toward a greater reliance on high-ranked small animals and plant resources (50), which are more abundant in such modified landscapes, and more reliably acquired, serving as a substantial incentive to women, the elderly, and children, for whom such resources are staples (47). People could also be drawn to well-used habitats because soaks, wells, and rockholes need to be continually dug out to ensure continued productivity, or because such landscapes typically offer more tools in the form of cached or discarded technology (grinding stones, cobbles, and cores) (51, 52), or because there are perceptual constraints in determining habitat quality and fire scars are a highly visible signal (53, 54). Alternatively, people may be drawn to places despite low food availability because they have high site fidelity to culturally significant places, such as important ritual and rock art sites (55). Rock outcrops suitable for art production provided a significant focal point for social aggregation, and may have been even more important where seasonal sources of extensive surface water (claypans and river pools) allow for large numbers of people to camp together in close proximity.

An alternative explanation of the relationship between past and present use is the possibility that as landscapes contain more past fire, the size of present fires is reduced. This might occur if more extensive fire mosaics reduce the size of burnable patches, or reduce the availability of patches to burn. In that case, the same foraging intensity (hectares searched per day) might produce fewer large fires in a coarse mosaic, and more smaller fires in a fine mosaic, making the number of fires a poor indication of foraging intensity. If this is the case, we would expect to see that median fire size among recent fires is much lower in more extensive fire mosaics. We do find that median fire size decreases slightly with the fire mosaic index, from 5.1 ha with no mosaic to 2 ha in the most extensive mosaic [generalized linear model, or GLM, (log), $\beta = -0.217$, L-R $\chi^2 = 4.34$, $P = 0.0370$]. However, when we control for differences in mean fire size, the fire mosaic index is still a strong predictor of recent fire [GLM(log), $\beta = 0.167$,

Table 2. SEM parameter estimates

Response	Predictor	Coef	SE	df	*P* value	Range coef	Model R^2
Log(mosaic index)	Distance to water	−0.0663	0.0152	344	0	−0.2265	0.18
	Total calories	0.0511	0.0064	344	0	0.4128	
	Road presence	0.6013	0.2914	344	0.0398	0.1015	
Log(present use)	Log(mosaic index)	0.1989	0.0188	344	0	0.4876	0.29
	Distance to water	−0.0193	0.0054	344	0.0004	−0.1616	
	Road presence	*0.1457*	*0.1109*	*344*	*0.1899*	*0.0603*	

Parameter estimates from the most supported piecewise structural equation model, including raw coefficients (coef), SEs, *P* values, standardized relevant range coefficients (range coef), and model fit (R^2). Italicized variables do not have a significant (i.e., $P < 0.05$) relationship with the respective node.

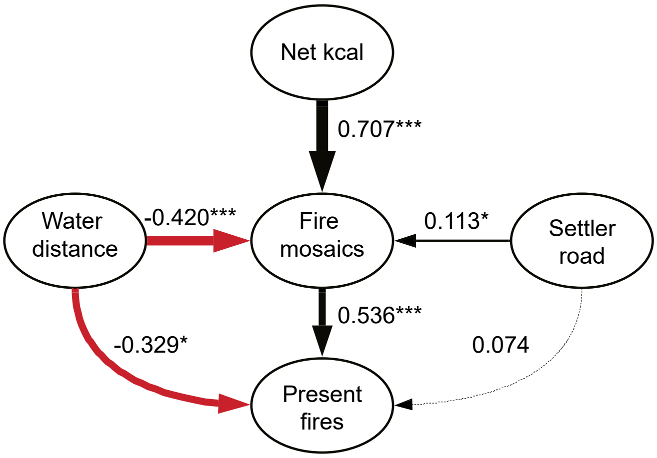

Fig. 5. SEM results. The most supported model of the drivers of past and recent land use in the Western Desert was a version of the weak Allee IFD without the effects of food availability. Road presence was not significant, but remained in the final model. Red, negative relationship; black, positive relationship; line width, effect size determined by relevant range method. Significance levels ***$P = 0.0001$, *$P = 0.01$ or 0.05.

