Ecological and economic benefits to cattle rangelands of restoring an apex predator

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Summary

1. The conservation of terrestrial carnivores is hampered by economic conflicts between predation and livestock production. The dingo *Canis dingo* is the top predator in Australia's terrestrial ecosystems but its abundance is controlled because it preys on livestock. Dingo control (poisoning, shooting) is associated with increased densities of wild herbivores, which can lead to reduced cattle condition and fertility through competition for pasture. We investigated whether the restoration of dingoes might provide a net benefit for rangeland vegetation and the profit margins of cattle pastoralists.

2. We developed a dynamic, multi-species metamodel to represent the trophic linkages and economics of a rangeland cattle enterprise. To estimate the strength of dingo-mediated trophic cascades, we underpinned the metamodel with a detailed simulation of pasture growth, grazing pressure and cattle live-weight gain. An economic model that calculated the costs and revenues associated with maintaining the cattle herd was used to examine trade-offs between livestock density, kangaroo abundance, calf losses and dingo control.

3. We simulated the effects of dingo abundance on rangeland ecology (pasture biomass, kangaroo density) and enterprise performance (cattle live-weight gain, gross margin). Assuming a typical stocking density for semi-arid rangelands, we estimated that kangaroo control by an unbaited dingo population would increase pasture biomass by 53 kg ha^{-1}, improve gross margins by \$0·83 ha^{-1} and reduce inter-annual variability in profits.

4. The increase in pasture biomass due to dingoes was greatest at low stocking densities (that permitted high kangaroo abundance in the absence of predation), while improvement in profits was strongest at intermediate stocking densities (when cattle density was high enough to take advantage of the additional pasture biomass). At high stocking densities, the abundance of kangaroos was low, so if dingo abundance exceeded that required to control kangaroos, some dingo baiting could produce small economic gains.

5. *Synthesis and applications*. There is little incentive for pastoralists to reduce livestock densities in mixed wildlife–livestock systems unless wildlife grazing can be controlled. Our results demonstrate that top-down herbivore control by dingoes should allow cattle pastoralists to profit from conservative stocking densities while reducing the risk of pasture over-utilization.

Key-words: animal production, large carnivores, livestock, predator–prey dynamics, rangelands, sustainable agriculture, trophic cascade

Introduction

The removal of apex predators is one of humankind's most pervasive ecological impacts and has modified the trophic structure and functioning of ecosystems worldwide (Estes *et al*. 2011; Ripple *et al*. 2014). Apex predators exert direct, top-down effects on their prey, but their

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influence also propagates through food webs, creating trophic cascades such that fluctuations in predator abundance modify herbivore density and thereby alter the biomass of primary producers indirectly (Paine 1980; Croll *et al.* 2005). Despite increased recognition of the importance of predators in structuring ecological communities, the conservation and recovery of terrestrial predators remains controversial due to perceived impacts of predators on livestock (Mazur & Asah 2013).

Australia once supported diverse guilds of mammalian predators and herbivores, but human hunting, together with a consequent and irreversible change in vegetation structure, are implicated in the prehistoric extinction of about 50 mammal species, including a complex assemblage of large carnivores (Johnson 2014b; Prowse *et al.* 2014). Australia's last remaining apex mammalian predator is the dingo *Canis dingo* (Crowther *et al.* 2014), an Asian wolf introduced to Australia approximately four thousand years ago (Johnson 2014b). Since the arrival of Europeans in Australia, dingoes have been widely regarded as a pest species because they prey on livestock. During the 1880s, a 5614-km long 'dingo fence' was constructed to protect south-eastern Australia's grazing rangelands from dingo incursions, and dingoes are still poisoned and shot on both sides of this barrier. Dingoes are now listed as Vulnerable by the IUCN (2013), and their top-down influence is missing or heavily reduced throughout much of the continent (Fleming *et al.* 2001).

The most obvious ecosystem impact of apex predators is the suppression of populations of large herbivores (Ripple *et al.* 2014). Dingoes selectively hunt medium- to large-sized prey, although they can also consume small mammals, reptiles and invertebrates when larger prey is scarce (Allen & Leung 2012; Johnson 2014a). There is strong evidence that dingo predation can control populations of kangaroos, the largest native herbivores in Australia. The persecution of dingoes following the arrival of Europeans apparently caused a rapid rise in kangaroo abundance (Johnson 2014a). Further, kangaroo density is higher inside (south of) the dingo fence where control is intensive than outside where control is less coordinated and less effective (Pople *et al.* 2000; Letnic *et al.* 2009), although other factors such as the provision of new water points might contribute to this difference. It follows that, whereas optimizing rangeland profits and restoring top-down predatory control are currently viewed as conflicting goals, the potential improvement in vegetation biomass and structure through dingo-mediated trophic cascades might actually benefit cattle production by providing more forage for cattle. With grazing rangelands now covering approximately 75% of Australia (ACRIS 2001), it is important to quantify the net influence of dingoes on rangeland production.

Choquenot & Forsyth (2013) used a dingo–kangaroo–vegetation–rainfall model to demonstrate that trophic cascades caused by dingoes should be weaker in unproductive landscapes where dingo density is low, and also where dingoes have ready access to alternative, non-herbivorous prey. Modelling trophic cascades in pastoral landscapes is more complicated, however, because stocking densities are the primary determinants of long-term pasture biomass and condition (Johnston *et al.* 2000). Predation of kangaroos by dingoes should benefit pastoralists because kangaroos compete directly with livestock for forage (Wilson 1991), but the true impact of dingoes on prey populations, vegetation condition and the financial performance of rangeland enterprises is inextricably linked to the management strategies employed by graziers.

We constructed a multi-species simulation to investigate the impacts of dingoes on beef cattle enterprises in the Australian rangelands, assuming typical stock management scenarios. Our dynamic metamodel (i.e. an integrated model composed of linked component models; Lacy *et al.* 2013) represented the important trophic levels and economics of a rangeland cattle-grazing system. We quantified the expected consequences of dingoes on rangeland ecology as well as enterprise performance. Our results indicate that the net influence of functioning dingo populations should be positive, leading to improved native pasture biomass, cattle growth rates and enterprise profits.

Materials and methods

METAMODEL OVERVIEW

We constructed the metamodel to simulate the rangelands occupied by a self-replacing beef cattle enterprise in New South Wales (Figs 1 and 2) and assumed a typical area for the enterprise of 50 000 ha (Chudleigh 1971). We simulated the bottom-up influence of pasture growth using the GRASP forage production model (Rickert, Stuth & McKeon 2000) which, in turn, was modified by Caughley's (1987) interactive model of red kangaroo *Macropus rufus* population dynamics and grazing pressure. Exploitation competition for pasture by kangaroos affected simulated cattle live-weight gain (LWG), mortality and fertility rates, and consequently influenced a population model developed for the enterprise cattle herd. Dingoes consumed both calves and kangaroos and their population growth rate responded accordingly. Dingo density could be modified by poison baiting (i.e. through the distribution of baits laced with the sodium fluoroacetate poison compound commonly known as '1080'). We linked a previously developed economic model to the cattle population model and used current pricing estimates to calculate the costs and revenues associated with maintaining the cattle herd.

