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Incorporating disturbance into trophic ecology: fire history shapes mesopredator suppression by an apex predator

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Abstract

1. Apex predators can suppress smaller bodied ‘mesopredators’. In doing so, they can provide refuge to species preyed upon by mesopredators, which is particularly important in regions where mesopredators are invasive. While most studies of mesopredator suppression focus on the response of mesopredators to human control of apex predators, other factors –including natural and anthropogenic disturbance – also drive the occurrence of apex predators and, in doing so, might shape spatial patterns of mesopredator suppression.
2. We examined the role of fire in shaping the occurrence of an apex predator and, by extension, mesopredators and small mammals in a fire-prone region of semi-arid Australia. We measured the activity of an apex predator (the dingo, *Canis dingo*); an invasive mesopredator it is known to suppress, the red fox (*Vuples vuples*); and two species of native small mammal (Mitchell’s hopping mouse, *Notomys mitchelli*; silky mouse, *Pseudomys apodemoides*) that are potential prey, across 21 fire mosaics (each 12.56 km^2). We used piecewise structural equation modelling and scenario analysis to explore the interactions between fire, predators and prey.
3. We found that dingoes were affected by fire history at the landscape scale, showing a preference for recently burned areas. While foxes were not directly affected by fire history, a negative association between dingoes and foxes meant that fire had an indirect impact on foxes, mediated through dingoes. Despite the suppression of foxes by dingoes, we did not observe a trophic cascade as small mammals were not negatively associated with foxes or positively associated with dingoes.

4. *Synthesis and applications.* Disturbance regimes have the capacity to shape patterns of mesopredator suppression when they alter the distributions of apex predators. Environmental change that promotes native predators can therefore help suppress mesopredators – a common conservation objective in regions with invasive mesopredators. The indirect consequences of disturbance regimes should be considered when managing disturbance (e.g. fire) for biodiversity conservation.

Keywords: Disturbance-induced trophic cascades, integrated ecosystem management, dingo, red fox, small mammals, predator-prey interactions, structural equation modelling, mesopredator suppression, apex predator, fire

Introduction

Predators shape ecosystems around the world by killing and instilling fear in competitors and prey (Creel & Christianson 2008; Laundré *et al.* 2014), sometimes triggering trophic cascades that impact entire ecosystems (Crooks & Soulé 1999; Ripple & Beschta 2004; Letnic *et al.* 2009). One common pathway through which apex predators affect ecosystems is by suppressing smaller predators ('mesopredators') (Elmhagen *et al.* 2010; Pasanen-Mortensen, Pyykönen & Elmhagen 2013), leading them to be more scarce where apex predators are most active (Ripple & Beschta 2004; Brook, Johnson & Ritchie 2012). This can benefit species preyed upon by mesopredators in turn (Letnic *et al.* 2009; Elmhagen *et al.* 2010), particularly in regions where mesopredators have been introduced and become invasive (Johnson, Isaac & Fisher 2007).

Evidence that apex predators can suppress mesopredators and trigger trophic cascades comes largely from experiments comparing areas where apex predators are abundant with areas in which they have been controlled or exterminated (Letnic & Koch 2010; Newsome & Ripple 2014). These studies have provided ample evidence that persecution of apex predators—such as grey wolves (*Canis lupus*) in North America (Levi & Wilmers 2011), Eurasian lynx (*Lynx lynx*) in Europe (Pasanen-Mortensen, Pyykönen & Elmhagen 2013) and jaguars (*Panthera onca*) in Central America (Moreno, Kays & Samudio 2006)—can result in mesopredator release. However, factors other than human persecution, including natural and anthropogenic disturbances, also drive the distribution and abundance of apex predators (Dees, Clark & Van Manen 2001; Schuette *et al.* 2014). In doing so, disturbance has the potential to shape trophic relations among species (Cherry, Warren & Conner 2016).

Disturbance-induced trophic effects are particularly important from a management perspective. The difficulties associated with lethal control of mesopredators are increasingly well-known (Doherty *et al.* 2015b). Compensatory immigration of individuals from surrounding areas means that lethal management must be intensive, sustained and broad-scale—and therefore costly—to be effective (Lazenby, Mooney & Dickman 2015). By creating conditions that favour apex predators, manipulation of disturbance regimes may be an alternative, or complementary strategy, to help mitigate the impacts of invasive mesopredators (Doherty *et al.* 2015b).

Fire is a widespread disturbance with the capacity to affect the relationships between apex predators, mesopredators and their prey. Evidence from both tropical (Leahy *et al.* 2016; McGregor *et al.* 2016), and temperate environments (Conner, Castleberry & Derrick 2011), suggests that fire exposes native prey to greater risk of predation by invasive mesopredators by creating open habitats that increase hunting success. However, mesopredators may themselves be more at risk of being attacked by apex predators in open habitats (Birtsas, Sokos & Exadactylos 2012), and therefore perceive them as more risky. If mesopredators avoid more open environments due to their fear of apex predators, this could confer an indirect benefit to smaller prey post-fire, and may be a means of diminishing the impacts of invasive predators on native prey in fire-prone landscapes (Doherty *et al.* 2015b).

