**The collapse of a continent: Aboriginal Australian ecosystem engineering and the maintenance of complexity under climatic uncertainty**

**Or—**

**Ecological Meltdown: Indigenous population losses contribute to biodiversity loss at a continental scale**

**Or--?**

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**Abstract**

Multiple organisms have been considered critical to the maintenance of biodiversity in Australia's unique and unpredictable climatic regime: dingos, burrowing bettongs, quolls, tiger sharks, wedge-tailed eagles, large varanids, megafauna. However, the single most significant indigenous organism on the continent—humans-- has rarely been given any role in ecosystem interactions other than as a primary source of species extinctions on the continent's initial colonization. This is surprising, given the substantial history of human occupation of the continent (ca 50k years), and recent evidence of an extensive history of place-based knowledge systems, genetic continuities, and substantial impacts of natural selection linking Aboriginal populations to specific habitats and environments. As a large-bodied, high trophic level organism with extensive niche construction capabilities and a substantial history of integration into local ecosystems, Aboriginal Australians should be considered a major source of positive ecological impacts. Here, we survey the potential sources of positive feedbacks between Aboriginal Australians and continental biota, and compare their impacts with those of other hypothesized trophic regulators and ecosystem engineers. We propose the hypothesis that the loss of Aboriginal ecosystem interactions, enhanced by increased climatic variability and the spread of invasive species, is one of the most significant forces affecting the rapid and unprecedented decline in the continent's indigenous biota.

**Introduction**

Australia, the continent with the lowest density of human occupation (save Antarctica) has one the highest current rate of species decline and extinction in the world (Woinarski et al. 2015). The causes of this decline are manifold: the spread of introduced meso-predators, namely foxes and cats (Short et al. 1992; Gibson et al. 1994; Dickman 1996a,b; Smith & Quin 1996; Short 1998; Burbidge & Manly 2002; Johnson 2006), the loss of apex predator regulation, or mesopredator release, on the part of wedge-tailed eagles and dingos (Glen et al. 2009, Glen and Dickman 2005, Richards and Short 1998, Glen et al. 2016) and post-colonial changes to fire regimes (Bolton and Latz 1978, Burbidge et al. 1988, Southgate et al. 2007, Burrows 2006, Burbidge and McKenzie 1989, McKenzie et al. 2006). Recently, the focus has also turned toward the loss of species functioning as ecosystem engineers, especially burrowing and digging organisms, as an important source of 'bottom up' impacts on biodiversity (Fleming et al. 2014).

Rarely considered as a source of diversity-enhancing effects, humans also have the potential to serve as potent apex predators and ecosystem engineers, particularly in Australia. Human populations entered Australian ecosystems between 45 and 50 thousand years ago, and quickly spread throughout the continent. Once established, populations appear to have significant site fidelity: both cultural/linguistic and genetic evidence suggesting substantial histories of local occupation and adaption to environments (Hamacher and Goldsmith 2013, Nunn and Reid 2016, Tobler et al. 2017). Furthermore, archaeological evidence shows few major shifts in subsistence strategies outside of a broadening of the diet around 3k to 5k years ago (Smith 2013). Finally, for a 50k year period, Aboriginal foraging strategies included a broad range of resources at all trophic levels, fairly evenly split between vertebrates, invertebrates, and plants, many of which required digging or other soil excavation techniques, as well as a substantial history of the use of fire for subsistence purposes (Keen 2004). The loss of Aboriginal populations, beginning at European invasion in 1788, and continuing slowly toward the interior by the mid-20th century, mirrors both the spread of invasive species and the decline of native mammal fauna (Burbidge 1988), suggesting a significant role for Aboriginal people in maintaining species diversity through both top-down regulation and bottom-up enhancement.

**Humans as 'uniquely different' predators**

Objections to the role of humans as an important source of positive effects often begin with the assumption that human predation is substantially different from other predators. Humans have been argued to focus greater attention on fewer, more vulnerable species; to be highly efficient at locating and killing prey, with exploitation rates that are 15 times higher than any other organism; and to be the only organism with the potential to drive other species to extinction (Darimont et al. 2015, Worm and Paine 2016, Gill et al. 2009).

