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RESEARCH ARTICLE OPEN ACCESS

Reconstructing Fox Invasion of Australia: A Process-Based Approach Using Historical Sightings

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ABSTRACT

Aim: European colonisation of Australia triggered a cascade of processes that continue to threaten biodiversity today. These include the introduction of invasive species, responsible for rapid and widescale extinctions. Here, we integrated process-based models with thousands of first sighting records to reconstruct the arrival and spread of European red foxes (*Vulpes vulpes*) in Australia at a high spatiotemporal resolution. *Location*: Continental Australia.

Methods: We constructed tens of thousands of spatially explicit population models of fox colonisation dynamics, using historical records, demographic estimates and spatiotemporal patterns of climate and environmental change. We then tested model outputs against inferences of timings of fox arrival from newspaper articles and empirical estimates of population sizes.

Results: We show that it took just 60 years for foxes to infill their entire potential distribution of Australia. Foxes colonised mesic regions of Australia earlier than the more arid regions of central and north-western Australia, reaching carrying capacity shortly after the middle of the 20th century.

Conclusions: These new insights into the temporal pattern of spread of foxes across Australia, its underpinning processes, and associated maps of abundances promise to help better explain past losses of biodiversity, providing critical information needed to avert future extinctions of Australia's unique fauna. Our process-based approach for projecting invasion histories should prove similarly useful for reconstructing the biogeography of other invasive species, including cryptic populations at the early stages of invasion.

1 | Introduction

Global rates of species loss and population decline have accelerated in recent centuries (Ceballos et al. 2017; Dirzo et al. 2014), threatening ecosystem functions and vital services they provide for both nature and people (Cardinale et al. 2012; Díaz et al. 2006). Invasive predators have contributed enormously to this downward trend in biodiversity (Doherty et al. 2016; Duenas et al. 2021). Averting future extinctions from invasive predators requires a more detailed understanding of their invasion history as well as ecological interactions and impacts (Doherty et al. 2016; Tomlinson et al. 2022).

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However, invasion pathways generally remain poorly understood across both space and time, hindering efforts to quantify and mitigate the decline of native fauna caused by these introduced predators (Spear et al. 2021).

Invasion patterns and pathways are generally poorly understood because locations and timings of initial introductions are rarely well documented (Spear et al. 2021). This is because releases often were unintentional (Ruesink et al. 1995). Moreover, introduced species can be cryptic and difficult to detect, particularly in the early stages of an invasion, or at the invasion front where densities are often low (Cunningham et al. 2022; Spear et al. 2021). Therefore, populations of invasive species can be present, exerting ecological influence, for substantial periods of time prior to their detection and the formulation of a management response. However, emerging process-based modelling techniques are providing new opportunities to reconstruct the range dynamics of invasive species, even when data on their invasions are spatially and temporally sparse (Botterill-James et al. 2024). Modelled outputs describing invasion histories can include time of first appearance at locales, rates and directions of expansion and trajectories of population growth. Such information is needed to quantify the contributions of invasive species to biodiversity losses (Tomlinson et al. 2024).

Process-based models simulate the ecological and evolutionary processes that drive the structure and dynamics of patterns of biodiversity (Pilowsky, Colwell, et al. 2022). In invasion biology, process-based models have been used to simulate spatial population processes for introduced species at fine spatiotemporal resolutions, projecting population and distributional changes across land and seascapes (Briscoe et al. 2022; Fordham, Akçakaya, Araújo, et al. 2013; Mellin et al. 2016). When combined with pattern-oriented modelling (POM) methods (Grimm and Railsback 2012), such models can be used to reconstruct population processes and their spatial dynamics over time frames ranging from decades to thousands of years (Botterill-James et al. 2024; Canteri et al. 2022; Tomlinson et al. 2022). This makes them very capable of establishing the arrival and expansion of invasive species and their underlying spatiotemporal patterns of abundance, including across entire continents.

While the processes of biodiversity loss in Australia are complex (Legge et al. 2023), invasive predators are to blame for large losses of Australia's unique terrestrial wildlife (Woinarski et al. 2019). Many species that once fulfilled key ecological functions (e.g., bioturbation and pollination) have now gone, weakening ecosystem structures and functions (James et al. 2011; Valentine et al. 2018). European red foxes (*Vulpes vulpes*) and domestic cats (*Felis catus*) brought to Australia by European colonists now kill many millions of native animals in Australia each year (Stobo-Wilson et al. 2022), and are the major driver of past and current extinctions and range collapses of Australia's endemic vertebrate species (Legge et al. 2023). While changed fire regimes and habitat conversion from natural vegetation to agricultural landscapes can amplify the impacts of these invasive species (Cremona et al. 2022; Downs and Brown 2012; Legge et al. 2023), averting future extinctions is dependent on mitigating predation by foxes and cats.