We ran simulations using historical daily climatic inputs for three New South Wales rangeland sites. To remove the influence of starting values (e.g. pasture state, herbivore and dingo densities), we allowed the model runs to burn in for 20 years using climate inputs for the period 1891–1910. Climatic inputs for the following 100 years (1911–2010) were used to produce model output. Default values for all ecological parameters are listed in Table 1, as are discrete values or ranges used for scenario testing and sensitivity analysis. The metamodel components and linkages are summarized below (for complete methods, see Appendix S1 in Supporting information).
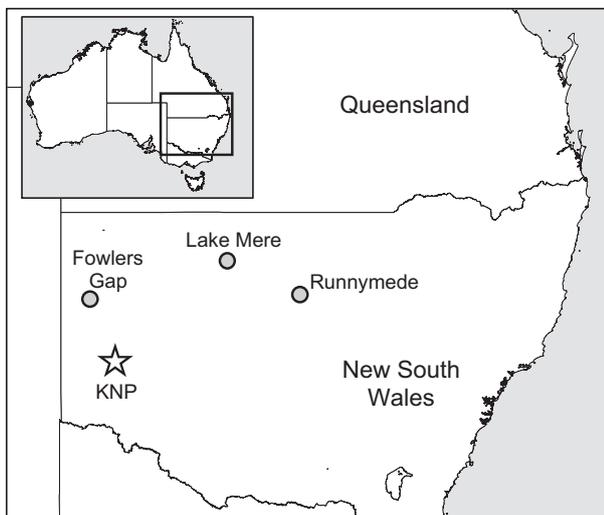
Fig. 1. Locations of the three semi-arid sites in New South Wales for which calibrated parameter sets for the GRASP pasture model were available (points). Also shown is Kinchega National Park (KNP, star) where Caughley (1987) parameterised the interactive kangaroo model.

GRASP PASTURE MODEL

GRASP simulates the climate–soil–plant–livestock interactions for Australian rangelands (Rickert, Stuth & McKeon 2000). We used GRASP parameterizations that had been developed previously for three semi-arid rangeland sites in north-western NSW (Fig. 1) where the pasture growth model validated particularly well against empirical data (Richards *et al.* 2001): Fowlers Gap (31.09°S, 141.70°E), Lake Mere (30.17°S, 144.99°E) and Runnymede (30.98°S, 146.72°E). We sourced the daily climate data required for each site from the SILO-enhanced climate data base (www.longpaddock.qld.gov.au/silo/index.html). Baseline simulations used the climate and GRASP parameter files for Fowlers Gap, the closest site to Kinchega National Park (Fig. 1) where Caughley's (1987) interactive kangaroo model was parameterized.

KANGAROO MODEL

Caughley's (1987) foundational 'interactive model' simulates kangaroo population dynamics as a function of pasture biomass, which is itself a function of rainfall-driven pasture growth and the density of kangaroos grazing the vegetation. We replaced the original vegetation component of the interactive model with the GRASP forage production model. Grazing by kangaroos is governed by their functional response (I_k), such that pasture intake by each kangaroo (kg individual^{-1} day^{-1}) is given by:

$$I_k = I_{\max,k}(1 - e^{-\text{TSDM}/f_k})$$

where $I_{\max,k}$ is the maximum intake rate of kangaroos, TSDM is total standing dry matter (kg ha^{-1}) derived from the GRASP model, and f_k is the foraging efficiency that controls the shape of the functional response. The numerical response of kangaroos is given by:

$$r_k = r_{\min,k} + (r_{\max,k} - r_{\min,k})(1 - e^{-\text{TSDM}/d_k})$$

where r_k is the annual population growth rate (exponential rate of increase), $r_{\min,k}$ and $r_{\max,k}$ are the minimum and maximum population growth rates for kangaroos, and d_k is the demographic efficiency that controls the shape of the numerical response (see Appendix S1, Supporting information).

CATTLE LWG

We used MacLeod, Ash & McIvor's (2004) approach to modelling LWG for pastures consisting of a mixture of perennial and annual species. Daily LWG was calculated as:

$$\text{LWG} = 0.23 - (0.005 \times U) + (0.005 \times \text{GD})$$

where U is the percentage utilization of new growth (by all herbivores) and GD is the percentage of growing days over the year. Growing days are defined as those when there is sufficient water
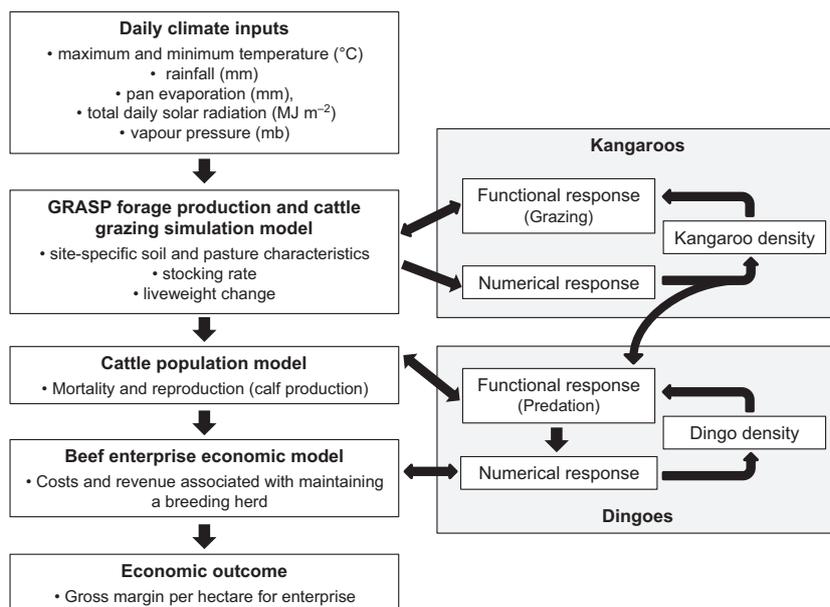

Fig. 2. Structural overview of the meta-model subcomponents and linkages.

