Conservation or Co-evolution? Intermediate Levels of Aboriginal Burning and Hunting Have Positive Effects on Kangaroo Populations in Western Australia

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Abstract Studies of conservation in small scale societies typically portray indigenous peoples as either sustainably managing resources, or forsaking long-term sustainability for short-term gains. To explain this variability, we propose an alternative framework derived from a co-evolutionary perspective. In environments with long histories of consistent interaction, we suggest that local species will frequently be well adapted to human disturbance; but where novel interactions are introduced, human disturbance may have negative environmental consequences. To test this co-evolutionary hypothesis, we examine the effect of Aboriginal burning and hunting on hill kangaroo (*Macropus robustus*) abundance. We find that hill kangaroo populations peak at intermediate levels of human disturbance, showing that in ecosystems characterized by long-term human-environmental interactions, humans can act as trophic mediators, resulting in patterns consistent with epiphenomenal conservation. Framing the question within this co-evolutionary perspective provides an explanation for the underlying mechanisms that drive environmental outcomes of subsistence practices.

Keywords Anthropogenic fire · Human behavioral ecology · Applied human ecology · Intermediate disturbance · Niche construction · Aboriginal Australia

Introduction

Studies of conservation among small scale societies produce varied characterizations. Some see sustainable practices as evidence of purposeful management grounded in traditional ecological knowledge (e.g., Lepofsky and Caldwell 2013; Lightfoot *et al.* 2013; Welch *et al.* 2013). Others point to the negative effects of human subsistence practices on biotic communities as evidence that individuals optimize short-term gains at the expense of long-term conservation (e.g., Alvard 1993, 1994; Kay 1994).

Debates that cast indigenous peoples as either intentional conservationists or environmental devastators oversimplify human-environment interactions and ignore existing theoretical frameworks in ecology that account for greater diversity in species interactions. These include direct interactions between species with positive effects to one (i.e., commensalism) or both species (i.e., mutualism) and indirect interactions which can benefit species several trophic levels removed (e.g., habitat facilitation), all of which result from interspecific co-evolution. Such positive effects, whether direct or indirect, are increasingly recognized as a significant force in community assembly, and may be critical in sustaining population stability in complex food webs (Bruno *et al.* 2003; Kikvidze and Callaway 2009). Stabilizing effects are often associated with "keystone species" which have disproportionate influence over other species (Paine

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1969; Power *et al*. 1996; Terborgh *et al*. 2001) and are crucial to ecosystem function (Cottee-Jones and Whitta-ker 2012). Keystone species include those with strong directional ties (such as top predators, Ripple *et al*. 2014), many weak ties (such as generalist omnivores, Neutel *et al*. 2002) or those that significantly modify their environments, sometimes referred to as ecosystems engineers (Jones *et al*. 1994; Smith and Wishnie 2000; Smith 2013) or niche constructors (Odling-Smee *et al*. 1996, 2003, 2013). The latter may be particularly im-portant where species interactions cause intermediate levels of environmental disturbance (Connell 1978; Huston 1979; Sousa 1979), thereby producing direct or indirect benefits to species at intermediate levels of interaction.

Though rarely included as a keystone species, humans often have strong top-down links, many weak ties and subsis-tence practices that significantly alter the environment. As such, species that have coexisted with stable human activities for long spans of time should be adapted to intermediate levels of anthropogenic disturbance. In ecological communities that have co-evolved alongside human subsistence strategies, tra-ditional practices may introduce positive and stabilizing ef-fects on complex community networks (Bliege Bird *et al*. 2013). Within such environments, we should expect human interaction to produce outcomes consistent with what some have called "epiphenomenal conservation" (e.g., Alvard 1993, 1998; Borgerhoff Mulder and Coppolillo 2005; Smith and Wishnie 2000) or "emergent sustainability" (Moritz *et al*. 2013). These outcomes are neither intentional conservation, which requires short-term loss in order for potential users to realize longer-term public gain, nor are they sustainable man-agement, which requires design and intent to ensure future benefit for users. Rather, they are an emergent outcome resulting from co-evolved interactions between humans and other organisms in a biotic community. However, these co-evolutionary outcomes are expected only in communities associated with a long history of stable human-environment interactions. When the scale and scope of human interaction changes rapidly, as with initial human colonization, sudden shifts in mobility or subsistence practices, the introduction of new technologies or new forms of ownership, it may result in extensive ecosystem disruption and a wave of species extinc-tions in the short term (e.g., Estes *et al*. 2011).

The co-evolutionary approach therefore provides predic-tions about where and when we should expect to find practices consistent with sustainable resource management in small-scale societies, and when the results of subsistence practices may be detrimental. Such a framework provides the means to explain variability across diverse societies and environments; specifically, to understand why some indigenous practices seem to produce effects consistent with conservation, while others do not. We suggest that the underlying patterning can

be explained as a process of co-evolution between human subsistence practices and those of other organisms in the local environment.

