LETTER

Predator control promotes invasive dominated ecological states

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Abstract

Invasive species are regarded as one of the top five drivers of the global extinction crisis. In response, extreme measures have been applied in an attempt to control or eradicate invasives, with little success overall. We tested the idea that state shifts to invasive dominance are symptomatic of losses in ecosystem resilience, due to the suppression of apex predators. This concept was investigated in Australia where the high rate of mammalian extinctions is largely attributed to the destructive influence of invasive species. Intensive pest control is widely applied across the continent, simultaneously eliminating Australia's apex predator, the dingo (*Canis lupus dingo*). We show that predator management accounts for shifts between two main ecosystem states. Lethal control fractures dingo social structure and leads to bottom-up driven increases in invasive mesopredators and herbivores. Where control is relaxed, dingoes re-establish top–down regulation of ecosystems, allowing for the recovery of biodiversity and productivity.

INTRODUCTION

Observations of ecosystems subjected to changing conditions suggest that a loss of resilience is often the underlying cause of catastrophic shifts to degraded states (Scheffer *et al.* 2001). The few remaining pristine environments display extraordinary resilience in the face of global change (Sandin *et al.* 2008 . This highlights the importance of identifying and strengthening the mechanisms that provide for resilience. However, these ecological mechanisms are often overlooked in favour of controlling the instruments of change (Scheffer *et al.* 2001).

The invasion of exotic species is considered one of the top five global causes of biodiversity loss (Sala *et al.* 2000), due to mounting evidence that invasive species directly cause extinctions (Vitousek *et al.* 1997; Wilcove *et al.* 1998). Invasive species are drivers not only of decline of individual species, but may also shift ecological systems to alternative states (Croll *et al.* 2005). Not surprisingly, when ecosystems are invaded by exotic species and native biodiversity declines, human intervention in the form of pest control is swiftly called upon. Vast resources are devoted to the

development of best practice pest control, from upper-trigger harvest (Baxter *et al.* 2008) to catching the very first rat ashore (Russell *et al.* 2005).

Despite the scale and intensity of pest control, evidence in support of this approach is lacking (Reddiex & Forsyth 2006; Warburton & Norton 2009), and its application has often backfired. Successfully established exotic species integrate into the complex web of ecological interactions (Glen & Dickman 2005). Eradication or control may therefore cause unforeseen ecological damage. For example, fox (*Vulpes vulpes*) control can lead to increased cat densities (*Felis catus*), which may in turn devastate small mammal populations (Risbey *et al.* 2000); eradication of cats can cause increased predation of rats (*Rattus* spp.) on birds (Rayner *et al.* 2007); and rat control can increase seabird predation by house mice (*Mus musculus*) (Wanless *et al.* 2007). The recent successful eradication of cats from Macquarie Island, Australia, resulted in a dramatic increase in rabbits (*Oryctolagus cuniculus*) causing extensive grazing damage, even though the eradication was conducted within an integrated pest management framework (Bergstrom *et al.* 2009).

Some authors have argued that invasives are not necessarily drivers of extinctions, but instead suggest that changes in environmental conditions (e.g. due to anthropogenic disturbance) may be favouring invasives over natives (Gurevitch & Padilla 2004; Didham *et al.* 2005). This view is certainly supported in instances where native species do not recover despite the removal of exotics (e.g. MacDougall & Turkington 2005; Reld *et al.* 2009). However, it fails to encompass the numerous cases of native species persisting on exotic-free islands, and increasing following successful control or eradication (Johnson 2006; Salo *et al.* 2007). We propose instead that although invasive species are often drivers of biodiversity loss, they are not the ultimate cause. Instead, the shift to invasive-dominated states is driven by an underlying loss or lack of ecological resilience. One of the leading hypotheses that might explain resilience loss in many ecosystems is the widespread control and absence of apex predators.

Across the globe there is compelling evidence for a keystone role of large predators in enhancing ecological resilience to the damaging effects of environmental stressors (Wilmers & Getz 2005; Johnson 2006; Wilmers *et al.* 2006; Rooney *et al.* 2008; Sandin *et al.* 2008). By suppressing the abundance and changing the behaviour of opportunistic species, apex predators enhance biodiversity. Striking examples include coyotes (*Canis latrans*) suppressing mesopredators such as cats thereby indirectly protecting birds (Crooks & Soulé 1999); wolves (*C. lupus*) regulating elk (*Cervus canadensis*) densities thereby facilitating a trophic cascade resulting in the recovery of vegetation, beaver (*Castor canadensis*) and riparian songbird populations (Hebblewhite *et al.* 2005); 'ecological meltdown' of forest fragments due to the loss of top–down regulation driven by jaguars (*Panthera panthera*) (Terborgh *et al.* 2001); and evidence that coral reef survival is related to the abundance of sharks (Sandin *et al.* 2008). Worldwide large predators have become rare and endangered due to human persecution, overexploitation and habitat loss (Sandin *et al.* 2008; Prugh *et al.* 2009), thereby compromising global ecosystem structure and stability (Rooney *et al.* 2006, 2008). The destructive influence of invasive species may therefore be masking an underlying ecosystem fragility and dysfunction resulting from the suppression or absence of apex predators.

