

Shrub encroachment is linked to extirpation of an apex predator

Christopher E. Gordon^{*,1,2,3}, David J. Eldridge⁴, William J. Ripple⁵, Mathew S. Crowther⁶, Ben D. Moore¹ and Mike Letnic^{2,4}

¹Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2751, Australia; ²Centre for Ecosystem Science, University of New South Wales, Sydney, NSW 2052, Australia; ³Centre for Environmental Risk Management of Bushfires, University of Wollongong, Wollongong, NSW 2522, Australia; ⁴School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia; ⁵Global Trophic Cascades Program, Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA; and ⁶School of Life and Environmental Sciences, University of Sydney, Sydney, NSW 2006, Australia

Abstract

1. The abundance of shrubs has increased throughout Earth's arid lands. This 'shrub encroachment' has been linked to livestock grazing, fire-suppression and elevated atmospheric CO₂ concentrations facilitating shrub recruitment. Apex predators initiate trophic cascades which can influence the abundance of many species across multiple trophic levels within ecosystems. Extirpation of apex predators is linked inextricably to pastoralism, but has not been considered as a factor contributing to shrub encroachment.

2. Here, we ask if trophic cascades triggered by the extirpation of Australia's largest terrestrial predator, the dingo (*Canis dingo*), could be a driver of shrub encroachment in the Strzelecki Desert, Australia.

3. We use aerial photographs spanning a 51-year period to compare shrub cover between areas where dingoes are historically rare and common. We then quantify contemporary patterns of shrub, shrub seedling and mammal abundances, and use structural equation modelling to compare competing trophic cascade hypotheses to explain how dingoes could influence shrub recruitment. Finally, we track the fate of seedlings of an encroaching shrub, hopbush (*Dodonaea viscosa angustissima*), during a period optimal for seedling recruitment, and quantify removal rates of hopbush seeds by rodents from enriched seed patches.

4. Shrub cover was 26–48% greater in areas where dingoes were rare than common. Our structural equation modelling supported the hypothesis that dingo removal facilitates shrub encroachment by triggering a four level trophic cascade. According to this model, increased mesopredator abundance in the absence of dingoes results in suppressed abundance of consumers of shrub seeds and seedlings, rodents and rabbits respectively. In turn, suppressed abundances of rodents and rabbits in the absence of dingoes relaxed a recruitment bottleneck for shrubs. The results of our SEM were supported by results showing that rates of hopbush seedling survival and seed removal were 1.7 times greater and 2.1 times lower in areas where dingoes were rare than common.

5. Our study provides evidence linking the suppression of an apex predator to the historic encroachment of shrubs. We contend that trophic cascades induced by apex predator extirpation may be an overlooked driver of shrub encroachment.

Key-words: arid lands, dingo, fire, herbivore, mesopredator release hypothesis, shrub encroachment, top predator, trophic cascade

*Correspondence author. E-mails: gordonc@uow.edu.au and cgor6229@hotmail.com

Introduction

Recent studies show that apex predators play a pivotal role in the functioning of ecosystems and that their importance in shaping ecological communities has been enormously underestimated (Estes *et al.* 2011; Ripple *et al.* 2014). Apex predators' suppressive, typically nonlinear effects on populations of herbivores and smaller predators (mesopredators) can have cascading, indirect effects on species at lower trophic levels. The disruption to ecosystems caused by the widespread removal of apex predators, such as big cats, canids and sharks, can shift ecosystems to alternate states across vast areas due to over-abundant mesopredators and herbivores regulating trophic pathways (Estes *et al.* 2011; Colman *et al.* 2014).

Numerous studies have demonstrated the existence of trophic cascades whereby the biomass of plants palatable to herbivores is depleted in areas where apex predators are absent due to an increase in herbivore abundance and impact (Terborgh *et al.* 2001; Beschta & Ripple 2009). A similar cascade of effects is predicted by the mesopredator release hypothesis (MRH). According to the MRH, reduced abundance of top-order predators results in an increase in the abundance and predatory impact of smaller mesopredators (Ritchie & Johnson 2009). Consequently, the prey of mesopredators may decline in abundance in the absence of apex predators (Ritchie & Johnson 2009).

Shrub encroachment is a global phenomenon characterised by an increase in cover and density of mostly indigenous woody plants at the expense of grasses, particularly in arid and semiarid grasslands (van Auken 2000; Eldridge *et al.* 2011). Encroachment has increased dramatically over the past century, but its drivers are not well understood. Encroachment is thought to result from complex interactions among grazing, burning and increased atmospheric concentrations of CO₂ altering the competitive relationships between woody seedlings and grasses (Briggs *et al.* 2005; Knapp *et al.* 2008).

The livestock grazing model for shrub encroachment posits that sustained overgrazing by livestock depletes aboveground grass biomass, reducing competition for resources between grasses and shrub seedlings and hence facilitates the recruitment of shrubs (Roques, O'Connor & Watkinson 2001). Livestock grazing also reduces fuel loads and consequently the frequency and intensity of fires which favour grasses over shrubs. Thus, by suppressing fire, grazing can further promote the recruitment and survival of shrubs (Scholes & Archer 1997).

Existing models to explain shrub encroachment have not considered whether vertebrate apex predators could play an indirect role in determining shrub abundance through their effects on consumers of shrubs. Extirpation of large mammalian carnivores is a world-wide phenomenon linked to livestock husbandry because people kill predators in order to protect livestock (Woodroffe

2000). The removal of large carnivores has the potential to influence shrub population dynamics because it frequently results in changes in the abundance and impact of consumers and dispersers of grasses, shrubs and their seeds such as large herbivores, burrowing herbivores and rodents (Weltzin, Archer & Heitschmidt 1997; Browning & Archer 2011; Davidson, Detling & Brown 2012).

In this study, we ask if multilevel trophic cascades (Box 1), triggered by the removal of Australia's largest terrestrial predator, the dingo (*Canis dingo*), could be a driver of shrub encroachment. Specifically, we use a sequence of aerial photographs spanning a 51-year period to examine the effect that dingo extirpation has had on shrub cover on either side of the Dingo Fence in the Strzelecki Desert, Australia. Extending over 5000 km, this fence excludes dingoes from its eastern and southern sides and thus provides a rare, large-scale experiment to examine the effects that top predators have on ecosystems (Letnic, Ritchie & Dickman 2012). Because our analyses of aerial photographs linked dingo suppression to marked

Box 1. Our *a priori* hypotheses to explain how dingoes may influence the abundance of shrub seedlings

Mesopredator cascade hypothesis: The suppression of consumers of shrub seeds and seedlings by foxes and cats in the absence of dingoes facilitates an increase in shrub density. This occurs because dingo removal results in an increase in fox and cat abundance owing to a reduction in direct killing and competition (Moseby *et al.* 2012). In turn, irrupting foxes and cats suppress the abundances of rabbits and mice through predation (Letnic, Crowther & Koch 2009). Rabbits consume shrub seedlings and mice consume shrub seeds (Auld 1995; Gordon & Letnic 2015). Where dingoes have been removed, decreased consumption on seedlings and seeds of shrubs by rabbits and mice, respectively, facilitates an increase in shrub recruitment and abundance.