Table 1. The default metamodel parameterization and details of the sensitivity analysis implemented using Latin hypercube sampling. Where no range is given, the parameter remained fixed across all scenarios

Parameter	Default	Sensitivity analysis
GRASP and climatic inputs		
Site	Fowlers Gap	Fowlers Gap, Lake Mere, Runnymede
Kangaroos		
Maximum intake rate, $I_{max,k}$	0·99*	0·99
Foraging efficiency, f_k	34*	34
Minimum population growth rate, $r_{min,k}$	−1·6*	$U(-2, -1)$
Maximum population growth rate, $r_{max,k}$	0·4*	$U(0.2, 0.8)$
Demographic efficiency, d_k	143*	143
Starting density, N_k	0·1	0·1
Dingoes		
Attack rate on kangaroos, a_k	0·0015[†]	$U(0.001, 0.01)$
Handling time for kangaroos, h_k	2·96	$U(1, 10)$
Attack rate on calves, a_c	0·005[‡]	$U(0.001, 0.1)$
Handling time for calves, h_k	10·5	$U(5, 20)$
Minimum population growth rate, $r_{min,d}$	−1·22[§]	$U(-2, -1)$
Maximum population growth rate, $r_{max,d}$	0·63[§]	$U(0.2, 0.8)$
Demographic efficiency, d_d	1·62[¶]	Derived from $\bar{I}_d$ for $r_d = 0$
Theta-logistic parameter, θ	2**	$U(1, 3)$
Predation rate $\bar{I}_d$ required for $r_d = 0$	1·75	$U(0.5, 5)$
Carrying capacity, K_d	0·0025[§]	$U(0.001, 0.040)$
Starting density, P	0·00035[§]	0·00035
Contribution of alternative prey (% of intake required for stable P)	10,50,90	$U(0, 100)$
Annual probability of environmental catastrophe affecting N_{alt}	0	$U(0, 1)$
Reduction in N_{alt} (%) in catastrophe year	0	$U(0, 100)$
Management strategies		
Stocking density	0·005, 0·010, … , 0·050, 0·055[††]	$U(0.005, 0.055)$
Dingo baiting (% reduction in P)	0,50,100	$U(0, 100)$

*Parameters derived from Caughley (1987).

[†]Initially, a_k was derived to produce a reasonable shape for g_k when kangaroos were the only prey source.

[‡]Initially, a_c was set equal to a_k.

[§]Parameters derived from Choquenot & Forsyth (2013).

The default value for d_d was derived such that the dingo population was stable when the mean dingo intake rate $\bar{I}_d = 1.75$ kg dingo^{-1} day^{-1}.

**With θ = 2, the dingo population growth rate is only reduced substantially at high dingo densities.

[††]A typical stocking density for these rangeland site is 0·03 AE ha^{-1} (Richards *et al.* 2001).

in the soil profile, and temperature is sufficiently high, to maintain pasture growth.

CATTLE POPULATION MODEL

We simulated a self-replacing cattle enterprise that sought to market steers, while also culling breeders and surplus heifers (see Appendix S1, Supporting information). This livestock model was formulated after MacLeod, Ash & McIvor (2004) and assumed a constant breeding herd was maintained through the purchase or marketing of heifers as necessary at the end of each simulated year. We modelled the cattle herd using an age-structured matrix population model with a pre-breeding census design (Caswell 2001) and adjustments to account for the culling or purchase of stock. We calculated annual mortality and fertility rates as a function of simulated LWG using established relationships (MacLeod, Ash & McIvor 2004):

Breeder mortality $(\%) = 6 + 94\mathrm{e}^{-0.027(\mathrm{LWG}+50)}$

Non-breeder mortality $(\%) = 2 + 88\mathrm{e}^{-0.03(\mathrm{LWG}+50)}$

Fertility $(\%) = 15 \cdot 6 + 0 \cdot 488 \mathrm{LWG}$

Fertility includes survival to the weaner stage (i.e. the ratio of calves weaned per 100 breeders) and a maximum fertility of 80% is imposed. We assumed bull numbers were maintained at 4% of the breeding herd (MacLeod, Ash & McIvor 2004).

DINGO MODEL

We based the dingo model component on the interactive dingo–kangaroo model developed by Choquenot & Forsyth (2013), but modified it to include calves as prey for dingoes, as well as an alternative (non-herbivorous) prey source to account for the generalist dingo diet. We adopted Type II, ratio-dependent functional responses for dingoes (prey killed dingo^{-1} day^{-1}) on calves (g_c), kangaroos (g_k) and alternative prey (g_a):

$$g_c = \frac{a_k N_c}{(P + a_k N_c h_c + a_k N_k h_k + a_{alt} N_{alt} h_{alt})}$$

$$g_k = \frac{a_k N_k}{(P + a_k N_c h_c + a_k N_k h_k + a_{alt} N_{alt} h_{alt})}$$

$$g_{alt} = \frac{a_{alt} N_{alt}}{(P + a_k N_c h_c + a_k N_k h_k + a_{alt} N_{alt} h_{alt})}$$

where subscripts c, k and alt refer to calves, kangaroos and the alternative prey, N is the density of prey, and P is the density of predators (Fig. 3). The attack rate a is the instantaneous rate of predation per predator and the handling time h is the time taken per prey killed (d dingo^{-1} prey^{-1}).

We constructed the default metamodel parameterization by first deriving a handling time for kangaroos (h_k) of 2·96 (Shepherd 1981). We assumed that the difference in handling times between calves and kangaroos was directly proportional to their relative mass (m_c/m_k) (Garrott *et al.* 2007). We then iteratively set the attack rate of dingoes on kangaroos ($a_k = 0.0015$) to generate a realistic functional response (g_k) when no other prey were in the system. Initially, we assumed that dingoes were equally likely to attack calves as kangaroos, which we consider conservative with respect to the possible benefits of this predator.

We assumed that alternative prey items had an average mass $m_{alt} = 2$ kg and were present at a constant density $N_{alt} = 1$ ha^{-1}. The handling time h_{alt} was derived so that, when no other prey was available and dingo density was low (close to zero), the daily rate of alternative prey consumption was sufficient to produce a stable dingo population, thereby preventing the extinction of dingoes when prey was scarce. The default parameterization set a_{alt} such that a maximum of 50% of that requirement could be met by alternative prey when dingoes were at carrying capacity.