Current reconstructions of fox and cat arrival and expansions across Australia are spatially and temporally coarse (Abbott et al. 2014; Fairfax 2019). This makes it difficult to decouple the roles of cats and foxes in the timing and rates of population declines and extinctions of native species using pattern- and process-based ecological models (Tomlinson et al. 2022). Here, we combine historic newspaper reports of first sightings of an invasive predator (Fairfax 2019) with Spatially Explicit Population Models (SEPMs) (Fordham et al. 2021) to reconstruct likely patterns of population expansion at high spatiotemporal resolutions. Using foxes as a case study, we generated thousands of plausible models of fox expansion across Australia and tested these against inferences of distributional change from sightings records, sourced from archival news media (Fairfax 2019). Our aim was to estimate the timing of fox arrival and establishment at high resolution across the Australian continent, providing a more complete understanding of the demographic and spatial processes underpinning the rapid colonisation of Australia by foxes. Our detailed reconstructions show that foxes filled their potential distribution in Australia in just 60 years, providing new biogeographic data needed to quantify past losses of fauna and to avert future extinctions.

2 | Methods

We used a new statistical-simulation approach to reconstruct the invasion dynamics of foxes in Australia at high spatiotemporal resolution. The approach integrated historical observations with SEPMs (Fordham et al. 2021) to simulate population and distributional dynamics and invasion pathways (Figure 1), capturing uncertainty in fox demography, dispersal, habitat suitability and density. This was done by varying parameters across plausible ranges and simulating tens of thousands of conceivable models of fox introduction, establishment and spread (Figure 1). These SEPMs were subsequently validated using pattern-oriented modelling (POM) methods, which compared simulated patterns with inferences of demographic change from historical records. Models that closely reconciled these validation targets were used to annually reconstruct the most likely patterns of fox establishment and expansion over a period of more than 200 years. All modelling was done in the poems package (Fordham et al. 2021) in the R statistical environment.

2.1 | Fox Sightings

We used the first sighting records of foxes from newspapers collated by Fairfax (2019) to reconstruct the time of fox arrival at specific locations and eco-climatic regions in Australia. First sightings of foxes were newsworthy at the end of the 19th and beginning of the 20th century in Australia, owing to the threats that foxes posed to sheep and poultry. These data encompass 865 reliably dated and geolocated records spanning continental Australia, with a spatial bias towards mesic and semi-arid regions. We statistically accounted for uncertainty in the timing of first arrival

