Aboriginal hunting buffers climate-driven fire-size variability in Australia's spinifex grasslands

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Across diverse ecosystems, greater climatic variability tends to increase wildfire size, particularly in Australia, where alternating wet-dry cycles increase vegetation growth, only to leave a dry overgrown landscape highly susceptible to fire spread. Aboriginal Australian hunting fires have been hypothesized to buffer such variability, mitigating mortality on small-mammal populations, which have suffered declines and extinctions in the arid zone coincident with Aboriginal depopulation. We test the hypothesis that the relationship between climate and fire size is buffered through the maintenance of an anthropogenic, fine-grained fire regime by comparing the effect of climatic variability on landscapes dominated by Martu Aboriginal hunting fires with those dominated by lightning fires. We show that Aboriginal fires are smaller, more tightly clustered, and remain small even when climate variation causes huge fires in the lightning region. As these effects likely benefit threatened small-mammal species, Aboriginal hunters should be considered trophic facilitators, and policies aimed at reducing the risk of large fires should promote land-management strategies consistent with Aboriginal burning regimes.

climate change | patch mosaic burning | trophic facilitation

hroughout Earth's history, periods of high climatic variability are associated with greater levels of biomass burning (1-3). Across diverse ecosystems including subalpine forests (4), ponderosa pine forests (5, 6), and desert grasslands (7, 8), interannual and interdecadal climatic variability increases fire size and extent by enhancing vegetation growth and reducing landscape heterogeneity during wet periods, subsequently increasing fire risk during the droughts that follow. This is particularly evident in Australia, where climate has been increasingly dominated by El Niño/Southern Oscillation (ENSO) and ENSO-like variability in precipitation over the last 5,000 y. Periods of high rainfall alternating with extreme drought drive periodic pulses of fire that extend across vast expanses of the arid zone (9-12), threatening habitats and facilitating predation by invasive species (8), leading to declines in the abundance of many endemic smallmammal populations.

Some suggest that these contemporary climate-driven fire cycles were exacerbated by the removal of Aboriginal hunters through persecution, disease, and migration following the European invasion; without the successional mosaics created through patch burning, large lightning fires driven by rainfall variability were able to spread across vast extents of desert grassland (13-17). Others, however, suggest that climate overshadows any anthropogenic effects (18), either dampening the effect of human ignitions in wet years (19) or enhancing it in dry years, when human fires cause more area to be burnt than would "naturally" be the case (20-22). If climatic effects are so large as to swamp any anthropogenic effects on fire size, then there is little hope for management regimes aimed at mitigating the effect of climatic variability on fire size and its associated detrimental effects on endangered small-mammal populations, particularly if these patterns increase with global climate change (23). Indeed, over the last 30 y, northwestern Australia has seen an increase in the number of heavy-rainfall events during the monsoon season and a decreasing number of low-rainfall events during the dry season

(24). Coupled with more frequent extreme ENSO and El Niñorelated sea-surface temperature anomalies, this has increased interannual rainfall variability in the region over the last 50 y, and this pattern is likely to continue in the future (25). As ENSOdriven bust periods increase mammalian dispersal distances simultaneously with an increase in fire size, buffering such effects could substantially reduce mortality through both predation and resource limitation, mitigating declines and species extinction among mammals in the critical weight range (50–3,000 g), most of which have occurred in desert regions (17, 26). If Aboriginal fire regimes do buffer climate-driven variability in fire size, then the deterioration of Aboriginal fire mosaics following their removal from the desert around the mid-20th century (15) likely explains observed increases in catastrophic fires and subsequent declines and extinctions of many small- to medium-sized mammal populations (27, 28), and provides a strategy to mediate these effects in the future.