The spread and increase of exotic species parallels the global rise of native mesopredators (Prugh *et al.* 2009). Indeed, most of the damage caused by exotic mammals is attributed to a small number of highly opportunistic mesopredators or herbivores such as rats, cats, foxes, goats, rabbits and pigs (Courchamp *et al.* 2003; Johnson 2006). Salo *et al.* (2007) compared the effect of native against exotic predators on native prey, and concluded that exotic predators are more harmful. However, as these exotic predators are mesopredators, their analysis may not necessarily reflect the destructive influence of invasive predators per se, but of mesopredator release (Crooks & Soulé 1999) more generally. Once released from the influence of an apex predator, native mesopredators, like their feral counterparts, can devastate biodiversity (Prugh *et al.* 2009; Ritchie & Johnson 2009). The recovery of large predator populations may therefore facilitate the functionality and resilience of ecosystems.

Australia presents a unique opportunity to test these ideas because here invasive species are considered the main drivers of extinction since European occupation, pest control is intensively applied, and only a single large-mammalian-terrestrial predator, the dingo (*C. l. dingo*), is extant (Johnson 2006). Furthermore, in Australia the widespread use of the toxin sodium monofluoroacetate (1080) to control invasive mesopredators and herbivores is also the main method used to destroy dingoes (Reddiex *et al.* 2006). Evidence of negative associations between dingoes and mesopredators and herbivores, and positive correlations with native biodiversity (O'Neill 2002; Glen *et al.* 2007; Johnson *et al.* 2007; Johnson & VanDerWal 2009; Letnic *et al.* 2009; Wallach *et al.* 2009a) has spurred a call to reintroduce dingoes into degraded rangelands (Dickman *et al.* 2009). However, the relative effectiveness of dingoes as suppressors of invasive species remains controversial, mainly due to a lack of experimental evidence. Predator control therefore remains the main management approach.

Here, we make use of a 'natural experiment' involving large-scale predator manipulations, to test the prediction that pest (predator) control inadvertently promotes, rather than suppresses, invasive mammals by disrupting top–down regulation (Fig. 1). The link between apex predators and ecosystem stability (Rooney *et al.* 2006, 2008) suggests that the loss of large predators may increase ecosystem
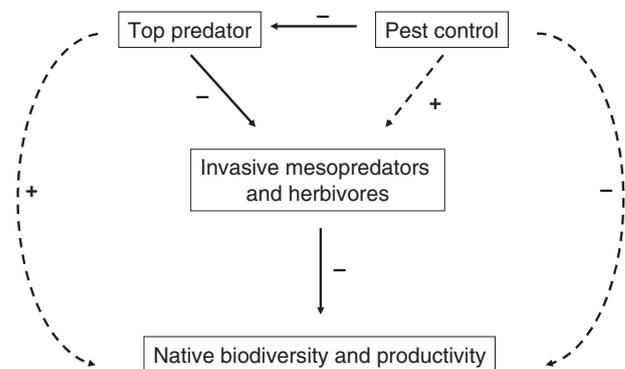
Figure 1 Theoretical model of the pathway to biodiversity loss. Invasive species cause biodiversity loss only when the apex predator is suppressed (or absent). Pest control therefore inadvertently exacerbates the problem it is attempting to solve.

susceptibility to invasive species. Previously, Johnson *et al.* (2007) found that the collapse of marsupial diversity across mainland Australia was particularly severe in areas where dingoes were scarce, and Letnic *et al.* (2009) found two distinct community compositions on either side of the 5600-km-long dingo barrier fence (DBF). We therefore predicted that the relaxation of predator control restores top–down regulation by dingoes, resulting in the suppression of invasive species and the recovery of native small mammals and vegetation. We also hypothesized that top–down regulation is not merely a function of dingo density, but is largely determined by social stability.

Dingoes, like other wolf species, have complex social systems, and social stability and abundance are not linearly related (Wallach *et al.* 2009b; Rutledge *et al.* 2010). Population abundance can either decrease or increase following control (Wallach *et al.* 2009b), suggesting that abundance may not be a fully reliable indicator of top–down regulation potential. The social group, rather than the individual, may form the fundamental structure driving predator top–down influence on ecosystems. Sociality influences a range of biological and behavioural traits such as hunting abilities, demography and fitness (Haber 1996), which are expected to affect ecological functioning.

We compared dingo abundance and social stability, composition of mammal communities, and vegetation cover and diversity at seven sites across the Australian arid zone, where the majority of extinctions have occurred (Johnson 2006). Sites represented different intensities of predator control, and at several sites responses to changed predator control regimes were measured. One site was surveyed before and after relaxation of control, two sites were surveyed before and after intensification of control, and one site was surveyed in successive years with no control. This study therefore combines both correlative and quasi-experimental analyses of community compositions, across space and time, under different management regimes, to investigate the consequence of predator control on ecosystem resilience to invasive species.

We found that dingoes successfully regulate invasive and opportunist mesopredators and herbivores, to the benefit of small native mammals and vegetation, particularly when social stability increases. Our results suggest that the resilience of ecosystems to perturbations such as alien species invasions is dependent upon the functionality of large predator populations.