Co-evolutionary Dynamics in Australia

Here we test predictions from this co-evolutionary hypothesis by examining the spatially variable effects of Aboriginal burning and hunting practices on hill kangaroo (*Macropus robustus*, also known as the common wallaroo or euro) in Western Australia. In Australia's remote western deserts, Martu, Aboriginal owners of their ancestral estates, maintain a number of traditional foraging practices, including fire-stick farming (Jones 1969)—a practice that may date back several thousand years (Codding 2012; Smith 2013) or more (Miller *et al*. 2005). Martu light fires for many reasons, but most frequently in the context of winter-time sand monitor lizard (*Varanus gouldii*) hunts (Bird *et al*. 2005; Bliege Bird *et al*. 2008). Sand monitor lizards are burrowed in the winter and hunters burn off patches of mono-specific climax vegetation composed of spinifex grass (*Triodia* spp. or *Plectrachne* spp.) in order to more easily spot the fresh mounds of sand at their entrances. This practice increases in-patch foraging returns during winter hunts, and increases foraging efficiency in the summer months when foragers can more easily track animals across the newly burned sandplain (Bird *et al*. 2005; Bliege Bird *et al*. 2008, 2013).

Because these hunting fires are smaller and more numerous than lightning caused fires, repeated burning and hunting results in the build-up of a more fine-grained and locally diverse mosaic of vegetation communities that vary in the time since fire (seral stages) (Burrows *et al*. 2006; Bliege Bird *et al*. 2008, 2012). Many of the species endemic to the desert region seem to be adapted to a tightly woven mosaic of alternating post-fire successional stages; especially smaller marsupials, such as the brushtail possum (*Trichosurus vulpecula*) and the spinifex hare-wallaby (*Lagorchestes hirsutus*), both of which have been argued to be dependent upon an Aboriginal fire regime (e.g., Lundie-Jenkins *et al*. 1993). Beyond reducing the likelihood of devastatingly large fires that could destroy habitat or actually cause mortality (Bliege Bird *et al*. 2012; Bradstock *et al*. 2005), the greatest benefits may center on the reduced costs of access to alternat-ing patches of varying seral stages, allowing for predator refugia in older seral stages adjacent to high quality foods occurring in patches of younger ages (e.g., Firth *et al*. 2010).

We recently showed that the indirect benefits sand monitor lizards receive from anthropogenic fires outweigh the associ-ated negative impacts of human hunting pressure (Bliege Bird *et al*. 2013). Along with sand monitors and other small mar-supials, larger species such as the hill kangaroo may also benefit from living within an anthropogenic fire mosaic. Pre-vious research has shown that fire can have a positive effect on

in-patch kangaroo densities. In the eucalyptus forests of Arnhem Land, kangaroo seem to prefer newly emerging shoots in the first stages of post-fire succession (Murphy and Bowman 2007). In the hummock sedgelands of Tasmania, fire incidence has a positive effect on kangaroo densities by removing dominant climax vegetation with limited forage value, and replacing it with a diverse set of colonizing plants that provide a higher density of high quality forage (Styger *et al.* 2011). However, studies examining the impact of fire on mammal populations typically look only at the in-patch effects, and as such, there is still very little research on how landscape-level patterning in fire affects kangaroo populations. Because hill kangaroo range over unusually small areas for arid-adapted mammals of their body size (Clancy and Croft 1990; Croft 1991; Fisher and Owens 2000), hill kangaroo may benefit from living within more fine-grained vegetation mosaics as they might more easily transition between shelter in old growth patches to resource-rich patches of younger seral age. The greater diversity of seral patches available within the average hill kangaroo day range may also buffer individuals from seasonal and inter-annual variability in resource distributions. This suggests that hill kangaroo populations may be higher in regions characterized by greater levels of human interaction. However, because hill kangaroo are commonly hunted by Aboriginal foragers who favor regions with higher kangaroo population densities, the negative effects of hunting may outweigh the potential positive effects of burning. If hill kangaroo are adapted to living within vegetation mosaics structured by Aboriginal fire-regimes, but are negatively impacted by predation, then their populations should be highest at intermediate levels of human interaction. If however, there are no positive effects of anthropogenic fire on hill kangaroo, then hill kangaroo populations should decrease monotonically with increasing human interaction and their populations should be highest away from anthropogenic influence.

