Invasive mesopredator release

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Abstract

1. Background.

2. Methods.

3. Results.

4. *Synthesis and applications.*

Key words: Camera trap; Felis catus; invasive predator; interspecific competition; mesopredator release; population density; spatial capture-recapture; spatial mark-resight; species interactions; Vulpes vulpes.

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1. INTRODUCTION

Understanding species interactions is critical for effective invasive species management (Zavaleta et al., 2001). When several invasive species co-occur, management actions that suppress the dominant invasive species may inadvertently benefit subordinate invasive species (Jackson, 2015; Kuebbing & Nuñez, 2015). Subordinate invasive species may be released from direct top-down pressure following a decline in the dominant predator or benefit indirectly from an increase in availability of shared resources (often referred to as mesopredator or competitor release - Crooks & Soulé, 1999; Doherty & Ritchie, 2017; Ruscoe et al., 2011). The release of a subordinate invasive species, particularly predators, can have serious negative implications for native taxa and ecosystem function (Ballari et al., 2016; Courchamp et al., 1999). However, integrated predator management is often far more costly and less feasible than single species control, and so it is important to identify when the extra cost if justified (Bode et al., 2015).

Most knowledge of predator interactions stems from unreplicated "natural experiments" (e.g. range contractions - Crooks & Soulé, 1999) or ad-hoc management interventions (e.g. invasive species eradications - Rayner et al., 2007). However, the occurrence, nature (positive or negative, direct or indirect) and strength of species interactions can vary among species assemblages, predation risk, environmental productivity, management regimes, and other landscape contexts (Alston et al., 2019; Finke & Denno, 2004; Hastings, 2001). Replicating management programs in an experimental framework is logistically challenging, but important for understanding these complexities, discriminating between plausible hypotheses and producing generalisable results in order to inform effective pest management (Christie et al., 2019; Glen & Dickman, 2005; Smith et al., 2020).

Unbiased estimates of invasive predator density are important to infer native prey impacts and set meaningful control targets (Moseby et al., 2019). Controversy around the mesopredator release hypothesis partially stems from the inability to separate behavioral and numerical population processes using traditional modelling approaches (Hayward et al., 2015; Stephens et al., 2015). The suppression of an apex predator may change the behaviour and density of a mesopredator, both of which impact detection rates (Broadley et al., 2019; Rogan et al., 2019). And so–even with experimental designs–it is difficult to interpret changes in unidentified counts or presence-absence records of mesopredators in relation to apex predators. While spatially explicit capture-recapture methods have been developed to robustly estimate predator density by separating out behavioural and observational processes from population density, they have seldom been used experimentally or to investigate multispecies interactions (although, see Forsyth

2

et al., 2019).

Predation by two invasive species, the red fox *Vulpes vulpes* and feral cat *Felis catus*, has played a major role in Australia's high rates of mammalian extinction (Woinarski et al. 2019). Integrated invasive predator management programs are rare. Introduced red foxes (hereafter foxes) are far more commonly controlled than feral cats, as they are more susceptible to poison-baiting, have greater direct economic impacts and fewer legal impediments to their control (McLeod & Saunders, 2014; Reddiex et al., 2007). Nonetheless, feral cats are one of the most widespread and damaging vertebrate species (Doherty & Ritchie, 2017; Legge et al., 2020; Medina et al., 2011). As foxes are larger-bodied (~2 kg difference) and have high dietary overlap with feral cats (Catling, 1988; Glen et al., 2011; Short et al., 1999), the mesopredator release hypothesis predicts that feral cat impacts will increase as fox populations are managed (Soulé et al., 1988). This is alarming because feral cats are extremely difficult to manage in open populations (Fisher et al., 2015; Lazenby et al., 2015).

Evidence that foxes suppress feral cats is inconclusive (Hunter et al., 2018). In parts of Australia where the native apex mammalian predator (the dingo *Canis familiaris*) is functionally extinct and introduced foxes are the largest terrestrial mammalian predator, four studies have observed an increase in feral cat detections following fox control (Marlow et al., 2015; Risbey et al., 2000; Stobo-Wilson et al., 2020). However, two other studies in similar systems did not see any change (Molsher et al., 2017; Towerton et al., 2011). One study with spatial replication detected an increase at one site but not another (Davey et al., 2006), and one study observed a decrease in feral cat activity (Claridge et al., 2010). No previous studies have directly estimated feral cat density in response to fox control.

In this study, we experimentally investigated the role of introduced foxes in top-down suppression of feral cat density in two regions of south-eastern Australia. Foxes and feral cats are the only functional terrestrial mammalian predators in these regions, and each region included at least one area in which foxes were subject to continuous lethal poison-baiting (hereafter "impact landscape"), and a paired area were foxes were not controlled (hereafter "non-impact landscape"). This allowed a sharp focus on the interactions between the two invasive predators, across a gradient of apex predator (fox) occupancy and landscape productivity. Firstly, we investigated finescale linear and nonlinear associations between fox occupancy and feral cats in each region. Secondly, we tested whether fox control increased feral cat densities using traditional experimental approaches: a replicated Control-Impact design in the region with long-term fox control, and a Before-After Control-Impact Paired Series (BACIPS) design in the

3

region with newly implemented fox control. In accordance with the mesopredator release hypothesis, we predicted that (1) feral cat density would be negatively correlated with spatial fox occupancy, and (2) fox control would increase feral cat density. We based inference on direct estimates of feral cat density using spatially explicit mark-resight models.

2. MATERIALS AND METHODS

2.1. Study area

We conducted our study across two regions of south-west Victoria, Australia (Fig. 1). The native temperate forests in both regions are fragmented to varying degrees, primarily by livestock farming and tree plantations. Although once widespread, dingoes are now absent throughout, and a native mesopredator, the tiger quoll *Dasyurus maculatus*, is long absent from the Glenelg region and recently absent in the Otway Ranges (last sighted in 2014 despite extensive camera-trapping). The terrestrial mammalian predator guild is therefore depauperate, with the introduced fox and feral cat being the primary functional mammalian terrestrial predators; birds of prey and snakes are the only other predators present.