METHODS

Study sites

We conducted surveys in the arid zone at five predator control sites [Mungerannie, Red Lake, Andamooka, Vulka-thunha-Gammon Ranges National Park (GRNP), and Nantawarrinna] and two control-free sites (Pandie Pandie and Curdimurka) (Table 1). Red Lake, Andamooka, Nantawarrinna and Curdimurka were surveyed annually over 2–3 years. At Red Lake, predator control was relaxed, in Andamooka (above average rainfall) and Nantawarrinna (below average rainfall) predator control intensified, and at Curdimurka there were no management changes and pest control was not applied (Wallach *et al.* 2009b). Study sites were 200–500 km², and each included at least three permanent water sources.

Table 1 Study site location, habitat and management practices

Site	Location	Rain (mm year⁻¹)*	Habitat	Land use	DBF	PB†	LHC
Pandie Pandie	26°38′ S, 139°43′ E	137	Gibber	PS	Out	0	0
Mungerannie	28°04′ S, 138°37′ E	121	Gibber	PS	Out	1	0
Curdimurka 07	29°28′ S, 137°03′ E	126	Sand dunes	PS & HA	Out	0	0
Curdimurka 08						0	0
Red Lake 06	30°11′ S, 136°51′ E	157	Sand dunes	PS	Out‡	1	0
Red Lake 07						0	0
Red Lake 08						0	0
Andamooka 07	30°32′ S, 137°05′ E	166	Sand dunes	PS	In	0	1
Andamooka 08						1	1
GRNP	30°29′ S, 139°14′ E	222	Rocky hills	NP	In	1	1
Nantawarinna 07	30°46′ S, 139°02′ E	221	Rocky hills	IPA	In	0	1
Nantawarinna 08						1	1

DBF, dingo barrier fence; PB, poison-baiting; PS, pastoral station; HA, heritage agreement site; NP, National Park; IPA, Indigenous Protected Area; LHC, large herbivore control.
*Average rainfall from: http://www.bom.gov.au.
†Within the past 12 months.
‡Inside the baited buffer zone along the DBF.

Poison-baiting was the main method of dingo and fox control and the most intensive pest control method applied. Dingoes were the declared target of poison-baiting campaigns in Mungerannie and Andamooka, whereas foxes were the main target at Red Lake, GRNP and Nantawarrinna. Baiting was generally conducted as a management practice irrespective of predator densities. Dingoes were controlled in all study sites during historic times, most for over 100 years. Four study sites are located outside and three sites inside, the DBF. None of the sites can be said to be completely devoid of dingo control, because locals and travellers have on occasion shot dingoes on our study sites, which is a common practice in Outback Australia. Rabbit control (mainly the introduction of rabbit calicivirus) was ubiquitous at all sites (Table 1).

Survey methods

At each site and year, we measured an index of relative abundance of dingoes, exotic mesopredators (foxes and cats) and herbivores (e.g. rabbits, goats *Capra hircus*, and donkeys *Equus asinus*), large native herbivores (e.g. kangaroos *Macropus* spp. and emus *Dromaius novaehollandiae*) and small native mammals (not distinguished by species). In Australia, mammalian species of intermediate body mass (50–5500 g, the 'Critical Weight Range', CWR) are particularly vulnerable to decline and extinction in low rainfall areas (Burbidge & Mckenzie 1989; Johnson & Isaac 2009), and are therefore a potential indicator of ecosystem diversity and stability. Therefore, we analysed small mammals as two separate groups of species: small (< 50 g) and CWR (50 < 300 g).

Relative abundance was estimated with a passive track survey method described previously in Wallach *et al.* (2009a). For each surveyed species, or group of species, we calculated an index of abundance by combining an estimate of relative density and distribution. Relative density was determined by dusting 500 m random transects and counting the number of animal crossings each day over 3 days, giving an average transect value of tracks per 500 m per day (10–12 transects per site). Relative distribution represents the proportion of the study site occupied, which was assessed by recording the presence or absence of fresh tracks in random 2-ha plots (20–40 plots per site). Transects and plots were positioned both on and off road, and at varying distances and directions within 7 km from water points. The Index of Abundance (IA) was calculated by multiplying relative density by the relative distribution of the site. Cattle abundance was estimated using the 2-ha plot data only (both fresh and old tracks included), as their management frequently involved their rotation between paddocks.

Dingo social stability was assessed based on scent-marking rates as described in Wallach *et al.* (2009b). Predator scats, urine and ground rakings are signs of scent-marking, and have a wide array of communicative purposes. In the Australian arid zone, dingo scats are concentrated at distinct focal points such as water points, animal warrens and carcasses. The accumulation of dingo scat deposits at focal points is predicted by lethal control, rather than abundance, and linearly increases the longer an area is left undisturbed (Wallach *et al.* 2009b). We conducted a survey of dingo scent posts, at the most prominent focal points (average of 80 focal points per site), as an index of social stability.

Vegetation was surveyed at five of the study sites in 2008 (Nantawarrinna, GRNP, Red Lake, Andamooka and Curdimurka) along 10×10 m lines running parallel, and 2 m away, from the passive animal track transects. Vegetation too high for browsing animals (generally > 2 m) was excluded from analysis. Each set of 10 vegetation transects were averaged for each dusted transect. Because grazing pressure can influence vegetation communities in various ways, we measured cover and richness, estimated relative palatability (to the most common herbivores), and calculated diversity and evenness with the Shannon index. However, all variables were strongly correlated (e.g. vegetation cover and richness: $R^2 = 0.95$, $P < 0.005$), and therefore we focused on measurements of cover and diversity as indicators of productivity and biodiversity.