L-R $\chi^2 = 34.95$, $P < 0.0001$], suggesting that in this dataset the number of fires remains a good measure of foraging intensity. Because fires are linked to foraging effort, this relationship between past and present fire could also be driven by prey switching: In poorly developed mosaics, people may be more likely to switch to alternative resources that do not rely on landscape burning, reducing hunting effort for sand monitors or other sandplain prey. If this is the case, we might expect more prey switching (and fewer fires) in sandplain habitat closer to the edges of other habitat types (mulga woodlands, rocky ranges, and eucalypt woodlands), where the cost of prey switching is lower (controlling for water access). But this prediction is not supported. Using a multivariate model predicting recent fire (log+1) with habitat edges, mosaic index, and distance to water, we find there is a negative effect of mean distance to habitat edges on the use index: That is, there are more fires near edges than farther [linear GLM(log), $\beta = -0.121$, L-R $\chi^2 = 4.62$, $P = 0.0316$], and this relationship is stronger where mosaics are more extensive, not weaker (edge × mosaic interaction, $\beta = -0.127$, L-R $\chi^2 = 5.43$, $P = 0.0198$).

People could also be drawn to previously used areas if ownership regimes prevent free movement between high-ranked habitats: A variant of the IFD known as the despotic distribution (56). In the despotic distribution, weaker competitors are pushed to lower-quality habitat because better competitors exclude them from resource access (57). Active despotism is unlikely to shape patch choice decisions in this case, as ownership in the Western Desert was not exercised over resources, but rather over knowledge; different linguistic groups typically did not exclude others from hunting and gathering and, in fact, shared a large overlapping region (Fig. 2*B*). Rights to burn while hunting were typically granted through kinship, residence, or familiarity with country, and in the absence of either of these, permission. However, in practice, women [comprising the majority of group membership (35)] tended to be more likely to remain in familiar places, and with the early departure of some residential bands on the periphery, those remaining may have felt uncomfortable about using core places of other family groups in their absence, or may not have had much knowledge of those regions. Thus, some high-quality water sources and habitats may have gone unused because people were unfamiliar with that country.

We have accounted for the two most probable measures of intrinsic habitat quality—food availability and proximity to water—and only one of these (water) was related to our index of recent landscape use, despite the fact that both are strongly related to past land-use. This difference in the drivers of past and present land use suggests that different factors drive the formation of mosaics than determine concurrent use. This might occur if mosaics are built up through increases in visitation frequency or length of occupation in regions with greater access to food, while the number of recent fires is a function of group size or sand monitor hunting effort increasing in regions with more developed fire mosaics. That recent fires are not linked to food availability may also be a function of the constraints of dry season travel; in moving between distant permanent water sources during the winter months, people may be stopping over in less-preferred habitats and increasing their sand monitor foraging effort to compensate for reduced food availability.

Another potential source of unmeasured variability in our dataset are Allee effects that arise through social facilitation. Strong social Allee effects can result in small groups choosing to reside in a region not because it is necessarily the most productive, but because another group is currently present. As our ethnographic work has suggested, there are powerful incentives to cooperation and sharing in this environment (35, 47). In this era, Martu women were heavily dependent on other women for cooperative hunting, childcare, and other activities, and there was continual anxiety about keeping people together and finding more people to live with. Elders who lived through this time recall small family groups visiting from long distances, and themselves traveling long distances to join relatives by searching the horizon for distant columns of smoke, often well outside their core estate. Additionally, during this period of escalating de-population, small groups and those without men were becoming increasingly vulnerable to violence and raiding by *wanmula*, or landless uninitiated males. During the 1950s, for example, two marauding brothers, Tirinji and Yawa, roamed the Great Sandy Desert on a violent rampage, murdering younger men and kidnapping women (58). Rumors of the brother's serial killings circulated the surrounding settlements and the fear engendered by their violence lasted years (59); in 1964, when Western Australia Native Welfare officer Terry Long encountered a group of 20 Aboriginal women and children at the Percival Lakes, he reported that the women were "desperate to quit the area [. . .] they had no men for years and were frightened that if they did run into a group containing men that some of them would be killed, if they were considered unsuitable as wives" (60). Given the potentially powerful effects of social life, which we cannot see in this unique snapshot of hunter-gatherer landscape use, we do not know whether it was the loss of ecological facilitation, social facilitation, or some combination of both that contributed the push factor promoting desert abandonment.