While commercial and market-driven foraging tends to deplete populations of vulnerable species (e.g. Darimont et al. 2015), subsistence hunting is not particularly efficient. Pursuit success rates by human hunters on terrestrial animal prey are generally equivalent to than that observed for many species of Carnivora (Table 1), ranging from a 5% daily success rate among hunters of large, mobile prey, to a 20-30% success rate for medium sized mobile animals to a 70% success rate for smaller less mobile animals in open habitats. While humans may have average hunting success rates, they eat only a tenth as much meat per day (.01 kg per kg body weight) as other predators (.11 kg) (Hill 1982).

Despite long histories of indigenous hunting, there is little evidence of long-term unsustainable hunting yields or species extinctions caused solely by traditional hunting practices, even with recent shifts toward greater use of rifles and shotguns (Alvard 1995, Levi et al. 2009). While larger prey might be scarce near central places and settlements, there is generally little impact of indigenous hunting on prey availability at larger spatial scales due to considerable source-sink dynamics (Hill and Padwe 2000, Peres and Nascimento 2006). While there is strong evidence for the local extirpation of rare and patchily distributed species, especially on islands (flightless duck, elephant bird, etc), and declines in the population density of larger animals around settlements, evidence for a human role in the extinction of widely-distributed species, such as Pleistocene megafauna, is highly contested (Choquenot and Bowman 1998). This is especially the case in Australia, where the only megafaunal remains to appear in archaeological sites as direct indicators of consumption are Genyornis eggshells.

Species lists compiled for human subsistence hunters do not show obvious biases toward the unequal exploitation of large or high trophic level species: few carnivores, if any, are ever taken in either South American rainforest (Alvard 1993), or East African plains: in 188 days, despite frequent encounters, Hadza only killed 1 lion and 1 hyena (O'Connell et al 1988). As well, the common assumption that larger prey are preferred due to their high profitability is not supported by the data: larger bodied animals do not predictably have higher on-encounter return rates than smaller bodied animals (Winterhalder 1981, Bird et al. 2009, 2012; also see tables in Alvard 1993, Hawkes et al. 1982). Human hunters tend to hunt more or less optimally: that is, prey are pursued on encounter relative to their profitability (Smith 1991, Winterhalder 1981, Bird et al. 2009) and hunters often switch to lower ranked prey late in a hunt if higher ranked prey have not been encountered (Alvard 1993). That is not to say that large, rare, lower ranked, and difficult to capture prey are never hunted: indeed, such prey (like kangaroo, emu, and freely swimming sea turtle) may be an important source of status for some hunters (e.g. Bliege Bird et al. 2001, Jones et al. 2014), but their acquisition is usually minor compared to the frequency of acquisition of prey targeted for consumption.

Humans are also highly omnivorous, rarely (with the exception of arctic environments) depending on animal prey for more than 50% of their daily average caloric requirements. As Dunne and colleagues show, in the marine and intertidal food webs of Sanak Island, the indigenous Aleuts exceeded nearly all other species in the generality and omnivory of their foraging and subsistence strategies (Dunne et al. 2016). The Aleuts were not unusual in this regard: inventories of hunter-gatherer diets routinely show the use of 100-200 different species for food alone. Omnivory, rather than efficiency, is what makes human predation very different from that of other top predators.