We used two types of rainfall data for analyses: long-term mean annual rainfall and total rainfall over the 3 years preceding surveys (http://www.bom.gov.au). The annual average rainfall variable provides a measurement of potential productivity that is related to habitat type and may influence management. The 3-year rainfall variable was used as a measurement of short-term productivity, while accounting for delayed response to wet or dry periods.

Analysis

We calculated correlations among all original variables and constructed a correlation matrix. This provided a basis for identifying groups of variables that were strongly correlated with one another so that they could be replaced by single composite variables to reduce the effects of multicollinearity in other analyses.

We used generalized linear models (GLMs) to test the strength of top–down control by dingoes on native and exotic herbivores, exotic mesopredators, and smaller mammals that are the prey of mesopredators, in comparison with other variables that could plausibly have influenced them. Such models were constructed for the following dependent variables: CWR mammals, small mammals < 50 g, foxes, cats, rabbits and large herbivores. In each case, we generated candidate models using all possible configurations of the independent variables, and compared the support for models according to differences in their AIC scores

(Burnham & Anderson 2002) and Akaike model weights (*wi*) (Link & Barker 2006). We retained all models that were within a 95% confidence set (Burnham & Anderson 2002), and the relative importance of each predictor variable was calculated by summing *wi* across all models in which the variables occurred. Models were constructed using a Poisson distribution and log link function.

We constructed separate versions of each model using dingo abundance and scent-marking as predictor variables. We did this to determine which of these two 'dingo' variables had the strongest effects, but we did not use them in the same models because they were strongly correlated. When selecting other independent variables, we made various combinations of the original variables, for three reasons: to reduce the number of candidate variables, to reduce the incidence of intercorrelation among candidate independent variables and to create ecologically meaningful categories (such as rabbits plus smaller mammals, as a prey guild for foxes and cats). The candidate variables (in addition to dingo abundance/scent marking) used for model building were:

(1) for CWR and < 50 g mammals: mesopredators (foxes plus cats), 3-year rainfall and all herbivores (i.e. rabbits plus large herbivores);
(2) for foxes: prey (rabbits plus small mammals) and poison-baiting (a categorical variable indicating whether 1080 baiting had been conducted within the past 12 months, included because foxes are susceptible to poisoning);
(3) for cats: foxes and prey (rabbits plus small mammals);
(4) for rabbits: mesopredators, 3-year rainfall and large herbivores;
(5) for large herbivores: 3-year rainfall and rabbits.

All variables were log + 1 transformed and standardized (to a 0–100 scale) to allow direct comparison of effect sizes between variables.

We used a Principal Components Analysis (PCA) to describe differences in ecological states among sites (and among years at several sites). For this analysis, we used the incidence of dingo scent-marking as the dingo population index, because this was more influential than dingo abundance in most models. The PCA was constructed using the intrinsic variables dingo (scent-marking), fox, cat, rabbit, large herbivores, and small (< 50 g) and CWR mammals (all variables log + 1 transformed). We then tested for correlations of PCs with average rainfall, vegetation and cattle. Vegetation was not included in the model because data were not available for some sites. Cattle were not considered an intrinsic variable because people dictated their density and movement.

To investigate causality, we compared community composition within and between sites undergoing changes in predator control. A comparison of species' or guilds' relative abundance between years was analysed with nonparametric tests because the data were not normally distributed. Mann–Whitney *U*-tests (Curdimurka, Andamooka) and Kruskal–Wallis tests (Red Lake) were used where sampling location changed between years, and Wilcoxon-signed ranks tests were used where sampling location was tied (Nantawarrinna).

RESULTS

Correlations among original variables are shown in Table 2. There were strong positive correlations of dingo activity with the abundance of small and medium-sized (CWR) mammals, and strong negative correlations with kangaroos, emus, goats and donkeys. Correlations were mostly stronger for dingo activity measured by scent-marking than by track abundance. Abundances of all large herbivores were intercorrelated and so were combined into a single large-herbivore category for subsequent analyses. Both fox and cat abundance increased with rabbit abundance, and there was a strong negative correlation of combined fox and cat (mesopredator) abundance with abundance of CWR mammals.

GLMs showed that dingoes were present in all the preferred models accounting for variation in community composition (Table 3). The index of dingo scent-marking had stronger effects in models than did the index of dingo abundance. In some cases, the direction of association (+ or −) was reversed for scent-marking and abundance. Both dingo variables were positively related to the abundance of small native mammals. Scent-marking was the stronger predictor of CWR mammal abundance, whereas dingo abundance was a better predictor of small (< 50 g) mammal abundance. Both dingo variables, especially scent-marking, were negatively related to the abundance of foxes and cats. Dingo scent-marking was also negatively related with rabbits and large herbivores, but dingo abundance (a weaker variable) was positively related.