Our study landscapes in the Glenelg region, Gunditjmara country, are primarily lowland forest (with an overstorey of *Eucalyptus obliqua* and *E. ovata*, a sparse midstorey and a fern-rich understorey) and heathy woodland (with an overstorey of *E. baxteri s.l.* and *E. willisii*, a sparse midstorey and a diverse understorey of narrow or ericoid-leaved shrubs). It has gently undulating terrain and frequently experiences prescribed burns and wildfires, creating a mosaic of fire histories and vegetation complexity. The area receives an average annual rainfall of 700 mm, with average minimum temperatures of 8.1°C and maximum of 17.6°C (*Bureau of Meteorology*, 2021).

Our study landscapes in the Otway region were in the western section of the Otway Ranges, Gadubanud country. Here, the vegetation is a mosaic of shrubby wet forest and cool temperate rainforest, with an overstorey of tall eucalyptus species (primarily *E. regnans*), *Acacia melanoxylon* and *Nothofagus cunninghamii*. The midstorey is dominated by tree ferns, *Acacia verticillata*, *Pomaderris aspera* and *Olearia argophylla*. The understorey predominantly comprises a dense layer of ferns and graminoids but can be relatively sparse in steep rainforest gullies. Maximum daily temperatures average 19.3°C in summer and 9.5°C in winter; annual rainfall averages 1955 mm (*Bureau of Meteorology*, 2021). This region rarely experiences fire and is nearly ten times more rugged than the Glenelg region (based on the terrain ruggedness index; Riley et al., 1999, averaged within a 10 m radius of each camera-trap site).

2.2. Lethal fox control

Across broad sections of each region, government land managers conduct ongoing fox control for biodiversity conservation. Manufactured poison baits (FoxOff, Animal Control Technologies, Somerton) containing 3 mg of sodium mono-fluroacetate (1080) are buried at a depth of 10 cm at 1-km intervals along accessible forest tracks and roads (Fig. 1). Different road densities across the two regions therefore result in variable poison-bait densities. In the Glenelg region, fox-baiting in the impact landscapes has been ongoing since October 2005, with baits checked and replaced fortnightly (Robley et al., 2014). In the Otway region, fox-baiting commenced in the impact landscape in November 2017. Poison baits were replaced weekly for six weeks until December 2017, before changing to monthly bait replacement until July 2018. The fox control program then lapsed for approximately six months until December 2018 due to logistical constraints, when monthly bait replacement recommenced for the duration of our study (Fig. S1).

2.3. Study design and camera-trapping

We designed experiments around the implementation of fox-baiting in each region. We simultaneously surveyed one impact and one non-impact landscape at a time using camera-traps. Each landscape pair was chosen based on similarity in landscape context, namely vegetation groups, with the aim of maintaining spatial independence with respect to predator range movements.

In the Glenelg region, we used a replicated control-impact design to test for differences in areas that have been poison-baited for foxes for more than 13 years compared with unbaited areas. We deployed a pair of camera-trapping grids in Cobboboonee National Park (impact) and Annya State Forest (non-impact) in January – April 2018, then moved these cameras to Mt Clay State Forest/Narrawong Flora Reserve (hereafter "Mt Clay"; impact) and Hotspur State Forest (non-impact) in April – June 2018 (Fig. S1). Each grid was separated by at least 8 km, a distance very unlikely to be traversed regularly by these invasive predators (B. A. Hradsky et al., 2017b).

In the Otway region, we undertook a BACIPS study to assess changes related to the introduction of the fox control program. We deployed camera-trap grids in an impact – non-impact pair of landscapes in June – September from 2017 to 2019, in the Great Otway National Park and Otway Forest Park (Fig. S1). Our first survey occurred approximately three months before fox-baiting began. The second survey was

conducted six months post-commencement of fox-baiting, however poison bait replacement lapsed at the beginning of the survey until nearly three months afterwards. Fox-baiting recommenced six months prior to the start of the final survey (Fig. S1). The impact and non-impact landscapes were at least 4.2 km apart, a distance unlikely to be traversed by these invasive predators, although possible (B. A. Hradsky et al., 2017b). In this study, and a concurrent study which identified individual foxes through genetic sampling (M. Le Pla, in review), we found no evidence of either species of predator moving between these landscapes.

In each of the six survey landscapes, we deployed a grid of camera-traps (67 – 110 cameras; mean = 94), with sites spaced on average 448 m apart (range: 194 – 770 m; Fig. 1). At each site, we deployed a single Reconyx trail camera (Reconyx, Holmen, Wisconsin) with an infrared flash and temperature-in-motion detector on a tree, facing a lure of oil-absorbing cloth doused in tuna oil (Fig. S2). More information on the camera-trapping methods is provided in Section 1.2 of the Supporting Information. Overall, we deployed 938 functional camera-traps, which operated for an average of 68 days (range: 12 – 93 days), totalling 62,415 trap nights (Table S1) across a total study duration of five months and three years in the Glenelg and Otway regions respectively (Fig. S1).

2.4. Individual feral cat identification

We sorted the cats into five categories based on their coat type: black, mackerel tabby, classic tabby, ginger and other (cats with multiple colour blends or other distinctive coats; Fig. S3). We did not attempt to identify any black cats, even the few with white splotches on their underside, as these markings could not always be seen. Within the other four coat categories, multiple observers identified individual cats based on their unique coat patterns where possible. Detailed information on this process is provided in Section 2 of the Supporting Information.

2.5. Spatial fox occupancy

To estimate density spatially, spatial mark-resight models require covariate values for each grid cell density is estimated across, and so we could not directly use the fox data from the camera-trap sites as independent variables. We therefore used the fox presence-absence data for each camera-trap site to generate a spatially-interpolated layer of fox occupancy probability using binomial generalised additive models (Wood, 2017). We did so using the "mgcv" R package (version 1.3.1; Wood, 2011). We modelled

7

fox presences and absences (response variable) across space (explanatory variable) separately for each region, with a duchon spline spatial smooth as these provide better predictions at the edge of surveyed space than other splines (Miller & Wood, 2014). In the Otway region, we included a random intercept for each camera-trap site to account for repeat sampling and did not share spatial information across the years (using a "by variable" smooth with year as a factor). Differences in camera-trap deployment lengths were accounted for using a model offset. We did not use occupancy-detection models because factors which impact fox detectability on camera-traps may also impact fox detectability to feral cats - which is more important than predictive performance in this context. We predicted generalised additive models estimates into the respective spatial mark-resight habitat masks and trapfiles (detailed below).