Australia is a fire-prone continent with a single terrestrial mammalian apex predator (other than humans), the dingo (*Canis dingo*). The dingo has been extirpated across a quarter of the continent and is controlled across the majority of the remainder (Letnic, Ritchie & Dickman 2012). Australia also has the worst record of modern mammal extinction, with >25 modern extinctions due in part to two widespread invasive mesopredators—the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) (Woinarski, Burbidge & Harrison 2015; Doherty *et al.* 2016). There is accumulating evidence that the ongoing decline of Australia's mammals is exacerbated by an interaction between altered fire regimes and invasive mesopredators (McGregor *et al.* 2014), as more intense fires increase the susceptibility of native mammals to predation by invasive mesopredators (Hradsky *et al.* 2016). Further, there is mounting evidence that dingoes suppress both species (Nimmo *et al.* 2015), particularly foxes (Johnson & Van Der Wal 2009; Colman *et al.* 2014), and, in some ecosystems, favour recently burned vegetation due to its open nature favouring pursuit hunting (Southgate *et al.* 2007). What has not been considered is whether dingoes—through their suppression of invasive mesopredators and preference for larger prey such as kangaroo species (Letnic, Ritchie & Dickman 2012)—could confer a net benefit to small- and medium-sized native mammals in recently burned areas.

We undertook a landscape-scale natural experiment to examine evidence for disturbance-induced trophic cascades in a fire-prone ecosystem of southern Australia. We examined the relationships between dingoes/wild dogs/hybrids (hereafter, referred to collectively as 'dingoes'), red foxes, and two species of native small mammal (Mitchell's hopping mouse, *Notomys mitchelli*; silky mouse, *Pseudomys apodemoides*) in relation to fire history across 21 replicate landscapes. We used structural equation modeling to examine whether fire can indirectly affect mesopredators by favoring an apex predator, and thereby benefit potential prey species in turn. We predicted that: 1. Dingoes and foxes would have a negative relationship (Johnson & VanDerWal 2009); 2. Foxes would have a negative relationship with both small mammals (Risbey *et al.* 2000); 3. Due to the role of dingoes in suppressing foxes, dingoes and small mammals would have a positive relationship (Johnson, Isaac & Fisher 2007; Colman *et al.* 2014); and 4. Spatial variation in fire age of vegetation would shape the distribution of all species, and therefore the magnitude of these trophic relationships.

Materials and methods

Study region

The ~7000 km^2 study area extends through a complex of conservation reserves in the Murray-Mallee region of northwest Victoria (the Big Desert Wilderness Park, the Big Desert State Forest and Wyperfeld National Park), collectively referred to as 'Big Desert Wilderness' (Figure S1). The region experiences a semi-arid climate, with mean annual rainfall of ~330 – 400 mm (Australian Bureau of Meteorology 2014). Two distinct vegetation types occur in the region. 'Mallee' vegetation possesses a heathy shrub understorey with a *Melaleuca uncinata* and/or mallee eucalypt (*Eucalyptus leptophylla* and *E. incrassata*) canopy. 'Heathland' vegetation generally lacks eucalypt trees, instead dominated by a mixed layer of small (<2 m), heathy shrubs. The Big Desert Wilderness is home to a diverse mammal community.

The region is fire-prone, with large fires occurring every 10-20 years (Pausas & Bradstock 2007; Avitable *et al.* 2013). Vegetation structure within semi-arid mallee ecosystems is strongly influenced by the time since it was last burnt (Haslem *et al.* 2011). Typically, fire is stand replacing, whereby a fire event will remove all above-ground biomass, resetting a patch's successional trajectory to year zero. As such, any patch within a landscape can be given a 'fire age,' based upon when it last burnt.

Landscape and site selection

This study employed a 'whole-of-landscape' experimental design, such that each experimental unit was a circular landscape 12.56 km^2 (diameter = 4 km) in size (following Taylor *et al.* 2012). A whole-of-landscape design allows both response variables (e.g. measures of predator and prey activity) and predictor variables (e.g. extent of fire ages within a landscape) to be measured for entire landscapes (e.g. Nimmo *et al.* 2013). Several of the study species are wide-ranging, such as dingoes (home range > 40 km^2; Robley *et al.* 2010), red foxes (home range >5 km^2; Coman, Robinson & Beaumont 1991) and Mitchell's hopping mice (movement of 2 km per night; Letnic 2001). Therefore, a whole-of-landscape approach allowed measuring both response and predictor variables at an ecologically meaningful spatial scale for the focal species.

Landscapes were chosen according to (1) the proportional cover of three fire-ages: areas which have experienced <11 years post-fire ('RECENTLY BURNED'), 11-35 years post-fire ('MID SUCCESSIONAL'), and >35 years post-fire ('LONG UNBURNED'); and (2) the extent of the mallee vegetation in the landscape ('MALLEE'), which is negatively correlated with the extent of heathy vegetation types. These age classes were selected as they represent key post-fire successional stages in semi-arid, mallee ecosystems (Haslem et al. 2011). Fire history and vegetation digital overlays was determined through 55 years (1958-2013) of LANDSAT satellite imagery, state agency records and local knowledge, and were ground-truthed at each site. Landscapes were chosen to sample a broad area across the reserve complex (Figure S1), and all landscapes were distributed > 2 km apart to help ensure spatial independence. A total of 21 study landscapes were selected.