The first two PCs accounted for 75% of the variation across the variables dingo (scent-marking), fox, cat, rabbit, large herbivores, and small (< 50 g) and CWR mammals (Fig. 2). PC1 explained 45% of the variance and represented a shift from sites dominated by dingo scent-marking ($r = 0.88$) with abundant small ($r = 0.58$) and CWR mammals ($r = 0.92$), to sites with less dingo scent-marking and more rabbits ($r = -0.54$), large herbivores ($r = -0.71$), foxes ($r = -0.38$) and cats ($r = -0.48$). PC2 explained 25% of the variance and represented a trend towards more foxes ($r = 0.63$) and cats ($r = 0.63$) along with their prey (rabbits, $r = 0.62$, and small mammals < 50 g, $r = 0.52$) and fewer large herbivores ($r = -0.49$). Cattle were positively related to PC2 ($F_{1,10} = 9.78$, $P = 0.01$) but not PC1 ($F_{1,10} = 0.02$, $P = 0.89$).

Table 2 Correlation matrix for the set of predictor variables. Entries in bold identify correlations significant at the .05 level

	RainAve	Rain3y	TSC	DScent	Dingo	Fox	Cat	Meso	Rabbit	Kang	Emu	Goat	Donkey	THerb	CWR
Rain3y	0.38														
TSC	**−0.59**	−0.30													
DScent	**−0.78**	−0.29	**0.92**												
Dingo	−0.43	−0.18	**0.90**	**0.85**											
Fox	0.14	0.55	−0.23	−0.24	−0.02										
Cat	0.13	0.54	−0.13	0.00	−0.01	0.47									
Meso	0.23	0.50	−0.33	−0.29	−0.15	**(0.86)**	**(0.78)**								
Rabbit	−0.11	0.42	−0.21	−0.01	−0.05	**0.73**	**0.75**	**0.80**							
Kang	**0.94**	0.38	**−0.69**	**−0.80**	−0.46	0.27	0.22	0.36	0.10						
Emu	**0.60**	−0.27	−0.42	−0.52	−0.20	−0.02	−0.27	0.02	−0.27	**0.59**					
Goat	**0.77**	−0.02	−0.42	**−0.62**	−0.27	−0.03	−0.35	−0.07	−0.41	**0.72**	**0.86**				
Donkey	**0.75**	−0.02	**−0.59**	**−0.76**	**−0.61**	−0.32	−0.42	−0.29	−0.53	**0.66**	**0.63**	**0.83**			
THerb	0.14	0.48	−0.51	−0.34	−0.32	**0.73**	**0.66**	**0.78**	**(0.92)**	(0.38)	(−0.10)	(−0.17)	(−0.23)		
CWR	**−0.83**	**−0.62**	**0.68**	**0.76**	0.48	−0.55	−0.45	**−0.64**	−0.34	**−0.87**	−0.41	−0.56	−0.46	**−0.57**	
< 50	−0.54	−0.23	**0.63**	**0.65**	**0.69**	0.16	−0.02	−0.01	0.11	−0.46	−0.39	−0.50	**−0.73**	0.06	0.53

RainAve, annual average rainfall; Rain3y, 3-years accumulated rainfall; TSC, time elapsed since predator control; DScent, dingo scent-marking; Meso, mesopredators (foxes plus cats); Kang, kangaroo; THerb, total herbivore (rabbits plus large herbivores); CWR, medium-sized mammals; < 50, small mammals.

Table 3 Generalized linear models of species' relative abundance using Akaike's Information Criterion (AIC), with either dingo abundance or scent-marking as predictor variables

Model				AIC	Δi	wi
CWR mammals						
Dingo SM (+0.03)		Rain (−0.08)	Herb (−0.10)	108.31	0.00	0.66
Dingo SM (+0.03)	Meso (−0.03)	Rain (−0.08)	Herb (−0.10)	109.65	1.34	0.34
Dingo A (+0.06)	Meso (−0.28)	Rain (−0.09)	Herb (−0.12)	174.07	65.76	0.00
Small mammals < 50 g						
Dingo A (+0.02)	Meso (+0.04)	Rain (−0.04)	Herb (−0.09)	212.83	0.00	1.00
Dingo SM (+0.01)	Meso (+0.03)	Rain (−0.03)	Herb (−0.02)	260.57	47.74	0.00
Fox						
Dingo SM (−0.09)	Prey (+0.02)	243.17	0.00	0.71		
Dingo SM (−0.09)	Prey (+0.02)	PB (+0.06)	245.00	1.83	0.29	
Dingo A (−0.004)	Prey (+0.01)	PB (+0.94)	293.00	49.83	0.00	
	Prey (+0.01)	PB (+0.94)	293.83	50.66	0.00	
Cat						
Dingo SM (−0.02)	Fox (+0.004)	Prey (+0.02)	384.11	0.00	1.00	
Dingo A (−0.02)	Fox (+0.008)	Prey (+0.01)	402.11	18.00	0.00	
Rabbit						
Dingo SM (−0.02)	Meso (−0.005)	Rain (+0.04)	L herb (−0.02)	95.31	0.00	0.74
Dingo SM (−0.02)		Rain (+0.04)	L herb (−0.02)	97.39	2.08	0.26
Dingo A (+0.005)		Rain (+0.05)	L herb (−0.01)	132.45	37.14	0.00
		Rain (+0.05)	L herb (−0.01)	133.24	37.93	0.00
Dingo A (+0.005)	Meso (−0.002)	Rain (+0.05)	L herb (−0.01)	133.95	38.64	0.00
Large herbivores						
Dingo SM (−0.07)	Rain (+0.02)	Rabb (−0.02)	139.56	0.00	1.00	
Dingo A (+0.004)	Rain (+0.05)	Rabb (−0.03)	383.53	243.97	0.00	
	Rain (+0.05)	Rabb (−0.03)	384.25	244.69	0.00	