Omnivory tends to have a stabilizing effect on complex ecological interactions. Interaction strength is the strength of the demographic relationship between two organisms and can be defined by the probability that one species will consume (or otherwise cause the mortality) of another or more generally, as the correlation between the population sizes or reproductive rates of two different species. Interaction strength can be negative, as in predation, or positive, as in mutualism or other form of facilitation. Interaction strength is a function of foraging strategy. Generalist foragers tend to have more weak ties than specialists, omnivores and herbivores more than carnivores, and inefficient consumers more than efficient ones. The distribution of interaction strengths throughout the network influences stability: a network dominated by strong ties induces coupled population cycling (as in the classic Lotka-Volterra models of snowshoe hare and lynx populations) that can result in extinction and trophic cascades, while one with predominantly weak ties tends to dampen such cycles and improve population persistence (McCann et al. 1998, Gellner and McCann 2016, Emmerson and Yearsley 2004). While human foragers may utilize a high number of species, observations of actual diet reveal that most of the interactions foragers have are fairly weak: foragers tend to rely heavily on a few species more than others, taking some only rarely or when conditions deteriorate. For example, among the !Kung San (Lee 1979), 14 out of 105 plant species eaten comprised 75% of the vegetable diet by weight; of 58 animal species, 11 comprised the majority of prey taken, being both common and regularly hunted.

Unlike other predators, humans employ extensive ecosystem engineering in the process of acquiring resources: they dig, and they burn. Digging mammals significantly increase soil turnover, increase soil nutrients by reworking organic matter into the soil, improve water infiltration which increases soil moisture, disperse beneficial fungal microorganisms, and increase plant recruitment both by providing more favorable sites for plant growth, and by the caching or burying of seeds, which reduces seed predation (Fleming et al 2014). Annual soil turnover by some digging mammals can be as high as 23 cubic meters per individual. Thus, declines in population of some keystone engineers may have a significant impact on food availability for all plant consumers. As central place foragers, humans also tend to create zones of heavy influence around camps and settlements through vegetation clearing and the use of broadcast fire. In some cases, this disturbance increases the diversity of plant communities and landscape structure, and possibly also the biomass of generalist species that thrive in such diverse landscapes (Robinson and Bennett 2004; Smith 2005).

**Indigenous Australians and their ecosystems**

What is notable about observational studies of human interaction with native (and non-native) fauna in Australia is the wide range of prey types commonly exploited: Aboriginal hunters routinely targeted smaller predators, such as wedge-tailed eagles and their eggs, feral cats, large Varanids, and occasionally dingos and foxes, as well as the prey of such predators, including smaller lizards (Varanus and Amphibolurus spp), small to medium sized mammals, even mice and insect larvae. There is thus significant dietary overlap between Aboriginal Australians and both native and non-native predators.

Compared to other apex predators in Australia, Aboriginal Australians were more extreme generalists, utilizing a much broader range of species. In the more temperate regions of southern Australia, Gott (1993) reported 1248 plants utilized for food, and 1479 species utilized for all purposes, including as medicines or artifacts. In arid Central Australia, O'Connell and Latz reported the Alyawarra recognized 122 economically useful plants, 92 of which were considered edible, about 30% of the total plant species available. Of animal species hunted, much less is known; however, what is clear is that a wide range of species larger than about 250g were routinely included in the optimal diet. In the temperate Southwest, animal foods taken routinely included a wide range of fish, mammals, reptiles, and birds, ranging in size from red kangaroo to kangaroo rats (Keen 2004). In the tropical north, Altman (1982) reported 90 different species of vertebrates and invertebrates and 80 species of plants observed to be acquired during a year-long study in 1970's Arnhem Land. Clarke (2007) recounted Edward Stirling (a member of the Horn Expedition to Central Australia in 1894) noting that most of the animal species available in the region were included in the diet to some degree, particularly the mammals. Prior to the contact period, mammalian fauna between 500g and 2 kg were moderately abundant, and likely provided an important weekly source of food, particularly burrowing bettongs, hare wallabies, and brushtail possums. Larger mammals and birds, including euros, bustards, plains kangaroos, and emus, were, in most environments, difficult to capture and comprised a much smaller proportion of the diet than did smaller prey (invertebrates, reptiles, birds and bird eggs, and plant resources). Invasive fauna were also incorporated into Aboriginal hunting strategies, especially as populations of native fauna declined, particularly feral cats, rabbits, and most recently, camels.