We used a numerical response for dingoes modified from Choquenot & Forsyth (2013):

$$r_d = \begin{cases} r_{min,d} + (r_{max,d} - r_{min,d})(1 - e^{-\bar{I}_d/d_d}), & r_{min,d} + (r_{max,d} - r_{min,d})(1 - e^{-\bar{I}_d/d_d}) < 0 \\ [r_{min,d} + (r_{max,d} - r_{min,d})(1 - e^{-\bar{I}_d/d_d})][1 - (P/K_d)^{\theta}], & r_{min,d} + (r_{max,d} - r_{min,d})(1 - e^{-\bar{I}_d/d_d}) < 0 \end{cases}$$

where r_d is the annual population growth rate, $r_{min,d}$ and $r_{max,d}$ are the minimum and maximum population growth rates for dingoes, d_d is the demographic efficiency that controls the shape of the numerical response, and $\bar{I}_d$ is the average daily intake (kg dingo^{-1} day^{-1}) by dingoes. Rather than estimate d_d directly, we estimated that an average intake of 1·75 kg dingo^{-1} day^{-1} was required for a stable dingo population (i.e. for $r_d = 0$) and then set d_d accordingly (see Appendix S1, Supporting information). The equations above account for density dependence when the population growth rate is positive due to the theta-logistic term $1 - (P/K_d)^{\theta}$, in which K_d is the carrying capacity for dingoes (individuals ha^{-1}) and θ is the shape parameter.

ECONOMIC MODEL FOR ENTERPRISE

We used a simplified version of MacLeod, Ash & McIvor's (2004) economic model to quantify the gross-earnings margin from cattle production for the simulated enterprise (see Appendix S1, Supporting information). First, we calculated the gross animal revenue as:

Gross animal revenue = total live weight of sale animals (kg)
× price per kg

The gross animal cost was then calculated as:

Gross animal cost = (bull + husbandry + marketing costs)
+ dingo baiting costs

The gross margin per hectare is then the difference between gross animal revenue and cost, divided by the station area.

We also examined scenarios where landholders controlled dingo populations to a certain percentage of the dingo densities derived from simulations with no poison baiting. To estimate the associated costs, we first assumed that dingo density could be reduced by 100% (i.e. to an ecologically negligible density) as a result of the annual distribution of DOGGONE® 1080 baits across the station at a density of 0·1 baits ha^{-1} (as recommended by the manufacturer, www.animalcontrol.com.au/dog-baits.htm). We then assumed a linear relationship between the expenditure on dingo baiting and the proportional reduction in dingo density.

SIMULATION STUDIES

Scenario testing using the default parameterization

We initially conducted metamodel simulations using the default parameterization for three scenarios: (i) cattle only, (ii) cattle and kangaroos and (iii) both herbivores plus top-down control by dingoes (i.e. no dingo baiting). For each scenario, we investigated a range of fixed stocking strategies quantified in terms of adult cattle equivalents (AE), where one equivalent reflects feeding by a 455 kg steer, because it remains general practice for pastoralists to adhere to relatively fixed stocking densities (MacLeod, Ash & McIvor 2004). We quantified the expected consequences of dingoes for rangeland ecology (mean annual pasture biomass and kangaroo density) as well as enterprise performance (mean annual LWG and gross margin per hectare) over the 100-year simulation time frame. We then modified the third scenario above to account for the population-level and economic impacts of different dingo-baiting regimes and different contributions of alternative prey to the diet of dingoes. Finally, since dingo populations bolstered by alternative prey might kill many calves in years when alternative prey becomes scarce, we tested a stochastic scenario in which random environmental catastrophes caused a reduction of alternative prey density by 95%, occurring with an average frequency once every 5 years.

Sensitivity analysis

To investigate whether the scenarios tested above produced results that were robust to different model parameterizations, including site-specific GRASP parameter and climatic input files, we did a thorough sensitivity analysis on the key model inputs (Table 1). To cover the multi-dimensional parameter space thoroughly, we generated 10 000 distinct parameter sets using Latin hypercube sampling, implemented using the R package lhs (Carnell 2009). We analysed the sensitivity analysis output with boosted regression trees (BRT) using functions in the R package

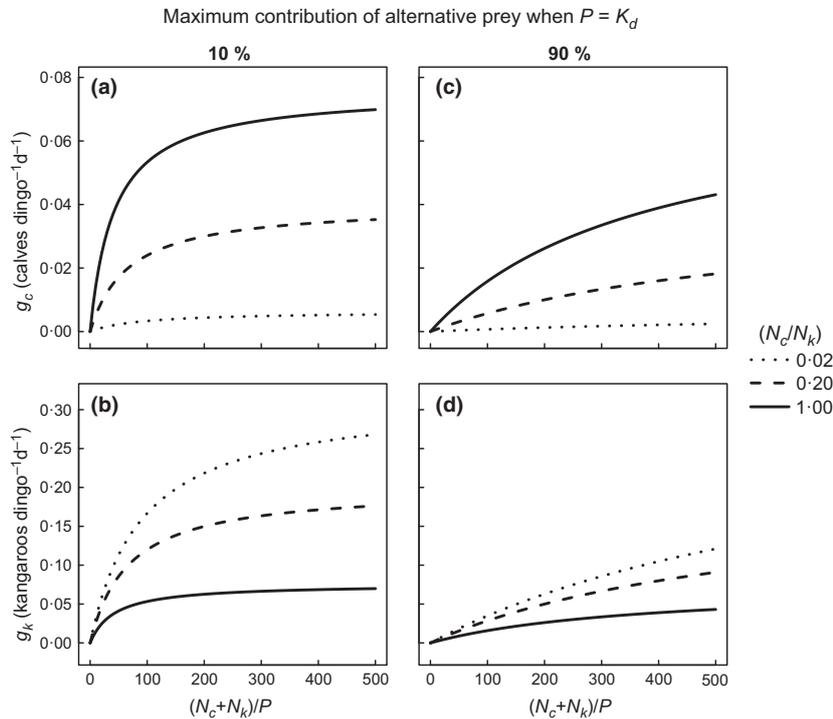Maximum contribution of alternative prey when $P = K_d$

Fig. 3. Functional responses of dingoes on calves and kangaroos with low (a, b) and high (c, d) alternative prey availability. These Type II, ratio-dependent responses are illustrated for different ratios of calf to kangaroo density (N_c/N_k) as a function of the ratio of total herbivore density ($N_c + N_k$) to dingo density (P).

dismo (Hijmans *et al.* 2013). BRT can fit nonlinear relationships and automatically handle interactions between predictors, so this technique is particularly useful for exploring the output from simulation studies (Prowse *et al.* 2013). We fit the BRT models using a Gaussian error, a learning rate of 0·01, a bag fraction of 0·75 and a tree complexity of 5.

Results

Our simulations demonstrated that the top-down influence of dingoes should improve herbivore control and pasture biomass and therefore provide financial benefits for cattle stations in the Australian rangelands (Fig. 4). In the absence of an apex predator, total grazing pressure was relatively insensitive to stocking density because, at low cattle densities, the reduction in livestock grazing was largely offset by kangaroos (Fig. 4b,c). For example, in simulations including cattle and kangaroos only, a reduction in cattle density from 0·05 to 0·01 adult equivalents ha^{-1} produced little improvement in enterprise performance: an increase in total standing dry matter from 328 to 341 kg ha^{-1} (Fig. 4a), a reduction in the pasture utilization rate from 40·2 to 36·3% (Fig. 4c) and an increase in cattle LWG from 120 to 126 kg individual^{-1} year^{-1} (Fig. 4d). These minor gains were restricted by the concurrent increase in kangaroo density from 0·093 to 0·291 ha^{-1}.