Five camera sites were nested within each landscape (21 x 5 = n = 105 in total; see Figure S1). Sites within landscapes were allocated according to area-proportionate sampling in terms of fire history and vegetation type (following Nimmo *et al.* 2012; Taylor *et al.* 2012). For example, a vegetation type or fire-age class that made up 0-20% of the landscape was allocated 1 site, those that comprised 20-40% were allocated 2 sites, and so on. Sites were distributed throughout the landscape as much as was logically feasible. Camera sites were > 200 m apart to increase spatial independence. Camera sites were placed > 50 m from minor dirt tracks, and ≥100 m from fire-scar edges and ≥50 m from boundaries between vegetation types to reduce the influence of ecotones.

Fauna surveys

To survey for predators (dingoes, foxes), we used camera traps (Reconyx Hyperfire HC600) at each site from April-August 2014 over three sampling rounds. Each site was surveyed for one round (i.e. one third of sites having cameras deployed in April 2014, one third of sites in May/June 2014, and the remaining third in July 2014), and the sites surveyed in each round were spread across the study area to ensure each round had maximized geographic coverage. Facing south (to avoid glare from the sun), cameras were attached to a wooden stake 0.5 m above the ground and angled slightly downward. Camera traps were set to take a burst of 10 photos, with a quiet period of 2 minutes between each trigger. Cameras were deployed at each site for a minimum of 33 days. Cameras were baited with tuna oil-soaked wadding placed in a PVC bait canister with steel mesh at one end and pegged to the ground 3 m in front of the camera. This bait mixture has previously been used to successfully survey for red foxes in mallee ecosystems (Payne *et al.* 2014). Four chicken necks were also buried (N, S, E and W) 50 cm from the PVC canister.

We obtained an additional measure of dingo occurrence by conducting two scat surveys at each site of the 105 study sites (n = 10 surveys per study landscape), up to three months apart (each site surveyed once in April 2014, then one third of sites in May/June 2014, one third in July 2014 and the remaining third in August 2014). Surveys were undertaken over 15 minutes by walking 400 m transects along roads next to each camera site (i.e. 200 m each side of the camera site and both sides of the road), recording all dingo scats.

We surveyed for small mammal species using camera traps (ScoutGuard 550V) at the same time as predator surveys. Small mammal cameras were paired with predator cameras, but located 50 m away. Cameras were downward facing and mounted on a wooden stake 1 m from the ground (De Bondi *et al.* 2010; Rendall *et al.* 2014). Small mammal cameras recorded a 15 second video upon triggering, with a 60 second quiet period between triggers. To attract small mammals, a super-absorbent wadding soaked in a peanut butter/fish oil solution was pegged to the ground inside a PVC canister directly below the camera trap. A small amount of rolled oats and sunflower seeds was also spread around the lure to attract rodents. For both predator and small mammal cameras, vegetation was cleared from each camera's field of view to reduce false trigger events. Predator and small mammal camera trapping was conducted over three separate sampling rounds, each round surveying seven landscapes.

Statistical analysis

Species' occurrence

In order to examine how confident we could be that observed absences from camera trapping or scat surveys were 'true' absences, we calculated the survey-level detection probability of all species using the unmarked package in R (Fiske & Chandler 2011). We used the following equation to calculate confidence that observed absences are 'real' absences:

$$N\ min = \log(\alpha) / \log(1 - p)$$

Where α is the desired level of confidence and p is the probability of detection (Kéry 2002). This analysis revealed that we could not be confident that observed absences were true for dingoes using the camera trap data. The nightly detection of dingoes at the landscape scale (i.e. considering nightly detections at any site within a landscape) was 0.03, meaning that we could only be ~60% confident in absences after 30 nights of camera trapping across all five sites within a landscape. Dingoes were far more detectable during scat surveys. Here, the detection probability at the landscape-scale was 0.63, meaning we could be ~ 87% confident that absences were true absences after the two rounds of five scat surveys in each landscape. The nightly detection probability of the red fox (from camera traps) was 0.16, meaning that we could be >95% confident of absences after 17 nights of sampling. The silky mouse and Mitchell's hopping mouse were highly detectable, with nightly detection probabilities of 0.38 and 0.39, respectively. This meant we could be >95% confident that observed absences were true absences for both species after 7 nights of sampling.

Structural equation modelling

We used piecewise structural equation modelling (SEM) to model the relationships between our four study species (the dingo, red fox, Mitchell's hopping mouse, and silky mouse) and landscape-scale predictor variables (i.e. extent of fires ages and vegetation types). Where *a priori* knowledge of potential relationships is available, SEMs can be used to examine a network of ecosystem processes, testing for relationships between two factors, but also how effects might flow through a system (Grace 2006; Grace *et al.* 2012). Unlike classical SEMs, where global estimation is used to construct a graph, the piecewise approach allows each 'node' or response variable to be modelled individually (Grace *et al.* 2012; Pasanen-Mortensen, Pyykönen & Elmhagen 2013).