That aboriginal foragers have a predominance of weak ties is suggested by the fact that not all species were equally important in the diet. In most cases, only a fraction of those ever consumed were important staples. For example, Latz (1997) records a total of 183 plant species consumed across the Central Desert as a whole, of which only 14 (7.6%) were consumed frequently enough to be considered a staple resource. The vast majority of species (78.7%) were only taken rarely or occasionally, when preferred species were not available. Staple resources were those that tended to be high-ranked (having a high rate of energetic return on encounter), abundant--such that they could be exploited frequently without depressing populations, and available for long periods of time (or were easily storable).

The extractive strategies of Aboriginal women throughout much of the continent primarily involved digging and soil disturbances (Keen, Clarke). In arid Australia, some of the major plant staples, including Ipomoea yams, Vigna yams, Cyperus corms, most mammals, reptiles and insects, including honey ants and witchetty grubs, are acquired by digging. Excavations for honey ants (Camponotus inflatus) typically reach 1 m3 or more as women follow the tunnels beneath mulga trees to the chambers where the storage ants, the repletes, cling to the ceiling. Nests can be more than 1.5 meters below the surface and 2 meters wide, and the first chambers between 20 and 60 cm below the surface (Conway 1991). One researcher noted 76 honey ant excavations over the course of one year at a density of 26 per hectare from a single community of 22 people (Conway 1991).

In SE Australia, 32% of all plant foods acquired were USOs, underground storage organs (Gott 1982). Here, the major staple was the yam daisy, Microseris lanceolata, known as murnong. M. lanceolata is a herbaceous perennial with non-fibrous, shallow tubers that was formerly at high abundance throughout the SE region. Vast fields of yellow-topped flowers were reported by early European observers, populated by multitudes of Aboriginal women with heavy loads of tubers (Gott 1982, 2005, 2007). Various ecological impacts of this tuber digging included extensive soil mounding, soil aeration, improvement of soil texture, and the incorporation of organic matter, all of which may have functioned to maintain this species at such a high density. With the loss of Aboriginal soil turnover in the region, and the establishment of cattle and sheep pastoralism, densities of this formerly common species have declined substantially. Other staples that persisted in the patches in which they were exploited included Dioscorea hastifolia, the warran yam, which grew more than 50 centimeters below the surface in SW Australia. Patches were so dense and extensive that early explorers described miles of fertile ground dug for yams (Atchison and Head 2012). In the tropical north, USOs, including tubers and corms, were also staple foods: "Women and children spent many hours with digging sticks following the creeping stems of yam vines down to their tubers over a meter below in the sand" (Clarke xxxx: 76). If the average woman spent 35% of her foraging time digging, foraged for 5 hours per day, and excavated at the rate of about .5 cubic meters per hour of digging, the rate of soil turbation would be .875 cubic meters per day, or 319 cubic meters annually.

Unlike nearly all other soil disturbing organisms, humans also dig so extensively that they influence hydrological patterns. More than 6000 years ago, Gunditjmara people in Southeastern Australia constructed extensive channels and drainage systems to manage wetlands and increase access to shortfinned eels, *Anguilla australis* (Lourandos 1997). Hundreds of meters of stone and earthwork channels were constructed, connecting previously isolated swamp drainage systems with coastal rivers systems, and creating a network of diversion channels and holding ponds that concentrated eel populations in easily accessible habitats for year-round exploitation. This had the effect of extending the range of eels into interior swamps that had formerly been inaccessible, as well as regulating water levels in the swamps, which prevented climatic variability from causing drastic shifts in eel population numbers. It was not just in mesic environments where indigenous Australians manipulated the availability of water; in more arid environments, people expanded the spatial distribution of ground water sources through digging soaks and wells and clearing sediment from rockholes and other points of rainwater catchment (Gould 1969).