We investigate this hypothesis by linking remotely sensed data on fire size with climatological data and ethnographic observations of Aboriginal hunting fires in the Martu Native Title situated in the Great and Little Sandy Desert bioregions of Western Australia. Our analysis uses a 10-y sequence (1999-2010) of satellite imagery to compare fire size and spatial patterning in regimes dominated by Aboriginal hunting ignitions with those under a lightning ignition regime (see Materials and Methods for fire regime definitions). Whereas lightning fires ignite seasonally in time and randomly across space, anthropogenic fires are mostly lit in the context of hunting (13, 29) (Materials and Methods). Among Martu, the Traditional Owners of this region, nearly all hunting fires are ignited within 50 km of the hunters' community or 5 km of a hunting track to burn patches of mature spinifex grass (Triodia spp.) hummocks in sandplain and dune country. Burning aids in search for game, increasing foraging returns for burrowed prey, particularly sand monitors (Varanus gouldii) and other herpetofauna (13, 29). Whereas some spot fires are lit during the summer months, the vast majority of broadcast fires are ignited during the winter months, when fuels are dry and winds are strong and consistent. This region of the Western Desert is extremely remote, with no urban infrastructure, no fire suppression, no pastoralism, and low tourism impact. Lightning is thus the major source of any ignitions in regions more than 50 km from the community and more than 5 km from a vehicle track, and all fires spread until they are naturally extinguished. If Aboriginal ignitions buffer climate-driven variability in fire size through the creation of small-scale habitat mosaics, then (i) regions dominated by Aboriginal ignitions should produce smaller or more closely clustered fires compared with lightning-dominated regions in both summer and winter

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seasons; (ii) this should produce greater pyrodiversity at small spatial scales, increasing the availability of postfire refugia to dispersing mammals; and (iii) 24-mo antecedent rainfall, which closely predicts fire size in spinifex grasslands (9, 22), should increase fire size in a lightning regime but not in an Aboriginal regime.

Results

From November 1999 to March 2010, there were a total of 6,100 fires with a mean size of 886 ha and a median of 6.3 (range 0.09– 490,322 ha; Fig. 1). On average, 9.7% of the landscape burns each year, ranging from a high of 23% in 2000 to a low of 1% in the summer of 2010. Rather than more of the landscape burning under an Aboriginal regime, we find that less burns, although the year-to-year difference is not significant (4.2% compared with 5.2% in the lightning regime burns each season; t = 0.598, P =0.5556). Both mean and median fire size are significantly smaller and fires are more tightly clustered in both seasons (Table 1). The Aboriginal regime also disturbs contiguous habitat and provides more successional fire breaks that limit the spread of large fires. Using an area-weighted χ^2 analysis to standardize the expected number of fires per 100,000 km² in each regime, we find proportionately fewer fires above 100 ha than expected in the Aboriginal regime, and significantly more than expected in the lightning regime (Table 2). The difference is particularly pronounced for fires larger than 10,000 ha, where there are not only proportionately fewer but absolutely fewer in the indigenous

Table 1. Fire size and distribution

	Median (ha)	Mean (ha)	Distance (m)	n
Wet season				
Lightning	46.9	1,910 ± 325	$5,400 \pm 3,594$	647
Aboriginal	4.1	326 ± 83	$1,248 \pm 874$	1,342
Dry season				
Lightning	16.9	$6,255 \pm 3,099$	12,832 ± 15,589	163
Aboriginal	3.3	109 ± 41	661 ± 335	2,514

Mean and median fire size (ha), mean nearest-neighbor distance (±SE, m), and total number of fires (n) in regions dominated by lightning or Aboriginal fire regime, November 1999 through March 2010. All mean differences between each regime are significant at P < 0.05 or less (t test, unequal variances).

regime. For every 100,000 km² under a lightning regime, 237 fires larger than 10,000 ha are observed per 10-y period, whereas the same area under an indigenous regime experiences only 103.