We developed an *a priori* SEM based on our knowledge of the species and their interactions (Figure 1; Appendix S1). Nodes of the SEM (i.e. models of individual species) were fit with a generalised linear mixed-effect model (GLMM). The response variable of each node was the species' reporting rate —the number of times the species was detected as a proportion of the total number of surveys, modelled as multi-trial binomial distributions. We used reporting rates in preference to presence/absence because 1) occupancy alone can overlook relationships between predators and mesopredators (Nimmo et al. 2015), and (2) the red fox, the hopping mouse and the silky mouse were detected in the vast majority of landscapes (red fox = 17/21 landscapes, hopping mouse = 20/21 landscapes, silky mouse = 20/21 landscapes), and hence modelling occupancy would be of little value**.** As camera traps failed to detect adequate numbers of dingoes for statistical analysis, the reporting rate of dingoes was the proportion of scat surveys (*n*/10) in which one or more dingo scats were observed within a landscape. For foxes, the reporting rate was the number of sites in a landscape within which a red fox was observed over the 30 camera trap-nights (*n*/5). Not all small mammal cameras remained operational (affecting 8 out of 21 landscapes) for the entire sampling period, whereas all predator cameras remained operational. Camera nights for small mammals remained operational for an average of 93% of the possible camera nights (range =78%-100%). Therefore, for both the silky mouse and Mitchell's hopping mouse, the reporting rate was calculated as the number of nights each species was detected out of all operational camera trap nights within a landscape. As sampling occurred over three separate rounds, sampling round was included as a random effect. Predictor variables were either (1) the reporting rates of other species or (2) landscape-scale predictor variables describing the extent of fire ages and vegetation types (Table S1).

To represent each landscape's fire history, we included two variables (Table S1): the extent of recently-burned vegetation ('RECENTLY BURNED'), the extent of long-unburned vegetation ('LONG UNBURNED'). Mid-successional vegetation was not included as it is completely negatively correlated with the extent of recent and long unburned vegetation. As the extent of mallee ('MALLEE') and heathland were strongly negatively correlated (r_s = - 0.83), we included only MALLEE. We inspected the final SEMs for overdispersion. When models had dispersion parameters > 1.5, landscape was also included as an observation level random effect (Zuur & Ieno 2012). We calculated the marginal R^2 for each GLMM to determine the variance explained by the fixed predictors (Nakagawa & Schielzeth 2013).

We calculated the path coefficients of final GLMMs using the ‘relevant range’ method outlined by Grace and Bollen (2005). This measures how a variable is predicted to change in proportion to its range (i.e. minimum to maximum of the response variable) as a predictor variable changed from its minimum to its maximum, whilst all other predictors are held at their mean (as in Dorresteijn *et al.* 2015). This approach allows a direct comparison of coefficients across all predictor variables and across all species (Grace & Bollen 2005). We judged predictor variables as being influential if the 95% confidence intervals of the coefficients did not overlap zero. Indirect effects of variables were quantified when a response variable had at least one influential pathway leading to it (either directly or mediated by another variable). Indirect effects were calculated by multiplying the relevant range coefficients of the various pathways leading to a variable (Grace & Bollen 2005).

To further explore the consequences of indirect effects, we used queries-based scenario analysis (Grace *et al.* 2012). Based on the results of the SEM (outlined below), we focused on the relationship between dingoes and foxes, due to the likelihood of indirect effects of fire on foxes, mediated through dingoes. We compared how fox reporting rates would change if the entire study region transitioned from being in the < 11 year age class to being in the 11-35 year age-class. This was possible, despite the 11-35 year age-class not being a predictor in the final GLMMs, because the influence of the 11-35 age-class on fox reporting rate is completely negatively correlated with the influence of <11 year and >35 year age classes, thus landscapes are comprised entirely of 11-35 year old vegetation when the other two age classes are set to zero. To illustrate the importance of indirect effects of fire, we generated two sets of predictions for this scenario—one that ignored the effects of fire on dingoes (and their flow-on effects on foxes), and one that incorporated those effects.

Ignoring indirect effects of fire: We predicted the reporting rate of foxes across the study region by breaking the region into 557 hypothetical 4 km diameter landscapes (the entire study region, 7000 km^2, divided by the size of each landscape, 12.56 km^2). First, we specified that all 557 landscapes were <11 years since fire (i.e. in the RECENTLY BURNED age class). Next, we determined dingo occurrence through these landscapes by undertaking 557 Bernoulli trials with a probability of 0.17, which is the mean reporting rate of dingoes from the raw data. MALLEE was held at its mean (as it was for all scenarios). We then predicted the reporting rate of foxes in each of the 557 landscapes after adding the outcomes of the dingo trials (i.e. the predicted reporting rate for each of the 557 landscapes) to the design matrix. We repeated the same procedure but with the entire region 11-35 years since fire, by setting RECENTLY BURNED and LONG UNBURNED to zero. In this scenario, the fire history of the region changes, but dingo occurrence within landscapes varies in a way unrelated to fire history. Therefore, any change in then reporting rates of foxes between the two scenarios is due to the direct effects of fire on foxes.