Conclusions

There is every reason to suspect that strong Allee effects (positive-density dependence) characterize human landscape use decisions in many social and ecological contexts. Humans are intensely social and nearly obligate cooperators; such conditions generate substantial benefits for living in groups that may outweigh the costs of resource competition at lower population densities (17, 18, 61, 62). Allee effects can also occur at the population level, independently of group size, if individuals change environments in ways that improve habitat quality, and these changes are cumulative and positively correlated with population density (63, 64). Allee effects can also arise through the way that movement pathways across the landscape concentrate people in space and time, leading to opportunities for trade, marriage, or ritual business (65). The significance of both group-level and population-level Allee effects for understanding human settlement and landscape use has only just begun to be explored: They have been implicated in resource defense territoriality (61), the partial abandonment of high-quality habitats on the Channel Islands (66), the creation of persistent central places (63, 67), and in the highly clustered way people initially colonized North America (68).

The existence of strong ecological Allee effects challenges the notion that mobile populations simply consume resources and respond to intrinsic habitat quality until resource scarcity or population growth forces settlement and technological innovations. Rather, the history of past interaction with a landscape, even by nomadic people, offers both constraints and opportunities for future interactions (63, 69). Such positive feedback effects have been documented, and appear to be stronger in ecological habitats with lower productivity; for example, in African grasslands, concentrations of people and cattle at central places increases nutrient availability, leading to greater plant diversity and productivity, which then draws people and their cattle (as well as grazing wildlife) back to that location (70, 71). The history of these past interactions may be conceptualized as the creation of basins or nodes of attraction, persistent places on the landscape that, due to the ecological, physical, or ritual infrastructure created there, draw people in by either reducing the costs of aggregation or by increasing its benefits. A least-cost pathway in a central region may become a node of attraction that encourages people to linger and coordinates social interactions, often through stigmergic processes (65, 72). Regions that may otherwise not be as suitable for supporting high population densities may draw people in, at least temporarily, and the environmental changes that occur as a result of that occupation can create persistent places that offer positive (as well as negative) feedbacks to everyday life. While the notion of persistent places has been primarily attached to the construction of durable housing, storage pits, irrigation structures, nonportable tools, or agricultural clearings and terracing, it can also be extended to the types of ecological interactions, or landesque capital (73), created through ecological facilitation. These might include both intentional and emergent ecosystem engineering, such as the maintenance of water sources or the expansion of wetlands through hydrological modifications (52, 74), plant and seed dispersal that increases patch density (75) or enhances β-diversity (76) through the process of foraging or plant transport, disturbances that expand the habitat range of useful plants (67, 77), the construction of intertidal rock walls that expand bivalve habitat and increase recruitment (78, 79), and the long-term ecological effects of burning (43).

Because of this, the existence of strong ecological Allee effects poses some problems for "population packing" hypotheses as explanations for increases in diet breadth and intensification of local economies. Population or habitat packing refers to the infilling of all high-quality habitats, such that expansion to lower-quality habitats is the only way to compete for resource access, resulting in competition for high-ranked resources and a decline in overall foraging return rates, which leads to a broadening of the diet and (in suitable environments) toward domestication and agriculture (80). These types of economies, characterized by a reliance on small animals and a wide range of processing intensive plant foods, are often referred to as "broad spectrum," typical of hunters and gatherers from the Holocene onward (81, 82). Our results suggest that even under conditions of low population density, when many high-quality habitats are empty, people still may aggregate in large social groups or may be drawn back to persistent places on the landscape due to the substantial benefits provided by social and ecological facilitation. The benefits obtained through fire mosaics shift the optimal diet toward more reliable (and more quickly renewing) small animals and plant foods, one of the signature hallmarks of intensification (50, 83). Thus, the existence of strong ecological and social Allee effects creating positive-density dependence, conspecific attraction, and persistent places explains how broad-spectrum economies can emerge under conditions of low population density and high resource availability (82, 84, 85).

These results have profound implications for how we model and think about habitat use, mobility, and settlement patterns. What we offer here is a middle-range theory to link the behavioral ecology of landscape use with niche construction theory of landscape modification, to provide greater understanding of the individual-level, often unintentional processes that lead to persistent habitat modification and that recursively shape the potential of landscapes to support human occupation and influence human mobility, migration, and settlement patterns.