2.6. Spatial mark-resight models of feral cat density

We used a spatial capture-recapture approach to estimate feral cat density (Borchers & Efford, 2008). These models consider counts of detections and non-detections of individual animals at trap locations (accounting for trap-specific survey effort) to estimate the location of each individual's activity centre. These models generally assume that individuals have approximately circular home ranges and spend the majority of time in the centre of which ("activity centre"). The probability of observing an individual therefore decreases with distance from the activity centre. Two detectability parameters govern this process: g0, the probability of detecting an individual per occasion in their activity centre and sigma: a spatial scale parameter which is relative to the home range size. Multiple candidate shapes for this decline in detectability with distance from the activity centre ("detection function") can be modelled.

Spatial capture-recapture models have been extended to consider situations where not all individuals in a population are identifiable (i.e. marked) (Chandler & Royle 2013). These spatial mark-resight models typically assume unmarked individuals to be a random sample of the population, sharing the same detection process as marked individuals, and so allow density to be estimated for the entire population. Spatial mark-resight models have four categories of sightings: (1) marked individuals - detections with known identities identified to the individual level at least once each session, (2) marked but unidentifiable individuals - detections of individuals with known identities, but for which the individual could not be determined in a given session (we had no detections in this category), (3) unmarked individuals - unidentified detections which definitely do not belong to the first two categories (in our study, this category comprised black cats) and (4) mark status uncertain - detections in which individuals cannot be identified and it is not clear whether the individual is of the marked or unmarked category.

We used closed population, sighting-only, spatial mark-resight to estimate feral cat density using the maximum likelihood "secr" R package (Efford, 2021). Detections of the "mark status uncertain" category cannot be handled in the "secr" R package, we therefore added them to the unmarked detections rather than discard them (Moseby et al., 2020). We condensed detection histories of each mark category to a binary presence-absence record per each camera-trap for a 24-hour length duration ("occasion"), beginning at midday. We ran separate models for each region and treated each camera-trap grid deployment as a "session". We created a 4000 metre buffer zone around each camera-trap location to estimate feral cat density across, with a grid cell resolution of 200 metres. These habitat mask specifications were based on initial models and our knowledge of feral cats in these area - ensuring density is estimated over a large enough area to encompass the activity centres of all feral cats exposed to our camera-traps, at a fine enough scale to minimise bias in density estimates. We tested the half-normal and exponential detection functions in each region, carrying forward the function with the lowest Akaike's Information Criterion score adjusted for small sample size (AICc) for all subsequent model fitting (Burnham & Anderson, 2004).

For each of the two regions, we ran three sets of models where we: (1) chose "base model" covariates to carry through into subsequent model sets, (2) tested fine-scale associations between spatial fox occupancy and feral cat density, and (3) experimentally evaluated the effect of fox control on feral cat density at the landscape scale. We assessed the relative performance of models in each set using AICc score, with models within 2 delta AICc of the top-ranked model considered strongly supported compared to the other candidate models (Burnham & Anderson, 2004). We expected that foxes would impact both detectability parameters for feral cats concurrently, and so, always specified g0 and sigma consistently in relation to foxes or fox control (Efford & Mowat, 2014).

Feral cat detectability may have decreased over each survey duration due to the lure scent fading, and density may differ across vegetation types. While we chose landscape pairs based on the similarity of ecological vegetation class groups (DELWP, 2020), there were small differences in the relative proportion of each group across landscapes. To account for this, we first condensed vegetation groups into three categories for each region: cleared land, heathy woodlands, lowland forests (Glenelg region only) and wet forests (Otway region only). Detailed information on this process is provided in Section 6 of the Supporting Information. We included vegetation type as a habitat mask covariate. Camera-traps were lured with tuna oil scent, which likely faded over the survey duration and potentially reduced feral cat detectability (Rees et al., 2019). To account for this, we fit a model where g0 had a linear trend over over the survey duration for each camera-trap. We included year as a density covariate in the Otway

9

region models to account for repeat sampling. We compared these models to a null model without the vegetation and linear time trend covariates. We carried these covariates through to all subsequent models if their respective model had an AICc score which was lower than the null model by more than two.

To test direct associations between feral cats and foxes, we used the spatial fox occupancy estimates (detailed in the previous section) as an explanatory variable. We compared three model specifications in each region; (1) where fox occupancy only affected feral cat density, (2) where fox occupancy only affected feral cat detectability (both parameters), and (3) fox occupancy affected both the density and detectability of feral cats. We included year as a density covariate in the Otway region models to account for repeat sampling. Predator associations may be nonlinear (Johnson & VanDerWal, 2009), and so, we fit these three models again using regression splines (generalised additive models called within the secr R package). We assessed these six models per region relative to a null model which did not include fox occupancy covariates. We considered support for an association between feral cats and foxes if any of these models had an AICc score which was lower than the null model by more than two, presenting the top-ranked model.