Accounting for indirect effects of fire: We repeated the same process as above, except that the probabilities for the 557 Bernoulli trials for dingoes were informed by the SEM. The predicted reporting rate of dingoes in landscapes entirely composed of RECENTLY BURNED was 0.18. Therefore, to predict dingo occurrence across the 557 recently burned landscapes, we undertook 557 Bernoulli trials with a probability of 0.18. The predicted reporting rates of dingoes in a landscape for which RECENTLY BURNED and LONG UNBURNED were set to zero (i.e. region comprised solely of 11-35 year old vegetation) was 0.02. Therefore, to predict the occurrence of dingoes across the region under this scenario, 557 Bernoulli trials were undertaken with a probability of 0.02. We then made predictions for the reporting rates of foxes in the 557 landscapes after adding the outcomes of the dingo trials (i.e. the predicted reporting rate for each of the 557 landscapes) to the design matrix.

To characterise uncertainty in the relationship between dingoes and fire, we generated scenarios based on both the mean and upper and lower 95% confidence intervals for all scenarios.

Results

From over 8,369 camera trap nights (red foxes, small mammals) and 210 scat surveys (dingoes), red foxes were detected at 81% of landscapes and 42% of sites, Mitchell's hopping mice and silky mice at 95% of landscapes and 46% and 65% of sites respectively, and dingoes were detected at 62% of landscapes and 29% of sites.

The extent of fire-ages directly affected dingoes and silky mice, but not foxes and Mitchell's hopping mice. The reporting rate of dingoes was positively related to RECENTLY BURNED (<11 years post-fire) and LONG UNBURNED (>35 years post-fire) although only the former had 95% confidence intervals that did not overlap zero (Figure 2). The reporting rate of red foxes was strongly, negatively related to the reporting rate of dingoes—fox reporting rates decreased by 52% of its range as dingo reporting rates changed from its minimum to maximum. The reporting rate of neither of the small mammals was related to either of the predators. The reporting rate of the silky mouse was positively related to RECENTLY BURNED and LONG UNBURNED, but the effect of LONG UNBURNED was 2.5 times stronger. No predictors had a strong relationship with Mitchell's hopping mouse reporting rate (Figure 2).

Indirect and cumulative effects of fire on foxes were quantified given that fire was influential for dingo reporting rates, which was itself influential for fox reporting rates. There was an indirect effect of RECENTLY BURNED on fox reporting rate of -0.26 (i.e. [fire-dingo pathway = 0.50] * [dingo-fox pathways= -0.52]), and a modest direct impact on fox reporting rate (relevant range coefficient of -0.29, 85% CIs overlapping zero), indicating that as the extent of RECENTLY BURNED changes from 0 to 1, fox reporting rate is predicted to change by 26% of its relevant range due to the indirect effects of fire mediated through dingoes. Scenario analysis showed the substantial difference to fox reporting rates of either accounting for, or ignoring, the impact of fire on dingoes (Figure 3). When ignoring the indirect effect of fire mediated through dingoes, changes in the fire regime (from <11 to 11-35 years) resulted in a rightward shift in the distribution of fox reporting rates ($\tilde{x}$ =0.35, IQR = 0.11 compared to $\tilde{x}$ =0.67, IQR = 0.23). However, the rightward shift in reporting rates was far greater when the effects of fire on dingoes were incorporated into the model. Here, foxes, released from suppression by dingoes due to their avoidance of 11-35 year old vegetation, became far more common ($\tilde{x}$ =0.78, IQR = 0.00) compared to the recently burned scenario ($\tilde{x}$ =0.24, IQR = 0.11) (Figure 3).

Discussion

Our study highlights the importance of considering species interactions in the context of disturbance regimes. Although fire had a limited direct impact on mesopredator (red fox) occurrence, fire had flow-on effects for foxes as it altered the reporting rate of an apex predator (dingoes), which impacted foxes in turn. Hence, by affecting the apex predator, fire history shaped the spatial pattern of suppression of an invasive mesopredator across the landscape. However, suppression of the red fox was not sufficient to trigger a positive response by two native small mammals, and thus we did not observe evidence of a disturbance-induced trophic cascade. Despite this, our results highlight the need to consider the indirect outcomes of ecological disturbance on biological communities and trophic interactions.

The effects of fire

Fire is a strong driver of animal communities in ecosystems around the world, including mammals (Fox 1982; Kelly *et al.* 2011; Hale *et al.* 2016). Here, we found two species responded strongly to fire— the dingo and the silky mouse—both showing a preference for early successional habitat, while the silky mouse also was positively associated with the extent of long unburned vegetation (thus avoiding mid-successional areas). The response of animals to fire history is often explained in relation to how post-fire succession affects vegetation (Fox 1982; Kelly *et al.* 2011; Nimmo *et al.* 2014). This is likely to be the case for the dingo in our study region. In mallee ecosystems, recently burned areas have simpler vegetation structure compared to mid and later successional vegetation (Haslem *et al.* 2011). Large-bodied, coursing and pursuit predators, such as dingoes, often prefer more open habitat as it facilitates easier movement and hunting throughout landscapes (e.g. black bears (*Ursus americanus*) (Stratman & Pelton 2007), and grey wolves (Ballard *et al.* 2000)). Dingo hunting of kangaroos (their preferred prey in the region: Davis *et al.* 2015) may be more efficient in such areas due to the relatively simplified habitat.