To better understand the dynamics between Aboriginal subsistence practices and desert fauna, we collected data on hill kangaroo scat densities in the Little Sandy Desert Bioregion of Western Australia across different Martu Aboriginal hunting regions. These data were coupled with remotely-sensed and on-the-ground measures of seral diversity and habitat heterogeneity. We test three predictions to determine the combined effects of Aboriginal burning and hunting on hill kangaroo populations. First, we examine hill kangaroo distributions across patches of different seral stages to determine if they do indeed prefer particular stages of vegetative regrowth. If so, then more fine-grained mosaics of these different seral stages should provide hill kangaroo with greater access to preferred resources within their daily foraging range. Second, if hill kangaroo benefit from living within a fine-grained mosaic of alternating seral stages, then their densities should be higher in regions with greater seral-stage diversity

and heterogeneity. Finally, because hunting pressure may co-vary spatially with burning, hill kangaroo populations may be greatest at intermediate levels of human activity, where the net benefits of Aboriginal burning are high enough to offset any negative impact of Aboriginal hunting.

Materials and Methods

Study Area and Context

In the Little Sandy Desert Bioregion of Western Australia, Martu have Native Title to a vast expanse of their traditional estates (Fig. 1). Of the three Martu communities within the Native Title Determination Area (Punmu, Parnngurr and Kunawarritji), this work is centered on Parnngurr community. Residents of all three communities are highly mobile, frequently traveling between different communities, to nearby towns (e.g., Newman, Port Hedland) and along hunting tracks to establish temporary 'dinner-time camps' from which they will forage for, prepare and consume wild foods.

Martu classify post-fire succession in five ethnoecological stages that correspond to the dominant vegetation (Table 1). Following an initial period during which the ground is bare, (*Nyurnma*), early regrowth (*Waru-Waru*) begins typically 6 months to 1 year following the first post-fire precipitation. The mid-seral stage (*Nyukura*) begins 1 to 5 years following fire with herbaceous and fruiting plants (e.g., *Solanum* spp.), which are an important dry season resource for Martu and, according to Martu informants, for hill kangaroo as well (Codding 2012). Spinifex re-establishes dominance between 5 and 15 years since fire. Martu differentiate this late seral stage into two types: *Manguu*, when spinfiex is mature enough that a fire can carry and *Kunarka*, when old spnifex dominates with a decaying center. Because a fire generally cannot spread until spinifex again dominates the vegetation, fire-return intervals are limited based on the structure of spinifex growth.

This *Triodia* spp. and *Plectrachne* spp. (spinifex) sandplain dominated environment is interspersed with *Acacia* spp. (mulga) woodlands, eucalypt dominated water-course margins and rocky ranges of mixed cover. Hill kangaroo spend most of their days in the shade of shrubs, trees and caves atop these rocky ranges, traveling down to the sandplains in the mornings and evenings to forage. Since most Aboriginal patch mosaic burning occurs in the sandplains, reshuffling the mosaics of post-fire vegetation may alter the distribution of plants available within a typical hill kangaroo foraging radius. Our analyses test for this in-patch effect of increasing forage quality, as well as for a landscape level effect on kangaroo populations.

Fig. 1 Map showing locations of scat transects relative to a 10 year fire history classified by remote sensing. *Highlighted circles* mark the 3-km radii around each hill kangaroo habitat. *Black circles* are scaled proportionally to kangaroo scat counts. *Dashed lines* are 4WD tracks around Parnngurr community. The insert shows the location of the Martu Native Title Determination Area in black with Karlamilyi National Park in white

Parnngurr Community

Older Fires   More Recent Fires

0 3 6   12   18   24
Kilometers
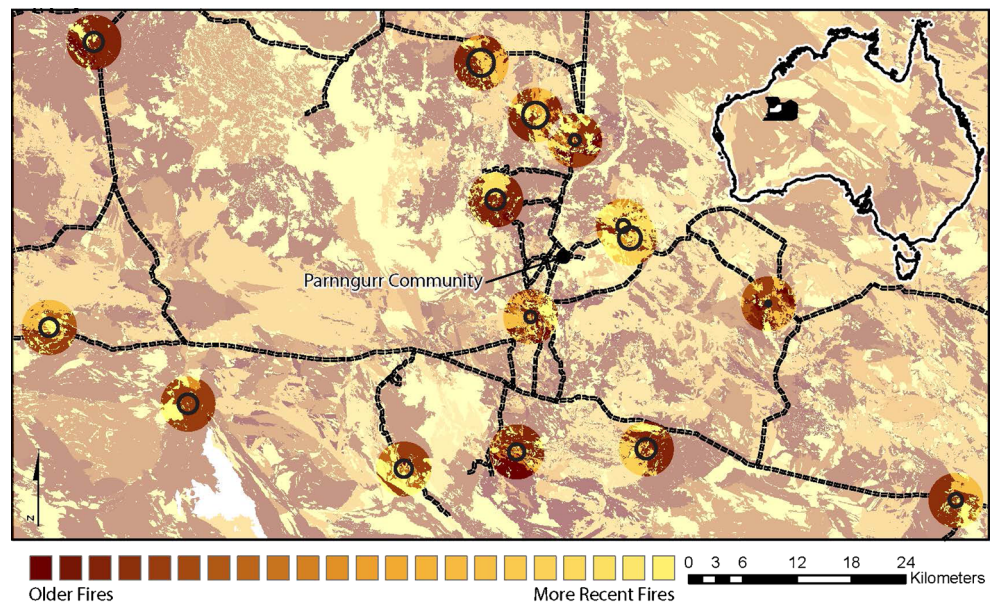
Data Collection