To investigate fox-baiting effects, we compared the difference in feral cat density between paired non-impact and impact landscapes. We estimated density separately for each landscape (coded as a separate "session") and considered statistical evidence for a difference between paired landscapes if 95% confidence intervals of the coefficient estimates of difference did not overlap zero. We used AICc scores to choose between different specifications of the detectability parameters: (1) constant, (2) an effect of fox-baiting (but with separate effects in each spatial or temporal replicate), (3) an effect of pair in the Glenelg region (due to possible seasonal differences) or an effect of year in the Otway region, (4) the combination of fox-baiting and pair/year effects, presenting the top-ranked model.
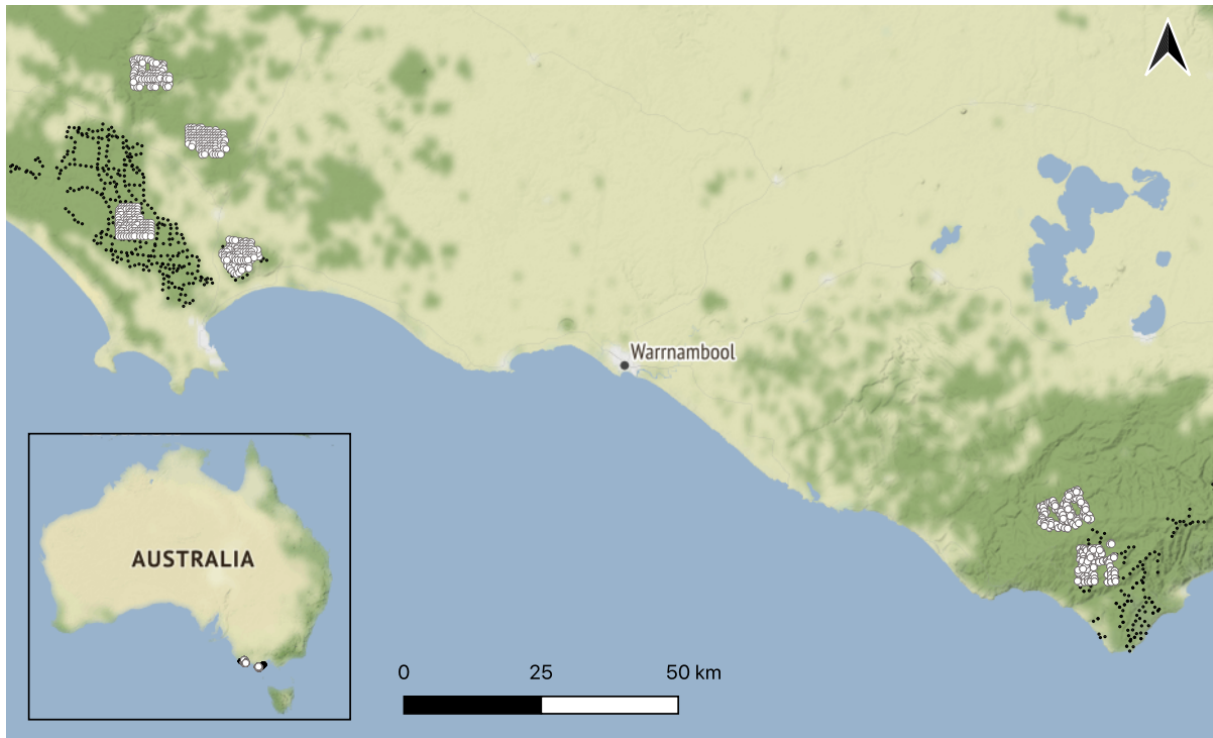
Figure 1: Locations of our six study landscapes in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots, the locations of fox poison-bait stations are denoted by smaller black dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. Map tiles by Stamen Design, under CC BY 3.0, map data by OpenStreetMap, under CC BY SA.

3. RESULTS

3.1. Fox occupancy

In the Glenelg region, foxes were detected on 0.55 and 0.26 of camera-trap sites in the non-impact and impact landscapes for the first replicate (Annya and Cobboboonee, respectively). For the second landscape pair replicate, foxes were detected at 0.48 and 0.35 of the camera-trap sites (Hotspur and Mt Clay, respectively). In the non-impact landscape of the Otway Ranges, naive fox occupancy rates increased from 0.13 in 2017, to 0.27 in 2018, to 0.43 in 2019. Foxes were detected at 0.36 of sites in the Otway impact landscape prior to poison-baiting in 2017, decreasing to 0.27 in 2018 (where fox-baiting occurred prior to, but lapsed during this survey), and further to 0.17 in 2019 (where fox-baiting occurred during the survey and had been for six months prior).

The generalised additive models of fox occupancy produced occupancy estimates which were largely consistent with the unadjusted naive occupancy rates, when back-transformed to the response scale and averaged at the landscape level. In the Glenelg region, mean fox occupancy was 0.51 (SE 0.13) and 0.34 (SE 0.12) for the first non-impact and impact replicate, with a mean estimate of 0.56 (SE 0.13) and 0.51 (SE 0.14) for the second replicate pair. In the Otway region, mean fox occupancy in the non-impact landscape changed from 0.18, 0.23, 0.36 in 2017, 2018 and 2019 (respective SEs: 0.07, 0.03, 0.11), whereas mean fox occupancy in the impact landscape changed from 0.31, 0.23, 0.18 in 2017, 2018 and 2019 (respective SEs: 0.09, 0.03, 0.08). There was higher fine-scale spatial variation in fox occupancy within the Glenelg region compared to the Otway region (Fig. 2). In fact, a completely smooth relationship (i.e. no spatial variation) with space was predicted for the 2018 survey in the Otway region (Fig. 2). The Glenelg region generalised additive model had an adjusted R-squared value of 0.142 and explained 14.8% deviance, whereas the Otway region model had an R-squared value of 0.24 and explained 27.8% deviance. Model summaries and spatial standard error estimates are presented in Section 5 of the Supporting Information.

3.2. Feral cats in the Glenelg region

In the Glenelg region, we recorded 222 feral cat detections from 26,792 camera-trap nights (Table S1). Sixty-five percent of detections were feral cats with unique natural markings; the remainder were black feral cats. We identified 85% of marked feral cats to the individual level; a total of 40 cats (9 − 13

12

individuals per grid). The exponential detector function was supported over the half-normal (Table S2). There was no support for a linear time trend on g0, nor for an impact of vegetation type on feral cat density (Table S3).

Feral cat density was negatively and linearly associated with spatial fox occupancy (coefficient -0.34; standard error 0.15; Fig. 3), with no effect on feral cat detectability. This model had an AICc score which was 2.76 less than the null; models which included an impact of fox occupancy on detectability parameters performed worse than the null model based on AICc scores (Table S3). Regression splines did not change model predictions (Fig. 3), with all nonlinear models performing consistently worse than their linear counterparts (Table S3).

When we estimated feral cat density separately for each landscape, there was statistical evidence (i.e., 95% confidence intervals of the parameter estimates did not overlap zero) that feral cat density was higher in the first impact landscape than its associated non-impact landscapes for the first replicate, but no difference for the second replicate (Fig. 5). The top-model in this set also had constant detectability.

