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Identifying historical and future global change drivers that place species recovery at risk

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Abstract

Ecosystem management in the face of global change requires understanding how co-occurring threats affect species and communities. Such an understanding allows for effective management strategies to be identified and implemented. An important component of this is differentiating between factors that are within (e.g. invasive predators) or outside (e.g. drought, large wildfires) of a local manager's control. In the global biodiversity hotspot of south-western Australia, small- and medium-sized mammal species are severely affected by anthropogenic threats and environmental disturbances, including invasive predators, fire, and declining rainfall. However, the relative importance of different drivers has not been quantified. We used data from a long-term monitoring program to fit Bayesian state-space models that estimated spatial and temporal changes in the relative abundance of four threatened mammal species: the woylie (*Bettongia penicillata*), chuditch (*Dasyurus geoffroii*), koomal (*Trichosurus vulpecula*) and quenda (*Isoodon fusciventor*). We then use Bayesian structural equation modelling to identify the direct and indirect drivers of population changes, and scenario analysis to forecast population responses to future environmental change. We found that habitat loss or conversion and reduced primary productivity (caused by rainfall declines) had greater effects on species' spatial and temporal population change than the range of fire and invasive predator (the red fox *Vulpes vulpes*) management actions observed in the study area. Scenario analysis revealed that a greater extent of severe fire and further rainfall declines predicted under climate change, operating in concert are likely to further reduce the abundance of these species, but may be mitigated partially by invasive predator control. Considering both historical and future drivers of population change is necessary to identify the factors that risk species recovery. Given that both anthropogenic pressures and environmental disturbances can undermine conservation efforts, managers must consider how the relative benefit of conservation actions will be shaped by ongoing global change.

KEYWORDS
climate change, drought, ecosystem management, ecosystem model, fire, interacting threats, invasive predators, multiple stressors, threatened species

1 | INTRODUCTION

Managing ecosystems requires identifying the key demographic drivers of species' populations, including anthropogenic pressures (e.g. habitat loss, invasive species) (Bergstrom et al., 2021), environmental disturbances (e.g. extreme weather, fire) (Feng et al., 2021; Maxwell et al., 2019) and species' interactions (Bartley et al., 2019). Importantly, these drivers rarely act in isolation (Côté et al., 2016; Simmons et al., 2021). Disturbance processes can shape the distribution of threats (Doherty et al., 2015; Martínez-Ramos et al., 2016), and changes in one species' abundance can lead to changes in others (Elmhagen & Rushton, 2007; Legagneux et al., 2012). Conservation managers must grapple with this complexity (Geary et al., 2019), and with the reality of being able to manipulate only a small subset of drivers acting on ecosystems (Beller et al., 2018). As the world's climate changes, the options for intervening—and the likelihood of achieving meaningful outcomes—are narrowing (Morelli et al., 2020). Yet studies of the drivers of single or multiple species' abundance rarely account for the flow-on effects of ecological change, nor for the leverage of managers to affect ecological outcomes (Pearson et al., 2022).

Environmental disturbances such as fire and drought are fundamental processes that shape ecosystems across the globe (Pausas & Keeley, 2021). Fire and rainfall often interact with anthropogenic threats, such as invasive species and habitat loss, to shape population dynamics (Doherty et al., 2015; Driscoll et al., 2021). Changes in the abundance of one species can then trigger changes in another through processes such as interference or exploitation competition (Cherry et al., 2016; Pasanen-Mortensen et al., 2017). Producing realistic and useful models of ecological communities and the factors that influence them requires approaches that can capture these dynamics (Geary et al., 2020). Ecosystem models, such as structural equation models, are well suited to this because they are able to account for direct and indirect effects on the ecological unit of interest and facilitate modelling of alternate future scenarios (Geary et al., 2020). Such approaches have been used to address complex ecosystem management questions at both the species (Bowd et al., 2021; Feist et al., 2017), and ecosystem scale (Yeates et al., 2020).

Global climate change is already altering local weather patterns (Sippel et al., 2020) and regional fire regimes (Abatzoglou & Williams, 2016; Mariani et al., 2018). Many recent extreme fire seasons have been attributed to climate change, including the western United States, eastern Australia and the Amazon (Barlow et al., 2020; Nolan et al., 2021). Numerous ecosystems, including those that occur in Mediterranean-type climate zones, are experiencing increasingly large, extreme fires as well as shorter fire return intervals, especially in times of prolonged drought (Bowman et al., 2020). These changes are likely to continue to intensify, particularly under current greenhouse gas emissions trajectories (Abatzoglou et al., 2019). More frequent extreme events, such as fire and drought, are likely to have flow-on effects to important ecological resources for species of concern (Maxwell et al., 2019). For example, the compounding effects of fire, drought and habitat loss have affected more than three quarters of Amazonian plant and vertebrate animal species in the last 20 years (Feng et al., 2021). Such disturbances can undermine conservation by cancelling out benefits gained by the actions of land managers (Tulloch et al., 2020). Therefore, as climate change and other global-scale pressures intensify these changes, the options for conservation managers to improve the persistence of species through local-scale actions narrow (Nimmo et al., 2015).

The biodiversity hotspot of south-western Australia is experiencing some of the world's most severe rainfall declines caused by climate change (Prudhomme et al., 2014), with peak wet season (May–July) rainfall already reduced by around 28% in the past 50 years (CSIRO & Bureau of Meteorology, 2020). These changes, alongside predation by invasive predators, habitat loss and fire, have contributed to significant declines in small- and medium-sized mammal populations in recent decades (Wayne et al., 2017). Some of the species that have experienced population change are expected to continue to decline due to further reductions in rainfall (Stewart et al., 2018). For example, populations of the woylie (*Bettongia penicillata*; a 1.3 kg marsupial) declined by ~90% between 1999 and 2006 likely driven largely by predation by invasive red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) (before recovering slightly) (Wayne et al., 2015). The climate envelope of the woylie is also expected to shift by up to 100% by 2080, leading to further declines (Stewart et al., 2018). Shifts in climate are likely to affect fire regimes, as the incidence of unplanned wildfire increases during drought in this region (Boer et al., 2009). The combination of fire and drought will further impact species, their habitats and the effectiveness of recovery actions (Collins et al., 2019; Tulloch et al., 2020).

Conservation in a time of hastening global change requires considering not only the drivers of historical decline and actions that can mitigate them (Lindenmayer et al., 2007), but also how future environmental change might affect the effectiveness of those actions. Previous research in this field focuses mostly on predicting the effect of future disturbances on surrogate metrics, such as habitat suitability rather than species populations (Morán-Ordóñez et al., 2018). Furthermore, studies on species populations themselves focused either on a single species or a single disturbance (Greenville, Brandle, et al., 2018; Lawson et al., 2010; Pauli et al., 2017). The mammalian community of south-western Australia is ecologically diverse, has undergone substantial declines, is vulnerable to multiple effects of climate change, and as such provides a suitable system in which to examine the complexities of ecosystem-based management. Therefore, to diagnose the drivers of spatial and temporal population change for four mammal species of conservation concern that have differing ecological traits and life histories, we built an ecosystem model using a long-term (19 years) monitoring program in the eucalypt forests of the Upper Warren region. We then used this ecosystem model to forecast the potential effects of future changes in weather, fire regimes and invasive predator management, learn what are the implications for the persistence of these threatened species and discuss what management actions are required in the context of future global change.