Fire was a fundamental component of small-medium sized game acquisition, that in turn supported many of the most important staple plant resources (Gould 1971, Jones 1969, Kimber 1983, Latz 1995). In the arid regions, broadcast fires were used primarily during the cool-dry season in the process of clearing tracts of older-growth spinifex to facilitate search for burrowed prey, especially sand monitor (*Varanus gouldii*) and other herpetofauna, but also small to medium sized mammals such as bilby (*Macrotis lagotis*, now rare in the arid zone), mulgara (*Dasycercus cristicauda*, also rare), burrowing bettong (*Bettongia lesueur*, extinct on the Australian mainland), and rufous hare wallaby (*Lagorchestes hirsutus*, highly endangered). Spot fires for flushing prey were used while hunting for larger monitors (*V.* *giganteus* and *V.* *panoptes*), brushtail possum (*Trichosurus vulpecula*, endangered in Western Desert), and invasives, especially cats. Work on contemporary Aboriginal hunting fires in this region shows that where people are actively hunting with fire, fires are smaller, patches of unburned habitat are more evenly distributed, pyrodiversity is higher, and climate-driven increases in fire size with rainfall are buffered (Bliege Bird et al. 2008, 2012, 2016). This increase in pyrodiversity affects populations of two important prey species for Aboriginal hunters: monitor lizards, and euro (*M. robustus*). Both experience higher population densities in more pyro-diverse habitats. The positive effects of pyrodiversity exceed the negative effects of predation for both species in all regions except those with the highest levels of human hunting pressure (Bliege Bird et al. 2013, 2014).

Fire has also been argued to be significant in maintaining the abundance and distribution of many herbaceous perennials and other important staple plant resources, including yam daisy (*Microseris lanceolata*) in western plains of Victoria (Gott 1983); warran yam (Dioscorea hastifolia) in SW WA (Hallam 1989); bulrushes (Typha spp.) in wetlands across southern Australia (Gott 1999); seed-producing plants and Solanum fruits in the Central Desert (Latz 1995); and cycads (Beaton) in the tropical rain forests of northwest Queensland. Aboriginal fire also maintains landscape level diversity in vegetation (pyrodiversity)in the tropical North….blah blah. Herbaceous perennials generally flower more abundantly following fire, and many of the food plants important for humans do not compete as well with other species, and are higher in abundance 2-4 years following fire (Wark 1996).

**The maintenance of diversity on a climatically variable continent**

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: burrowing bettongs up to 5km (Short and Turner 1999), rodents and dasyurids moving more than 10 km (Dickman et al. 1995), and fat-tailed dunnarts (*Sminthopsis crassicaudata*) 5 km (Read 1984). Their foraging strategies seem to be highly nomadic across the landscape, moving from one rich foraging patch to another. These vagrant types of dispersal strategies are tied to ENSO- and ENSO-like pulses of rainfall alternating with period of drought, which have strongly dominated Australia’s climate for the last 3000-4000 years (Donders et al. 2007). 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 (Dickman et al. 2010). Boom years also cause population explosions, which subsequently crash during the droughts which inevitably follow (Dickman et al. 1999). Population booms are fueled by increases in seeds and vegetation growth that follow the pulses of rainfall; ephemeral and annual plants respond first, then perennial grasses and shrubs. Herbivorous and granivorous mammals then respond with a flurry of reproductive activity, which subsequently fuels increases in the predator population. The predator population surges just as the droughts arrive, and mammal populations are brought down to very low levels by a combination of increased predation and resource competition (Letnic and Dickman 2006).

In the arid zone, interannual and interdecadal variability in rainfall also brings pulses of fire driven by those same increases in vegetation growth (Turner et al. 2011). In drier years following one or more heavy rainfall years, the accumulation of fuel due to spinifex growth leads to large fires that burn 15-20% of the landscape in a single season; outside of these events, most years see only between 1 and 3% burned (Gill et al. 2002). The extensive fire events which follow the high rainfall period have two devastating effects on small mammal 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 (Letnic & Dickman 2005, 2006). Secondly, larger fires during drought years coincide with the long-distance dispersal animals must make in order to find food, exposing them to increased risks of predation (Letnic et al. 2005). Open habitats increase predation rates, exposing dispersing mammals to aerial as well as terrestrial predators (Smith and Quin 1996, Letnic and Dickman 2006, Kortner et al. 2007). Large fires in combination with pulses of boom and bust intensify population cycles, leading to mortality events that could be severe enough that recovery is unlikely.