Methods

Present and Prior Use of Landscapes as Visible in Early 1950s Fire Histories. In the 1950s, the Royal Australian Air Force began photographic surveys of the desert interior in the first attempt to create detailed topographic maps of the remotest regions of the continent. These high-resolution black-and-white images have been used previously to demonstrate evidence of altered fire regimes, as many areas were still occupied by Aboriginal people living a nomadic lifestyle as full-time hunter-gatherers, and clearly exhibit extensive anthropogenic fire scars (86, 87). For this study we obtained more than 1,200 individual aerial photos imaged between May and August 1953 and scanned to 2-m pixel accuracy by Geosciences Australia. The images were georeferenced and mosaicked for a 35,300-km^2 region of the contemporary Martu native title. For georeferencing, one of us (M.H.P.) developed an automated image registration algorithm implemented in Matlab, which is freely available at https://bitbucket.org/mpatmudd/opengeoreg (see *SI Appendix* for details). We utilized adaptive histogram matching in ArcGIS to color-balance the images against a high-resolution base image and the radiometry method to generate seamlines for mosaicking.

Following mosaicking, we used the region-growing algorithm implemented in QGIS to digitize the boundary footprints of all visible recent fire scars. Because some parts of the mosaic were imaged on more than one date during the May to August 1953 window, we were able to observe both the relative brightness of the most recent scars and to see how quickly the scars darkened over time as vegetation began to regrow. The most recent scars were highly reflective, showing up as white to light gray, similar to unvegetated sand and soil, while older scars and thick vegetation were much darker. Recent scars had clear boundaries with angular shapes oriented in the direction of prevailing winds, distinctly separating them from neighboring vegetation. Many (but not all) recent fires also contained visible ignition lines, straight edges on the upwind side of the fire created by a person dragging a burning fire-stick perpendicular to the wind (87). In each local region, R.B.B. assessed the relative reflectance of unvegetated substrates, and digitized the fire scars with distinct boundaries that came close to matching those reflectance values. When classification was completed, we calculated an average reflectance value of 110 as the cutoff for designation as a "recent fire"; recent fires are bright white to light gray (reflectance value 110 or more on a scale of 0 to 255), while denser vegetation reflects much darker (reflectance value less than 110) (Fig. 2). Those fires averaging less than 110 were removed from subsequent analysis. Surprisingly, when we completed digitizing the recent fire scars, we observed spatial patterning in their distribution that seemed to follow pathways of movement; recent scars were clustered in space, with linearly oriented scars connecting these clusters, suggestive of people lighting fires while traveling between camping places (Fig. 2). We refer to the number of recent fires as the "use index."

Following the collection of recent fire scars, we generated a vector grid of 100-km^2 cells (n = 353 habitats) (Fig. 2). Recent fires were attached to a habitat if any portion of the fire boundary overlapped. In each habitat, we assessed the fire mosaic by counting the approximate number of older but still visible fire scars, excluding those already marked as recent fires. Unlike for the enumeration of recent fires, there was no expectation that older scars have distinct boundaries. In order to count as a separate fire, scars with adjacent edges had to have slightly different reflectance values, or differences in shape due to differences in prevailing wind direction at the time of the burn. If there were no internal differences in reflectivity or external differences in shape, the scar was counted as a single burn instance. This may underestimate the number of fires in regions where many fires are burning in close temporal and spatial proximity, causing their boundaries to merge together. Similarly, it could overestimate the number of fires in regions where there are a few larger fires that experience differential regrowth causing variation in internal reflectivity. As such, because the count may conflate vegetation diversity and number of older fires in each habitat, it is better conceptualized as a qualitative scoring of pyrodiversity, or fire-related patchiness (which we refer to as the "fire mosaic index"), rather than an absolute count of the number of older fires.

Tracks and Trade Routes. There were two non-Martu tracks visible on the aerial photo mosaic, one north–south graded track in the far western region of the image on the Balfour Downs cattle station, and one northeast/southwest ungraded track on the far eastern side: The CSR. Tracks were attached to a habitat if any part of the track overlapped with the grid cell.

Mean Distance to Permanent or Semipermanent Water. Mean distance to water in each habitat was averaged from a Euclidean distance raster calculated from a water source dataset of potable water point sources compiled from satellite observations, ground-truthed topographic maps, local knowledge, and ground observations by several of the authors. Each water source was given a rank score relative to its permanence and significance (size and amount of water), where 1 is an ephemeral source that only holds water a few weeks following rain, and 4 is a source that nearly always contains water year-round). The distance raster includes only sources ranked 3 and 4 for permanence as these are most likely to still contain water in the winter dry season.