2 | MATERIALS AND METHODS

2.1 | Study region

This study focusses on approximately 140,000 ha of land managed by the Department of Biodiversity, Conservation and Attractions (DBCA) within the Upper Warren region of south-western Australia, which is fragmented to some extent by freehold land used principally for agriculture or forestry (Wayne et al., 2013) (Figure 1). It has a Mediterranean climate, with warm summers, cool winters and mean annual rainfall of ~650 mm in the north-east and ~1000 mm in the south-west (BoM, 2020). The dominant habitat types are dry eucalypt forest and woodland, dominated by jarrah (*Eucalyptus marginata*), marri (*Corymbia calophylla*) and wandoo (*E. wandoo*). Fire is a prominent disturbance in the region, with regular prescribed burns and occasional wildfires (Boer et al., 2009). Most of the fire within the study region is prescribed fire, and the current fire management policy stipulates that 45% of the study region be less than 6 years postfire at any one time to reduce the likelihood of large-scale severe fires. Therefore, fire history in the region is driven mostly by anthropogenic factors rather than environmental factors (e.g. rainfall) (Boer et al., 2009). Most of the study area has been subject to one or more native timber harvesting events over the last 100 years and while most of the area is now either Nature Reserve or National Park, about a third is State Forest and remains available for timber harvesting until the end of 2023 (Wayne et al., 2006).

Introduced red foxes (*V. vulpes*) and feral cats (*F. catus*) have contributed to the decline of multiple threatened species in the region since the mid- to late 19th century (Wayne et al., 2017). Since 1977, fox control programs have been implemented across the region at varying levels of intensity, ranging from irregular ground baiting to frequent aerial baiting using sodium fluoroacetate (1080 poison) (Wayne et al., 2017). The spatial extent and frequency of baiting across the region was increased considerably in the 1990s, moving to annual or twice-yearly frequencies (Wayne et al., 2017). Quarterly aerial baiting began in 1997 across the region as part of the Western Shield program and still operates today (Wayne et al., 2017).

In this study we focussed on four mammal species that have undergone significant population change and subsequently been the focus of numerous recovery efforts in recent decades: the woylie—a medium-sized fungivorous marsupial, the chuditch (*Dasyurus geoffroii*; 1.1 kg) a carnivorous, wide-ranging marsupial, the koomal (*Trichosurus vulpecula*; 1.6 kg) an arboreal marsupial, and the quenda (*Isoodon fusciventor*; 0.8 kg) a ground-dwelling omnivorous marsupial
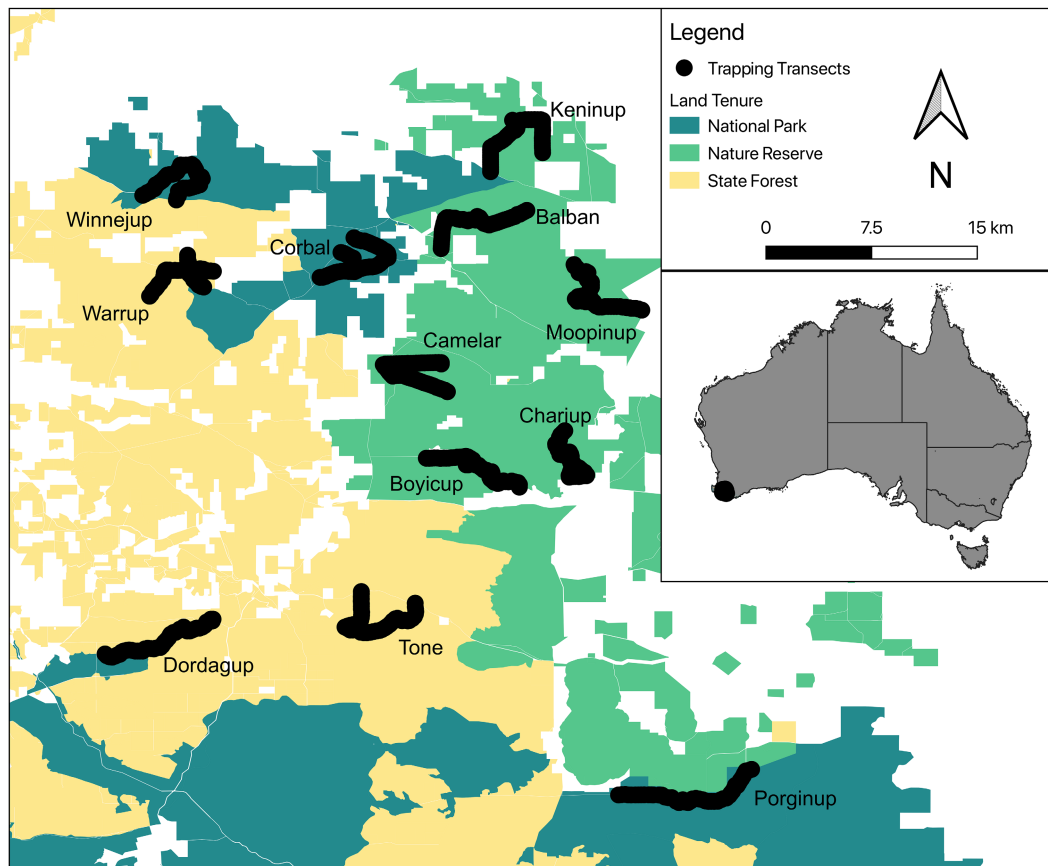
FIGURE 1 Location of 12 mammal trapping transects in relation to public land tenure (National Park, Nature Reserve and State Forest) within the study region in south-west Western Australia, Australia. Labels next to each transect indicate the transect name. White sections of the main map are predominantly cleared private land. *Inset*: Approximate location of the study region (black dot) in south-western Australia.

(Table S1). The north-east and northern parts of the study region (e.g. Balban and Camelar transects, Figure 1) are important locations for each species, due to the presence of more suitable habitat provided by drier, more open jarrah woodlands (Figure 1). All four species are threatened by predation by red foxes and feral cats, but vary in their sensitivity to other disturbances. Table S1 outlines key ecological information on each of the four species in this study.