Aboriginal fire may interfere with this process, buffering smaller animals both from climatically induced variation in resource availability and increases in predation…more…

The tendency for Aboriginal Australians to prey both on smaller-bodied predators and the prey of those predators has the potential for creating conditions where the loss of that influence creates substantial mesopredator release (Nishijima et al. 2014). When apex predators compete with, and directly prey on smaller predators, they have the potential to increase the persistence of vulnerable prey species by reducing total predation pressure [CITATIONS]. Varanids are the most abundant mesopredators in Australia, and dietary studies indicate extensive niche overlap with quolls, cats and foxes. Removal of these competitors can increase varanid populations, and varanids have the potential to severely reduce the populations of other animals (Sutherland et al. 2011). Varanids could be particularly devastating mesopredators in the absence of an apex predator to control their populations: unlike mammalian predators, reptile populations often boom during a bust (Read et al. 2011), and as strongly generalist foragers, varanids may be highly resilient in the face of shifts in fire regime (Pianka and Goodyear 2011). Varanids are also widespread throughout the arid zone, and likely were at much higher population densities than other predators given the low density of mammals in Australian deserts (Morton 1979). While reptiles generally have lower metabolic rates than mammalian predators, their higher abundance might compensate for their lower feeding rate. Aboriginal control of wedge-tailed eagle populations may also have played a significant role in the persistence of small to medium sized mammals in more open country. Wedge-tailed eagles consume primarily larger mammalian prey, and are significant sources of predation on endangered mammals where they still exist (Richards and Short 1998, Glen et al. 2016).

**Conclusions**

As large-bodied central place foragers who interact with a wide range of plant and animal species, humans have the potential for substantial positive effects on ecosystems. Dunne and colleagues have proposed that the ecological networks incorporating human interactions in foraging societies may be more stable over the long term because subsistence foragers are highly generalist prey-switchers with rather inefficient capture rates. Given the extreme generalism of Aboriginal foraging strategies, the dominance of weak interactions, the persistence of predation on smaller predators as well as on their prey, and evidence for substantial positive effects of Aboriginal fire mosaics and other ecosystem engineering activities, we suggest a high potential for the absence of indigenous ecosystem services in Australia to cause an 'ecological meltdown' (sensu Terborgh 1991).

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| **Species** | **Condition** | **Prey** | **Pursuit Success** | **Reference** |
| Aquila fasciata | Open ground | Rabbits | .40 | Martinez et al. 2014 |
|  |  | All | .28 |  |
| Aquila pomerina |  | All | .24 | Collopy 1983 |
| Aquila clanga |  | All | .34 | Grazynski et al. 2002 |
| Canis lupus | At optimal group size | Elk | .34 | MacNulty et al. 2014 |
|  | At optimal group size | Bison | .28 | MacNulty et al. 2014 |
| Canis lupus dingo |  | Rabbits | .09-.12 | Thomson 1992 |
|  |  | Kangaroo | .10-.20 | Thomson 1992 |
|  |  | Sheep | .66 | Thomson 1992 |
| Felis catus | Open habitat | All | .70 | McGregor et al. 2015 |
|  | Closed habitat | All | .17 |  |
|  |  | All | .30 |  |
| Lycaon pictus |  | Adult gazelle | .35 | Fanshawe and Fitzgibbon 1993 |
|  | Overall | Adult wildebeest | .45 |  |
| Felis leo | Overall | Solitary prey | .50 | Orsdol 1984 |
| Homo sapiens | Martu women, digging stick+fire | V. gouldii, recently burnt ground | .69 | Bliege Bird, n.d. |
|  | Martu women, digging stick | V. gouldii, unburnt ground | .38 | Bliege Bird, n.d. |
|  | Martu men, Rifle | M. robustus | .30 | Bird et al. 2009 |
|  | Martu men, Rifle+ vehicle | A. australis | .32 | Bird et al. 2009 |
|  | Semaq Beri men, poison dart + blowgun | Primates | .28 | Kuchikura 1988 |
|  |  | Squirrels | .43 |  |
|  | Agta women + dogs | Deer, pigs | .31 | Estioko-Griffin 1986 |
|  | Agta men | Deer, pigs | .17 |  |
|  | Efe men + bow | All | .33 | Wilkie and Curran 1991 |
|  | Iowa hunters + bow | White-tailed deer | .10-.30 | Gladfelter et al. 1983 |
|  | Animal control officers+shotguns | Feral cats | .20 | Bester et al. 2002 |
|  | Hadza men + bow | Large animals | .05 (daily) | Hawkes and O'Connell 1991 |

Table 1.