This spatial patterning in fire has two substantial ecological effects that increase the availability of postfire habitat refugia: First, it produces an anthropogenic landscape with greater pyrodiversity at smaller spatial scales, and second, it preserves more long-unburned habitat and disperses it more evenly across the landscape (Table 3). Subdividing each landscape into hexagonal regions of 23 km² reveals that Aboriginal regions have significantly higher successional patch richness, diversity, and evenness. In Aboriginal regions, unburned patches from year to

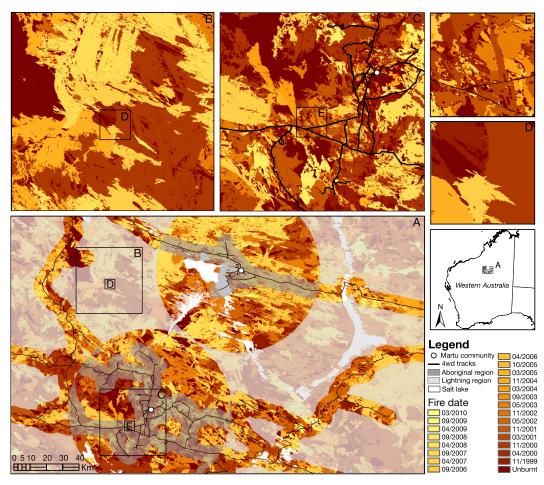


Fig. 1. Fires in the study region. (A) The spatial extent of the Aboriginal regime (a buffer of 5 km around tracks within 50 km of a community) and the lightning regime (areas more than 5 km from tracks and more than 50 km from a community). (B and C) Fires at the 40-km scale. (D and E) Fires at the 6-km scale.

Table 2. Distribution of fires per 100,000 km² of area in each regime

	Fire size (ha)	0.1–1	1–10	10–100	100–1,000	1,000–10,000	10,000–100,000	100,000-1,000,000
Aboriginal	Count	15,282	43,822	18,607	4,812	1,115	103	0
	Total %	17.54	50.29	21.35	5.52	1.28	0.12	0.00
	Column %	99.44	97.94	95.16	87.31	68.82	31.92	0.00
	Row %	18.25	52.33	22.22	5.75	1.33	0.12	0.00
	Deviation	512	823	-184	-485	-442	-208	-17
	Cell χ ²	17.77	15.76	1.80	44.40	125.54	138.69	16.60
Lightning	Count	86	920	946	700	505	220	17
	Total %	0.10	1.06	1.09	0.80	0.58	0.25	0.02
	Column %	0.56	2.06	4.84	12.69	31.18	68.08	100.00
	Row %	2.54	27.10	27.86	20.61	14.89	6.49	0.51
	Deviation	-512	-823	184	485	442	207	16
	Cell χ ²	438.41	388.71	44.49	1,095.24	3,097.02	3,421.37	409.56

Area-weighted χ^2 analysis. Cell χ^2 values greater than 2 indicate significant deviations from expected values. n = 87,136, likelihood ratio $\chi^2 = 4,467.66$, P < 0.0001.

year are associated with significantly higher proximity indices than in lightning regions, indicating they are distributed in larger, closer, more contiguous patches. The difference in area burned year to year accumulates to reach significance at 10 y, with Aboriginal regions averaging more mature habitat (>10 y unburned) than lightning regions.

Mean fire size in the lightning regime is not only larger across both seasons, it exhibits significantly more temporal variation than in the Aboriginal regime (Levene's F test, F = 4.9, P = 0.0302; Fig. 2). This variability in fire size is linked to climatic variability in cumulative rainfall: Variation in 24-mo antecedent rainfall is a significant predictor of mean seasonal fire size in the lightning regime [log generalized linear model (GLM), estimate = $e^{0.015}$ $\chi^2 = 6.9$, P = 0.0085] but not in the Aboriginal regime (log GLM, estimate = $e^{0.008}$, $\chi^2 = 1.1$, P = 0.2925; Fig. 3). In the lightning regime, mean fire size increases 10-fold from 2 drought years (400 mm) to 2 wetter than average years (1,200 mm), and more than doubles the number of lightning regime fires larger than 10,000 ha, from 4.6 to 10.5 (Poisson log GLM, estimate = $e^{0.01}$, $\chi^2 = 5.6$, P = 0.0179). Although there were two high antecedent rainfall seasons (>1,200 mm) in the Aboriginal regime that produced a larger than average number of big fires, overall the relationship between rainfall and the number of large fires was not significant (Poisson log GLM, estimate = $e^{0.006}$, $\chi^2 = 0.9$, P = 0.3233).