The context of hunting and burning was recorded over a long-term ethnographic project starting in 2000 (Bird *et al.* 2004, 2005; Bliege Bird *et al.* 2008, 2012, 2013). Hunting bouts—defined as the total time an individual forager spent searching for, pursuing and field processing a particular suite of resources associated with a given activity or patch—were monitored through a combination of focal-individual follows and continuous camp-scans (Altmann 1974). Intensive focal-follows of kangaroo hunters occurred between 2007 and 2010 (Codding 2012). These provide fine-grained detail on Aboriginal hunting practices and quantitative data on hunting time and returns which can be used to generate estimates of hunting pressure.

In order to investigate potential anthropogenic influences on populations, hill kangaroo distributions were quantified through a series of two stratified-random-bearing 1-km-x-4-m pedestrian transects in each Martu hunt region (Codding 2012). Transects were restricted to rocky ranges and adjacent sand plains, occasionally crossing watercourse margins. The relative densities of kangaroo were measured using fresh scat-

event counts as a proxy (Hill 1981; Murphy and Bowman 2007; Styger *et al.* 2011). Fresh scat-events were tallied within each discrete successional patch and ecological habitat (rocky, sand plain, watercourse margin). While intra-genus identification is unreliable (Telfer *et al.* 2006), hill kangaroo are the most abundant, if not the only, large macropod in these hunt regions. In-patch fire-history was recorded following the ethnoecological stages identified by Martu (Table 1). Transects were walked from 2007 to 2009. The results include scat densities recorded across 30 transects in 15 different hunt regions.

Seral-stage diversity was calculated by developing fire histories for the area using a time series of 22 30-m resolution Landsat 7 TM+(1999–2002) and Landsat 5 TM (2003–2010) images taken at roughly 6 month intervals (barring cloud-free days) from November 1999 to April 2010 (see Fig. 1). Each fire scar was hand-digitized in ENVI using a ratio of bands 7 and 4. A sample of 50 randomly distributed points was ground-truthed in May 2011 (Bliege Bird *et al.* 2012). Remote sensing data was used to calculate the number of different seral patches ("Seral Richness"), a measure of seral-stage diversity. Seral diversity was measured as the number of

Table 1 Martu ethnoecological stages of vegetative succession following fire

Seral stage	Martu Stage name	Min age (years)	Max age (years)	Description
Burned-ground	*Nyurnma*	0	≈ 0.5	Burned ground
Early	*Waru-Waru*	≈ 0.5	≈ 1	Green shoots emerge
Mid	*Nyukura*	≈ 1	≈ 5	Herbaceous and fruiting plants
Late	*Manguu*	≈ 5	<15	Spinifex begins to dominate
Late (climax)	*Kunarka*	>10	>15	Old spinifex dominates

different Martu classification stages within a 3-km buffer encompassing both transect locations in each region constructed in ArcMap (ESRI 2011). Each 3-km radii polygon was then used to summarize values from a raster (30-m^2 pixels) dataset classified by burn age calibrated appropriately according to the year the transect was walked (see Fig. 1). Diversity values were calculated from the raster data by treating each seral stage as a 'species'; values were extracted from the raster dataset using Hawth's Analysis Tools for ArcGIS (Beyer 2004) and then imported into R where richness values were calculated using the *vegan* library (R Development Core Team 2012; Oksanen and Simpson 2011). On-the-ground measures included the area of each seral stage along each transect, the area of each substrate (habitat) and the number of seral transitions, or edges ("Seral Edge"), used as a measure of seral-stage heterogeneity.

Statistical Analyses

To determine the effect of each measure of anthropogenic burning and hunting on counts of kangaroo scat events, analyses relied on generalized linear models of the poisson family (or distribution) with the canonical log-link (Faraway 2006). These were implemented in R (R Development Core Team 2012). Model results report the null deviance (D_0), which includes only the intercept, and the deviance explained by the model (D_M) reported in negative two log-likelihood.

Models constructed to determine the in-patch effect of each seral stage (Table 1) on scat counts controlled for substrate and area, and interactions between seral stages and habitats. Additionally, Wald's test was used to determine if the parameters significantly improve model predictions (R Development Core Team 2012). For display purposes, these values are shown (Fig. 2) following a continuity corrected log or $log(x+0.5)$ (Zeileis *et al.* 2008). Because models assume a log link, interpretation relies on the exponent of model coefficients.