Δi, model score differences; wi, Akaike model weights; A, dingo abundance; SM, scent-marking; Meso, mesopredators (foxes plus cats); Herb, total herbivores (rabbits plus large herbivores); PB, poison-baiting; L Herb, large herbivores (native and exotic); Rabb, rabbits. The estimate values are indicated in brackets.
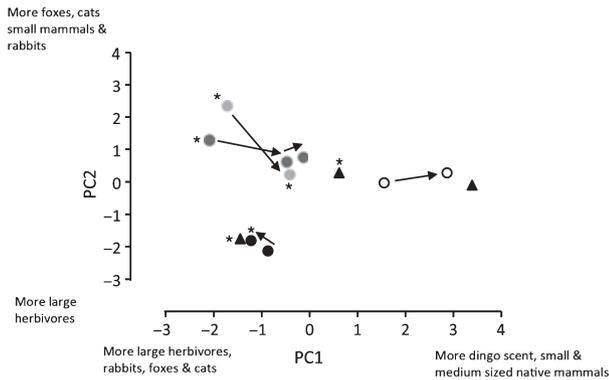
Figure 2 Changes in ecosystem states as shown by principle component scores for each site and year on an axis of the two strongest models. PC1 describes the span of top–down regulation strength and PC2 represents a range of conditions driven mainly by bottom–up forces. Sites that were measured across years are connected by arrows, indicating the direction of time (open circles – Curdimurka; light grey circles – Andamooka; dark grey circles – Red Lake; black circles – Nantwarrinna). The three properties that were surveyed once only are indicted with triangles. Sites and years where poison-baiting was conducted within 1 year of the study are starred. The relaxation of control moves sites to the right (top–down regulated state), whereas instituting it moves them to the left (bottom–up driven state).

Sites with positive PC1 values varied mainly along this axis, whereas sites with negative PC1 values fluctuated widely along the PC2 axis. Poison-baited sites and years tended to be pushed towards negative PC1 values ($t = 2.48$, d.f. = 11, $P = 0.03$) inducing a shift to PC2-driven conditions. The disruption of top–down regulation caused by predator control is also evident in the GLM of fox abundance. Foxes were positively related to 1080 poison-baiting (Table 3), even though this is the very method used to control them, and the decision to poison-bait was independent of fox abundance. Poison-baiting had no discernible association with PC2 ($t = −0.24$, d.f. = 11, n.s.).

Interestingly, both the GLM and PCA revealed that rainfall in our arid study sites was negatively related to small native mammals and vegetation. Rainfall was negatively related to both-size categories of small mammals, but positively related to invasive and opportunistic herbivores (Tables 2 and 3). Average rainfall was negatively related to PC1 ($F_{1, 10} = 7.24$, $P = 0.03$), PC2 ($F_{1,10} = 7.73$, $P = 0.02$) and vegetation (cover: $F_{1,3} = 23.54$, $P = 0.02$, diversity: $F_{1,3} = 11.18$, $P = 0.04$), whereas vegetation was positively related to PC1 (cover: $F_{1,3} = 23.35$, $P = 0.02$, diversity: $F_{1,3} = 39.07$, $P = 0.008$). Thus, sites with more stable dingo packs had more plant cover and diversity despite being drier. This relationship follows the trend of predator control intensification as average annual rainfall increases ($F_{1,10} = 6.21$, $P = 0.03$).

The comparison of community composition before and after management changes provides quasi-experimental evidence that human induced disruption of top–down regulation causes shifts to invasive dominated ecosystem states. Where dingoes were not controlled (Curdimurka) mesopredators and herbivores remained uncommon whereas dingoes and small native mammals (including CWR mammals) were abundant (Fig. 3a). Although species abundance did not change significantly between years (n.s. for all species), the PC1 value of this site did move a considerable distance towards a healthier state (Fig. 2). Similarly, the cessation of poison-baiting in Red Lake caused immediate discernible improvement: the site shifted towards a positive PC1 value (Fig. 2) as dingo and small mammal abundance increased (including the appearance of a CWR mammal after two years), and foxes and herbivores decreased (Kruskal–Wallis dingo: $H = 7.89$, d.f. = 2, $P = 0.02$; small mammals: $H = 12.24$, d.f. = 2, $P < 0.01$; fox: $H = 8.61$, d.f. = 2, $P = 0.01$; cat: $H = 1.37$, n.s.; rabbit: $H = 14.59$, d.f. = 2, $P = 0.001$; kangaroo: $H = 13.71$, d.f. = 2, $P = 0.007$; Fig. 3b).