2.2 | Mammal capture data

This study uses data from a long-term monitoring program from 2000 to 2018 to detect spatial and temporal population changes in small- and medium-sized mammals (Wayne et al., 2017). Cage traps were deployed across 12 transects along forest management tracks and roads, with each transect comprising 50 traps spaced 200m apart (i.e. 600 trap sites total). In each survey session, traps were deployed for four nights and checked every morning. For each individual capture event, the species was recorded, and the animal was marked with a unique ear tag to differentiate between new and re-captured individuals. This allowed for more robust estimates of abundance at each transect by ensuring individuals are not counted twice (Link et al., 2018). While this trapping approach captures a wide array of species, we focus on the four previously mentioned—the woylie, chuditch, koomal and quenda. We used the minimum number of individuals alive for each species at each transect during each survey session, that is, the number of unique individuals captured per session. We used this approach because detections of the four species of interest were too sparse in some instances over the spatial and temporal extent of our study to fit robust mark–recapture models.

We grouped surveys into half-year seasons based on when surveys were conducted each year (January–June but predominantly in the austral autumn, or July–December but predominantly in the austral spring) over the study period (2000–2018). In this analysis, each trap site was only surveyed once in any half-year period, resulting in 38 separate survey periods across the 12 transects. We therefore modelled abundance as the minimum known number of individuals at a given transect and half-year period.

2.3 | State-space abundance models

Hierarchical state-space abundance models are useful for modelling the relative abundance of species across space and time because they allow for explicit partitioning of the latent state of the system (i.e. true abundance), and the observation process (Buckland et al., 2004; Hostetler & Chandler, 2015), which enables differentiation between observation error and process error. This approach has been successfully used to estimate spatial and temporal trends in abundance from long-term monitoring data in a range of species and ecosystems (Greenville, Nguyen, et al., 2018; Scroggie et al., 2018). While state-space models are rarely able to estimate true abundance (Link et al., 2018), the models are consistently able to provide robust

estimates of changes in relative abundance of species through space and time and so are well suited to studying drivers of population change (Kery & Royle, 2020).

State-space models use a dynamic specification of how the abundance at site i will change from time t to time $t+1$. In our specification of the state-space model, we assumed a Poisson distribution for the expected initial abundance ($N_{i,1}$) and for the abundances at $t+1$. We use a Poisson generalised Markov model specification (Sollmann et al., 2015), rather than the traditional Gaussian specification because a generalised specification allows for non-Markovian population dynamics, such as multiple site-scale extinction and re-colonisation events over the course of the time series (Kery & Royle, 2020). For the process model, each site (i) represents an individual transect, and each time step (t) represents a half-year survey period at a given transect.

As each species' abundance varies spatially across the study region, we modelled the initial abundance ($N_{i,1}$) of each species at each site using a Poisson distribution with transect-level overdispersion, where λ_i is the expected initial abundance at transect i.

$$N_{i,1} \sim \text{Poisson}(\lambda_i) \tag{1}$$

We parametrised our generalised state-space models to predict abundance estimates ($N_{i,t+1}$) as a function of abundance at the previous time step ($N_{i,t}$), a population growth rate ($\gamma_{i,t}$) with transect and time-specific random effects, and the expected number of colonising individuals at time t (ρ_t).

$$N_{i,t+1} \sim \text{Poisson}(N_{i,t} \times \gamma_{i,t} + \rho_t) \tag{2}$$

$$\log(\rho_t) \sim \text{Normal}(0, \sigma_\rho^2) \tag{3}$$

For our observation model, we used the binomial model from Dail and Madsen (2011) where $C_{i,t}$ is the observed number of individuals at a given transect i at time t (i.e. the survey data), $N_{i,t}$ is the estimated abundance and $p_{i,t}$ is the probability of detecting an individual at transect i and time t. To account for variation in survey effort influencing detection probability, we included a coefficient term $\beta_{p,1}$ describing a linear relationship with survey effort (i.e. the number of trap nights a transect was surveyed at time t) to account for occasional variation in effort due to operational considerations. We also allowed for overdispersion in detection probability ($\alpha_{i,t}$) across space and time, which may have been caused by variation in trap availability and/or overall abundance of the species being trapped (Kery & Royle, 2020; Wayne et al., 2017).

$$C_{i,t} \sim \text{Binomial}(N_{i,t}, p_{i,t}) \tag{4}$$

$$\text{logit}(p_{i,t}) \sim \alpha_{i,t} + \beta_{p,1} \times \text{Effort}_{i,t} \tag{5}$$

Because chuditch captures were relatively sparse, we used a simplified state-space model to estimate chuditch abundance. The model for chuditch abundance allowed for overdispersion in

the population growth rate (γ_i) across sites and in random immigration rates over time ρ_t. The chuditch model did not allow for overdispersion in detection probability or initial abundance at a site ($N_{i,1}$). We used uninformative priors for all parameters in each model. For details on the priors used, refer to the Supplementary Material.

2.4 | Model fitting and checking

We fitted each species' state-space model to the count data using Bayesian Markov Chain Monte Carlo simulations using the R package jagsUI (Kellner, 2015). Each model was run with three chains and had a burn in of 500,000 iterations before sampling another 500,000 iterations. We retained every 500th value due to memory constraints, leaving 1000 values for inference. We assessed model convergence by ensuring all Rhat values were <1.1 (Gelman & Rubin, 1992), and visually inspecting the trace plots of each parameter. Model convergence was not achieved for the quenda state-space models after 1000,000 iterations. Therefore, we included the quenda in the structural equation modelling (SEM) framework using a reporting rate variable that represented the number of detections of the species at a transect out of the total sampling effort (trap nights) at a transect during a sampling period. Modelling the quenda reporting rate as a multi-trial binomial distribution therefore allowed us to account for variable survey effort across the study period.

2.5 | Structural equation model construction

To understand the drivers of landscape-scale spatial and temporal changes in the abundance of our four study species, we used a piecewise SEM approach. Piecewise SEM is a method that can facilitate modelling of individual relationships between two ecosystem components, while also accounting for how relationships can flow through a system (Grace, 2006; Shipley, 2009).