Models examining the effects of seral-stage diversity (richness) and heterogeneity (edge) on scat counts across hunt regions controlled differences in the area surveyed (due to unnavigable terrain) by weighting each observation by the max possible area less the area surveyed. A second-order polynomial was introduced if it improved the model fit as determined through an increase in the amount of deviance (D_M) explained. Because spatial variability in the distribution of hill kangaroo scat may be biased by underlying nonrandom neighboring relationships (Valcu and Kempenaers 2010), we tested for spatial autocorrelation using the *spdep* package in R (Bivand 2013).

To examine the effects of hunting on hill kangaroo abundance, a measure of hunting pressure was derived by summing the amount of time spent hunting in each region between July 2007 and August 2010 (Codding 2012). Because observations did not occur in precisely the same locations as transects,

hunting pressure across the region was predicted by a polynomial surface that represents the spatial trend in hunting time observed from 2007–2010. This was generated using the *spatial* package (Ripley 2011) in R (R Development Core Team 2012). The degree polynomial was selected from alternatives based on the greatest amount increase in r^2 and decrease in *AIC*. The surface was converted to a raster and values corresponding to the location of each scat transect were extracted using the *raster* package (Hijmans and van Etten 2012).

A secondary measure of human influence was calculated as the average travel time from the community to each hunt region. Because Martu are central place foragers, the amount of time required to travel from the community should provide a broad measure of human influence on the landscape. As above, the predictive effect hunting pressure and travel time on scat counts were determined through generalized linear models of the poisson family with a log link controlling for area surveyed and including a second-order polynomial where it improved model fit.

Results

Successional Patch Preference

Hill kangaroo differentially distribute themselves across patches of post-fire succession ($D_0=3006.1$, $D_M=1508.3$, $p<0.0001$, Table 2, Fig. 2). Scat densities are higher in early seral patches characterized by newly emerging green shoots and in mid-seral patches where they are able to target fruiting and herbaceous browse. The aggregate effect of these preferences should result in hill kangaroo being more abundant in areas characterized by greater seral-stage diversity and heterogeneity, where these preferred patches have a higher probability of falling within their daily foraging range.
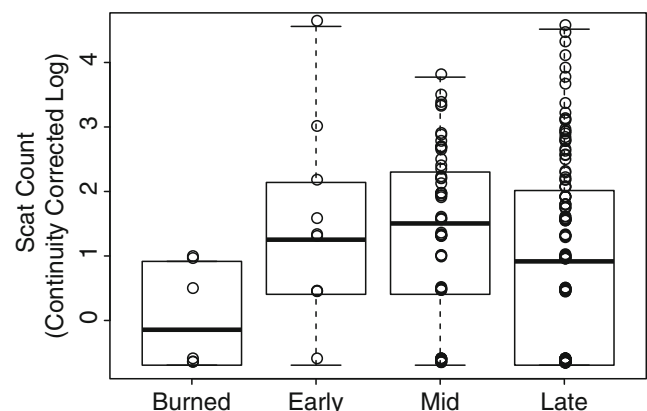

Fig. 2 In-patch scat counts (continuity corrected log) across seral stages. Circles represent the raw data. Box plots show the distribution of the data outlining the first and third quartile

Table 2 Summary of generalized linear model results examining in-patch variation in hill kangaroo density as a function of successional stage and habitat

Parameter †	Estimate	Std. Error	z	p	
Intercept	−1.06	0.74	−1.43	0.15204	
Early succession	1.51	0.72	2.10	0.03603	*
Mid succession	2.45	0.81	3.03	0.00242	*
Late succession	1.14	0.71	1.60	0.11032	
Rocky range	0.11	0.93	0.12	0.90651	
Sand plain	0.24	0.20	1.21	0.22678	
Watercourse margin	−0.26	0.45	−0.59	0.55647	
Area (m^2)	0.00	0.00	30.51	<0.0001	*

*Denotes statistical significance at $p<0.05$. † Wald's Test suggest that the inclusion of these parameters significantly improves model prediction ($F=140.17$, <0.0001). There were not enough observations of scat in freshly burned area to be included in the model

Effects of Fine-Grained Vegetation Mosaics

The distribution of hill kangaroo scat counts across each hunt region is not biased by spatial autocorrelation ($I=$ −0.04, $p=0.419$), but is predicted significantly by seral-stage diversity and heterogeneity. Scat counts increase significantly as a function of remotely sensed estimates of successional richness ($D_0=511.89$, $D_M=89.64$, $p<0.0001$, Fig. 3) and as a function of on-the-ground observations of successional edge density ($D_0=1312543$, $D_M=372597$, $p<0.0001$, Fig. 3). However, scat counts decline at the highest levels of edge density. This may signify that too many small fires have a detrimental effect on hill kangaroo populations, but it is more likely a function of covariance between Aboriginal burning and hunting pressure. Areas characterized by greater seral diversity as a result of burning while sand monitor hunting may also be areas where kangaroo are hunted more intensively. To further investigate these factors, we examine the interactive effects of Aboriginal burning and hunting on hill kangaroo abundance.