3.3. Feral cats in the Otway region

In the Otway region, we recorded 1022 feral cat detections from 35,623 camera-trap nights (Table S1). Sixty-one percent of detections were of feral cats with unique natural markings and we identified 86% of these, a total of 98 cats (20 – 30 per grid). The exponential detector function was strongly supported over the half-normal (Table S2). There was no support for a linear time trend on g0, nor for an impact of vegetation type on feral cat density (Table S3).

Spatial fox occupancy was negatively correlated with feral cat density (linear model coefficient -0.26; SE 0.14; Fig. 3) and also impacted feral cat detectability (Fig. 4). The linear model and nonlinear models were indistinguishable based on AICc scores (as was also the case for the other two model specifications), with at least 10.6 AICc scores lower than the null. Where fox occupancy was higher, feral cats were also less detectable in their activity centres (i.e. negative association with g0; coefficient -0.69; SE 0.21; Fig. 4A) and ranged further (i.e. positive association with sigma; coefficient 0.3; SE 0.09; Fig. 4B). The shape of nonlinear model differed from the linear model, although, estimates were mostly contained within the linear model 95% confidence intervals (Fig. 3; Fig. 4).

There was no statistical evidence that feral cat density differed between impact and non-impact sites

in any of the three years surveyed (Fig. 6A). The coefficient estimate of difference changed from a negative direction in 2017 and 2018 (i.e. feral cat density was lower in the impact site than the non-impact site) to a positive direction in 2019 (when fox-baiting occurred throughout the survey duration), however 95% confidence intervals of the parameter estimates still overlapped zero (Fig. 6A). There was strong evidence (based on AICc scores) that feral cat detectability differed across the three years, and in response to the fox-baiting (Table S5). In the non-impact site, there appeared to be a decline in feral cat density over the three years surveyed (although we did not explicitly test the statistical significance of this; Fig. 6B).
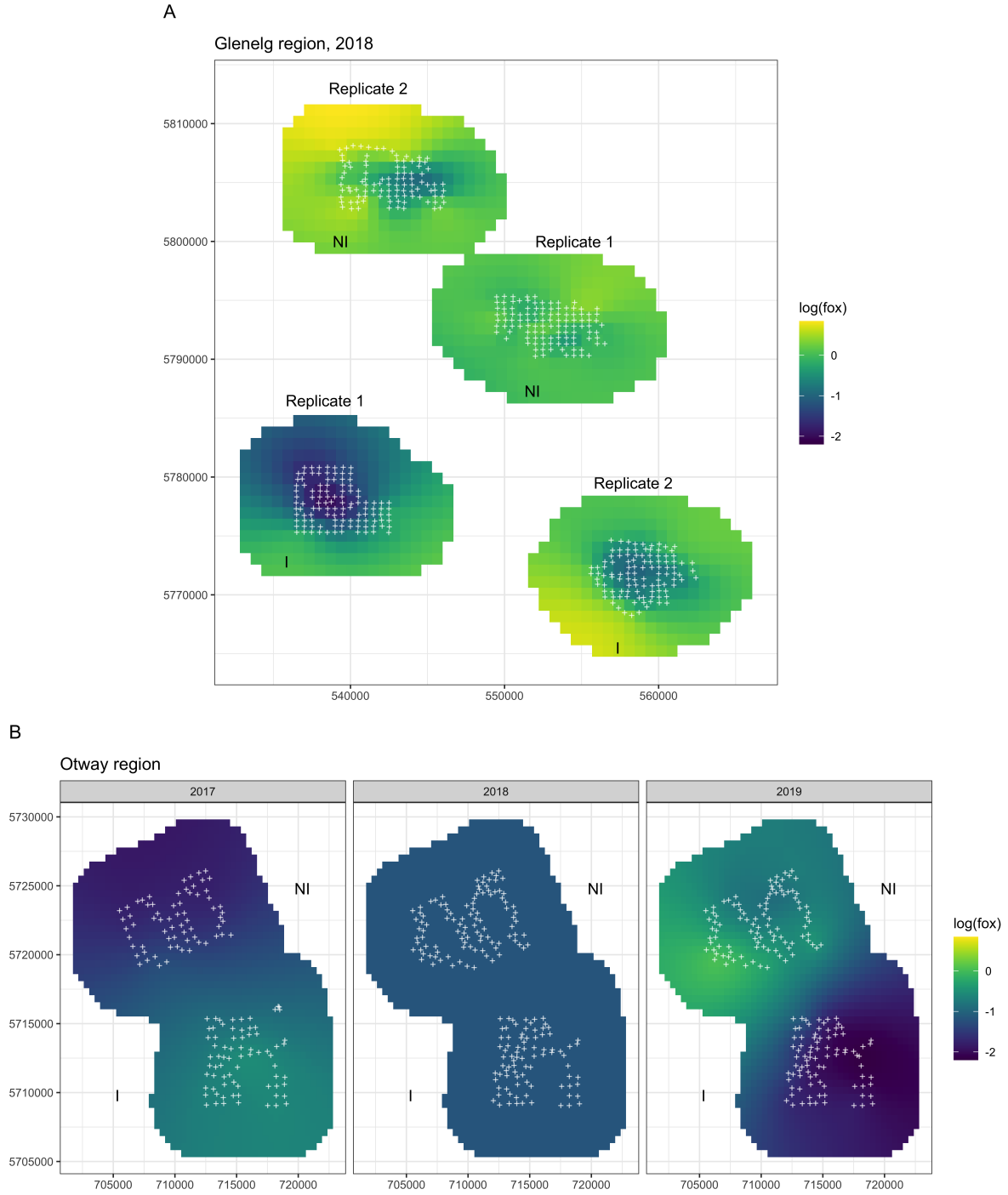
Figure 2: Fox occupancy predictions derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Glenelg (A) and Otway (B) regions, Australia. Estimates were used as predictor variables in the feral cat spatial mark-resight models.
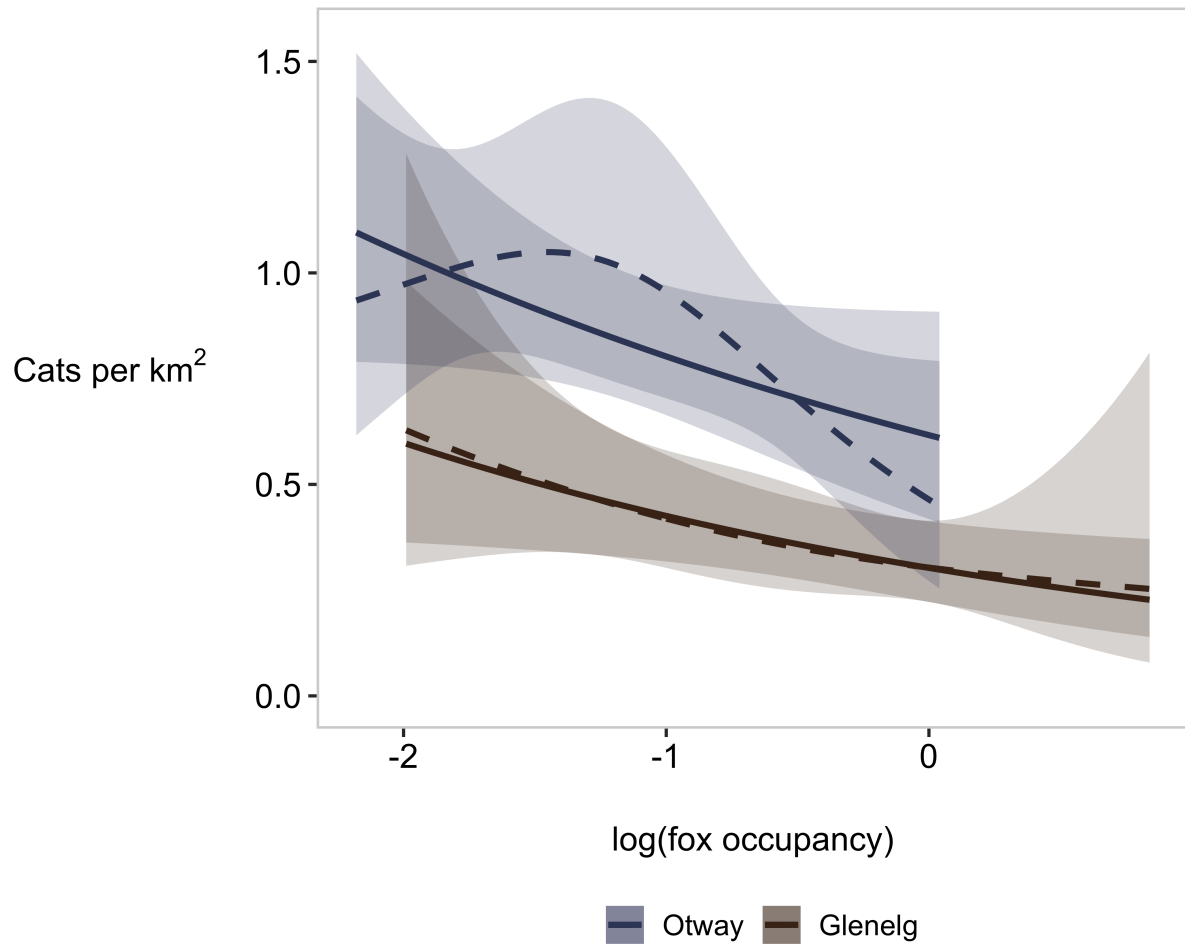
Figure 3: Linear (solid lines) and nonlinear (dashed lines) models of feral cat density and fox occupancy in the Glenelg and Otway regions, Australia. Shaded areas indicate 95% confidence intervals.
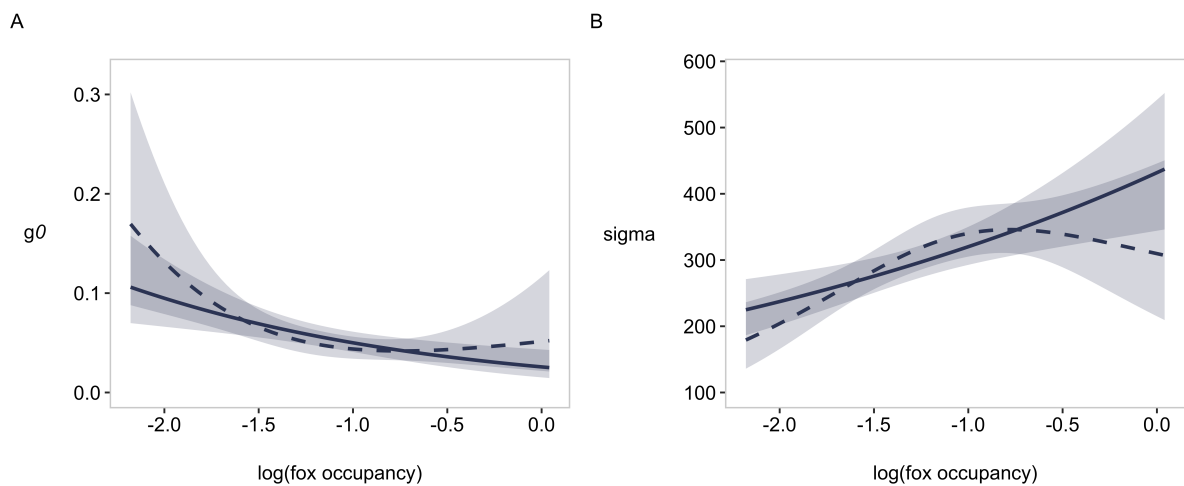
A