To develop our SEM, we first built a meta-ecosystem model based on our understanding and knowledge of the Upper Warren jarrah forest ecosystem (Wayne et al., 2015, 2017; Wayne, Liddelow, et al., 2011; Yeatman et al., 2016). Best-practice SEM development requires the development of a meta-model as it facilitates transparency regarding which potentially important ecosystem components are not represented in the SEM and therefore may be a source of structural uncertainty (Grace et al., 2012). The meta-ecosystem model for the Upper Warren jarrah forest is represented in Figure S2. Then, from the meta-ecosystem model, we developed our alternative a priori SEMs, based on our hypothesised causal relationships between ecosystem components with sufficient data to model (all links are shown in Figure 2; alternative a priori SEMs shown in Figures S4–S7). The a priori SEM included variables relating to predator management, fire management, timber harvesting, resource availability and landscape-scale habitat extent, as we expected these variables and the interactions between them to be important in explaining the spatial and temporal variation in abundance or activity of our four study species (Table S1). Details of how each
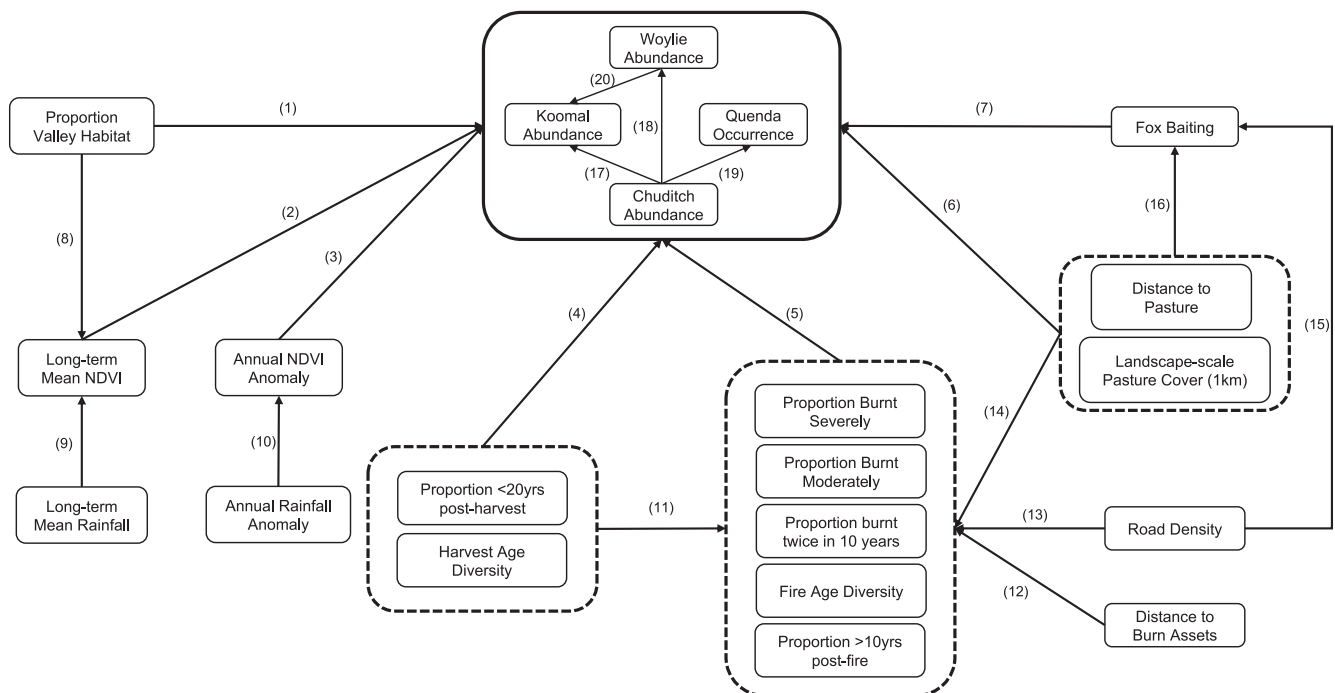
FIGURE 2 Conceptual diagram of the a priori structural equation model used to model drivers of changes in abundance or activity of the woylie, the chuditch, the koomal and the quenda. Numbers correspond to pathways identified in Table S1. Dashed boxes indicate sets of variables that are related to a common disturbance regime (e.g. fire, timber harvesting or habitat extent). Specific hypothesised causal pathways modelled in alternative structural equation modelling are shown in Figures S4–S7. The meta-ecosystem model from which this was developed is outlined in Figure S2. NDVI, Normalised Difference Vegetation Index.

covariate was compiled are located in the Supplementary Materials (Table S2).

2.6 | Structural equation model fitting

We implemented our structural equation model (SEM) analysis of the drivers of mammal population change using a Bayesian information theoretic framework (Garrido et al., 2021). We used Bayesian SEM because of the flexibility in terms of model form and for consistency in interpretation with our state-space models of mammal abundance. Our SEM had multiple sub-models with the following groups of response variables: (1) woylie abundance, (2) chuditch abundance, (3) koomal abundance, (4) quenda activity, (5) fire, (6) fox baiting and (7) primary productivity. Prior to fitting our SEM, we tested for correlation between predictor variables by calculating the Pearson correlation coefficient for each pair of covariates. Two pairs of our landscape-scale variables were correlated ($r_s > 0.7$ or < -0.7) (i.e. Road Density and mean Normalised Difference Vegetation Index [NDVI]; proportion of a transect <20 years post-harvest and the Shannon Diversity of harvest age-classes) and thus could not be included in the same sub-models of abundance or activity for the four species of interest. Therefore, to test the relative importance of including each of these four variables and their associated model structures we built four alternate SEMs to deal with this structural uncertainty and identify the most parsimonious SEM structure. The four alternate SEMs and rationale for hypothesised pathways can be found in the Supplementary Material (Table S3). Included in the SEM model selection phase was a null model (i.e. no covariates) and a random effects-only model, giving a total of six alternate SEMs. We used the Widely Applicable Information Criterion (WAIC) to identify the most parsimonious SEM structure, which is calculated using the posterior likelihood of each model (Gelman et al., 2014). The SEM with the lowest WAIC value within a candidate set can be interpreted as being the most parsimonious model, balancing model complexity and the fit of the model to the data (Gelman et al., 2014).

We implemented our analysis using a Bayesian framework in the R package brms, which uses the programming language *Stan* (Bürkner, 2017). By fitting each SEM in brms, the coefficients of each bivariate relationship are directly comparable in terms of effect size. Each sub-model was fit as a generalised linear mixed effects model and included Phase as a random intercept. Because we used the mean of the distribution of predicted abundance for each species at each sampling period (i.e. a positive non-integer), this necessitated fitting the woylie, chuditch and koomal abundance sub-models with gamma distributions. The quenda model of reporting rate (activity) was fit with a binomial distribution, and fire, fox baiting and primary productivity with Gaussian distributions. Prior to model fitting, all continuous covariates were scaled and centred using the R base function 'scale'.

Each SEM was run with three chains and a burn in of 2000 iterations before sampling another 2000 iterations, leaving 2000 values

for inference. We assessed model convergence by ensuring all Rhat values were <1.1 (Gelman & Rubin, 1992), and visually inspecting the trace plots of each parameter. The SEM with the lowest WAIC value was determined to be the most parsimonious and was used for subsequent inference. We calculated the Bayesian R^2 value for the SEM with the lowest WAIC, as well as the random effects-only SEM to determine the variance explained by both the fixed and random effects in each sub-model.

2.7 | Scenario analysis

We used scenario analysis to assess how implementing different management strategies might affect the abundance or activity of our four species of interest (Grace et al., 2015). Scenario analysis (i.e. queries) is a common application of structural equation models, particularly in the context of global change drivers (Grace et al., 2012). We identified 11 alternate plausible ecosystem management strategies that covered potential forest management futures, with a focus on fire and weather (Table 1). We implemented these scenarios by using the most parsimonious SEM to predict direct and indirect consequences of each scenario using the *fitted* function using the brms R package, sampling each prediction 10,000 times to account for uncertainty in the prediction. Where relevant, we first calculated the direct effects of the scenario on intermediate variables (e.g. rainfall anomaly→NDVI anomaly; scenarios 2, 5, 10 and 11), before using the outputs of this prediction to predict the abundance/activity of the species of interest.