Table 3. Regional-scale diversity and the availability of habitat refugia

	Aboriginal	Lightning	
	Mean ± SE	Mean ± SE	
Pyrodiversity		_	
Richness	11.72 ± 4.85	4.45 ± 1.40	
Simpson's diversity	0.692 ± 0.144	0.460 ± 0.206	
Simpson's evenness	0.773 ± 0.142	0.599 ± 0.252	
Availability of habitat refugia			
Proximity index to unburned patches	154.72 ± 21.99	56.89 ± 8.65	
Cumulative area long-unburned (%)	19.5 ± 15.5	12.9 ± 19.9	
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Richness, diversity, and evenness are measured by the number of different fire ages represented in March 2010. The availability of habitat refugia is given by the proximity index (area-weighted, 3-km radius) between unburned patches in each season. A higher index value indicates patches are larger, closer, and more contiguous. "Cumulative area long-unburned" includes the summed area of all patches that did not burn at all over the entire 10-y sequence. All mean differences between regimes are significant at P < 0.05 (t test, assuming unequal variances).

Discussion

This research expands upon our previous work (13, 29) supporting the notion that patch mosaic burning by Aboriginal hunters enhances biodiversity through pyrodiversity, increasing vegetational diversity at small spatial scales by manipulating plant succession (30, 31). We show that, contrary to the common assumption that climate controls fire size and that Aboriginal ignitions can only cause more extensive fire spread in dry years, Martu hunting fires mediate climate-driven effects on fire size. Increasing interannual variability in rainfall causes temporal and seasonal peaks in fire size under a lightning-driven fire regime,

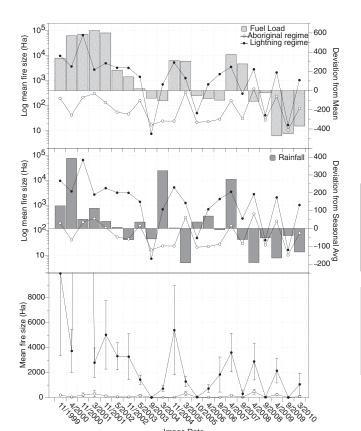


Fig. 2. Temporal variation in fire size. The relationship between mean fire size (ha), fuel load (mm 24-mo cumulative antecedent rainfall), and seasonal rainfall (mm) in Aboriginal and lightning regimes. Error bars show \pm 1 SE.

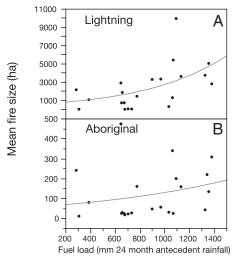


Fig. 3. Cumulative antecedent rainfall (mm) and mean fire size (ha) in Lightning (A) and Aboriginal-dominated (B) landscapes.

but not in landscapes buffered by indigenous hunting fires. Hunting fires remain small as fire risk increases, moderating the ENSO-related boom-bust cycles that can lead to devastatingly large wildfires. This more than doubles the number of fire ages present at the scale of a human day range (23 km²) and increases both the size and the proximity of unburned patches, supporting greater access to postfire refugia for animals living in the region. Indigenous subsistence fires in the Western Desert are thus an intermediate disturbance that dampens climate-driven fire cycles by increasing landscape heterogeneity and preventing large burns from propagating.