Herbivore cascade hypothesis: Shrub density increases in the absence of dingoes because suppression of grasses by grazing herbivores facilitates an increase in shrub density. This occurs because shrub seedlings, which are less palatable to grazers than grasses, are released from competition with grasses owing to herbivores' suppressive effects on grass abundance (van Auken 2000). The removal of dingoes exacerbates herbivores' effects on grasses because in the absence of dingoes pastoralists increase their stocking rates and kangaroo populations irrupt (Letnic, Crowther & Koch 2009; Letnic, Ritchie & Dickman 2012). Where dingoes have been removed, decreased competition from grasses and decreased mortality of shrubs and shrub seedlings facilitates shrub recruitment.

increases in shrub cover, we then quantified contemporary patterns of mammal and shrub seedling abundance at study areas situated on either side of the Dingo Fence and used structural equation modelling (SEM) to compare hypotheses to explain how dingoes might influence shrub cover and the abundance of shrub seedlings (Box 1). To corroborate the patterns generated by our aerial photograph and SEM analyses, we tracked the survival of seedlings of the dominant encroaching shrub species, *Dodonaea viscosa angustissima* (hopbush) over a 32-month period and manipulated the density of hopbush seed in the soil to assess seed removal by rodents.

Materials and methods

The study was conducted in the region surrounding the Dingo Fence in the Strzelecki Desert (Fig. 1). To prevent immigration of dingoes into New South Wales (NSW) and thus reduce their attacks on sheep (*Ovis aries*), the NSW state government constructed an c. 2 m tall dingo-proof fence along the NSW/South Australia (SA) border and NSW/Queensland (Qld) border between 1914 and 1917 (Fig. 1; Letnic & Dworjanyn 2011). The boundaries of NSW with Qld and SA along the meridians 29°S

and 141°E, respectively, were established by decree during the 19th century prior to colonisation of the region by European settlers (King William Henry the Fourth 1836). Thus, the borders are arbitrary administrative boundaries that do not reflect geographical features that may be expected to influence shrub or mammal abundance.

Dingoes are rare on the NSW ('inside') side of the fence where intensive control using poison baiting, trapping and shooting have been carried out since domestic livestock grazing commenced in the second half of the 19th century (Fleming *et al.* 2001). Dingoes are common on the SA and Qld ('outside') sides of the fence where they are controlled only sporadically (Letnic, Crowther & Koch 2009). Suppression of dingoes in western NSW has induced a trophic cascade evidenced by a marked difference in mammal assemblages across the fence. Kangaroos (*Macropus* spp.) and red foxes (*Vulpes vulpes*) are more abundant inside the fence where dingoes are rare, while dingoes, rabbits (*Oryctolagus cuniculus*), rodents and grasses are more abundant outside the fence where dingoes are common (Letnic, Crowther & Koch 2009).

The dominant landforms in the Strzelecki desert are longitudinal, west-east trending sand dunes reaching 8 m in height. Mean annual rainfall in the study region decreases from north to south and ranges from 188 to 227 mm (Australian Bureau of

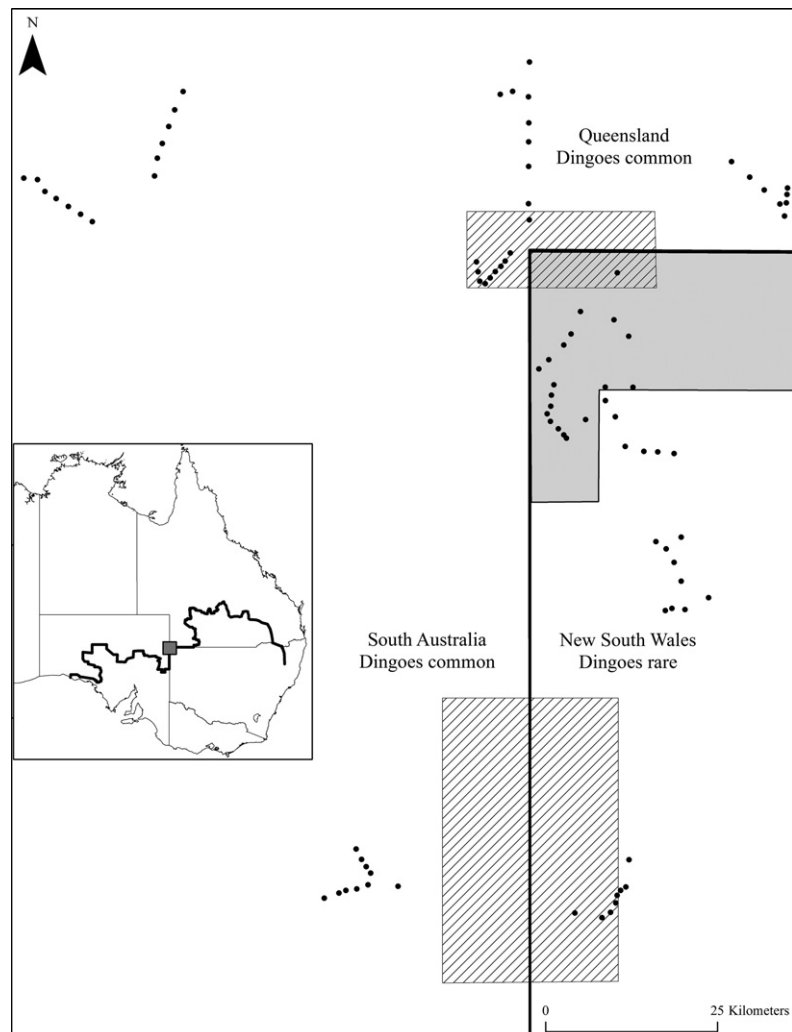


Fig. 1. Locations of the study areas in the Strzelecki Desert showing sites where historic shrub cover was assessed (diagonal lines within polygons; Fort Grey in the north and Hawker gate in the south) and sites where the contemporary patterns of hopbush seedling and consumer abundances were measured (black circles). Black lines represent the Dingo Fence. The grey polygon represents Sturt National Park. The insert map shows the location of the Dingo Fence (black line) and study area (grey square) in Australia.

Meteorology 2016). Vegetation on sand dunes is dominated by annual and perennial shrubs and inter-dunal swales are dominated by grasses and forbs.

Sheep were grazed at relatively high densities throughout the study area during the late 19th and early 20th century when dingo control was undertaken primarily by trapping and poisoning with strychnine and sheep were frequently shepherded. Following the erection of the dingo fence between 1914 and 1917 until the present day, sheep grazing has largely been restricted to areas situated 'inside' the dingo fence, due to the lower risk of dingoes attacking sheep (Letnic & Dworjanyn 2011). Historically, cattle have been grazed on both sides of the dingo fence (Letnic, Crowther & Koch 2009). Large areas not subject to commercial livestock grazing occur inside (Sturt National Park) and outside (vacant land in the northwest corner of the study area) the Dingo Fence (Fig. 1). Sturt National Park has not been grazed by livestock since 1972; however, dingoes are routinely killed in and around the park and are therefore rare.

HISTORICAL SHRUB COVER

We compared changes in shrub cover through time for areas where dingoes are historically rare (inside the Dingo Fence) and common (outside the Dingo Fence) at two separate locations, Hawker Gate (2770 sample units, defined below) and Fort Grey (2018 sample units; Fig. 1). The two locations fell within the same broad geological formation and vegetation type, but differed in their land-use. Cattle are grazed outside the fence at both locations, but sheep and cattle are grazed inside the fence at Hawker Gate, and no livestock are grazed inside the fence at Fort Grey (i.e. Sturt National Park). These land-use differences allowed comparisons of shrub cover between pastoral and non-pastoral areas inside the dingo fence. Such comparisons were not possible outside the Dingo Fence because no ungrazed areas occurred within the immediate sample area.