Recently burnt vegetation is often characterized by a flush of herbs and grasses, which, combined with their burrowing habit (and thus reduced reliance on vegetation structure), may provide food resources (e.g. seeds) for silky mice and explains their preference for burnt vegetation. Silky mice are also known to feed heavily on seeds of a fire-sensitive shrub, *Banksia ornata*. This explains their preference for landscapes with less mallee vegetation—as *B. ornata* is associated with heathy communities in the region—as well as their preference for long unburned areas, as *B. ornata* produces the most seed at ~40 years post-fire (Gill & Mcmahon 1986)

Interactions between apex- and meso-predators

We found evidence that dingoes suppress red foxes—a trend consistent with the mesopredator suppression hypothesis (Ritchie & Johnson 2009) and studies of predator interactions elsewhere (Glen *et al.* 2007; Colman *et al.* 2014). While this relationship has been observed in eastern Australian forests (Johnson & Van Der Wal 2009) and in the arid zone (Letnic & Koch 2010), our study suggests suppression of foxes by dingoes also occurs in semi-arid environments. Collectively, this body of evidence suggests dingoes are capable of suppressing red foxes across a considerable extent and range of Australian environments.

The effects disturbance and predation have in shaping the structure and function of ecological communities are well established (Hobbs & Huenneke 1992; Ripple *et al.* 2014). Emerging from our study though, is the important role disturbance may have in affecting the dynamics of predator-predator interactions, and hence the potential to initiate disturbance-induced trophic cascades. In consideration of how pervasive disturbance events (e.g. fires, floods, droughts and other extreme weather events) are across the globe, it becomes evident that interactions between disturbance, predators, and prey may be more common than appreciated. Natural experiments that take advantage of spatial and temporal variation in disturbance (e.g. fire applied to different parts of landscapes as part of planned management burns), coupled with the exclusion of certain predators from some of these same areas, would allow behavioural and population responses of other predators and prey to be monitored (for example approaches see box 2 in Ritchie *et al.* 2012), and hence, help to address important knowledge gaps.

Contrary to our prediction, we found that the two small, native mammal study species did not benefit as a result of mesopredator suppression. Foxes can be important predators of small mammals, and foxes are known to prey upon Mitchell's hopping mouse, silky mouse and house mouse (e.g. Davis et al. 2015). Further, foxes have a generalist diet (Spencer, Crowther & Dickman 2014), which depending on ecosystem context and state (Greenville *et al.* 2014), can include a high proportion of rodent species including hopping mice (Cupples *et al.* 2011). Further, experimental work shows small mammals (e.g. hopping mice) have higher abundance in the presence of dingoes where foxes are suppressed in arid (Gordon *et al.* 2017), and forest environments (Colman *et al.* 2014). That we did not observe the same relationship here may be because we only assessed the potential benefits of mesopredator suppression for two prey species. Given the many potential prey species in the study region (Davis *et al.* 2015), such benefits may be present for other, unstudied species (e.g. mallee ningaui *Ningaui yvonneae*, western pygmy possum *Cercartetus concinnus*).

It is also possible that the positive effects of fox suppression by dingoes were undone by another invasive predator in the region, feral cats. Feral cats are also major predators of rodents and other small mammals in Australia (Doherty *et al.* 2015a). We did not record feral cats frequently enough to analyses their relationships with fire, dingoes and foxes, but these relationships are likely to be complex given evidence that cats are known to be drawn to recently burned areas (McGregor *et al.* 2016) and to avoid both dingoes (Brook *et al*. 2012) and foxes (Molsher *et al.* 2017). If foxes suppress cats to a greater extent than dingoes, then it is possible that cats at times benefit from the suppression of foxes by dingoes. More work is needed to assess how cats respond to mesopredator suppression of foxes by dingoes, and how mesopredator suppression affects prey communities in this ecosystem, considering the response of other mammals, reptiles and birds.

Conservation and management implications

There is increasing need for integrated, whole-of-ecosystem approaches to managing landscapes and the simultaneous effects of disturbance (fire) and invasive or pest animals (Doherty *et al.* 2015b). Our study highlights the potential for fire management to influence predator management. Both are highly managed within the region—and in many regions across the world—but largely independently. We have shown that a particular fire regime—one that minimized the extent of mid-successional vegetation—can benefit dingoes. The presence of dingoes in recently burned landscapes is particularly noteworthy given recent evidence that invasive mesopredators can compound the impacts of fire on native mammals (McGregor *et al.* 2014; Hradsky *et al.* 2016; Leahy *et al.* 2016). Could dingoes reduce the impact of fire by suppressing invasive mesopredators in recently burned landscapes? Further work on a broader array of prey species and in different ecosystems is required to answer this question, but given that dingoes have benefited prey in others regions (Colman *et al.* 2014; Gordon *et al.* 2017), our results add to a growing body of evidence that supports this possibility.

Authors' contributions

All authors helped conceive the ideas for the paper and designed the methodology, WLG conducted the fieldwork, WLG, JAL and DGN analysed the data, WLG, EGR and DGN led the writing of the paper. All authors gave final approval for publication.

Data accessibility

Data available from the Dryad Digital Repository: doi:10.5061/dryad.m8k99 (Geary, Ritchie, Healey, Lawton, Nimmo, 2018).