Our results demonstrate clear ecological effects of anthropogenic fire at small spatial scales, refuting recent assertions that Aboriginal burning had no measurable effect on the continent's biota (18). Landscapes in the Western Desert have likely been shaped by a long history of anthropogenic fire, with human occupation extending to more than 36,000 y and intensifying over the last 5,000 y (32). Whereas contemporary large-scale patterns of anthropogenic fire are likely to differ in their spatial extent from those of the past, the local application of fire is identical to that observed in the ethnohistoric period, and contemporary hunting fires are similar in size to those observed in the 1950s before the desert exodus (15). Precontact landscape-level fire mosaics were localized around heavily used campsites near springs, wells, and rockholes; such a pattern was so evident that early European explorers in the desert linked the appearance of fire mosaics to the proximity of water (33). The network of mosaics across the desert region following the tracks between water sources would have created a patchwork of heterogeneous vegetation that prevented lightning fires from spreading the great distances they do today, creating critical refugia for many species during periods of drought.

Australia's mammalian populations exhibit complicated relationships between ENSO-related boom-and-bust climate cycles, fire, and predator-prey dynamics. Small mammals in the Australian desert are primarily ground-dwelling and have been recorded making fairly long-distance (5-10 km) movements between habitats (34). These vagrant dispersal strategies are tied to ENSO-influenced variability in the summer monsoon leading to pulses of rainfall alternating with period of drought. During boom years, small mammals are more sedentary and social, but in bust years, they disperse long distances in search of better forage, concentrating in well-watered refugia near rocky ranges (26). Boom years also cause population explosions, which subsequently crash during the droughts that inevitably follow (35). Population booms are fueled by increases in seeds and vegetation growth that follow the pulses of rainfall; this subsequently fuels increases in the predator population. The predator population surges just as the droughts arrive, and mammalian populations are brought down to very low levels by a combination of increased predation and resource competition (8). The extensive fire events following the high-rainfall period have two devastating effects on smallmammal populations. First, when burnt areas are small (<30 ha), resource availability does not seem to be adversely affected, but when fire depletes resources over larger spatial scales, it can have strongly depressive effects (8, 36). Second, larger fires during drought years coincide with the long-distance dispersal animals must make to find food, exposing them to increased risks of predation (37). Open habitats increase predation rates, exposing dispersing mammals to aerial as well as terrestrial predators (8, 38, 39). The predator population has increased over the past 50 y, with the loss of mesopredator regulation through the exclusion of apex predators such as dingoes and Aboriginal hunters, and the spread of invasives, mainly cats and foxes (40-43). The climatebuffering effects of Aboriginal fire have likely been particularly important for many species that benefit both from fine-grained mosaics of alternating resources and from enhanced shelter and protection from large catastrophic fires and the predators that hunt within them. This may explain the coincident decline or extinction of most small- to medium-sized mammals in the desert regions with the cessation of Aboriginal hunting and burning in many regions of the arid zone between 1920 and 1970 (34).

Given this, we suggest that the hunting practices of Aboriginal foragers in the arid zone provide an important trophic facilitation effect through fire-mediated disturbance of plant communities. Hunting fires have widespread ecosystem-engineering effects, creating small-scale habitats that prevent the spread of very large fires and, in so doing, may buffer small, ground-dwelling mammals from the effects of climate-driven fire regimes. Certainly such trophic effects are at least, if not more important than the dingo, recently proposed as a trophic regulator of small-mammal populations (44). Indigenous fire regimes in other environments strongly affected by ENSO-related climate cycling, such as Southern and Western Africa, have been shown to provide similar effects, creating small-scale fire mosaics that prevent interannual and interseasonal variation in lightning fire spread (45, 46). Future land-management strategies should either adopt strategies consistent with Aboriginal burning practices or promote the Aboriginal use of fire in the context of hunting in remote regions of arid Australia; doing so should buffer arid Australia from the threat of large wildfires with increasing climate change and reduce predation rates on native mammals.