B

Figure 4: Linear (solid lines) and nonlinear (dashed lines) models of feral cat detectability parameters in the Otway Ranges, Australia. The probability of detecting a feral cat in its activity centre per 24-hour occasion (g0) decreased with the probability of fox occupancy (B), while sigma (which is related to home range size) increased (C). Shaded areas indicate 95% confidence intervals.
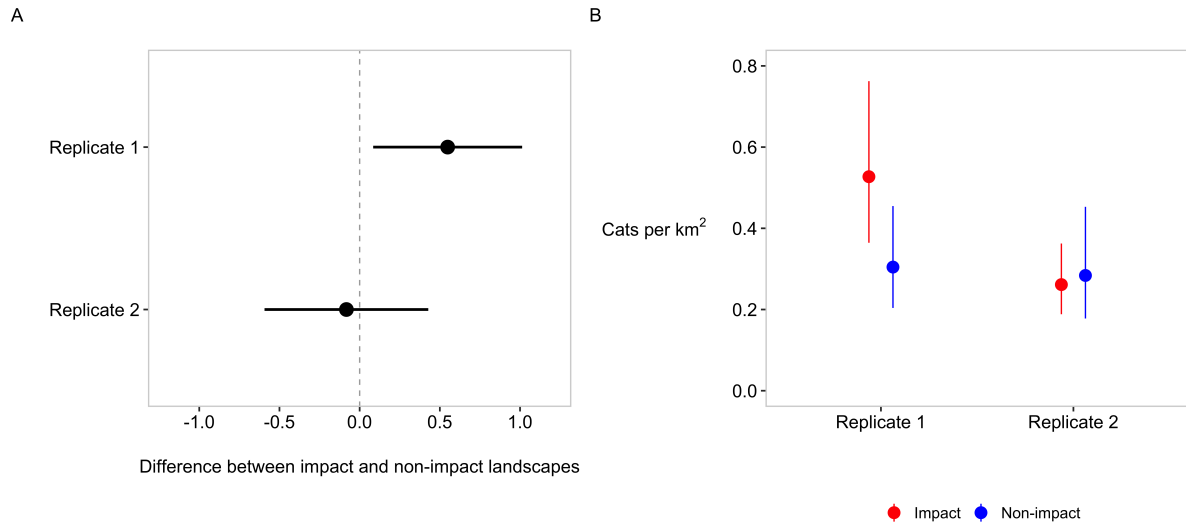
Figure 5: Estimates of difference between feral cat density in impact and non-impact landscapes (A) and predicted density estimates (B) in the Glenelg region, Australia. There was statistical evidence (i.e., 95% confidence intervals of the parameter estimates did not overlap zero) that feral cat density was higher in the landscape with more than 13 years of fox-baiting (impact) than landscapes without fox-baiting (non-impact) for the first replicate pair, but not for the second replicate pair. Error bars represent 95% confidence intervals.
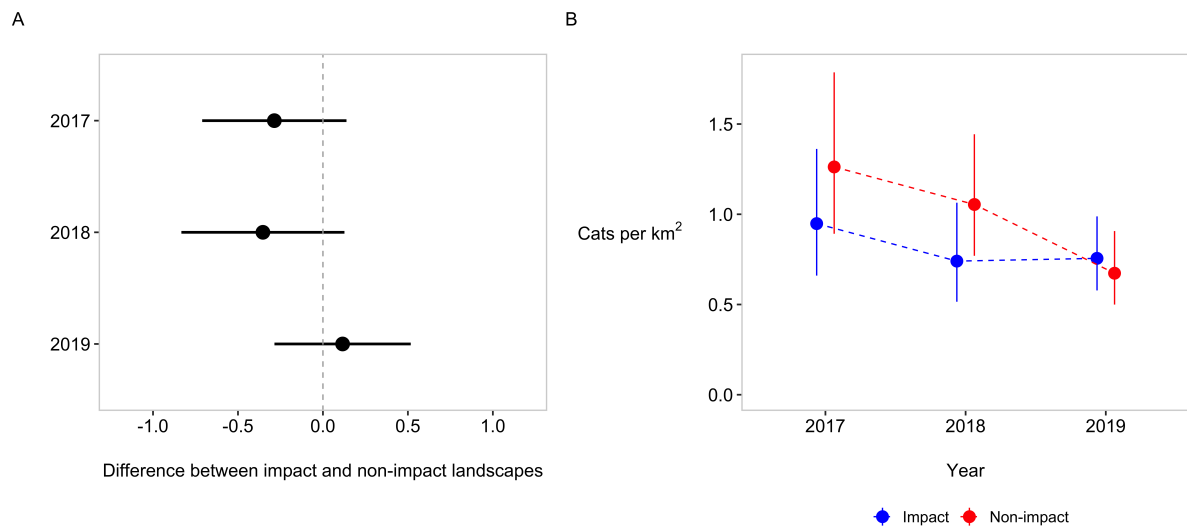
Figure 6: Estimates of difference between impact and non-impact landscapes (A) and predicted density estimates (B) in the Otway region, Australia. There was no statistical evidence (95% confidence intervals of the parameter estimates overlapped zero) that feral cat density differed between impact and non-impact landscapes in each year surveyed). In 2017, surveys were conducted approximately two months before fox control commenced in the impact landscape (red). Error bars represent 95% confidence intervals.

4. DISCUSSION

After individually identifying 137 feral cats, we found that feral cat density was highest where fox occupancy was lowest across both surveyed regions (supporting hypothesis 1). However, lethal fox control did not consistently increase feral cat density (mixed support for hypothesis 2). This is most likely due to fox-baiting the inconsistently suppressing fox occupancy, as well as our short sampling period in the Otway region post-baiting. Our study does provide evidence that foxes can impact the population dynamics and behaviour of feral cats, demonstrating potential for mesopredator release following intensive and sustained fox control. More broadly, our study highlights the nuance involved in detecting mesopredator release, demonstrating how correlative and experimental approaches provide complementary lines of evidence, as well as the importance of disentangling mesopredator population density from animal behaviour.

By using lethal control to manipulate fox occupancy across two separate ecosystems, we observed a consistent negative association with feral cat density (Fig. 3). There is contention around whether linear regression is appropriate for predator correlation studies, as subordinate predators may only be suppressed when apex predator abundance is high (Johnson & VanDerWal, 2009). However, there was no evidence of non-linear associations between foxes and feral cats in the Glenelg region, while linear and non-linear models performed equally well in the Otway region. Non-linear models in the Otway region predicted feral cat density to decline only in the mid-high range of fox occupancy (Fig. 3), while behavioural changes were seen in the low-mid range of fox occupancy (Fig. 4). Perhaps feral cats can successfully avoid foxes through behavioural change where foxes are rare, but this is ineffective where foxes are common. Fox avoidance strategies likely come at the expense of hunting success (Sih, 1980). This may be why we did not see signs of behavioural change in the Glenelg region where small mammal abundance is relatively low - fox avoidance strategies may be untenable for feral cats here (Wilson et al., 2010).