Shrub cover was assessed using monochromatic aerial photographs taken by government agencies in 1948, 1972, 1983 and 1999 (see Appendix S1, Table S1, Supporting Information for replication levels between sample areas). Aerial photographs were digitised at 800 dpi, homogenised to a 1:50 000 scale, and georeferenced through a first order rectification in ArcGIS (version 9.3; ESRI, Redlands, CA, USA). To estimate shrub cover, circular sample units (100 m diameter) were overlaid onto aerial photographs at regular 500 m intervals from a random location in the northwest corner. Shrub cover was calculated as the number of shrubs visible within each sample unit. Because shrubs mainly occur on sand dunes, and to ensure that replicate points were sampled from similar habitat types, we limited our sampling to sand dune areas (>30% of total coverage). Shrubs were readily distinguishable from understorey cover in aerial photographs (Appendix S1, Fig. S1). To minimise confounding owing to environmental variation, the sample units were always placed <15 km from the Dingo Fence, and repeated measures taken across the time-series were made from sample units within a 5 km diameter area.

For each sampling unit, we scored the following attributes hypothesised to influence shrub abundance for inclusion as predictor variables in generalized linear models (GLMs; Appendix S1, Table S2 shows predicted effects of variable on shrub cover): year of the photograph; distance to Dingo Fence; distance to closest artificial watering point (a proxy for historic

grazing activity; Landsberg *et al.* 2003); latitude; average annual rainfall in the previous 20 years; and the occurrence of fire within the last 20 years at the centroid of each sampling unit. Because historical information indicated that the intensity and efficiency of dingo control has increased over time (Allen & Sparkes 2001; Fleming *et al.* 2001), we included an interaction term between dingo presence (i.e. side of the Dingo Fence) and time in our models.

Maps of the distribution of artificial watering points were created using historical maps archived at the National Library of Australia. Average annual rainfall within the previous 20 years was assessed using annual gridded rainfall data obtained from the Australia Bureau of Meteorology (Australian Bureau of Meteorology 2016). Fire history maps were created for the entire sample period using aerial photographs (1948–1999), satellite imagery (1975–2012), archival maps held at the State Library of NSW and online fire-mapping resources (www.firenorth.org.au/nafi2/).

STATISTICAL ANALYSIS OF HISTORICAL SHRUB COVER

Continuous predictor variables were standardised to have a mean of 0 and standard deviation of 1. Spearman's rank correlation was used to assess collinearity between predictor variables. If the correlation between variables exceeded 0.7, then the two variables were considered proxies and one variable was removed from analyses (Zuur 2009). GLMs with a Poisson error distribution were used to assess the effects of predictor variables on shrub cover. We tested all combinations of predictor variables and ranked the fit of models using the Akaike's Information Criterion for small sample sizes (AICc; Burnham & Anderson 2002). Scaled coefficient strength and associated standard errors from GLMs were used to infer predictor variable influence within the best model. Residual and null deviance values were used to compare the fit of candidate GLMs (i.e. a candidate model is 'better' than the null model if it has a lower residual deviance value). Chi-squared values were used for statistical inference whereby: $\text{chi-squared} = \text{null deviance} - \text{residual deviance}$ with degrees of freedom ($\text{df} = \text{null deviance df} - \text{residual deviance df}$).

To account for spatial autocorrelation (SAC) within our data set, we used autocovariate models (10 km neighbourhood distance), which estimated the degree to which the response variable at any one site reflected the response variables at surrounding sites (Dormann *et al.* 2007). All GLMs included a distance-weighted SAC term. GLMs were conducted in the program R (R Development Core Team 2016). Spatial autocorrelation coefficients were generated using the package 'spdep' (spatial dependence; Bivand 2011).

CONTEMPORARY PATTERNS IN SHRUB SEEDLING AND MAMMAL ABUNDANCE

We quantified the abundances of shrub seedlings and shrubs, grasses, and mammals at 91 study sites spread on either side of the Dingo Fence over five sampling periods between May 2012 and June 2013 (see Appendix S2, Table S1 for replication levels among sampling occasions). The 1 ha sites were located on sand dunes adjacent to single-lane vehicle tracks and were >1 km (but normally >2 km) from artificial watering points. Sites were centred on dune crests and encompassed dune bottom, middle and top areas. Sampling occurred after a prolonged period of high

rainfall associated with the La Niña phase of the El Niño Southern Oscillation. Cumulative rainfall totals for the period between 2010 and the time of sampling were similarly high throughout the study area (Appendix S2, Table S1).

Because we were interested in identifying the effects that dingoes may have had on shrub seedling abundance and hence recruitment through 'mesopredator' and 'herbivore' cascade pathways (Box 1), we stratified sites across a range of contemporary grazing and dingo control regimes. These included sites with: sheep and cattle grazing where dingoes were rare (inside the Dingo Fence; $n = 22$); cattle grazing where dingoes were common (outside the Dingo Fence, $n = 43$); no livestock grazing where dingoes were rare (Sturt National Park inside the Dingo Fence; $n = 19$) and no livestock grazing where dingoes were common (vacant land outside the Dingo Fence; $n = 7$; Fig. 1). Constraints on access resulting from inclement weather or unpassable roads limited our sampling effort during some sampling periods.

The abundance of all shrub seedlings (<30 cm height) at each site was quantified by scoring the number of seedlings on three 2 m × 100 m belt transects. Seedling abundance was calculated at each site as the number of seedlings per 1000 m². The canopy cover of mature shrubs (>1 m height) was assessed at each site using a Bitterlich gauge (Friedel & Chewings 1988). This technique generates a shrub cover estimate which is proportional to shrub canopy size. Shrub cover was averaged across six evenly spaced points at each site using a Bitterlich gauge of 75 cm length, and with a 7.5 cm cross bar. *Dodonaea viscosa angustissima*, *Acacia ligulata*, *Acacia aneura*, *Acacia tetragonophylla*, *Hakea leucoptera*, *Casuarina pauper*, *Senna artemisioides* spp. and *Senna pleurocarpa* were the shrubs species included in counts.

Abundance of grasses was quantified using a step-point method (Landsberg *et al.* 2003). On each site, grass cover was scored on three 100 m transects at 1 m intervals resulting in a total of 300 points per site. Grass cover at each site was calculated as the percentage of points where grass was recorded. *Aristida* spp. and *Eragrostis* spp. were the dominant grasses at study sites.

Indices of dingo, fox and feral cat (*Felis catus*) activity were recorded at each site using a 40 m tracking plot located on single-lane dirt roads adjacent to each site. The track plots were swept daily. The presence of dingo, fox and cat tracks was recorded for two to three consecutive nights. An index of the activity of each species was calculated as the percentage of nights that each predator was detected.

Grazing activity of kangaroos, rabbits and livestock (cattle and sheep) was quantified in the same three 2 m × 100 m belt transects used to quantify seedling abundance by scoring the presence of fresh dung (dung with a black patina). An index of grazing activity for each species was calculated as the total number of dung groups per 1000 m² (Letnic, Crowther & Koch 2009). We chose dung counts over other estimators of grazing activity (e.g. livestock stocking rates) as our measurement of grazing activity because they can be used to index recent grazing pressure at the scale of our 1 ha study sites.

We used live-trapping to index the abundance of granivorous rodents (*Mus musculus*, *Notomys fuscus*, *Pseudomys hermannsburgensis* and *Pseudomys desertor*). Trapping was conducted at each site using 20 box traps (Sherman traps; 7.62 × 8.89 × 22.86 cm, H.B. Sherman Traps, Inc., Tallahassee, FL, USA) baited with peanut butter, oats and golden syrup. Traps were placed in a four by five grid with traps spaced 20 m apart. Sites were trapped for two or three consecutive nights. Bait was replenished daily.

To prevent double counting, captured mice were given a unique mark with a pen. Total mouse abundance was calculated as the number of individuals captured per 100 trap nights.