The poison-baiting treatment effectively removed dingoes in Nantawarrinna (during a period of below average rainfall) (Wilcoxon-signed ranks test: dingo $Z = 2.59$, $P = 0.01$), but in Andamooka (during a period of above average rainfall) dingo abundance increased significantly (Mann–Whitney $Z = 2.8$, $P = 0.004$). The loss of dingoes from Nantawarrinna shifted the site to a more negative PC1 value (Fig. 2): herbivore abundance increased (Wilcoxon-signed ranks test: rabbit $Z = 2.40$, $P = 0.02$; kangaroo $Z = 2.13$, $P = 0.03$), whereas mesopredators and small mammals remained uncommon in both years (n.s.; Fig. 3c). In Andamooka, the increase in dingoes was closely followed by an equivalent decrease in foxes (Mann–Whitney $Z = 2.64$, $P = 0.008$), whereas cat, herbivore and small mammal abundance remained unchanged (n.s.) (Fig. 3d).

DISCUSSION

The premise that invasive species are ultimate causes of biodiversity loss is not supported by this study. Rather than controlling invasives, pest control inadvertently promotes invasive and opportunistic species by disrupting dingo populations. Social stability, rather than abundance, was the stronger predictor of these effects. Two main ecosystem states were revealed by our analyses: those regulated by top–down or bottom–up processes. Comparison of sites before and after changes in predator management supports the notion that predator control causes shifts between these two states. Although this is not a full experimental study (with treatment replications), the evidence for these patterns derived from the correlative (spatial) and quasi-experimental (temporal) approaches is complementary and robust.
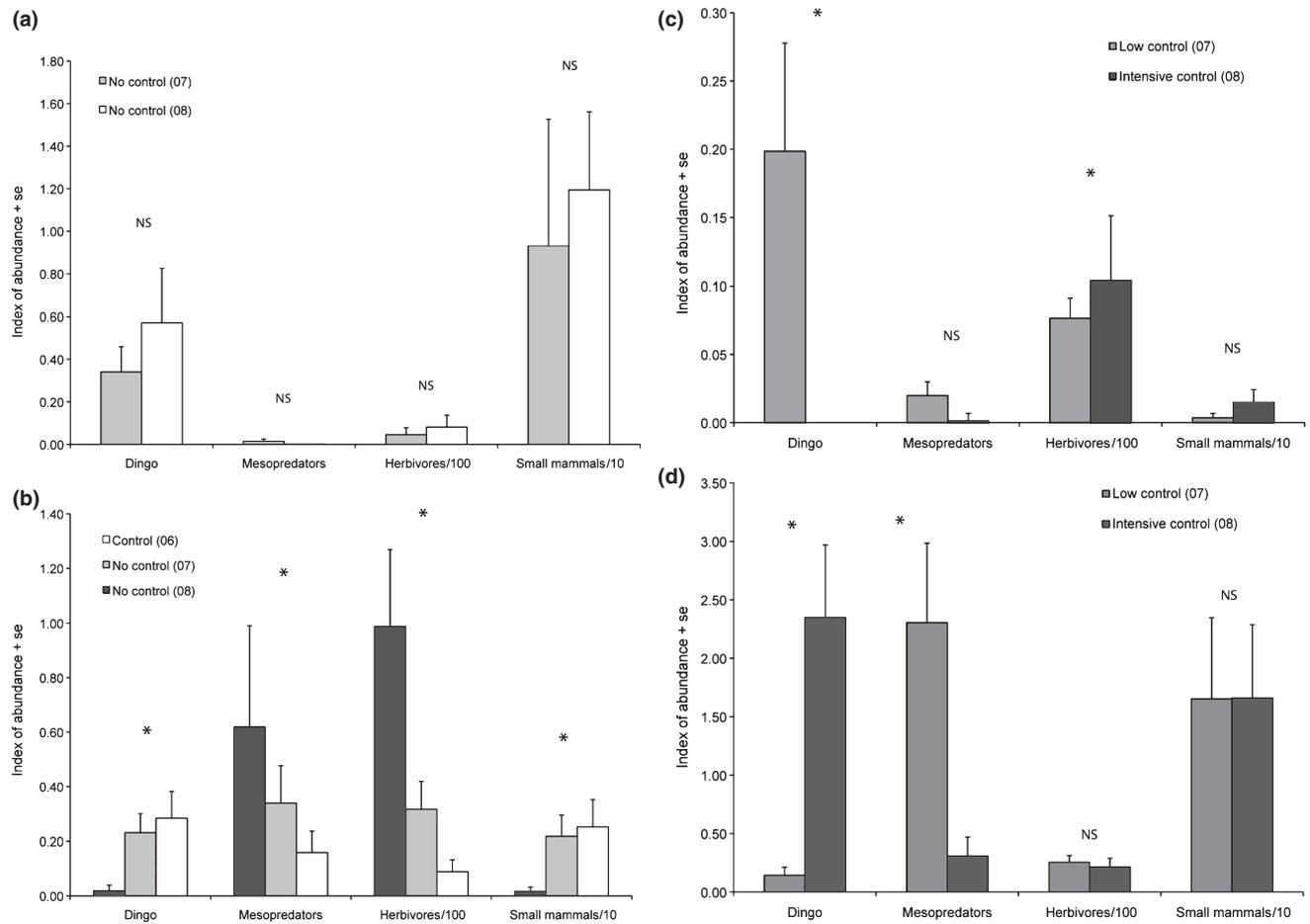
Figure 3 Change in mammal composition (mean ± SE) in response to predator management: under (a) no control (Curdimurka 2007–2008), (b) relaxation of control (Red Lake 2006–2008), (c) intensification of control during a dry period (Nantawarrinna 2007–2008) and (d) intensification of control during a productive period (Andamooka 2007–2008). Herbivore abundance was divided by 100 and small mammals by 10 to allow for a comparable scale. Significance is denoted with asterisks ($P < 0.05$).