Interactive Effects of Burning and Hunting

While hill kangaroo appear to benefit from living within fine-grained vegetation mosaics caused by Aboriginal burning, they may also be negatively affected by over-hunting. To test this, we first examine scat counts as a function of the amount of time kangaroo hunters spend in each region. A second-order polynomial surface significantly explains spatial variability in the distribution of hunting pressure across the landscape ($r^2=0.3727$, $F=$ 6.06, $AIC=461.93$, $p<0.0001$). Predicted estimates of hunting pressure significantly explains scat counts across each hunt region ($D_0=1312543$, $D_M=827375$, $p<0.0001$, Fig. 4). Hill kangaroo scat counts initially increase with the amount of time spent hunting in each region, but begin to decline at intermediate levels (Fig. 4). This could be caused by covariance between hunting and burning. Indeed, the amount of time spent hunting kangaroo in each region significantly predicts the amount of successional edge encountered along each transect ($D_0=$ 62053, $D_M=38812$, $p<0.0001$). As Martu burn in the context of sand monitor hunting, but rarely in the context kangaroo hunting, this reveals significant co-variance between the time spent hunting both taxa in each region.

As a proxy measure for the costs of access for central place foragers, travel time should provide a rough measure of the positive and negative effects that humans may have on hill kangaroo populations. Travel time significantly predicts variability in the distribution of hill kangaroo ($D_0=511.89$, $D_M=160.98$, $p<0.0001$, Fig. 5). Fig. 5 shows that densities are low closest to the Aboriginal community and increase until the limits of anthropogenic fire mosaics (approximately 60 min away from the community, see Bliege Bird *et al*. 2008, 2012). After this threshold, their relative abundance declines. This shows that hill kangaroo benefit most from intermediate levels of human influence, where the benefits of burning outweigh the effects of hunting.

Fig. 3 Scat count per hunt region as a function of (*left*) remotely sensed observations of seral-stage diversity (richness) and (*right*) on-the-ground observations of seral-stage heterogeneity (edge) shown with predicted model fits (*solid line*) and standard errors of the model fit (*dashed*)
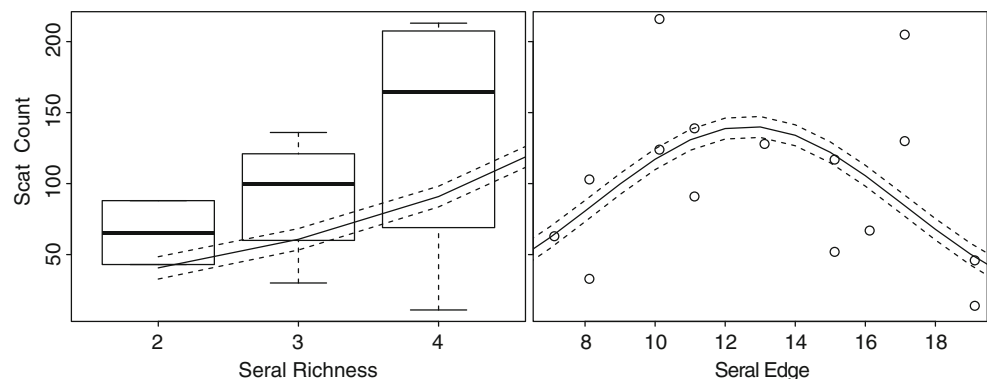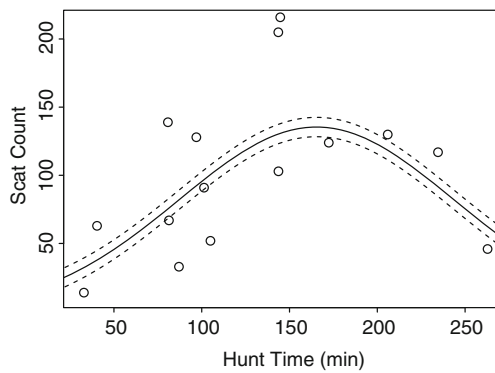
Fig. 4 Scat count as a function of the amount of time spent hunting in each region shown with the predicted model fit (*solid line*) and standard errors around the model fit (*dashed*)