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Figures

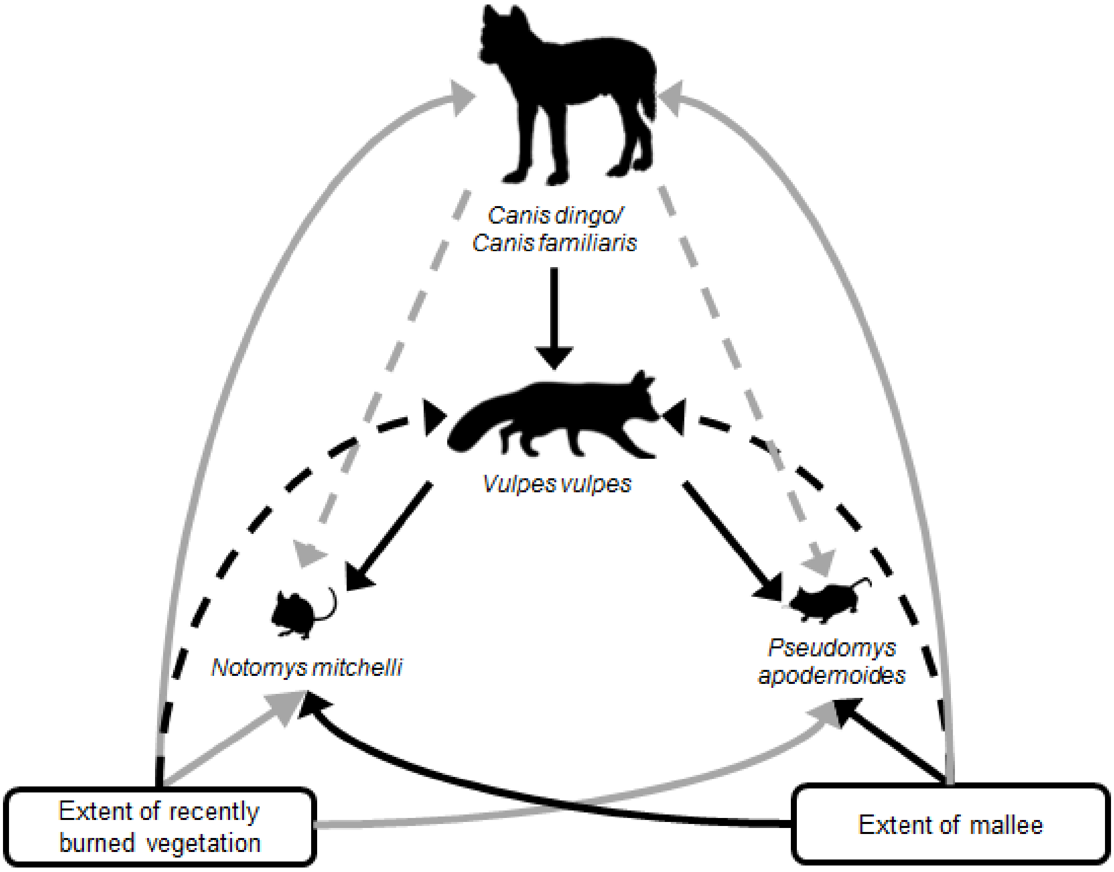

Figure 1: A priori piecewise structural equation model describing predator-predator, predator-prey interactions and effects of fire history and vegetation on each species for the Big Desert-Wyperfeld region, northwest Victoria. Grey lines represent predicted positive relationship pathways, black lines represent negative relationship pathways, and dashed lines represent indirect effects. Justification for the model is given in Table S1. For simplicity, only relationships between RECENTLY BURNED (not LONG UNBURNED) are included in this figure.