Annual rainfall in the Upper Warren region is expected to be 30% below the long-term average by 2030 due to climate change (Stewart et al., 2018). Therefore, our rainfall scenarios used a conservative decline in rainfall of 20% below the long-term average. In the Upper Warren region, prescribed burns are effective at reducing wildfire risk for 6 years post-burn (Boer et al., 2009), and so under the current fire management policy of having 45% of the landscape less than 6 years post-fire it is realistic to expect that 25% of the landscape could be 3 years or less post-fire at any given time (Table 1; Howard et al., 2020). Increases in the extent and frequency of fire (moderate or severe) are also expected under climate change, either through wildfire or the required increase in prescribed burning to combat increased wildfire risk. Therefore, we also included scenarios that represent large, but plausible, increases in the extent of moderate and severe fire (Table 1). For the increased fox baiting scenarios, we modelled a plausible increase in fox baiting efforts to 45 baits/km^2 per annum, which is the baiting intensity already occurring in one conservation hotspot within the study region. All covariates that were not changed for the scenario were held at their mean, and the Baseline scenario makes predictions based on all covariates being held at their mean (Table 1). We present the full distribution and a boxplot of the results of each prediction and compare to the median prediction of the baseline scenario. Figure S8 shows the distribution of observed values of each of the covariates when

TABLE 1 Table showing eight scenarios analysed using predictions from the best structural equation model to understand how alternate management scenarios may affect the abundance/activity of the woylie, the chuditch, the koomal and the quenda.

Scenario name	Description
1. Base	All covariates held at their mean
2. Low Rainfall	Rainfall anomaly of the previous 12 months is set to −0.2. All other covariates held at their mean
3. Moderate Fire	25% of a transect burnt moderately in the previous 3 years. All other covariates held at their mean
4. Increased Baiting Intensity	Baiting intensity set to 45 baits per km^2 per year. All other covariates held at their mean
5. Low Rainfall + Moderate Fire	Rainfall anomaly of the previous 12 months is set to −0.2. 25% of a transect burnt moderately in the previous 3 years
6. Increased Moderate Fire	50% of a transect burnt moderately in the previous 3 years. All other covariates held at their mean
7. Increased Severe Fire	50% of a transect burnt severely in the previous 3 years. All other covariates held at their mean
8. Increased Short-Interval Fire	50% of a transect burnt at least twice in the previous 10 years. All other covariates held at their mean
9. Increased Severe Fire + Increased Baiting Intensity	50% of a transect burnt severely in the previous 3 years. Baiting intensity set to 45 baits per km^2 per year. All other covariates held at their mean
10. Low Rainfall + Increased Severe Fire	Rainfall anomaly of the previous 12 months is set to −0.2. 50% of a transect burnt severely in the previous 3 years. All other covariates held at their mean
11. Low Rainfall + Increased Severe Fire + Increased Baiting Intensity	Rainfall anomaly of the previous 12 months is set to −0.2. 50% of a transect burnt severely in the previous 3 years. Baiting intensity set to 45 baits per km^2 per year. All other covariates held at their mean

Note: Where relevant (e.g. rainfall anomaly in the previous 12 months), scenarios are mediated by nodes and links that may fall between the abundance estimates and the focal covariate of the scenario.

trapping sessions were conducted, in relation to the covariate values tested in the scenario analyses.

3 | RESULTS

3.1 | Mammal abundance

Over the 19-year study period, mammal trapping resulted in 6278 woylie captures (0–0.165 unique individuals per trap night at a transect in a given session), 7363 koomal captures (0–0.126 unique individuals per trap night), 848 chuditch captures (0–0.055 unique individuals per trap night) and 167 quenda captures (0–0.008 unique individuals per trap night) from >39,800 survey nights. All four species exhibited considerable spatial and temporal variation in abundance or activity. Woylie abundance was highest in most transects in the early 2000s before undergoing a significant population crash then slight recovery from 2015 onwards (Figure S2a). Chuditch abundance showed similar variation, but with peaks in the period between 2010 and 2015 (Figure S2b), whereas koomal abundance peaked mostly between 2005 and 2015 (Figure S2c). Quenda abundance could not be modelled, but their capture rates were highly variable across the study period (Figure S2d).
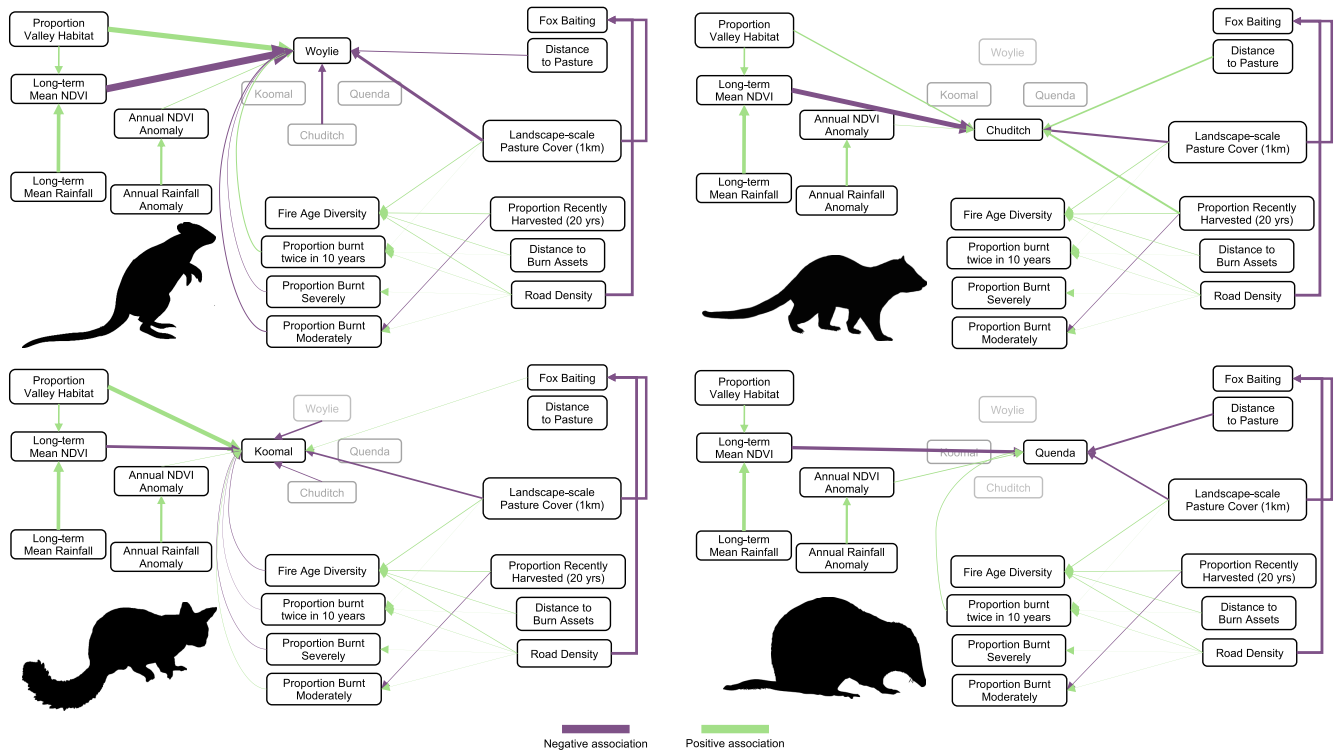
3.2 | Structural equation modelling