Discussion

Hill kangaroo are significantly more abundant in regions dominated by fine-grained seral-stage mosaics developed by Aboriginal burning. Because Aboriginal fires shuffle the spatial distribution of seral patches so that they occur in more fine-grained mosaics (Bliege Bird *et al.* 2008), areas characterized by greater levels of habitat heterogeneity and seral diversity are more likely to provide hill kangaroo with access to a greater diversity of vegetation and a greater number of preferred patches within their foraging range. This effect is likely so pronounced because Martu fire regimes differ most from lightning regimes at scalar extents ranging from 3 to 5 km (Kauhanen 2011), which brackets the estimated home ranges of hill kangaroo (Clancy and Croft 1990; Croft 1991; Fisher and Owens 2000). Gathering data at a scalar extent appropriate to the hill kangaroo home range was also likely crucial to revealing this pattern, as others have highlighted (Kelly *et al.* 2012). Our results are robust across measures derived from remote sensing
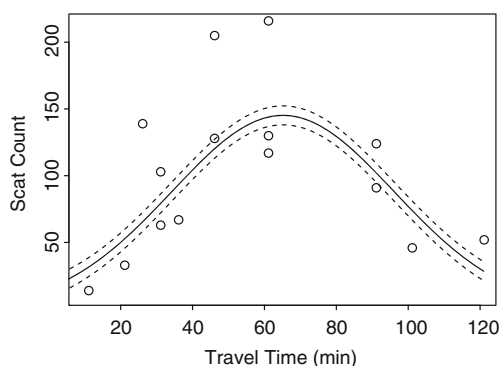

Fig. 5 Scat count as a function of travel time from the community shown with the predicted model fit (*solid line*) and standard errors around the model fit (*dashed*)

and on-the-ground observations. However, the overall positive effect is complicated by hunting pressure, which is negatively correlated with increasing travel distance from the community.

Hunting pressure appears to have a negative effect on hill kangaroo populations so that their populations are highest at intermediate levels of human interaction. Aboriginal burning occurs most frequently in the context of sand monitor hunting (Bird *et al.* 2005; Bliege Bird *et al.* 2008). Because sand monitor and hill kangaroo hunters (frequently women and men respectively, Bliege Bird and Bird 2008; Bliege Bird *et al.* 2009; Codding *et al.* 2010, 2011) often travel to the same regions and divide their labor between these two hunt-types, the positive and negative effects of burning and hunting tend to co-vary with one another. The fact that hill kangaroo are most abundant at intermediate levels of human predation likely reflects the dynamic interactions between hunters' decisions, fire regimes and prey abundance. Hunt regions currently characterized by low prey abundance near the community represent locations that have already been over-hunted. It is unknown whether the effects of predation pressure causes populations decline due to increased mortality or as a function of prey behavior which leads kangaroo to vacate areas frequented by hunters (*sensu* Charnov *et al.* 1976), though these effects are likely a combination of the two. The intermediate areas probably represent sweet spots where hunters are targeting dense kangaroo populations enhanced by the cumulative and indirect effects of anthropogenic burning. Here, hill kangaroo have increased access to anthropogenic landscapes characterized by higher densities of seral patches with early and middle stages of regrowth. In such areas hunting pressure has yet to, and may never, cause kangaroo populations to decline.

These results show that at intermediate levels of human disturbance, Aboriginal fire regimes have the greatest net effect on hill kangaroo populations, with populations declining outside the range of anthropogenic fire mosaics. Prior to European contact, this positive effect may have been more widespread as highly mobile hunter-gatherers traveling on foot would have a ranged across greater areas of the desert than today, where the impact of anthropogenic fires is restricted to the foraging radius around permanent communities and the vehicle tracks that provide access to the desert (Bliege Bird *et al.* 2012). Moreover, the negative impact of hunting would have been more dispersed, with greater periods of time between hunts in the same region, allowing prey populations to recover. However, hill kangaroo populations still persist near the community at densities similar to those regions far removed from human influence. This persistence is a direct outcome of the adaptive foraging decisions of kangaroo hunters. Post-encounter pursuit of hill kangaroo frequently results in acquisition failure due to their escape velocity

(Bird *et al.* 2009); in regions of low kangaroo density, a failed pursuit typically results in failed overall hunting bout as a second encounter is unlikely (Codding 2012). After several failed bouts, hunters are unlikely to return to that hunt region for some time. As with many predator–prey interactions at equilibrium, prey seem to persist largely due to the adaptive pre-switching decisions by predators—either to take other prey, or as in this case, to take the same prey from other locations (e.g., Abrams 1993; Winterhalder and Lu 1997).

Our results show that hill kangaroo benefit from living within regions dominated by anthropogenic fire regimes, which suggests that hill kangaroo may have co-evolved along-side an extensive history of Aboriginal burning and hunting practices. The onset of anthropogenic fire regimes may have allowed hill kangaroo (and likely other endemic fauna) to extend their range into more marginal landscapes and to occur at higher densities within their extant range. Because these processes represent behavioral responses that would increase kangaroo somatic and reproductive success, the patterns observed here would likely emerge quickly after initial introduction of anthropogenic fire and would likewise disappear with the removal of anthropogenic fire mosaics. However, these outcomes should not be confused with conservation management.