We calculated an index of the rainfall received at each study site during the recent La Niña event (see above) by summing the estimated amount of rainfall received between January 2010 and the month during which each experimental site was sampled using the Australian Bureau of Meteorology's monthly gridded data base (5 × 5 km grid resolution; Australian Bureau of Meteorology 2016).

Fire occurrence was quantified using the previously described historic fire maps. Information regarding the amount of dingo control at each site was obtained from landholders. The intensity of dingo control was treated as an ordinal variable whereby: areas inside the Dingo Fence subject to poisoning, exclusion by the fence and shooting were allocated a value of 3 ($n = 41$); areas outside the Dingo Fence where dingo baiting and shooting occurred were allocated a value of 2 ($n = 26$); and areas outside the Dingo Fence where no dingo baiting occurred were allocated a value of 1 ($n = 24$).

STATISTICAL ANALYSIS OF CONTEMPORARY PATTERNS IN SHRUB SEEDLING AND MAMMAL ABUNDANCE

Piecewise SEM was used to test hypotheses explaining how dingoes might influence shrub recruitment (Box 1, Fig. 2, see Appendix S3 for R script). Unlike classical SEM approaches which use a co-variance matrix to determine a global estimator, piecewise SEM uses localised estimators (Grace *et al.* 2012). Piecewise SEM are particularly useful for analysis of landscape-scale data sampled using a range of methods, like ours, because localised estimates can be specified using case-specific models. For example, Poisson models can be specified for count data and binomial models can be specified for binary data.

We created an *a priori* SEM model (Fig. 2) describing the expected relationships between test variables based on previous research in the area, and on our mesopredator cascade and herbivore cascade hypotheses (Box 1). In addition to pathways described in Box 1, mature shrubs were predicted to positively affect the recruitment of shrub seedlings due to nursery effects (Cunningham *et al.* 1992); fire which occurred at some of the study sites between 2010 and 2011 (19 sites) was expected to negatively affect grasses, shrubs and shrub seedlings due to burning; historic fire which burnt some of the study area in 1972 (12 sites) was expected to negatively affect mature shrubs due to burning; rain since 2010 was expected to positively affect grasses and shrub seedlings because seedling recruitment often occurs after episodic periods of high rainfall (Nicholls 1991); livestock and kangaroos were expected to negatively affect shrub seedlings because these species may episodically browse some shrub seedlings or kill them through trampling; and foxes were expected to negatively affect cats due to competition or predation (Letnic, Ritchie & Dickman 2012). We did not include linkages between: dingoes and rabbits, and dingoes and mice in our SEM because previous studies have demonstrated strong positive correlations between these variables and there is no *a priori* reason to believe that dingoes shepherd rabbits or mice (Letnic, Crowther & Koch 2009); livestock, kangaroos and rabbits because competition between these herbivores is low during periods of high rainfall (Dawson & Ellis 1994); or foxes and cats and livestock and

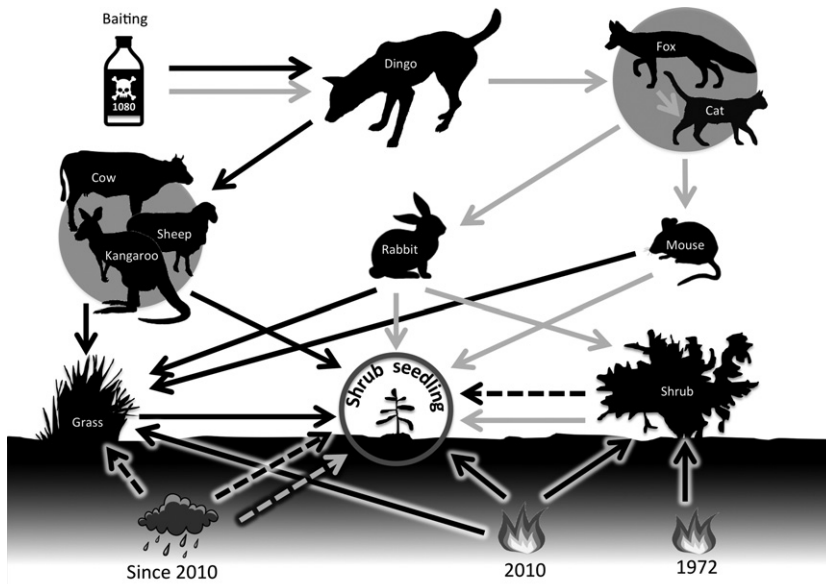


Fig. 2. The *a priori* structural equation model describing interaction pathways through which dingoes were predicted to influence shrub seedling abundance. Grey lines represent the mesopredator cascade hypothesis and black lines represent the herbivore cascade hypothesis (as described in Box 1). Solid lines represent predicted negative effects and dashed lines represent predicted positive effects. [Colour figure can be viewed at wileyonlinelibrary.com]

kangaroos because these herbivores typically fall above the prey size limit of foxes and cats (Letnic, Ritchie & Dickman 2012).

Quasi-Poisson and negative binomial GLM were used to calculate local estimators within our SEM analysis. Where test variables showed almost mutually exclusive relationships with one another – e.g. kangaroos were rarely observed where dingoes were present and vice versa (here and; Letnic & Crowther 2013) – binomial GLMs were used (see Appendix S2, Table S2 for a description of models). To account for SAC within the SEM, autocovariate models were used to calculate distance-weighted SAC terms for each of the dependant variables in the SEM (Dormann *et al.* 2007). SAC terms were then included as fixed factors in all component GLMs. Backward stepwise model reduction was used to simplify models whereby non-significant explanatory variables were sequentially excluded from analyses until all variables were significant. For this ‘best’ model, standardised path coefficient estimates were calculated using methods presented in Grace *et al.* (2012), and deviance explained was calculated as the residual deviance minus the null deviance divided by the residual deviance.

HOPBUSH SEEDLING SURVIVAL AND HOPBUSH SEED REMOVAL BY RODENTS

We compared the survival of hopbush seedlings at 15 sites on each side of the Dingo Fence over a 32-month period. We focused on hopbush because it is the most common shrub species in the study area and the abundance of hopbush seedlings and seeds are known to be greater inside than outside the Dingo Fence (Gordon & Letnic 2015). Further, hopbush is a widely distributed species which (i) is known to have increased in abundance over the past century and (ii) experiences mass recruitment events following periods of high rainfall (such as the 2010/2011 rainfall event; Noble 1998). Within the study area, mature hopbush plants reach a maximum height of 4 m, and produce seed annually during spring and summer. The seeds are wind or ant dispersed and are the foliage browsed by insects, livestock, kangaroo and rabbits. Sites were separated by 1–2 km intervals and were located at the bottom of dunes. Metal tags were attached to the bases of seven hopbush seedlings at each site (average seedling height \pm SE: inside the Dingo Fence

21.54 \pm 0.92 cm, outside the Dingo Fence 22.86 \pm 0.77 cm) during November 2012. Because seedlings were rare at some sites outside the Dingo Fence, only three seedlings were tagged at one site and six seedlings were tagged at three sites (total of 98 seedlings outside the Dingo Fence). Seedling survival was assessed in March 2013, September 2013, January 2014 and July 2015. Seedling death was identified by complete disappearance or desiccation of seedlings so that they were brittle to touch. Survival of hopbush seedlings on either side of the Dingo Fence was compared using Kaplan–Meier survival curves associated with Wilcoxon tests for statistical significance.