The most parsimonious SEM (SEM2; Figure S5) included the covariates such as the proportion valley habitat, mean NDVI, the proportion of buffered transect harvested within 20 years and landscape-scale pasture cover as predictors of mammal abundance/activity, and was

clearly best according to WAIC (Table S4). This SEM explained a considerable amount of variation in woylie ($R^2 = .59$), chuditch ($R^2 = .53$) and koomal ($R^2 = .72$) abundance, and moderate amounts of variation in quenda activity ($R^2 = .32$) (Table S6).

All four species had negative associations with mean NDVI and the landscape-scale amount of pasture, and positive associations with valley habitat (except quenda) and the annual NDVI anomaly (Figure 3). We found negative associations between distance to pasture for woylie and quenda abundance and activity, but a positive association for chuditch abundance (Figure 3). Proportion of recently harvested habitat had a positive association with chuditch abundance (Figure 3). Of the fire covariates, the proportion of severely burnt habitat had a negative effect on woylie and koomal abundance (Figure 3). Chuditch abundance was negatively associated with woylie and koomal abundance, and koomal abundance was negatively associated with woylie abundance (Figure 3). Fox baiting intensity had a positive association with koomal abundance, a slight positive association with woylie abundance and a negative association with quenda activity (Figure 3; Table 2). Coefficients and 90% credible intervals for all paths in the most parsimonious structural equation model are shown in Table 2 for the four species of interest and Table S5 for all other paths.

3.3 | Scenario analysis

The combination of increased extent of severe fire and a reduction in rainfall will likely reduce the abundance or activity of all four species, but this effect was mitigated somewhat for koomal and woylie by increased fox baiting (Figure 4). The woylie, the chuditch, the koomal and the quenda had much lower abundances in low rainfall scenarios compared with the baseline, as represented by the dotted lines in Figure 4.

FIGURE 3 Graphical representation of the final most parsimonious structural equation model, broken up into parts representing the paths for each of the four species studied: woylie (top-left), chuditch (top-right), koomal (bottom-left) and quenda (bottom-right). Paths shown are only those with 90% credible intervals that do not overlap zero. Purple paths indicate negative associations and green paths indicate positive associations between SEM nodes. The width of each path corresponds to the strength of the association between the two SEM nodes, with thicker paths indicating stronger associations. Coefficients and 90% credible intervals for all paths modelled in the SEM can be found in Table S3. NDVI, Normalised Difference Vegetation Index; SEM, structural equation modelling.

The severe fire scenario had a negative effect on woylie and koomal abundance (Figure 4a,c) and quenda activity, but a positive effect on chuditch abundance (Figure 4b). Increased fox baiting intensity had a positive effect on woylie and koomal abundance, and a negative effect on quenda activity. The scenario representing the current fire management policy (moderate fire) had no discernible effect on each of the four species (Figure 4). The response of quenda activity to any of the fire-only scenarios was highly uncertain, with no clear patterns except for a potential reduction in activity in the severe fire scenario (Figure 4d).

4 | DISCUSSION

Integrated and multi-species management is often a goal of conservation (Grumbine, 1994; Lindenmayer et al., 2007), but is hard to achieve due to the complexity of interacting abiotic and biotic factors (Côté et al., 2016), uncertainty (Geary et al., 2020), conflicting requirements of species (Connell et al., 2019) and limited conservation budgets (Wintle et al., 2019). In the face of global change, managers must also disentangle drivers of historical and potential future population changes for multiple species. Here, we modelled the influence of key demographic drivers (fire, habitat loss or conversion, predator management and primary productivity) on four threatened medium-sized mammal species with contrasting ecological traits, as

well as the interactions between the species. Analysis of future fire and rainfall scenarios revealed that all four species are vulnerable to ongoing declines in rainfall. In addition, severe fire events may compound declines, particularly when they occur in concert with low rainfall, but increased invasive predator management could mitigate these effects somewhat for two species. The mechanisms driving these declines are potentially linked to the effect of fire and drying climate on food and shelter availability, and management could be further improved by understanding the causal mechanisms (e.g. water and food availability, ecophysiological factors, etc.) driving these population changes. Our ecosystem-based approach allows conservation practitioners to pinpoint which drivers are likely to be most important to address in future management plans. Our results show that considering multiple species and multiple disturbances, and planning actions accordingly (Stephens et al., 2018), is increasingly important for managing ecosystems in this era of global change.

Our finding that mammal spatial and temporal population trends within our study region are associated more with environmental factors (specifically, habitat availability/amount and productivity) than land management actions within the range observed in this study (fox baiting and timber harvesting) is not surprising. Historical declines in biodiversity are mostly linked to habitat loss and fragmentation (Caro et al., 2022). However, a recent global study found that rapid warming associated with climate change was a stronger predictor

TABLE 2 Coefficient means and 90% credible intervals for the paths in the most parsimonious structural equation model directly influencing the abundance and activity of the woylie, chuditch, koomal and quenda.