Including dingoes in the metamodels initiated a trophic cascade that increased pasture biomass and LWG due to a reduction in kangaroo density (Fig. 4). Assuming a typical stocking density of 0·03 adult equivalents ha^{-1}, for example, dingo control of kangaroos increased total standing dry matter from 333 to 383 kg ha^{-1} (Fig. 4a), reduced kangaroo density from 0·174 to 0·022 kangaroos

ha^{-1} (Fig. 4b), lowered the pasture utilization rate from 39·1 to 25·4% (Fig. 4c) and increased cattle LWG from 121 to 147 kg individual^{-1} year^{-1} (Fig. 4d). The positive influence of dingoes on pasture biomass and the utilization rate was greatest at low stocking densities (Fig. 4a,c) because livestock grazing at high cattle densities restricted the kangaroo population in any case (Fig. 4b).

There was no peak in simulated profits over the range of stocking densities tested, reflecting the difficulty of simulating the long-term effects of heavy grazing (see the Discussion). Nevertheless, the net influence of dingoes on enterprise gross margins was positive, indicating that the beneficial influence of dingoes on pasture biomass (through herbivore suppression) outweighed the negative effects of predation on calves (Fig. 4e). Relative to metamodels with uncontrolled kangaroo populations, the net benefit of dingoes was $0·83 ha^{-1} at a stocking density of 0·03 adult equivalents ha^{-1} (Fig. 4e). However, this financial benefit weakened when stocking density was too low to take advantage of the trophic cascade (e.g. a benefit of $0·32 ha^{-1} at a stocking density of 0·01 AE ha^{-1}) or so high that heavy grazing by cattle suppressed the kangaroo population and dingo control was made redundant (e.g. an increase of $0·38 ha^{-1} at a stocking density of 0·05 AE ha^{-1}) (Fig. 4a,e). Predation of kangaroos by dingoes also reduced the inter-annual variability of pasture utilization rates (Fig. 4c), thereby producing more stable annual LWG and gross margin values (Fig. 4d,e), particularly for low stocking densities. For scenarios with (or without) dingo predation of kangaroos and a cattle density of 0·03 adult equivalents ha^{-1}, for example, the widths of 95% confidence bands around the mean model outputs were as
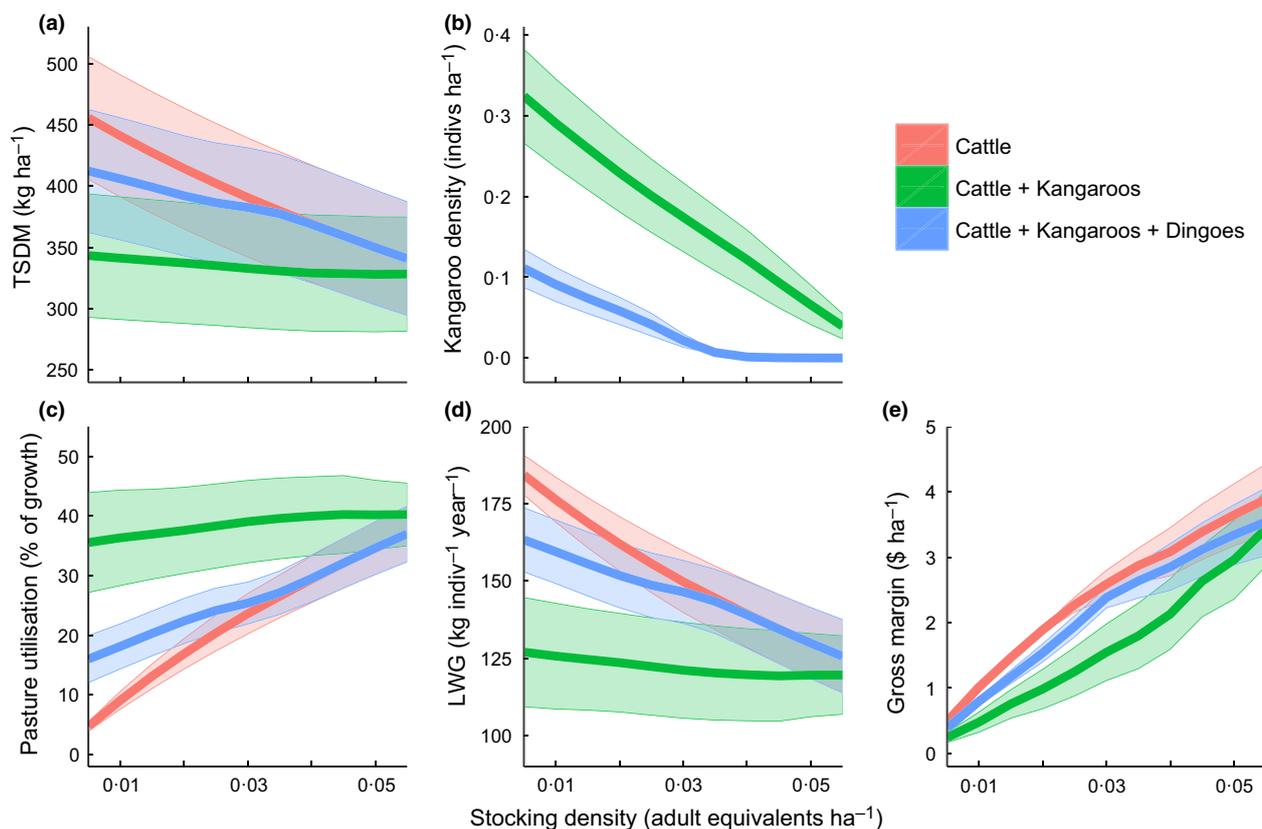
Fig. 4. Mean metamodel output (±95% confidence intervals estimated from the 100-year simulation time frame) using the default parameterization (i.e. using the GRASP parameterization for Fowlers Gap). Results are shown for (a) total standing dry matter (TSDM), (b) kangaroo density, (c) pasture utilization by herbivores, (d) cattle live-weight gain (LWG) and (e) gross margin per hectare for the simulated enterprise.

follows: 7·0 (13·8)% for the pasture utilization rate, 20·4 (31·0) kg individual^{-1} year^{-1} for cattle LWG and $0·32 ($0·87) ha^{-1} for the enterprise gross margin.