The PC1 axis represents the influence of top–down regulation by dingoes, and PC2 describes the range of bottom–up driven conditions where dingo influence is removed. Top–down regulated states (+PC1) are comprised of socially stable dingo populations, allowing higher abundance of small and CWR mammals and higher vegetation cover and diversity. Sites that are pushed into negative PC1 values fluctuate widely along the PC2 axis. Sites at the positive end of PC2 are presumably more productive, allowing for the higher availability of small mammals (< 50 g) and rabbits, which may support higher cat and fox populations. Cattle were positively related to PC2 because pastoral practices traditionally remove large predators and rely on bottom–up driven productivity. But high productivity on the PC2 scale is not sustainable, because the lack of top–down regulation eventually leads to ecosystem collapse. Sites at the negative end of PC2 are also negative on the PC1 axis, and these sites reflect the most

degraded conditions as mainly large mobile herbivores (e.g. kangaroos and goats) persist there.

The consequences of intensification and relaxation of predator control indicate that sites can potentially recover back into +PC1 states. Relaxation of control allows dingo populations to recover, leading to population control of mesopredators and generalist herbivores and an increase in small mammals (Red Lake). Sites that have been freed from predator control over an extended period of time may continue to improve in the absence of human intervention (Curdimurka). On the other hand, conditions in even highly degraded sites can deteriorate further where predator control is continued (Nantawarrinna). Sites that have shifted and been maintained in degraded states through long-term predator control may require an extended period of recovery. Vegetation loss, seed bank depletion, soil erosion and species loss may induce a positive feedback that locks systems in degraded states (Scheffer *et al.* 2001). Vast

stretches of Australia's arid and semi-arid rangelands have indeed reached a state best described as 'wastelands', requiring an urgent restoration of top–down regulation (Dickman *et al.* 2009).

The restoration of top–down regulation depends on the recovery of social stability rather than a mere increase in predator numbers. Previous studies suggest that social groups rather than individuals are the basic driving force of predator–prey dynamics, providing underlying stability of populations and ultimately ecosystems (Fryxell *et al.* 2007). Studies of large social predators have found that density dependent self-regulation maintains population size under a threshold level, irrespective of fluctuations in resource availability, suggesting that apex predators exert top–down regulation upon themselves (Kissui & Packer 2004; Fryxell *et al.* 2007; Rutledge *et al.* 2010).

The lack of stable territory holding packs releases apex predators to bottom–up processes that may increase reproductive rates and immigration, and results in populations dominated by juveniles (Knowlton *et al.* 1999; Wallach *et al.* 2009b). The highest abundance of dingoes detected in this study was in a −PC1 site (Andamooka) subjected to predator control following a high rainfall event. Although top–down regulation effects have frequently been demonstrated for numbers alone (Ritchie & Johnson 2009), inconsistencies may emerge if social stability is not accounted for (Letnic *et al.* 2009; this study). Thus, dingo social stability is a more powerful predictor of mesopredator and herbivore abundance, and dingo abundance may be positively related to herbivore densities (once social stability is removed from analysis). The abundance of different small mammal group sizes also respond in a distinct fashion to bottom–up and top–down driven conditions. Small (< 50 g) mammals appear to be more opportunistic as they feature on the positive end of both PC scales. Here, dingo abundance was the stronger predictor variable and mesopredator abundance was also positively related. CWR mammals on the other hand are more sensitive to changes in top–down regulation, as their abundance was closely tied with dingo social stability, and they occurred almost exclusively in +PC1 sites.

Extinctions in Australia have been most severe in the arid zone, even though this is where human population density is at its lowest, wilderness areas are vast and connected, and despite the fact that alien species were also introduced into mesic areas (McKenzie *et al.* 2007). This pattern may have emerged because dingo control is most effective where permanent water is restricted (Wallach & O'Neill 2009). In our arid zone study sites, the destructive influence of predator control even outweighed the benefits of rain. Although rainfall does initially increase productivity (Letnic *et al.* 2009), the build up of herbivores and mesopredators that occurs where the apex predator is controlled, eventually overwhelms any newly available resource. This result

challenges the popular view that the devegetated state of the Australian arid zone is drought induced.

The scale and intensity of pest control across the globe reflects a common belief that many ecosystems are incapable of adjusting to the arrival of alien species, and that human intervention can replace the role of apex predators. Neither of these notions is supported by this study. The limitations of human intervention (pest control) probably stems from a failure to mimic the full array of behavioural interactions driving direct and indirect effects by apex predators. To the best of our knowledge, invasive species have never caused extinctions where large predator populations remain intact. This study suggests that once an exotic species has successfully integrated into an ecosystem we should not attempt to remove it. Instead, we should apply strategies that promote the inherent strengths that enable ecosystems to maintain resilience to change.

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