Materials and Methods

The study region includes more than 46,000 km² of the Great and Little Sandy Desert bioregions of Western Australia. Within this area are four primary ecological communities: (i) spinifex (Triodia schinzii and T. basedowii) and Acacia (A. pachycarpa and A. ligulata, among others)-dominated sandplains and dunes covering 85.6% of the total land area; (ii) lateric uplands and clay-dominated soils with mulga (A. aneura) woodland (2.4%) and Senna shrubland (1.1%); (iii) Triodia-dominated but poorly vegetated rocky ranges (7.3%); and (iv) Eucalyptus (mainly E. victrix and E. camadulensis)-dominated watercourse margins and floodplains (3.2%). Australia's spinifex-dominated arid grassland fire regimes are strongly fuel- and climate-limited. Sources of natural ignition are frequent during summer monsoons, and fuel accumulation is rapid during years of good rainfall (10). Between fires there is generally a period when fuel loads are too low to support the spread of fire. a period depending upon the rate of growth of the dominant groundcover fuels. Spinifex is a perennial hummock grass, which grows slowly and with wide spacing, taking at least 5 y of good rainfall to become dense enough to carry a fire. Early and midsuccessional patches thus operate as fire breaks.

The study region includes a large portion of the Martu Aboriginal Native Title and Karlamilyi (Rudall River) National Park in which two Martu communities (Parnngurr, population 60-80 and Punmu, population 90-120) are located (Fig. 1). Punmu was established in 1982 by a group of Martu from Strelley Outstation, and Parnngurr was established in 1984 by a group from Jigalong attempting to halt uranium mining in the area, and have been continuously inhabited since. Many of the families returning to the communities include among their older members those who were living nomadically in the Karlamilyi region in the 1950s and 1960s.

The spatial and temporal patterning and size and spread of indigenous fires are shaped by social and economic processes. Most fires target habitat preferred for winter dens by sand monitor, Senna-dominated shrublands and Triodia-dominated grasslands, and although burning can occur throughout the year, the majority of indigenous ignitions are during the cool, dry months of April to September. This patterning is affected by how many men vs. women are foraging. Women use or rely on fire primarily to increase foraging returns in the search for burrowed sand monitor (Varanus gouldii), which comprise 74% of all foraging activity and 58% of total foraging production. There are immediate benefits from winter-season burning in the pursuit of sand monitor (12, 26). When individuals hunt in areas with low successional diversity, burning causes a 40% increase in return rate and a reduction in the percentage of hunts that end in failure, from 22 to 4% (12, 26). There are also some long-term benefits that are realized only at the landscape scale: Increases in habitat patchiness as a result of mosaic burning reduce the search cost for sand monitor in the hot season, when prev are mobile and tracked for long distances (12). Men spend less time involved in fire-related monitor hunting and more time in tracking during the summer when fires are generally not an important component of hunting, as they tend to make foraging more difficult by driving prey deeper into summer dens. Much of men's interaction with fire is in patch burning in all habitat types near roads to attract bustards, or in lighting small patches of spinifex during the hunt for feral cats. The presence of a vehicle track is an important determinant of travel time to the foraging patch, and thus tracks shape the spatial patterning of fires as well. Perhaps the most important determinant of spatial pattern is forager mobility: the tendency to forage (and burn) in a region of about 10 km² intensively for several consecutive days, then move on to a new region tens of kilometers away. This pattern of mobility tends to increase fire-age heterogeneity at a small spatial scale, as revisits to the same local area will occur only on an annual or semiannual basis.

Martu not only have incentives to burn, they also face social and economic disincentives to burn; especially in allowing hunting fires to spread beyond the area, one can immediately search during a single hunting trip. There is a common perception among land managers and pastoralists in Australia that Aboriginal burning is a form of pyromania, and that burns are conducted at random mainly by flicking matches out of moving vehicles. Despite the fact that burning is an important signal of ownership and a demonstration of one's rights to manage landscapes, among Martu, burning without foraging is considered wasteful and costly: It burns resources others might want to collect, exposes animal dens to predators such as dingoes, who also take advantage of fire clearings to hunt, and has the potential to burn areas one does not have the right to burn, exposing the fire starter to potential retribution from others. The number of fires in a region is not predicted simply by where people travel on the landscape, nor by whether or not they are foraging in a location, but by the amount of time they devote specifically to sand monitor hunting (12).