Sustainable Subsistence

While the subsistence practices of indigenous populations are often considered to be directed at either long-term management or short-term gains, here we show that the outcomes of human-environmental dynamics may have more to do with the co-evolutionary histories of human subsistence practices. While hill kangaroo benefit from living within fine-grained vegetation mosaics established through anthropogenic fire, these positive effects should not be confused with management. Because Martu fires are lit most frequently in the context of sand monitor lizard hunting, any effect on other species, like hill kangaroo, is necessarily indirect. While Martu are well aware of these indirect effects, they clearly state that they are not "managing" these populations. Instead, they suggest that these interactions are part of broader patterns of ecological and spiritual relationships known as the *Jukurrpa* or law passed down by the Dreamtime ancestors (Bliege Bird *et al.* 2013; Tonkinson 1993). This belief places people within—not apart from—ecological interactions. The empirical patterns shown here, supported by traditional Aboriginal knowledge, suggest a long history of interactions between humans and the environment in which the distribution of plants and animals is partially structured by anthropogenic fire regimes. While shaped over millennia, patterns observed today reveal a positive ecological effect of intermediate human interaction.

Such positive effects of indigenous resource use may also occur in other regions where human-fire dynamics have existed *in situ* for long periods of time, as in North and South America (e.g., Keeley 2002; McAdoo *et al.* 2013; Welch *et al.* 2013). These indirect positive effects need not be limited to fire (e.g., Fowler and Lepofsky 2011). For example, Moritz *et al.* (2013) suggest that what seems to be effective management of grazing commons among Fulbe pastoralists actually emerges from patterns of mobility that are in each individual's best interest. In such cases, indigenous practices may indeed promote species health, but again, this does not mean that subsistence practices are designed to have these conservation effects. However, better understanding these co-evolutionary dynamics can inform conservation strategies.

Applying Co-evolutionary Dynamics to Conservation

Today, Australia is experiencing some of the highest rates of mammalian species decline in the world (Cardillo and Bromham 2001; Short and Smith 1994), which is hypothesized to result not only from novel human intervention (including invasive species introduction), but also from the removal of traditional Aboriginal fire regimes. In Australia's arid center, species loss began coincident with the departure and removal of Aboriginal foragers (Burbidge and McKenzie 1989; Letnic and Dickman 2005). Because many of the extinct and endangered small mammal species are hypothesized to be sensitive to the scalar extent and grain of seral-stage habitat heterogeneity (Bolton and Latz 1978; Burbidge *et al.* 1988; Lundie-Jenkins *et al.* 1993); Southgate *et al.* 2007), the removal of Aboriginal fire regimes is potentially to blame for the observed increase in fire extent and intensity and the reductions in small mammal abundance and diversity (Burbidge and McKenzie 1989; Letnic and Dickman 2005; Woinarski *et al.* 2010).

Our results suggest that Aboriginal burning may provide a benefit to species whose distributions overlapped with these fine-grained mosaics for prolonged periods of time, including now vulnerable or extinct species. Other research suggests that fine-grained seral mosaics may be crucial in supporting threatened mammal populations within Australia's desert ecosystems (Burbidge and McKenzie 1989). For example, the vulnerable rufous hare wallaby (*Lagorchestes hirsutus*) likely benefits from Aboriginal fire regimes through reduced dietary variability (Lundie-Jenkins *et al.* 1993). Further, Aboriginal fire regimes may also reduce mortality by introducing fire-breaks that significantly reduce the probability of large fires which would otherwise cause heavy mortality in individual small- to medium-sized mammals (Burbidge and McKenzie 1989; Bliege Bird *et al.* 2012). A tighter mosaic of different seral stages may also reduce predation pressure (including that from invasive predators) by decreasing areas of exposure during feeding or dispersal. Given this, the recovery of these

populations may depend on reestablishing these mosaics (Richards 2005; Richards *et al.* 2008). This suggests that managing Australia's desert ecosystems requires understanding the long-term impacts of traditional land-use strategies employed by Aboriginal Australians. In order to be successful, management schemes should facilitate traditional burning and hunting regimes in remote communities and incorporate this traditional ecological practice into future management protocols.

Conclusion

Characterizations of human-environment interactions among small-scale societies that emphasize only the negative effects of predation, or the conscious attempts to minimize it, miss an opportunity to explore the diverse ecological dynamics that structure human interactions with the ecological communities of which they are a part. Human subsistence practices that have a long history in a particular region likely have keystone effects in the broader ecological community due to long-term co-evolutionary dynamics between human decisions and endemic species. Because endemic fauna likely adapted to living in environments where these practices were central to people for long durations, the outcomes of such practices may serve to mediate trophic interactions and facilitate the persistence of diverse species assemblages and ecosystem stability. Understanding the processes that sustain these ecological communities, regardless of whether they are intentional or not, will allow for more effective design of management protocols that can simultaneously satisfy conservation goals while facilitating the survival, well-being, and autonomy of traditional subsistence practices.

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