Importantly, these benefits were robust to assumptions regarding the availability of alternative (non-herbivorous) prey and different dingo-baiting regimes (Fig. 5). The dingo-mediated trophic cascade was strongest (i.e. the positive effect on pasture biomass was greatest) when kangaroos and calves were assumed to constitute the primary prey for dingoes and the contribution of alternative prey was small (Fig. 5a). In this case, simulated dingo density remained low due to prey scarcity, but calf losses could be high (up to 15%) (Fig. 5i). As the contribution from alternative prey was increased, the positive influence of dingoes on pasture biomass weakened because fewer kangaroos were killed by dingoes (Fig. 5e–g), and similarly, the percentage of calves lost to dingoes also decreased (Fig. 5n–o) despite the higher densities of dingoes supported (Fig. 5i–k).

Gross margins for the simulated enterprise were consistently greater for scenarios with no dingo control than those with complete removal of dingoes (Fig. 5u–w). However, profit margins could be slightly improved by a partial (50%) reduction in dingo density if stocking density was high and the contribution of alternative prey for

dingoes was low (Fig. 5u,v). Under these assumptions, few dingoes were required to reduce kangaroos to negligible densities (Fig. 5e,f), whereas higher dingo densities incurred the costs of calf predation (Fig. 5m,n) and produced no additional benefit for pasture biomass (Fig. 5a, b). When the availability of alternative prey was decreased by simulated periodic catastrophes, calf predation increased slightly (Fig. 5p), but the trophic cascade strengthened due to increased kangaroo predation (Fig. 5p), and the net effect was increased enterprise profits (Fig. 5x).

The sensitivity analysis demonstrated that pasture biomass was particularly responsive to, and inversely correlated with, the intensity of dingo baiting and the minimum and maximum population growth rates of kangaroos, since these affected the strength of trophic cascade (Fig. 6a,b). In particular, the improvement in pasture biomass due to dingoes was reduced substantially when the maximum population growth rate for kangaroos was small (<0·3, Fig. 6b). Importantly, trophic cascades due to dingo predation emerged from all three site-specific GRASP and climatic parameter sets we tested, despite primary productivity differences among sites (Fig. 6b[iv]). Total standing dry matter typically simulated for the three sites (Fig. 6b[iv]) differed from that reported in Richards
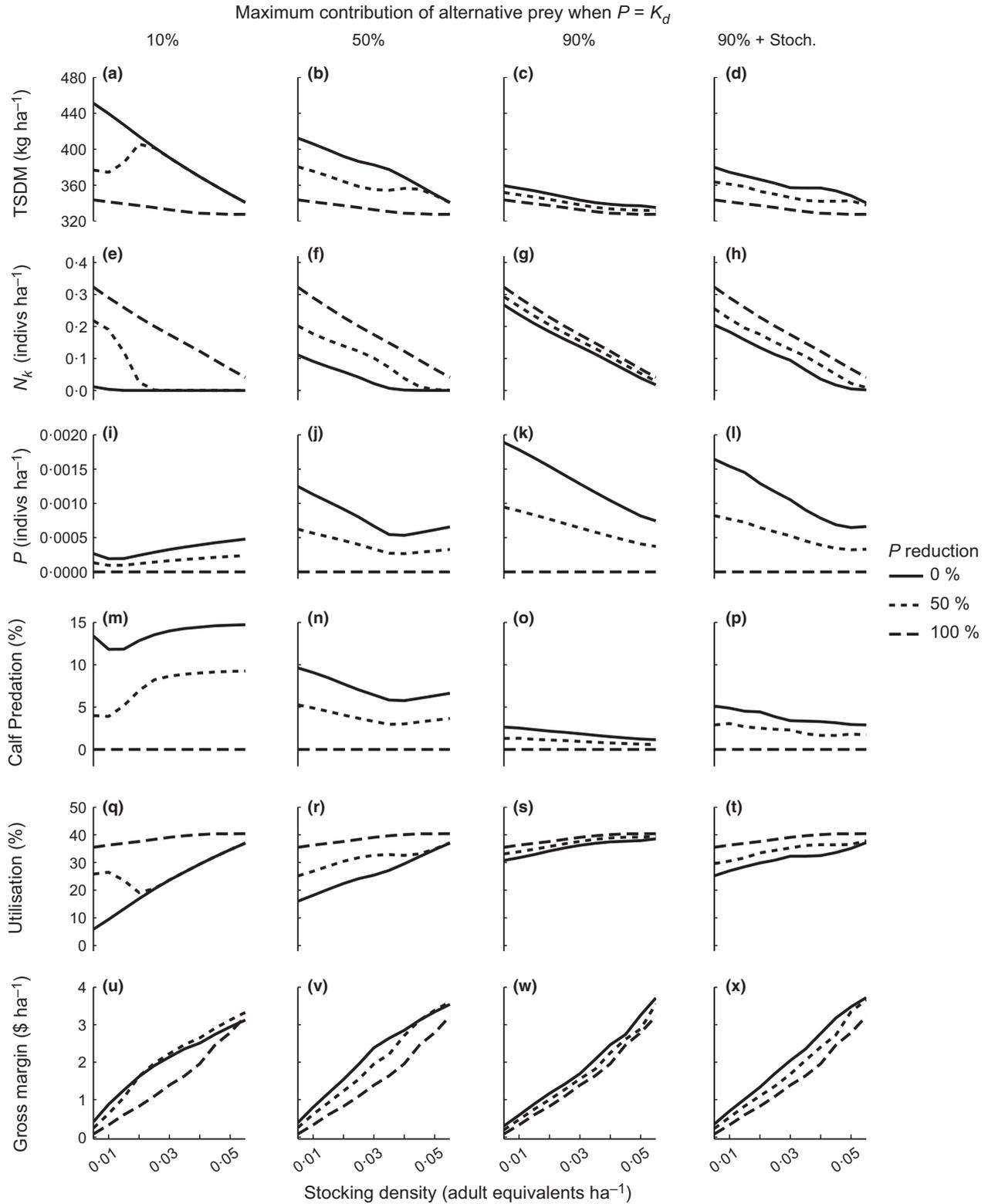
Maximum contribution of alternative prey when $P = K_d$

Fig. 5. The effect of dingo baiting and the availability of alternative prey on the ecological and economic performance of the simulated enterprise. Mean results over the 100-year simulation time frame are shown for the default parameterization for: (a–d) total standing dry matter (TSDM), (e–h) kangaroo density (N_k), (g–l) dingo density (P), (m–p) the percentage of calves predated by dingoes, (m–o) the total utilization of annual pasture growth by cattle and kangaroos and (p–r) gross margin per hectare. Dingo baiting was simulated as a 50 or 100% reduction in dingo density. Columns represent different assumptions regarding the availability of alternative prey for dingoes. The final column also includes stochasticity in the availability of alternative prey (i.e. a reduction of alternative prey density by 95% occurring with average frequency once every 5 years to simulate lean years) and presents the means from 10 stochastic replicates.

et al. (2001) because we included kangaroo grazing, made different assumptions regarding stocking densities and adopted a longer 100-year climatic period for simulations.