We used foraging trays to experimentally test whether mice readily consumed hopbush seeds. Five plastic bowls (15 cm diameter, 5 cm depth) filled with sand were buried flush with the ground on dune tops at 75 (34 sites inside, 41 sites outside the Dingo Fence) of the 91 study sites used in the contemporary patterns in shrub seedling and mammal abundance study. Forty hopbush seeds (winged capsules removed; 2 mm diameter) were then mixed through the sand matrix. The number of seeds eaten from each tray was recorded each night for two or three consecutive nights, and seed consumption was expressed as seed removal per night. Seed removed from trays was replenished daily. A linear model was used to test associations between seed removal and mouse abundance. To identify which vertebrate granivores were consuming seeds, we identified the tracks present at foraging trays and placed a portable trail camera (ScoutGuard, SG560-8M, HCO Outdoor Products, Norcross, GA, USA) at 26 of the 75 foraging trays outside the Dingo Fence. Cameras were not deployed inside the fence because preliminary surveys showed that rodents were extremely rare. Cameras were placed on 20 cm platforms at a distance of 3 m from foraging trays. Feeding granivores were identified from 30 s videos.

Results

HISTORICAL SHRUB COVER

Shrub cover increased from 1948 to 1999 on both sides of the Dingo Fence. However, the rate of increase was

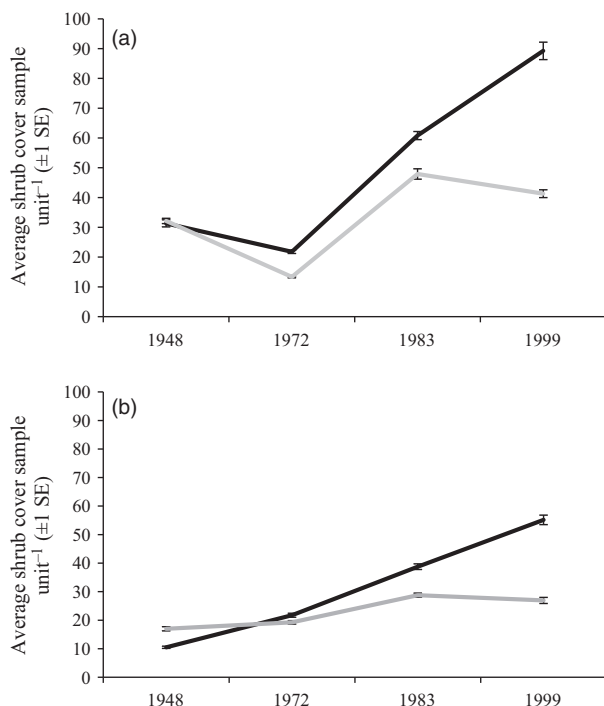


Fig. 3. Average shrub cover (± 1 SE) within 100 m diameter sample units at Fort Grey (a) and Hawker Gate (b) during 1948, 1972, 1983 and 1999. Black lines indicate areas with low dingo abundance 'inside' the Dingo Fence, grey lines indicate area with high dingo abundance 'outside' the Dingo Fence.

greater after 1972 in areas without dingoes, irrespective of whether the land was used for commercial livestock grazing or as conservation reserve (Fig. 3). On average, shrub cover increased by 33% on pastoral sites inside the Dingo Fence and 7% at pastoral sites outside the Dingo Fence in the southern Hawker Gate region, and by 89% on conservation reserve sites inside the Dingo Fence and 41% on pastoral sites outside the Dingo Fence at the northern Fort Grey region. Shrub cover was consistently higher at the northern Fort Grey region than the southern Hawker Gate region (Fig. 3).

Weak to moderate correlations were observed between predictor variables entered into GLMs (Appendix S1, Table S3). The most parsimonious GLM explaining shrub cover was the model that included all predictor variables except the occurrence of fire in the previous 20 years ($AICc = 63\ 677.33$, $w_i = 0.574$, residual deviance = 40 038). The only other supported model included all predictor variables ($AICc = 63\ 677.93$, $w_i = 0.425$, residual deviance = 40 036). Both models were substantially better than the null model ($AICc = 102\ 646.37$, null deviance = 79 023, $P < 0.0001$), indicating that the inclusion of the predictor variables substantially increased model fit. We focus on the former 'most parsimonious' model for inference. Year was the most important determinant of shrub cover followed by the interaction between year and dingo abundance, the SAC term, latitude and rainfall respectively (Fig. 4). The effect of distance to water (mean \pm SE: inside the Dingo

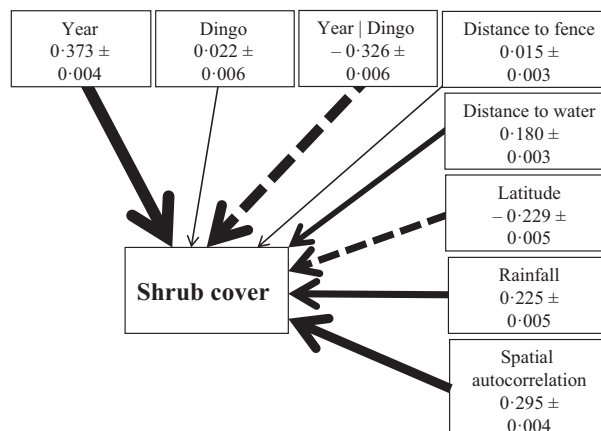


Fig. 4. Path diagram showing parameter estimates (± 1 SE) for standardized predictor variables included in the most parsimonious generalized linear model based on $AICc$ value. Solid lines indicate positive effects on shrub abundance, dashed lines indicate negative effects on shrub abundance. Line width is weighted by the magnitude of the coefficient estimate.

Fence = 5303 m \pm 89 m, outside the Dingo Fence = 5110 m \pm 78 m), a correlate of livestock grazing activity (Landsberg *et al.* 2003), was smaller than that of all other predictor variables excluding distance to the Dingo Fence (mean \pm SE: inside the Dingo Fence = 4550 m \pm 93 m, outside the Dingo Fence = 4353 m \pm 67 m; Fig. 4). Mean annual rainfall in the previous 20 years and fire occurrence (fire was recorded at 1% of sites inside the Dingo Fence in 1972 and was never observed outside the Dingo Fence) were poor predictors of shrub cover. The inclusion of the SAC term in the final GLM did not bias model parameter estimates. This is evidenced by the standardised coefficient estimates being similar between GLMs with and without the SAC term included as a fixed factor (Appendix S1, Table S4; Dormann *et al.* 2007).

CONTEMPORARY PATTERNS IN SHRUB SEEDLING AND MAMMAL ABUNDANCE

On average, dingo activity, rabbit grazing pressure and mouse abundance was greater outside than inside the Dingo Fence (Table 1). On average, fox activity, livestock grazing pressure, kangaroo grazing pressure, shrub seedling abundance and shrub cover was greater inside than outside the Dingo Fence (Table 1). Cat activity, grass cover and total rainfall since 2010 were similar on both sides of the Dingo Fence (Table 1).