Where fox occupancy was higher in the Otway Ranges, feral cats were less detectable in their activity centres and ranged further (Fig. 4). Low detectability is likely to correlate with fewer apex predator encounters, and has been observed in other predator interaction studies (e.g. Lombardi et al., 2017). Sigma scaling with fox occupancy probability supports observations made by Molsher et al. (2017), and may reflect a direct avoidance strategy. Animal movement rates are expected to increase in response to unpredictable threats (Riotte-Lambert & Matthiopoulos, 2020). Alternatively, feral cats may consider foxes predictable and avoid locations they frequent, thus having to range further to cover the same home-

range area. In a similar environment to the Otway region, Buckmaster (2012) observed large "holes" in the home range of each GPS collared feral cat, hypothesising apex predator avoidance to be the reason for this after ruling out prey differences. On the other hand, sigma scaling with fox occupancy probability may be an indirect effect - a symptom of the change in feral cat density. Feral cat density was lowest where fox occupancy was highest and animals, including feral cats, tend to have larger home ranges at low densities (Bengsen et al., 2016). Regardless of the mechanism, apex predator-dependent movement rates has serious implications for the interpretation of studies which compare the relative abundance (without disentangling behaviour from density) and spatial overlap of predator species (Broadley et al., 2019; Efford & Dawson, 2012; Neilson et al., 2018; Stewart et al., 2018).

Feral cat density in the Glenelg region was consistent across three out of the four landscapes surveyed (Fig. 5). This is unsurprising given that (1) feral cat density was negatively correlated with fox occupancy, and (2) landscape-wide fox occupancy estimates varied by less than 10% across these three landscapes. In contrast, average fox occupancy was more than 31% lower in Cobboboonee, and cat density at least 67% higher. We expect these differences between the two impact landscapes to be largely due to the Cobboboonee camera-trap grid being surrounded by mostly fox-baited forest, whereas Mt Clay was nearly entirely surrounded by unbaited farmland (Fig. 1). Landscape feral cat density estimates are averaged across the entire camera-trap grid interior and surrounding 4 km buffer zone. Hradsky et al. (2019) predicted that extending poison-baits 1 km into the adjacent farmland would more than halve fox density inside Mt Clay. Many previous studies of fox-cat (and other predator) interactions have relied solely on impact and non-impact as a proxy for apex predator abundance and distribution (e.g. Hunter et al., 2018). While experimental studies are fundamental in testing mesopredator release, direct measurements of apex predators are also necessary to reliably interpret the response of subordinate species (Salo et al., 2010).

We saw no statistical evidence that feral cat density differed between impact and non-impact landscapes in the Otway region (Fig. 6). There may not have been an effect because fox occupancy was already low prior to fox control commencing (Fig. 2). The non-linear correlative model predicted feral cat density to be unaffected by fox occupancy at such low levels (Fig. 3). However, we did see a small increase in feral cat density in the impact landscape relative to the non-impact landscape during our final survey in 2019. Our short sampling period post-baiting may have not allowed enough time for changes to manifest in the adult population, as foxes possibly suppress cats through lowered breeding and recruitment rates (**REFS**). Despite high feral cat density, the high proportion of unmarked cats in the Otway

21

region, and complex detectability covariates reduced our ability to demonstrate statistical evidence for weak fox-baiting effects. Our surveys here provide an important baseline for which to compare future changes in predators and prey against, particularly once fox-baiting has occurred over a longer (and more consistent) time frame.

Our study has several limitations. It is unclear whether foxes may suppress feral cats directly through top-down control, or indirectly through competition for shared prey. Instead of responding directly to foxes, feral cats may have responded to fox-induced impacts on native prey (Stobo-Wilson et al., 2020). Although, vegetation type drives native prey occurrence within these regions (B. A. Hradsky et al., 2017a) and we saw no evidence that vegetation type impacted feral cat density. Rather than avoidance or exclusion, negative correlation between foxes and feral cats may reflect differences in niche preference. However, this is less likely to be an issue for our study because foxes were artificially suppressed using lethal control. Because uncertainty from our fox occupancy models was not fully propagated into the spatial mark-resight models, we underestimate the true variance feral cat density and fox occurrence correlation. Unfortunately, a full bayesian integration of the fox occurrence analysis and the spatial mark-resight model is not yet implemented, but could emerge soon. The development of open population spatial mark-resight models would also improve parameter estimates for multi-season surveys.

Our study is among the very few which have tested the mesopredator release in terms of population density. Uncertainty around mesopredator release often stems from complex predator guilds (Jachowski et al., 2020; Levi & Wilmers, 2012)–a major difference is that our study was conducted it in a simple system where only two medium-large mammalian predators occur. We saw behavioural and numerical responses consistent with a mesopredator release of feral cats. This could explain why pest management that only targets foxes–one of the most prevalent conservation actions in Australia–does not consistently improve native prey persistence (Duncan et al., 2020; Lindenmayer et al., 2018; Wayne et al., 2017). However, more evidence is required to equivocally prove that lethal fox control consistently causes increases in feral cat density. Regardless, there will be circumstances where targeted fox control is worthwhile because some native prey species are more susceptible to foxes than feral cats (**REFS**). A more integrated approach to invasive predator management, whereby both foxes and cats are simultaneously or otherwise optimally controlled together could substantially improve biodiversity outcomes (Comer et al., 2020). If this is not feasible, changes in mesopredator density and the outcomes for prey species should be closely monitored with triggers for ceasing invasive apex predator control if it proves counterproductive for conservation of threatened prey species.

5. ACKNOWLEDGEMENTS

6. AUTHORS' CONTRIBUTIONS

M.W.R, B.H, J.H.P, B.A.W and A.R conceived the ideas and designed methodology; M.W.R, J.H.P, M.LP, E.K.B and B.H collected the data; M.W.R analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

7. OPEN RESEARCH

Raw data and code are on Github link xx.

Data will be deposited on the Dryad Digital Repository after acceptance.

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