Stocking density was the most important determinant of simulated gross margins (Fig. 6c,d). Parameters governing the strength of dingo-mediated trophic cascades also had a strong impact on simulated profits, while parameters controlling calf predation by dingoes were less influential (Fig. 6c,d). Again, the positive net influence of dingoes on enterprise profit was not dependent on site-specific parameterizations. Partial dependency plots for all metamodel inputs that support these conclusions are included in Figs S1 and S2 of the Supporting information.

Discussion

Although apex predators perform critical ecological functions (Estes *et al.* 2011; Ripple *et al.* 2014), the conservation of terrestrial carnivores is hampered by conflicts between predators and livestock production (Mazur & Asah 2013; Johnson 2014a). Dingoes have been controlled throughout the Australian rangelands for over a century because of the threat they are perceived to pose to the profits of graziers. In contrast to this prevailing view, our simulations suggest that the restoration of dingoes as an effective apex predator should have ecological and financial benefits for cattle rangelands.

The native grasslands of south-eastern Australia comprise some of the most modified ecoregions on Earth (Hoekstra *et al.* 2005), and overgrazing has contributed to the systematic degradation of these landscapes. Experimental fieldwork and modelling studies suggest that the most sustainable stocking densities for native pastures are those that limit pasture utilization to approximately 20–30% of annual growth (Hunt *et al.* 2014). In the absence of an apex predator, such utilization rates might be difficult to realize – as our models demonstrate, any reduction in livestock grazing pressure achieved at such low stocking densities is likely to be offset largely by other herbivores (Fig. 4c). This simulated result validates the attitudes of pastoralists who see little incentive in reducing stocking densities when wild herbivore populations cannot be controlled (Johnston *et al.* 2000).

In contrast, our metamodels show that predation of native herbivores by dingoes is expected to induce a trophic cascade that improves the standing biomass of pastures. Simulated trophic cascades were strongest at low stocking densities (when kangaroo densities were high if dingoes were absent), but attenuated at high stocking densities because overgrazing suppressed kangaroo populations. This suggests that where dingo populations are allowed to persist there will be greater incentive for graziers to conserve pasture biomass by maintaining low stock density. As well as increasing pasture yield, low stocking densities result in improved pasture condition (e.g. by increasing the abundance and cover of perennial grasses), reduced erosion potential, increased retention of native vegetation regrowth that provides habitat for small vertebrates and invertebrates, reduced greenhouse gas emissions and improved water infiltration (Bradshaw *et al.* 2013; Hunt *et al.* 2014).

Stocking density was the primary determinant of enterprise gross margins in our simulations (Fig. 4e, Fig. 6) as demonstrated by several other experimental and modelling studies (Johnston *et al.* 2000; MacLeod, Ash & McIvor 2004). There was no obvious peak in simulated margins; rather, profits were largest at the highest stocking densities because declines in per capita LWG were compensated by the increased size of the cattle herd (Hunt *et al.* 2014). However, pasture utilization rates simulated for the Fowlers Gap site exceeded 30% for all stocking densities above about 0·04 adult equivalents ha^{-1} (Fig. 4). In reality, livestock densities above this threshold probably exceed the long-term carrying capacity of these semi-arid environments. Although 'dynamic' pasture options have been developed within GRASP to account for the long-term effects of heavy grazing (e.g. Scanlan, MacLeod & O'Reagain 2013), these options were parameterized for sites in northern Queensland and they did not yield sensible results when tested for the three New South Wales sites we considered (results not shown).

At intermediate stocking densities around 0·03 adult equivalents ha^{-1}, trophic cascades initiated by dingoes improved cattle growth, survival and fertility rates, thereby more than compensating for calf losses due to predation and increasing gross margins. Enterprise profits were reduced in scenarios in which dingoes were allowed substantial access to alternative prey sources (Fig. 5u–x), despite smaller percentage calf losses, due to attenuation of the trophic cascade (i.e. where dingo-driven control of kangaroos was weakened by substantial reliance on other prey sources) (Choquenot & Forsyth 2013). However, the simulated net effect of dingoes on economic returns was always positive for intermediate stocking densities, even for scenarios that simulated periodic crashes of the alternative prey source due to random environmental variation (Fig. 5). Field studies indicate that predation of calves by dingoes is greatest during periods of prey shortage such as droughts (Allen 2014), and similarly, calf losses in our simulations were greatest when dingoes had little access to alternative prey.