Shrub seedling abundance was best explained by the mesopredator cascade hypothesis (Box 1, Fig. 5). In accordance with this hypothesis, dingo baiting was correlated negatively with dingo activity and dingo activity was correlated negatively with fox activity. Thus, high levels of dingo baiting had an indirect positive effect on fox activity. In turn, fox activity was correlated negatively with rabbit grazing pressure and mouse abundance. Rabbit grazing pressure and mouse abundance were correlated

Table 1. Mean (\pm SE) values for continuous variables in our structural equation model describing interaction pathways through which dingoes were predicted to influence shrub seedling abundance. Data is shown for: pastoral areas inside the Dingo Fence (DF; $n = 22$ sites), conservation areas inside the DF where livestock are absent ($n = 19$ sites), pastoral areas outside the DF ($n = 43$ sites) and vacant land outside the DF where livestock are absent ($n = 7$ sites)

Variable	Units	Livestock present inside the DF	Livestock absent inside the DF	Livestock present outside the DF	Livestock absent outside the DF
Dingo	Activity/night	0	0	42.88 \pm SE 5.76	56.71 \pm SE 9.53
Fox	Activity/night	74.86 \pm SE 6.29	44.52 \pm SE 7.66	1.53 \pm SE 1.07	18.85 \pm SE 9.81
Cat	Activity/night	17.31 \pm SE 5.81	0	17.76 \pm SE 3.77	0
Livestock grazing	Dung/1000 m ²	211.31 \pm SE 68.00	0	7.00 \pm SE 2.09	0
Kangaroo grazing	Dung/1000 m ²	573.54 \pm SE 124.78	391.26 \pm SE 64.56	1.58 \pm SE 0.76	0
Rabbit grazing	Dung/1000 m ²	59.09 \pm SE 14.86	28.10 \pm SE 11.52	202.67 \pm SE 28.32	278.42 \pm SE 88.57
Mouse	Captures/100 nights	1.13 \pm SE 1.13	0	160.65 \pm SE 38.47	85.85 \pm SE 32.45
Grass	Percentage cover	38.72 \pm SE 1.91	30.36 \pm SE 3.48	49.88 \pm SE 1.85	39.42 \pm SE 1.46
Shrub seedling	Seedling/1000 m ²	209.09 \pm SE 30.85	196.47 \pm SE 35.08	52.34 \pm SE 11.76	0
Shrub	Shrub cover index	14.27 \pm SE 1.13	13.57 \pm SE 1.10	4.88 \pm SE 0.43	4.57 \pm SE 0.75
Total rainfall	Millimetres	843.54 \pm SE 10.41	1014.52 \pm SE 9.05	1006.20 \pm SE 22.23	901.28 \pm SE 0.71

negatively with shrub seedling abundance. Thus, fox activity had an indirect positive effect on shrub seedling abundance. Further, because dingo activity was correlated negatively with fox activity, dingoes had an indirect negative effect on shrub seedling abundance. Fire since 2010 was correlated negatively with shrub seedling abundance. A number of exogenous pathways which did not indirectly impact shrub seedling abundance were present

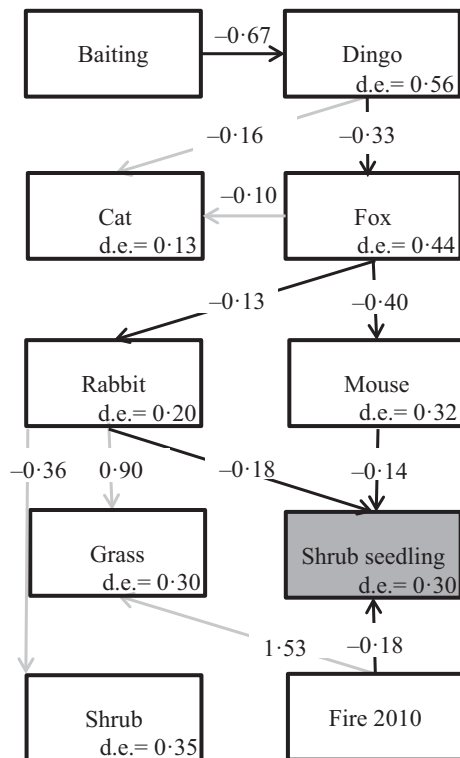


Fig. 5. The most parsimonious structural equation model describing interaction pathways through which dingoes were predicted to influence shrub seedling abundance. Numbers dissecting or lying above arrows show standardised path coefficient estimates and deviance explained (d.e.) is shown within boxes. Black lines show pathways effecting shrub seedling abundance and grey lines show exogenous pathways.

within the final SEM. These included negative correlations between dingo and cat activity, fox and cat activity, and rabbit grazing pressure and shrub cover; and positive correlations between rabbit grazing pressure and grass cover, and fire occurrence since 2010 and grass cover.

Spatial autocorrelation was observed in most GLMs comprising the final piecewise SEM (Appendix S2, Table S2). Spatial autocorrelation was particularly apparent in models describing dingo impacts on livestock and kangaroo grazing pressure. Although strong negative associations were observed between dingoes and livestock and kangaroo grazing pressure (Table 1), these pathways were not included in the final SEM (Fig. 5). This was because livestock and kangaroos were almost exclusively observed inside the Dingo Fence, and thus GLMs were strongly weighted by the autocorrelated term (Appendix S2, Table S2).

HOPBUSH SEEDLING SURVIVAL AND HOPBUSH SEED REMOVAL BY RODENTS

Survivorship of hopbush seedlings was greater inside the Dingo Fence where dingoes were rare than outside the

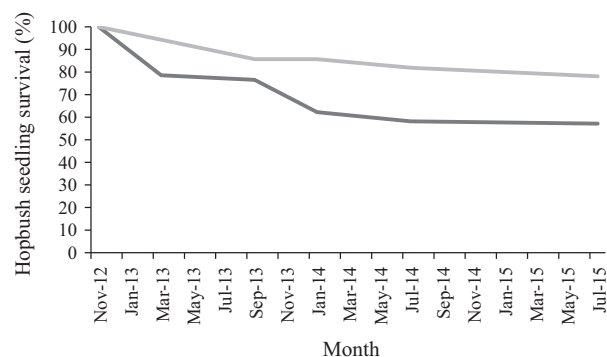


Fig. 6. Percentage survival of hopbush (*Dodonaea viscosa angustissima*) seedlings inside (light grey line) and outside (dark grey lines) the Dingo Fence between November 2012 and July 2015.

Dingo Fence where dingoes were common (Fig. 6; $\chi^2 = 4.81$, $df = 1$, $P = 0.0278$).

Total mouse abundance was positively correlated with the number of seeds taken from foraging trays ($R^2 = 0.445$, $F_{1,73} = 58.48$, $P < 0.001$, $y = 0.027x + 7.772$; Appendix S4, Fig. S1). Trail cameras showed that the rodent *N. fuscus* was the only vertebrate granivore to consume seed from foraging trays (*N. fuscus* was observed on 85% of sample nights and foraged on 81% of these nights). On average, *N. fuscus* consumed more hopbush seeds outside (mean $13.44 \pm SE 1.31$ seeds per trap night) than inside (mean $6.85 \pm SE 1.06$ seeds per trap night) the Dingo Fence.

Discussion

Our results provide evidence linking the suppression of an apex predator to the historic encroachment of shrubs (Figs. 3 and 4). Although there was a general increase in shrub cover over time on both sides of the Dingo Fence, the increase in cover was greater at locations where dingoes were rare. Our analysis of contemporary patterns of consumer abundances and vegetation revealed strong relationships between the abundances of dingoes, red foxes, consumers of shrub seeds and shrub seedlings that accord with our mesopredator cascade hypothesis (Box 1, Fig. 5). Our analysis of hopbush seedling survival and seed removal showed seedling survivorship was 1.7 times greater and seed removal by rodents was 2.1 times lower in areas where dingoes were historically rare than common (Fig. 6). Viewed collectively, our results are consistent with the hypothesis that shrub encroachment within our study area is linked to trophic cascades induced by the suppression of an apex predator, the dingo.

GENERAL CHANGES IN HISTORIC SHRUB COVER THROUGH TIME

The general increase in shrub cover in areas where dingoes were common (outside the Dingo Fence) and rare (inside the Dingo Fence) is consistent with the CO₂-enrichment hypothesis for shrub encroachment (Briggs *et al.* 2005); i.e. shrubs increase in abundance because the C₃ photosynthetic pathway used by most shrubs is more efficient at sequestering energy in high CO₂ environments than the C₄ photosynthetic pathway utilised by most grasses (Archer, Schimel & Holland 1995; van Auken 2000). However, the CO₂-enrichment hypothesis cannot explain the divergent trends in shrub abundance in areas where dingoes are common and rare. This is because CO₂ levels would have been similar on each side of the Dingo Fence through time.