Most observational studies of human hunting pursuit success rates suggest that humans are not particularly efficient hunters when pursuing prey larger or faster than the hunter. Pursuit success rates for Desert Aboriginal foragers range from 30% for fast, mobile prey like large birds and kangaroos, 47% for large monitor lizards, 89% for smaller monitor lizards, and 96% for the smallest, slowest skinks. Because men tend to focus on larger, more mobile prey, they tend to have lower success rates overall than women. Hadza large game hunters in east Africa have a 3% daily success rate on large animals (Hawkes 1993). Semaq Beri blowgun hunters pursuing monkeys and other aboreal prey in Malaysia had an 11.6% success rate per encounter (Kuchikura 1988). Agta women hunting with dogs have a 31% success rate on deer and other large animals, men have a 17% success rate (Estioko-Griffin 1986). Efe archers in the Ituri rainforest killed about 33% of the animals they encountered (Wilkie and Curran 1991). American bow hunters on white-tailed deer obtain success rates of about 10-30% per encounter depending on experience (Gladfelter et al. 1983). Cat hunters using shotguns attempting to eradicate feral cats from an Antarctic island had a 20% success rate (Bester et al. 2002).

Australian Aboriginal hunters have low intake rates and moderate pursuit success rates for animal prey. Central Desert male hunters acquired about 5 kg per observation day (or .08 per kg body weight) on foot hunts with rifles targeting large prey such as red kangaroo, bustard, or emu (O'Connell and Hawkes 1984); pursuit success rates for such prey are around 30% (Bird et al. 2009). In the Western Desert, contemporary foragers hunting 2-3 days per week take 4.57 kg of meat per person per foraging day, 3.65 kg of large prey and .92 kg of smaller prey (Bliege Bird and Crabtree in prep).

Semaq Beri: using poison darts and blowguns, actively avoided larger animals such as wild pigs, tapir, and elephant; were much more successful on slower moving primates than faster squirrels (11.6% vs. 9.6% of encounters led to successful capture; 28.4% of stalks (11.6% of encounters) led to capture for monkey prey; 43% of squirrel stalks (9.6% of encounters) ended in successful capture. Only captured one carnivore in 240 days of observation, a civet.

South America (Jerozolinski and Peres 2003) surveyed 31 settlements of varying ages and found that the age of settlement was the only significant effect on the prey profile of successful hunts: hunters in older settlements took a wider variety of species, and hunters in younger settlements took more larger-bodied prey.

Yost and Kelly 1983: Over 867 hunts, Waorani hunters using spears, blowguns, and shotguns captured a minimum of 37 animal species, only 1 carnivore (a caiman) out of 3165 individuals killed. 14 species, primarily pigs and tapirs, large birds, large rodents, and deer comprised 95% of total weight captured. Some of the largest prey, such as tapir (n=8), caiman (n=1), and brocket deer (n=6) were among the least frequently acquired.

Levi et al. 2009: concluded that Matsigenka subsistence hunting was unlikely to threaten large vertebrate species over most of Manu National Park except possibly some rare and patchily distributed species. Likewise, both Hill and Padwe (2000) and Peres and Nascimento (2006) found that while larger prey might be depleted near central places and settlements, there was no impact of indigenous hunting on prey availability at larger spatial scales due to considerable source-sink dynamics. Furthermore, the influence of indigenous landscape interactions affected the structure of plant communities in ways that tended to increase the ability of the ecosystem to support more biomass: smaller, more adventitious species increased populations in the more diverse forest structure created by human environmental manipulation (Robinson and Bennett 2004; Smith 2005).