For Martu, the landscape-scale patterns of fire express information about the relationship between the country and those who hold it (kanyinin). The patterning of fire is an honest signal of ownership, where fire footprints reflect the actual use of the land, the foraging activity of those who look after it. This allows fire to represent to other Martu the fact that people are actively reenacting the Jukurrpa (Dreamtime) through their embeddedness in ecosystem structure and function. Those who take the time to go out and hunt and make burned ground also provide a secondary public good in the form of increased production of important fruiting plants and seed grasses several years following the fire. Providing public goods such as fruit "gardens," or hunted game, is an important way that Martu gain and maintain social status, and is also reflective of a strong tie with the Jukurrpa. The fire process thus involves immediate foraging incentives that benefit individuals who light fires, social costs that provide incentives for individuals to limit fire

size and spread, and long-term benefits that are supplied as a public good in the form of increased fruit and seed production. The provision of these long-term benefits is stabilized by social incentives that reward those who provide public goods as "strong in the *Jukurrpa*."

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 6-mo intervals (barring cloud-free days) 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. Each fire footprint was hand-digitized in ENVI version 4.8 (Exelis Visual Information Solutions, Boulder, Colorado) 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 0.1 ha (2 pixels). Ground-truthing of the classified map was completed in May 2011. Fifty randomly selected points (constrained to be within 500 m of a road or track) were visually checked. Ninety percent were classified correctly relative to their estimated burn age.

The second classification layer we constructed was a fire regime map (Fig. 1), which breaks up our area of interest into two landscapes (Aboriginal and lightning) stratified by which ignition source is dominant. The Aboriginal (anthropogenic) regime was defined by the density of Martu foraging camps present in our database, which covers 347 sample days and 4,461 person-hours of search and pursuit in hunting and collecting (all seasons, June 2000 to September 2010) sampled during 12 of the 22 time-steps covered by the satellite imagery. 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 that served as the temporary home 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. Each foraging bout (n =1,811 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 processing of each resource type, as well as time spent in burning and the location of ignition points. Vehicle tracks used during foraging trips were mapped using a handheld Global Positioning System receiver and overlaid on the fire map to construct the buffer zones. A buffer zone of 5 km to either side of roads and tracks up to 50 km from an Aboriginal community is the indigenous regime, characterized by mainly Martu ignition sources (484,230 ha, or 10% of the total area of interest). The lightning regime (2,315,552 ha, or 50% of the total area of interest) are areas greater than 50 km from communities and 5 km from tracks.

To analyze fire size, we plotted the spatial location of each fire centroid on the regime map. Fires were attributed to regimes based on the location of this centroid. To analyze habitat diversity and patch distribution, we merged all seasons' fires into a single raster map showing successional patch diversity at the end of the time series (March 2010), and analyzed diversity and patchiness in each regime using a 3-km-radius hexagonal grid of 1,251 regions (each 23.38 km²) to clip the raster map. Hexagons were generated within each landscape (Aboriginal and lightning) and not allowed to cross the landscape boundaries. There were 695 regions in the lightning regime and 106 in the Aboriginal regime. Pyrodiversity (Simpson's diversity, Simpson's evenness, and richness) and measures of patch isolation (proximity index) were calculated on the hexagonal regions using FRAGSTATS version 3 (47).

Climate variables that influence the extent of fire spread are mainly those that influence fuel growth. Spinifex fuels are particularly dependent on a long period of rainfall to accumulate, and previous research has shown that fire spread in spinifex grasslands is strongly predicted by 24-mo antecedent cumulative rainfall (8). Climate data were obtained from the only recording station within the area of interest (Telfer Aero, 013030, 21.71° S, 122.23° E; http://www.bom.gov.au).

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