Another plausible explanation for the general increase in shrub abundance through time on both sides of the Dingo Fence is the reduced impact of rabbits as regulators of shrub recruitment following the introduction of the biological control agent myxomatosis in the early

1950s. Studies conducted since the introduction of myxomatosis have demonstrated that rabbits can suppress the regeneration of shrubs and trees by browsing on seedlings (Auld 1995; Booth, King & Sanchez-Bayo 1996). Following the release of myxomatosis, rabbit numbers crashed throughout Australia (Ratcliffe *et al.* 1952), and their influence on shrub and tree recruitment is thought to have been diminished (Crisp & Lange 1976). The effects of rabbits on shrub recruitment in the Strzelecki Desert may be expected to be greater both now and in the past in areas where there are dingoes, because dingoes facilitate higher numbers of rabbits (Newsome *et al.* 2001; Letnic, Crowther & Koch 2009).

A MESOPREDATOR RELEASE CASCADE HYPOTHESIS FOR SHRUB ENCROACHMENT IN ARID AUSTRALIA

According to our SEM, the most parsimonious explanation for the observed pattern of shrub seedling abundance at the time of our study is that in the presence of dingoes, granivory and browsing of shrub seedlings by rodents and rabbits, respectively, imposes a recruitment bottleneck on shrubs. Conversely, in the absence of dingoes, this recruitment bottleneck no longer exists because rodent and rabbit abundances are suppressed by high numbers of red foxes owing to the release of foxes from direct killing by and competition with dingoes.

While caution is required when interpreting correlative data, our mesopredator cascade hypothesis for shrub encroachment is well supported by previous studies and data collected in this study which demonstrate that mice and rabbits, which are consistently more abundant in the presence of dingoes (Newsome *et al.* 2001; Letnic, Crowther & Koch 2009), are important consumers of shrub seeds (Gordon & Letnic 2015) and seedlings (Auld 1995; Booth, King & Sanchez-Bayo 1996). Moreover, our field sampling for consumer, shrub seedling and mature shrub abundances occurred following one of the strongest La Niña events recorded in Australia during the last 100 years, and thus, represented an optimal recruitment period for shrubs (Nicholls 1991). Rodent and rabbit populations typically irrupt following La Niña driven rainfall events in arid Australia (Letnic, Tamayo & Dickman 2005). Thus, we propose that high levels of granivory and browsing by rodents and rabbits, facilitated by the presence of dingoes, could limit shrub recruitment in the wake of periodic La Niña events.

Although the Dingo Fence was constructed between 1914 and 1917, the cover of shrubs on either side of the fence measured from aerial photographs was not markedly different in 1948 or 1972, but began to differ after 1972. Because government and local pastoral records from the surrounding region show that livestock densities (and hence grazing pressure) were generally similar inside and outside the Dingo Fence between 1941 and 1980 (see Appendix S5, Fig. S1), it is unlikely that these divergent trends in shrub cover were caused by increases in total

livestock grazing. A second explanation for the divergent trends in historic shrub cover could relate to the introduction of the poison sodium fluoroacetate (1080) which greatly increased the effectiveness of dingo control from the late 1960s onwards (Fleming *et al.* 2001). Dingo control, primarily using meat baits impregnated with 1080, is undertaken extensively in western NSW but less so in adjoining areas outside the Dingo Fence in Qld and SA, where dingoes remain relatively common. Prior to the use of 1080, dingoes occurred at higher numbers than they do now in western NSW (Fleming *et al.* 2001), and although controlled by trapping, shooting, poisoning and exclusion by the Dingo Fence, they may have been sufficiently abundant to suppress red fox populations and hence facilitate higher populations of rabbits and mice (Letnic & Koch 2010).

Improvement in the efficiency of dingo control through time is evidenced in the study region and elsewhere in Australia by the reduction in dingo bounty payments paid following the introduction of 1080 (Allen & Sparkes 2001). Although bounty payments are not a particularly sensitive index of dingo abundance, the sharp decrease in bounties paid following the introduction of 1080 across Australia is thought to reflect a dramatic decrease in dingo abundance (Allen & Sparkes 2001). Thus, if our hypothesis is correct, a reduction in the influence of dingoes on mammalian assemblages and therefore increases in shrub populations in western NSW (inside the fence) could be expected following the introduction of 1080.

A HERBIVORE CASCADE HYPOTHESIS FOR SHRUB ENCROACHMENT IN ARID AUSTRALIA

Our results provide little support for the hypothesis that herbivore grazing pressure is a driver of shrub encroachment within the study area. The marked increase in historic shrub cover between 1972 and 1983 at sites where dingoes exist at low densities (inside the fence) occurred irrespective of whether sites were used for livestock grazing (Hawker Gate) or as conservation reserve (Fort Grey; Fig. 3). Distance to closest watering point, a proxy for livestock grazing intensity, also had a negligible correlation with historic shrub cover in our analysis. Our SEM which explored contemporary patterns of consumer and hopbush seedling abundance showed weak and non-significant associations between dingo activity and livestock or kangaroo abundance, grass cover, and seedling abundance during the wet climatic period associated with our field survey (Fig. 5).

Conclusion

Here, we provide evidence that the extirpation of an apex predator, the dingo, has initiated a trophic cascade that facilitates shrub recruitment and shrub encroachment. Apex predator extirpation is inextricably linked to shrub encroachment in many areas of the world; e.g. in the

south-west of the USA shrub encroachment has coincided with the decline of wolves (van Auken 2000; Ripple *et al.* 2013), expansion of livestock grazing (Dunlap 1991), reduced fire frequency (van Auken 2000), irruption of mesopredators and wild herbivores (Ripple *et al.* 2013; Newsome & Ripple 2015), and decline of rodents and lagomorphs (Weltzin, Archer & Heitschmidt 1997; Davidson, Detling & Brown 2012). However, our study is the first to suggest that trophic cascades initiated by apex predator extirpation could be a driver of shrub encroachment. Given the strong associations observed between apex predator extirpation and shrub encroachment globally, we suggest that trophic cascades and the loss of ecosystem functioning initiated by apex predator removal could be an important factor influencing shrub encroachment in many areas of the Earth.

Authors' contributions

C.E.G. and M.L. conducted field work. C.E.G., M.L., M.S.C. and B.D.M. analysed data. All authors wrote and edited the manuscript.

Acknowledgements

This research was funded by the Australian Research Council and Hermon Slade Foundation. Wildlife ethics approval was granted by the South Australian Department of Environment and Natural Resources (26/2011) and the University of Western Sydney's Animal Ethics and Care Committee (A8904). Marianne Pasanen-Mortensen and Bodil Elmhagen provided advice on SEM.

Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.g6m44> (Gordon *et al.* 2016).