	Woylie			Chuditch			Koomal			Quenda		
Predictor	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI	Mean	LCI	UCI
Bait Intensity	0.12	−0.03	0.27	−0.01	−0.12	0.10	**0.08**	**0.01**	**0.15**	−0.16	−0.35	0.04
Chuditch Abundance	**−0.49**	**−0.67**	**−0.29**				**−0.19**	**−0.27**	**−0.11**	−0.08	−0.26	0.10
Distance to Pasture	**−0.22**	**−0.39**	**−0.05**	**0.39**	**0.29**	**0.49**	−0.02	−0.09	0.05	**−0.39**	**−0.58**	**−0.20**
Fire Age Diversity	−0.08	−0.25	0.08	0.07	−0.03	0.17	**−0.12**	**−0.21**	**−0.04**	−0.17	−0.35	0.01
Mean NDVI	**−1.67**	**−2.00**	**−1.34**	**−1.17**	**−1.35**	**−0.99**	**−0.66**	**−0.80**	**−0.52**	**−0.79**	**−1.08**	**−0.50**
NDVI Anomaly	**0.16**	**0.03**	**0.30**	**0.10**	**0.02**	**0.18**	**0.06**	**0.00**	**0.12**	**0.19**	**0.05**	**0.33**
Prop <20 Years Post Harvest	−0.17	−0.39	0.06	**0.46**	**0.33**	**0.59**	0.04	−0.04	0.12	−0.25	−0.56	0.05
Prop Burnt Twice (10 Years)	**0.24**	**0.05**	**0.45**	0.10	−0.01	0.22	**−0.06**	**−0.13**	**0.00**	**0.17**	**0.06**	**0.29**
Prop Moderately Burnt (3 Years)	**−0.23**	**−0.42**	**−0.04**	−0.01	−0.11	0.09	**0.08**	**0.01**	**0.15**	−0.03	−0.18	0.11
Prop Pasture (1 km)	**−0.71**	**−0.98**	**−0.44**	**−0.51**	**−0.68**	**−0.35**	**−0.29**	**−0.40**	**−0.18**	**−0.39**	**−0.66**	**−0.12**
Prop Severely Burnt (3 Years)	−0.12	−0.25	0.02	0.05	−0.03	0.14	**−0.10**	**−0.16**	**−0.03**	−0.11	−0.32	0.07
Prop Valley Habitat	**1.22**	**1.02**	**1.41**	**0.32**	**0.21**	**0.43**	**1.05**	**0.95**	**1.16**	0.06	−0.18	0.30
Woylie Abundance							**−0.36**	**−0.45**	**−0.28**			

Note: Predictors with bolded means, LCIs and UCIs are those where the credible intervals do not overlap zero. Coefficients and CIs for all other paths are shown in Table S5.

Abbreviations: LCI, lower credible interval; NDVI, Normalised Difference Vegetation Index; UCI, upper credible interval.
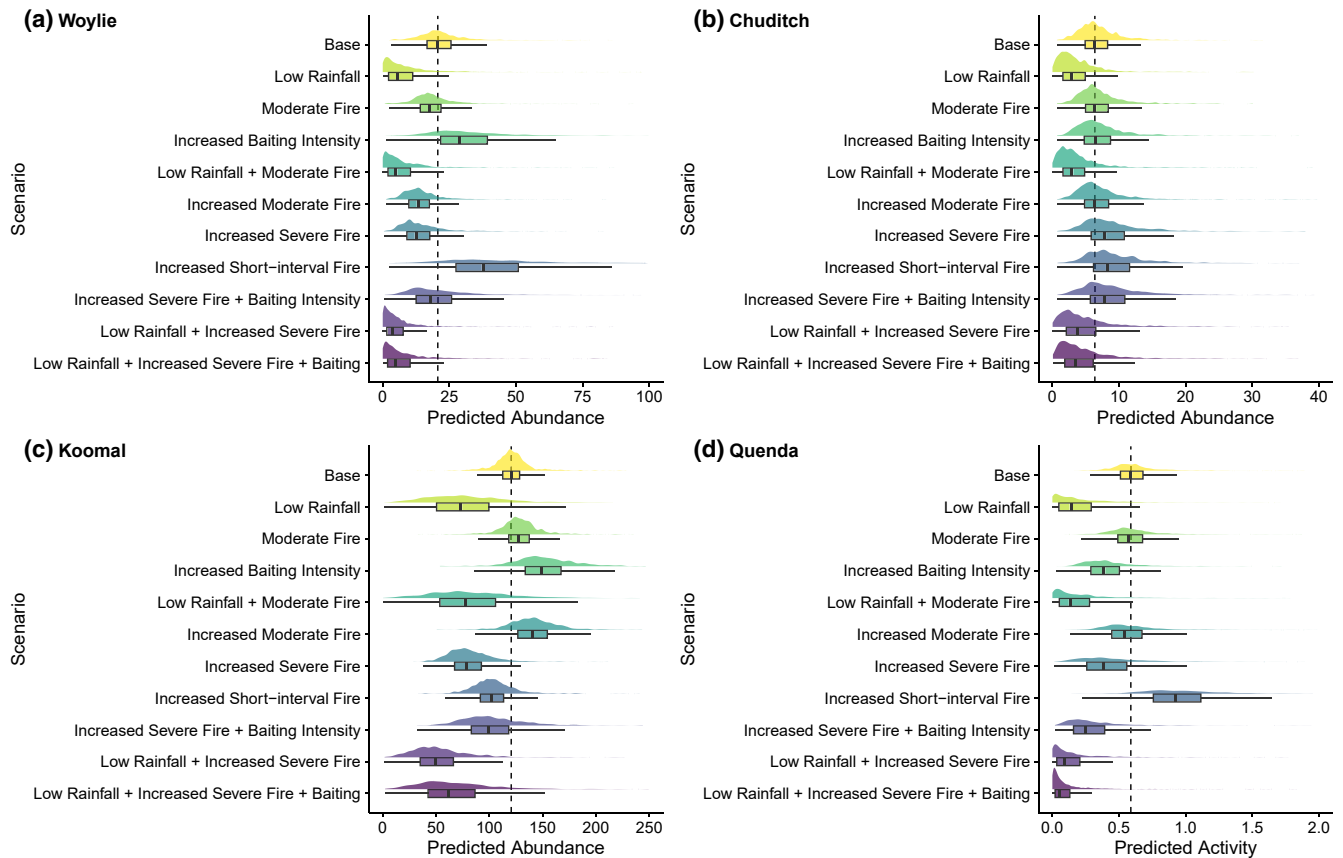
FIGURE 4 Distributions of abundance and activity estimates for each of the 11 scenarios modelled for the (a) woylie, (b) chuditch, (c) koomal and (d) quenda. *X*-axes for each species have been truncated slightly to aid visual interpretation. Predicted abundance represents the estimated number of individuals at a given transect, and predicted activity is the reporting rate of quenda at a transect.

of mammal and bird population declines than anthropogenic land use and protected areas (Spooner et al., 2018), and this trend is expected to continue (Thierry et al., 2022). We found a negative relationship with regional-scale mean long-term primary productivity for all four species. Historically, these species occurred across a wide range of habitats, with much of their former range being in relatively drier environments with more open woodlands and scrub (Wayne et al., 2017). The Upper Warren region is a relatively mesic system compared with typical habitats occupied by the woylie, chuditch and koomal in particular, and so the negative relationships with primary productivity fit with knowledge of these species' ecology (Wayne et al., 2017). However, our results also suggest that these species respond to local-scale patches of higher productivity, through their preference for valley habitat and increased abundance associated with food availability caused by periodic rainfall-driven productivity. In other parts of Australia, such as the arid zone, mammals are more limited by anthropogenic factors like introduced predators than climate change (Greenville et al., 2017). The stronger influence of environmental covariates compared with land management in this study may have arisen if the relatively uniform intensity of management actions across the study region (i.e. almost the entire region has been subjected to some amount of fox baiting, timber harvesting and fire) is sufficient to adequately address those threats. Therefore,

without true control sites (i.e. areas of no management) for each of the management interventions in this study, their modelled effect on the four species in our study may be dampened.