Dingoes can engage in surplus killing of livestock (Short, Kinnear & Robley 2002) which was not permitted in our models, so our simulations might underestimate the true economic impact of calf predation. However, simulated calf losses could be large (>15%) in models for which dingoes were left unbaited, which is within the upper range of empirical estimates (Holroyd 1987; Allen 2014). Further, our models might actually overestimate calf losses because we allowed calves to be killed from birth to weaning, whereas empirical evidence suggests that most calf predation occurs within the first few weeks of life (Allen 2014).
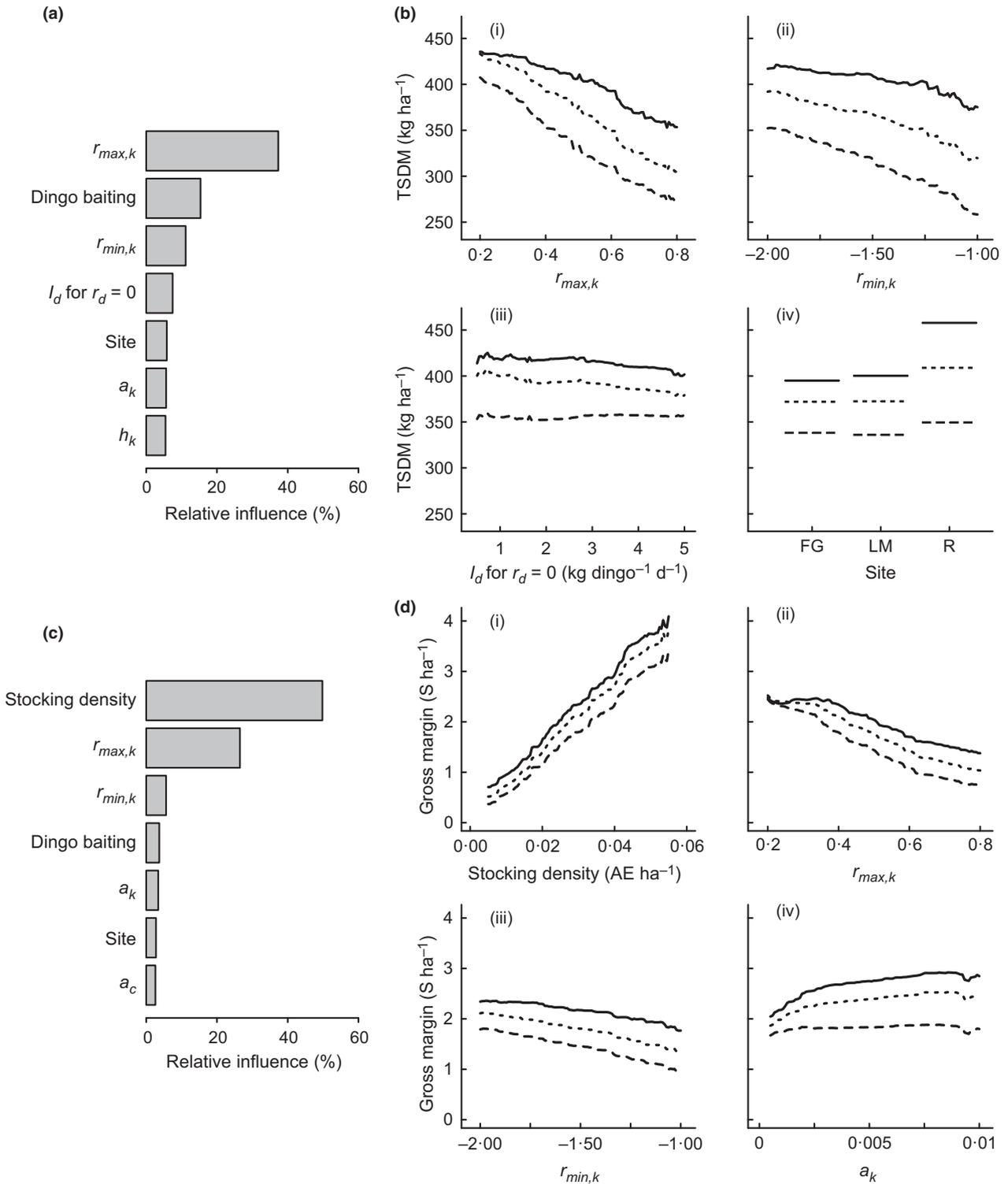
Fig. 6. Boosted regression tree (BRT) summary of the metamodel sensitivity analysis for two simulation outputs: (a, b) total standing dry matter (TSDM) and (c, d) gross margin per hectare. Relative influence metrics from the BRT analyses are shown for the simulation parameters to which each output was most sensitive (a, c). Partial dependency plots (b, d) are also shown in each case for the four most important parameters at three dingo-baiting intensities simulated as a 0, 50 and 100% reduction in dingo density (solid, short-dashed and long-dashed lines, respectively). These plots assume all unplotted parameters are set at their mean values (i.e. the average of all values used in the sensitivity analysis). Parameter abbreviations are as detailed in Table 1.

Our models identified a restricted set of conditions under which some dingo control (i.e. a reduction of dingo density by <100%) might have financial benefits.

Specifically, when stocking density was high, the density of kangaroos was low, so if dingo density exceeded that required to control kangaroos, some baiting could

produce small economic gains (Fig. 5u,v). This result is conditional on our assumption that baiting once per year is always sufficient to control dingo populations successfully. In contrast, dingo baiting is regarded as necessary at least twice yearly in many rangeland regions. Further, some evidence suggests that baiting can actually increase livestock losses by disrupting dingo pack structures and permitting breeding by non-dominant dingo pairs (Eldridge, Shakeshaft & Nano 2002). On balance, therefore, we consider that even under the aforementioned conditions, our models provide little evidence to support dingo control in cattle rangelands.

Although empirical research could best elucidate the ecological effects of trophic regulation by dingoes, the large temporal and spatial extent necessary for such an experimental programme renders this logistically and financially infeasible (Glen *et al.* 2007). A multi-species simulation-based approach provides one alternative, but our metamodels are necessarily a simplification of reality and there are several assumptions that should be made explicit. First, depauperate ecological systems with low herbivore diversity are most likely to exhibit a trophic cascade when exposed to an apex predator, because fewer grazing species are available to compensate for the predation of preferred herbivore prey (Duffy 2002). We simplified the rangeland ecosystem to three main species (dingoes, kangaroos, cattle), which neglects the contribution of other native and feral herbivores. In particular, invasive rabbits *Oryctolagus cuniculus* are capable of rapid population growth during periods of favourable rainfall (Pech & Hood 1998) and might attenuate the expected trophic cascade due to dingoes in some Australian regions. Second, our models do not include human harvesting of kangaroos that, where implemented, is governed by annual quotas of up to 10–20% of estimated kangaroo population sizes. Third, we used equations governing cattle LWG, mortality and fertility rates that were parameterized in Queensland; ideally, these equations should be calibrated specifically for the NSW sites we tested. Finally, we stress that our results are specific to cattle enterprises only, whereas mixed-farming strategies that include both cattle and sheep are common in many rangeland areas. Dingoes can kill sheep more easily than calves, so if dingoes were restored to regions where sheep farming is common (i.e. inside [south of] the dingo fence), additional measures such as the use of guardian animals might be required to protect flocks (van Bommel & Johnson 2012).

In the absence of top-down predatory control, the contribution of non-domestic herbivores to total grazing pressure is substantial in Australia; for example, up to 30–40% of pasture growth in south-western Queensland (Johnston *et al.* 2000). Our simulations demonstrate that trophic cascades initiated by dingoes killing native herbivores are expected to be strong enough to improve the biomass of native pastures and, as a consequence, the gross margins of cattle enterprises. These results not only challenge the conventional perception of dingoes as an economically damaging pest species that must be controlled, they also contribute quantitative estimates of the expected ecological and financial benefits of this apex predator. However, our study represents just the first step towards quantifying the ecosystem services that could be provided by dingo restoration. For example, our metamodels could potentially be expanded to include the landscape-scale impacts of dingoes on rangeland carbon emissions and erosion regulation. Spatial metamodels could also be developed to examine the source-sink dynamics resulting from the dispersal of dingoes from restored regions and the impact of such a strategy on sink areas. Finally, frameworks for quantifying the cultural services provided by dingoes, such as the conservation of small native mammals and birds through the suppression of invasive mesopredators (Letnic *et al.* 2009; Wallach *et al.* 2010), could also be implemented (Butler *et al.* 2013).

Acknowledgements

Data accessibility

Data are not archived because this manuscript does not use data. Please see Appendix S1 (Supporting information) for full details of the model structure and parameterization.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Partial dependency plots from the sensitivity analysis for total standing dry matter.

Fig. S2. Partial dependency plots from the sensitivity analysis for gross margin per hectare.

Appendix S1. Supplementary methods.