References

- Allen, L.R. & Sparkes, E.C. (2001) The effect of dingo control on sheep and beef cattle in Queensland. *Journal of Applied Ecology*, **38**, 76–87.
- Archer, S., Schimel, D.S. & Holland, E.A. (1995) Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change*, **29**, 91–99.
- van Auken, O.W. (2000) Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics*, **31**, 197–215.
- Auld, T. (1995) The impact of herbivores on regeneration in four trees from arid Australia. *The Rangeland Journal*, **17**, 213–227.
- Australian Bureau of Meteorology (2016) Archive - monthly gridded rainfall totals. Available at <http://www.bom.gov.au>.
- Beschta, R.L. & Ripple, W.J. (2009) Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, **142**, 2401–2414.
- Bivand, R. (2011) Spdep: spatial dependence: weighting schemes, statistics and models. R package version 0.5-40. Available at <http://cran.r-project.org/src/contrib/Descriptions/spdep.html>.
- Booth, C., King, G. & Sanchez-Bayo, F. (1996) Establishment of woody weeds in western New South Wales. 1. Seedling emergence and phenology. *The Rangeland Journal*, **18**, 58–79.
- Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S. & McCarron, J.K. (2005) An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience*, **55**, 243–254.
- Browning, D.M. & Archer, S.R. (2011) Protection from livestock fails to deter shrub proliferation in a desert landscape with a history of heavy grazing. *Ecological Applications*, **21**, 1629–1642.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY, USA.

- Colman, N., Gordon, C., Crowther, M. & Letnic, M. (2014) Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20133094.
- Crisp, M.D. & Lange, R.T. (1976) Age structure, distribution and survival under grazing of the arid-zone shrub *Acacia burkittii*. *Oikos*, **27**, 86–92.
- Cunningham, G.M., Mulham, W.E., Milthorpe, P.L. & Leigh, J.H. (1992) *Plants of Western New South Wales*. CSIRO Publishing, Collingwood, Australia.
- Davidson, A.D., Detling, J.K. & Brown, J.H. (2012) Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment*, **10**, 477–486.
- Dawson, T.J. & Ellis, B.A. (1994) Diets of mammalian herbivores in Australian arid shrublands: seasonal effects on overlap between red kangaroos, sheep and rabbits and on dietary niche breadths and electivities. *Journal of Arid Environments*, **26**, 257–271.
- Dormann, C.F., McPherson, J.M., Araujo, M.B. *et al.* (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.
- Dunlap, T.R. (1991) *Saving America's Wildlife*. Princeton University Press, Princeton, NJ, USA.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. & Whitford, W.G. (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters*, **14**, 709–722.
- Estes, J.A., Terborgh, J., Brashares, J.S. *et al.* (2011) Trophic downgrading of planet earth. *Science*, **333**, 301–306.
- Fleming, P., Corbett, L., Harden, R. & Thompson, P. (2001) *Managing the Impacts of Dingoes and Other Wild Dogs*. Bureau of Resource Science, Canberra, Australia.
- Friedel, M.H. & Chewings, V.H. (1988) Comparison of crown cover estimates for woody vegetation in arid rangelands. *Australian Journal of Ecology*, **13**, 463–468.
- Gordon, C.E. & Letnic, M. (2015) Functional extinction of a desert rodent: implications for seed fate and vegetation dynamics. *Ecography*, **39**, 815–824.
- Gordon, C.E., Eldridge, D., Ripple, W.J., Crowther, M.S., Moore, B.D. & Letnic, M. (2016) Data from: Shrub encroachment is linked to extirpation of an apex predator. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.g6m44>.
- Grace, J.B., Schoolmaster, D.R., Guntenspergen, G.R., Little, A.M., Mitchell, B.R., Miller, K.M. & Schweiger, E.W. (2012) Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere*, **3**, Article 73.
- King William Henry the Fourth (1836) *Letters Patent Establishing the Province of South Australia*. Privy Council, Westminster, UK.
- Knapp, A.K., Briggs, J.M., Collins, S.L. *et al.* (2008) Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*, **14**, 615–623.
- Landsberg, J., James, C.D., Morton, S.R., Müller, W.J. & Stol, J. (2003) Abundance and composition of plant species along grazing gradients in Australian rangelands. *Journal of Applied Ecology*, **40**, 1008–1024.
- Letnic, M. & Crowther, M.S. (2013) Patterns in the abundance of kangaroo populations in arid Australia are consistent with the exploitation ecosystems hypothesis. *Oikos*, **122**, 761–769.
- Letnic, M., Crowther, M.S. & Koch, F. (2009) Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? *Animal Conservation*, **12**, 302–3012.
- Letnic, M. & Dworjanyan, S.A. (2011) Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? *Ecography*, **34**, 827–835.
- Letnic, M. & Koch, F. (2010) Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology*, **35**, 167–175.
- Letnic, M., Ritchie, E.G. & Dickman, C.R. (2012) Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews*, **87**, 390–413.
- Letnic, M., Tamayo, B. & Dickman, C.R. (2005) The responses of mammals to La Niña (El Niño southern oscillation)-associated rainfall, predation, and wildfire in central Australia. *Journal of Mammalogy*, **86**, 689–703.
- Moseby, K.E., Neilly, H., Read, J.L. & Crisp, H.A. (2012) Interactions between a top order predator and exotic mesopredators in the Australian rangelands. *International Journal of Ecology*, **2012**, 15–30.
- Newsome, T.M. & Ripple, W.J. (2015) A continental scale trophic cascade from wolves through coyotes to foxes. *Journal of Animal Ecology*, **84**, 49–59.
- Newsome, A.E., Catling, P.C., Cooke, B.D. & Smyth, R. (2001) Two ecological universes separated by the Dingo Barrier Fence in semi-arid Australia: interactions between landscapes, herbivory and carnivory, with and without dingoes. *The Rangeland Journal*, **23**, 71–98.
- Nicholls, N. (1991) The El Niño/Southern Oscillation and Australian vegetation. *Vegetatio*, **91**, 23–36.
- Noble, J.C. (1998) *The Delicate and Noxious Scrub: CSIRO Studies on Native Tree and Shrub Proliferation in the Semi-arid Woodlands of Eastern Australia*. CSIRO Publishing, Clayton, Australia.
- R Development Core Team (2016) A language and style for computer programming. (ed. R.f.f.s. computing). Available at <http://www.R-project.org>.
- Ratcliffe, F.N., Myers, K., Fennessy, B.V. & Calaby, J.H. (1952) Myxomatosis in Australia: a step towards the biological control of the rabbit. *Nature*, **170**, 7–11.
- Ripple, W.J., Wirsing, A.J., Wilmers, C.C. & Letnic, M. (2013) Widespread mesopredator effects after wolf extirpation. *Biological Conservation*, **160**, 70–79.
- Ripple, W.J., Estes, J.A., Beschta, R.L. *et al.* (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**, 1241484.
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.
- Roques, K.G., O'Connor, T.G. & Watkinson, A.R. (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, **38**, 268–280.
- Scholes, R.J. & Archer, S.R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.
- Terborgh, J., Lopez, L., Nuñez, P. *et al.* (2001) Ecological meltdown in predator-free forest fragments. *Science*, **294**, 1923–1926.
- Weltzin, J.F., Archer, S. & Heitschmidt, R.K. (1997) Small-mammal regulation of vegetation structure in a temperate Savanna. *Ecology*, **78**, 751–763.
- Woodroffe, R. (2000) Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*, **3**, 165–173.
- Zuur, A.F. (2009) *Mixed effects models and extensions in ecology with R*. Springer-Verlag, New York, NY, USA.

Received 6 June 2016; accepted 14 October 2016

Handling Editor: Anne Loison

Supporting Information

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

Appendix S1. Additional information relating to our analysis of historical trends in shrub cover.

Appendix S2. Additional information relating to our assessment of contemporary trends in shrub seedling and mammal abundance.

Appendix S3. R script used to conduct the structural equation model described in the contemporary trends in shrub seedling and mammal abundance section of the manuscript.

Appendix S4. Additional information relating to our assessment of hopbush seed removal by rodents.

Appendix S5. Livestock densities and grazing pressure within the wider sample area between 1941–1980.