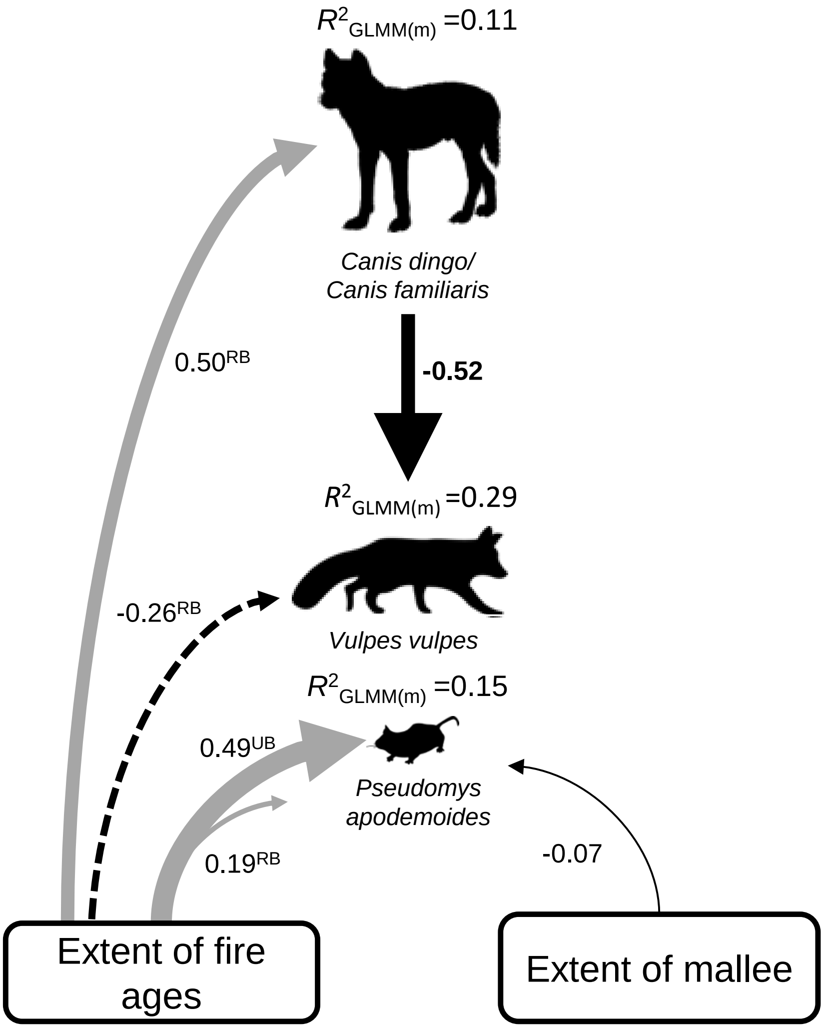

Figure 2: Final piecewise structural equation model showing relationship pathways influencing predator and prey incidence in the Big Desert-Wyperfeld region, northwest Victoria. Black lines indicated a negative relationship pathway, grey lines indicate a positive relationship pathway, solid lines represent direct effects and dashed lines represent indirect effects. Pathways for which 95% confidence intervals overlap zero are not shown. The fit for each node is indicated by the R^2 value. Fire history pathways are included as superscripts to the coefficients (UB = long unburnt, RB = recently burnt).

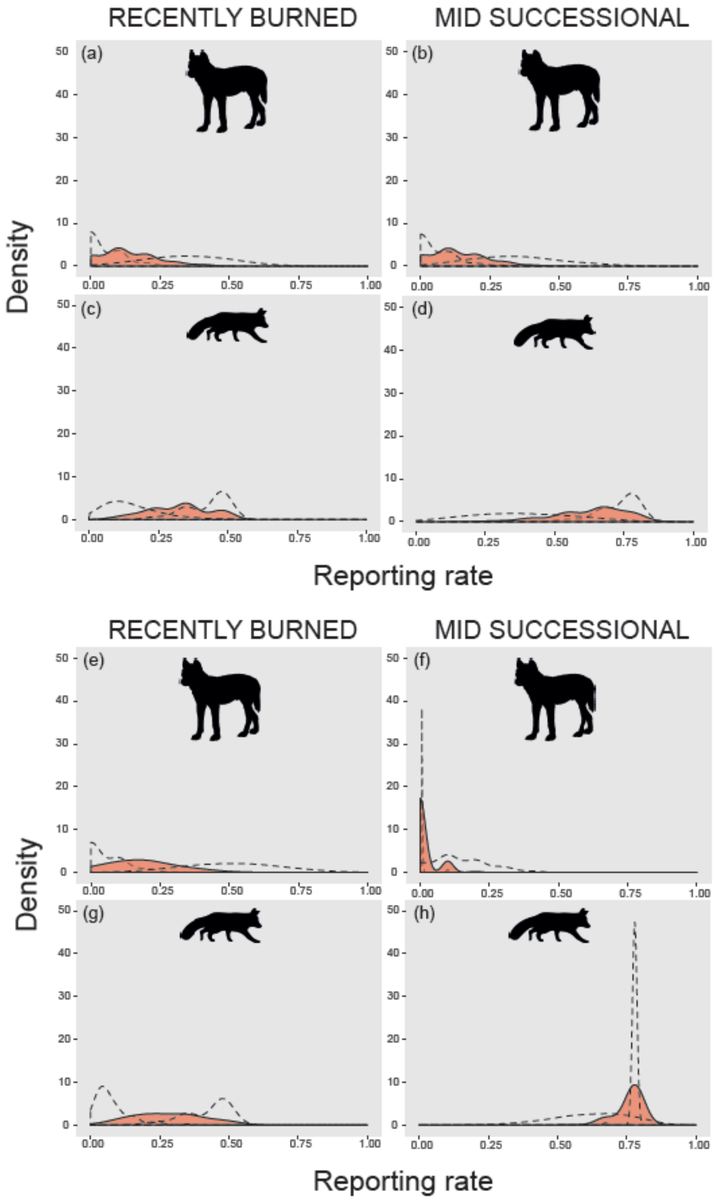

Figure 3. Kernel density plots of dingo and fox reporting rates derived from scenario analysis. In the first scenario (top, a-d), the relationship between dingoes fire history (as seen in the fitted SEM) is ignored. Vegetation of the entire study region shifts from being RECENTLY BURNED (< 11 years since fire, a, c) to being entirely within the 11-35 age class (b, d) (i.e. both RECENTLY BURNED and LONG UNBURNED set to zero). In the second scenario (bottom, e-h), the same shift in successional states occurs, but the relationship between dingoes and fire (derived from the fitted SEM) is included, such that dingoes become less common as the fire age transitions from RECENTLY BURNED to mid successional. Solid line = predictions derived from the mean, dotted lines = predictions derived from upper and lower 95% confidence intervals.