When we predicted future population abundance and activity under different combinations of weather, fire and predator management, we found that the severe fire scenario had a large effect on species abundance and activity, especially when severe fires and drought co-occur in space and time. Like other parts of the globe (Dore, 2005), where rainfall has become less reliable and extended droughts more common, the rainfall in our study region has declined by 28% over 50 years and is likely to continue to decline (CSIRO & Bureau of Meteorology, 2020). This will increase the likelihood of larger, more frequent and severe fires (Abatzoglou et al., 2019; O'Donnell et al., 2014). Our scenario analysis suggests that this rainfall decline combined with increased area of severe fires is likely to compound and hasten declines in each of the four species, especially when these drivers of population change co-occur in space and time. However, increased predator management may be able to mitigate these effects slightly for the koomal and the woylie. These declines would likely be related to reductions in survival and reproductive output when resources are scarce following severe fires that occur during droughts. Our results suggest that the koomal, woylie and quenda are particularly vulnerable. The koomal is a forest dwelling and

hollow-dependent species (Wayne et al., 2005, 2017), and severe fires would reduce shelter resources (Etchells et al., 2020; Inions et al., 1989). Similarly, for the ground-dwelling woylie and quenda, severe fires likely remove important habitat that provides food resources and cover from predators (Collins et al., 2019). By contrast, the chuditch appears to prefer landscapes with recently burnt habitat, which may facilitate improved hunting success for invertebrates and small vertebrates (Wheatley et al., 2020). Our results highlight the need to carefully plan fire management in Mediterranean-type ecosystems (Bradshaw et al., 2018), balancing the needs of multiple species while also ensuring prescribed fire is having a net benefit for fauna vulnerable to severe fire.

Each of the four species had varying responses to the other major driver of disturbance within the region—timber harvesting. Koomal and woylie abundances were not related to the amount of recently harvested habitat at a transect, while chuditch abundance was positively associated. The chuditch has relatively large home ranges and den in diverse successional stages (McGregor et al., 2014), they are able to take advantage of the mix of forest structures present at transects with higher diversity of harvest ages. Woylie abundance is typically unaffected by recent timber harvesting (Wayne et al., 2016), but frequent landscape-scale disturbance by severe fire may reduce resource availability and therefore influence the ability for woylie populations to persist. In jarrah forests, hollow-dependent mammals, such as the ngwayir (western ringtail possum *Pseudocheirus occidentalis*), are negatively associated with recently harvested sites due to declines in hollow availability and food resources after harvesting (Wayne et al., 2006; Wayne, Liddelow, et al., 2011).

We found small positive effects of fox baiting intensity on koomal and woylie abundance and a negative effect on quenda activity. There is evidence that targeted predator baiting can lead to large local population increases of prey (Dexter & Murray, 2009; Kinnear et al., 2010; Orell, 2004), including in the Upper Warren (Burrows & Christensen, 2002; Morris et al., 2000; Wayne et al., 2006). The uncertain signal in our results is likely due to several factors including, (1) fox baiting for conservation began, and associated population recovery occurred, before the period of this study (i.e. the initial effects of fox control on native prey species were not included in this study), (2) the lack of an adequate comparison area in which little or no fox control was conducted and (3) the targeting of high intensity fox baiting in areas where the species in this study have exhibited large population change. It is therefore possible that the current baiting regimes are adequately mitigating the effects of foxes across the region for these four species. However, it is also possible that the true relationship between the four mammal species and fox baiting effort may be masked by other factors, such as the effects of cat predation or, in the case of the woylie, disease (Wayne et al., 2015). When fox abundance is reduced, woylie populations are able to expand rapidly (Wayne et al., 2017). However, an increase in feral cats following fox control has been implicated in the decline of woylie populations in the Upper Warren (Wayne, Maxwell, et al., 2011) and elsewhere (Marlow et al., 2015). Populations responding positively to a reduction in predation pressure, such as those in this region

(Wayne et al., 2017), can also experience subsequent density dependent effects such as overexploitation of resources or disease (Duncan et al., 2020). If this is true, the concurrent decline in rainfall may have reduced the overall carrying capacity of some parts of the region, placing a 'ceiling' on the recovery of species such as the woylie.

In the face of increased frequency of severe fire and drought, conservation of vulnerable species will require renewed focus on actively maintaining climate and fire refuges or areas of known high-quality habitat (Meddens et al., 2018; Morelli et al., 2020). In regions where most fire is prescribed, this means identifying important factors driving population change and mitigating wherever practically possible. Actions such as reducing the frequency, severity and/or extent of fire during fire management and its impact on key resources (e.g. food and shelter) and reducing the effects of other threats such as invasive predators will be especially important in times of low rainfall. This is particularly relevant in Mediterranean-type ecosystems because unburnt refuges are where species often recover from after fire (Jones et al., 2016). Within the Upper Warren, our results suggest that prioritising the careful management of locally productive areas such as valleys that support higher density populations with limited habitat loss may be critical for all four species. In years where drought and severe wildfire risk is high, managers may also need to pre-emptively reduce the impacts of other co-occurring threats that are easier to control (e.g. invasive predators), or plan for more intensive management interventions after disturbances, such translocations.

Our study attempts to synthesise a large amount of information to identify the major historical and future drivers of population change for four threatened species. However, its inferential power is limited by important data gaps. All four species are known to be severely affected by predation by red foxes and feral cats (Wayne et al., 2017). However, there were no available data on predator density or abundance, meaning we used fox baiting intensity to as a proxy for the level of pressure put on the fox population, despite predator management not being a reliable predictor of predator abundance and or of benefit to prey species (Walsh et al., 2012). Quantifying variation in predator abundance over space and time would improve the inferential power of future research, allowing further exploration of how the impact of predators might interact with the fire and climate trends identified in this study. Our future climate and fire scenarios, while informative, were relatively simplistic. Future research should explore short- and long-term spatial and temporally explicit forecasts of future fire regimes and climate to develop fire management strategies that improve the persistence of fauna in the region. Similar approaches have been used elsewhere to identify optimal forest management strategies for species such as the spotted owl *Strix occidentalis* (Jones et al., 2022) and Leadbeater's possum *Gymnobelideus leadbeateri* (Nitschke et al., 2020). Given the complexities identified in this study, management experiments that measure the impact of key variables and drivers of population change on the species of interest will become increasingly necessary to address future ecosystem management challenges (Foster et al., 2016).

CONFLICT OF INTERESTS

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Relevant data and code associated with this study are available on GitHub at https://github.com/billygeary/UpperWarrenSEM and is archived at Zenodo (DOI: 10.5281/zenodo.7686363).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.