Land Cover and Food Availability. Our contemporary observations of land use show that different vegetation communities contain different sets of resources and different expected resource densities; some, like rocky ranges, are the source of ritually and socially important resources like kangaroo; others, like spinifex sandplains, are important for supplying the fruit, seeds, and small animals that support daily subsistence. To facilitate our assessment of habitat quality, we converted vegetation cover into the expected net caloric value of resources found within that landscape (ignoring any effects of fire mosaic) (*SI Appendix*, Table S1). To calculate this for the 1950s imagery, we relied on contemporary vegetation maps constructed by hand-drawing major habitat boundaries on high-resolution satellite imagery: Mulga woodland, open eucalypt woodland, and gallery forest; rocky range and upland with a mix of tree, grass, and shrub cover; lakes, including salt flats, and claypans; and spinifex-dominated sandplain. These maps were analyzed in Fragstats (v4.3) using the overlaying 10-k grid to calculate percent cover of each vegetation community for each grid cell.

Our primary measure of habitat quality is net caloric monthly food availability. In this region of Australia, there are 10 contemporary subsistence staples considered to be within the optimal diet: Sand goanna, hill kangaroo, witchetty grub, two types of *Solanum* fruit, grass seed (represented here by *Eragrostis*), sandplain *Acacia* shrub seed (represented here by *Acacia ligulata*), two watercourse margin resources (the underground storage organs of *Cyperus* and *Vigna*), and Mulga tree seed (*Acacia aneura*). Total net caloric availability was calculated by multiplying average species density in each vegetation community (generated through our own vegetation surveys) with monthly average caloric production and subtracting the energetic costs of pursuit and processing. To estimate caloric production, we multiplied density by average annual production by weight of edible parts (for plants, weighted by months available) and average body weight (for animals). Gross weights were converted to gross caloric gain using published tables of nutritional content (88). Net calories were calculated by subtracting the average energy cost of collection and processing per kilogram, assuming (for ease of analysis) a flat 200 calorie expenditure per hour of activity. The resulting value per hectare was multiplied by the number of hectares in each landscape grid for each habitat type and summed across all habitat types. Net caloric gain is represented here as megaKcals (10^6 kcals).

Statistical Methods. SEMs allow modeling of multiple response and predictor variable within a single model (89). SEMs differ from other modeling approaches in that variables can be considered as both a response and predictor variable within the same causal network, allowing for the quantification of indirect or "flow-on" effects (90). While SEMs have traditionally been estimated as a global model, piecewise SEMs facilitate the modeling of nodes separately, while allowing for a broader array of error distributions, such as binomial and Poisson distributions (91). Piecewise SEMs were appropriate in this case because of the interrelationships among distance to water, net caloric availability, and past and present land use, represented by the mosaic index and use index, respectively, such that the mosaic index was both a response and predictor variable (of the use index).

We followed the method outlined by Shipley (92) to employ an information theoretic approach to compare the support for each structural equation model, given the data (93). We calculated Akaike's Information Criterion (AIC) to compare models within the candidate set; those that receive a low AIC have greater support (93). We calculated AIC differences (Δi)—the difference between the AIC with the lowest value and all other AIC values—to examine support for models other than the most supported model. Models with Δi values <2 are considered to have substantial support (93). We also calculated Akaike weights (w_i) for each model to measure the probability that each was the best within the candidate set. Models with $w_i > 0.9$ are regarded as "clearly best" among a candidate set (93). We present both raw and standardized coefficients for models with strong support (i.e., $\Delta i, < 2$).

One complication is that AIC cannot be calculated for an entirely saturated SEM (i.e., one with all possible links), and our weak Allee IFD is entirely saturated. To overcome this, we fit the model without the link between the count of recent of fires and total calories, and then undertook a d-sep test to examine whether the model contained missing links. A significant d-sep test (i.e., $P < 0.05$) would suggest that there are missing paths in the SEM and therefore refute the notion that recent fires are independent of total calories, whereas a nonsignificant relationship ($P > 0.05$) would confirm the independence of recent fires and total calories. Standardized coefficients were calculated to allow a direct comparison of effect sizes among predictor variables, based on the relevant range method (94). We used the *piecewiseSEM* package (described in ref. 89) v2.0.2 in R v3.5.3 (R Core Development Team, 2019).

Data Availability. Due to confidentiality agreements with the Martu community, all datasets are available only by request.

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