Whether or not introduced predators impact vulnerable prey populations depends on how they interact with other species. Introduced predators may be particularly devastating when they are smaller-bodied and where apex predators are missing or in decline (Johnson et al. 2007). Apex predators keep mesopredator populations in check through both competition and direct predation (Glen et al. 2009, Glen and Dickman 2005).

However, when mesopredators experience abundant alternative prey, coexistence of predators and prey may depend critically on the ability of apex predators to keep mesopredators in check: under these circumstances, modeling suggests the removal of an apex predator will have strong suppressive effects on vulnerable prey, including the possibility of extinction (Nishijima et al. 2014).

Australia is unusually deficient in apex predators; thus the loss of any should have substantial effects on the persistence of native fauna. Wedge-tailed eagles (*Aquila audax*), and dingos. Dingos consume a wide variety of prey items, [dingo diet here].

While introduced mesopredators, dingo suppression, feral herbivores, and land clearance for agriculture and pastoralism may have profoundly affected mammalian populations in more mesic regions of Australia, paradoxically, species loss and decline has been most severe in the desert, a region with the lowest footprints of agro-pastoralism, industrialization and land conversion, and the lowest population densities of both invasive mesopredators and dingos (Marlow et al. 2000, Marlow 1992, Fleming et al. 2001). In the deserts, small native mammal populations persisted alongside introduced predators for many decades (Abbott 2002), declining only very recently, sometime during the period between 1920 and 1960 (Finlayson 1961, Bolton and Latz 1978, Burbidge et al. 1988, Wohling 2001, Burrows et al. 2006). While dingoes generally are found at their lowest population densities in the Western Desert, there is no clear evidence for a shift in dingo populations coinciding with mammalian population losses in the region. their populations have not been as strongly affected by eradication programs as those in pastoral areas (Fleming et al. 2001). In the desert, there may be another apex predator more important than the dingo, one resident in the arid zone 40,000 years prior to the dingo’s arrival: humans. Small mammals disappeared from the desert at the same time as the exodus of Aboriginal inhabitants from the region (Finlayson 1961, Burbidge et al. 1988).

**Mesopredator suppression and generalist human predation**

SYNTHESIS.

Arid zone

Australia was first colonized about 45,000 years BP, with the first evidence for occupation of the Western Desert after 40,000 BP (Smith et al. 1997, Veth et al. 2010). Prior to 22,000 BP, the desert was wetter than present and occupation probably focused on dense, high quality resource patches, oases of diversity and abundance in a generally arid sea of sand (Veth 2000, Veth 2005, Veth 1993). Between 22,000 and 18,000, the height of the last glacial maximum created hyperarid conditions, which appears to have reduced population densities in the desert regions. As climates ameliorated, use of desert environments increased, possibly beginning about 13,000, but increasing especially in the late-Holocene (Veth 2000, Smith et al. 2008). Concomitant changes in subsistence patterns are probable, especially with late-Holocene reductions in climatic variability leading to increased human populations and intensified use of high handling-cost seeds (Edwards and O’Connell 1995, Smith et al. 2008, Williams et al. 2010). While mesopredators, especially varanids, were proabably always an important component of human hunting in the desert, they may have become even more central in the intensified economies of the late-Holocene (Codding 2012). Foraging strategies at the ethnohistoric period were highly flexible, but focused around the acquisition of small-medium sized animals, both mammals and herpetofauna mesopredators, with a heavy reliance on seasonal collection of seeds from grasses, trees and shrubs, fruits from the desert Solanum species, geophytes from *Cyperus bulbosus*, *Vigna lanceolata* and [*Ipomoea costata*](http://en.wikipedia.org/wiki/Ipomoea_costata), and occasional large game (kangaroo, *Macropus robustus* and *M. rufus*, and emu, *Dromaius novaehollandiae*) (O’Connell et al. 1983, Cane 1987, Gould 1969, 1991, Meggitt 1965, Kaberry 1939).