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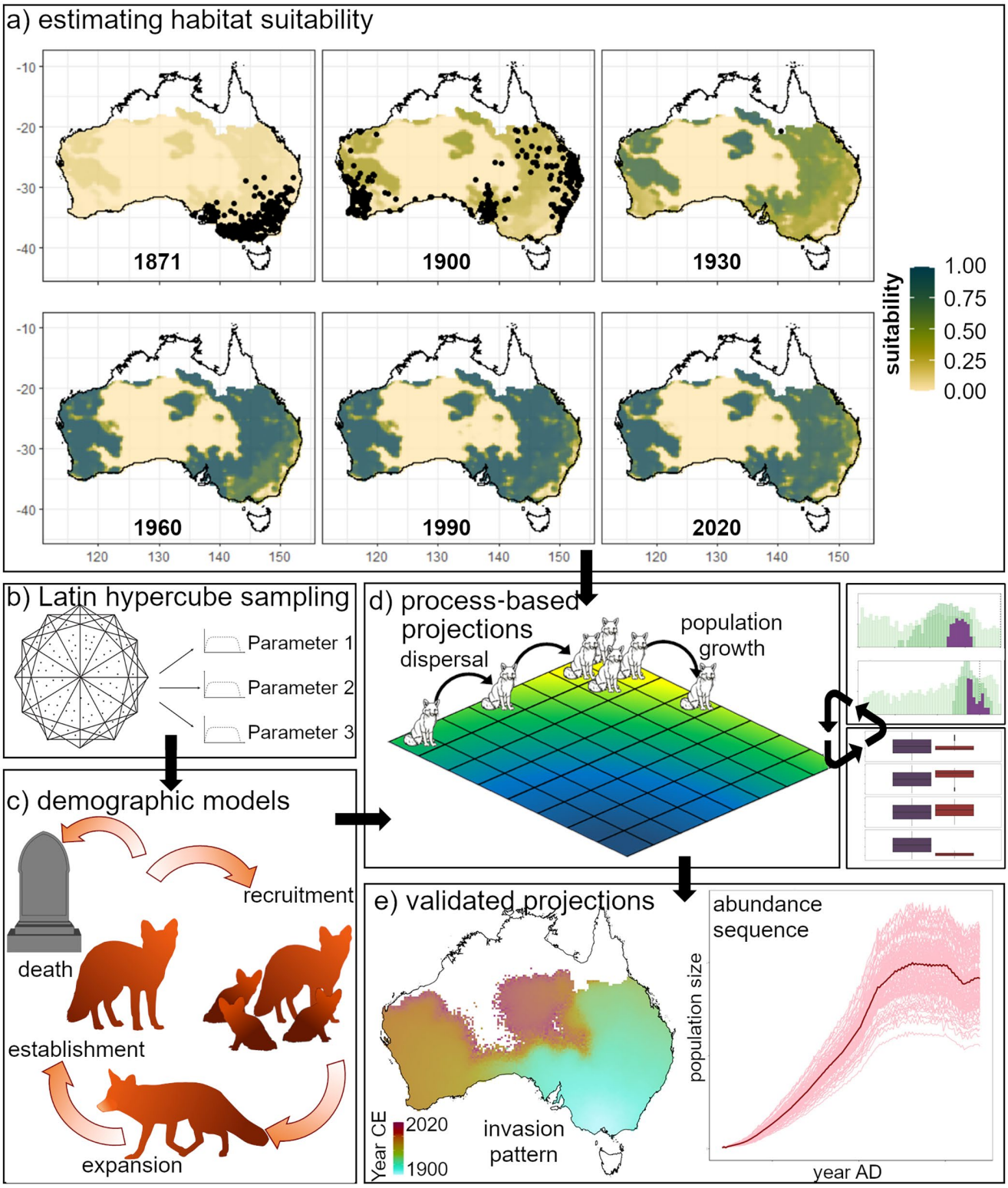


FIGURE 1 | Reconstructing establishment and spread of foxes in Australia. Workflow for the development and validation of SEPMs implemented using the poems R package (Fordham et al. 2021) begins by (a) *estimating habitat suitability* in space and time that aligns with first sighting records (points). Demography is introduced using (b) *Latin hypercube sampling* to capture paramater uncertainty, resulting in (c) many plausible *demographic models* of the focal species. This produces (d) *process-based projections* of spatiotemporal occurrence and abundance, validated against evidence of observed or inferred spatiotemporal patterns of colonisation dynamics. The most accurate subset of simulations is then used to generate (e) *validated projections* of invasion dynamics, including abundance through time. Fox silhouettes modified from Phylopic.

in eco-climatic regions (Figure S1) using the Gaussian-resampled, inverse-weighted McInerny ('GRIWM') method (Bradshaw et al. 2012), which statistically accounts for the likelihood that the first sighting of a fox in an area is likely to underestimate the time of arrival because very low densities of animals are difficult to detect. This method was originally developed to estimate the time

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of extinction but has since been adapted to estimate the time of arrival (Canteri et al. 2025; Saltré et al. 2016).

2.2 | Spatiotemporal Habitat Suitability

The suitability of the Australian landscape and its environment for foxes was modelled using spatial estimates of fox density at 1km^2 resolution (Stobo-Wilson et al. 2022), which we upscaled to ~25km^2 resolution. We scaled density values between zero and one to calculate a measure of habitat suitability, using an upper density threshold centered on the 95th percentile. The assumption being that density and habitat suitability are correlated (de la Fuente et al. 2021). The upper density threshold value was allowed to vary between the 90th and 100th percentile in different SEPMs (see below), the latter representing no threshold being applied.

Since foxes tend to occur in high abundances in urban and agricultural landscapes (Sharp et al. 2001), we treated habitat suitability as having a positive relationship with post-European vegetation change, owing to agricultural land use conversion (Saunders et al. 2010). We used decadal reconstructions of the areas of each grid cell devoted to grazing, cropland, irrigation, or urbanisation following the arrival of Europeans in Australia (Ellis et al. 2021). These temporal snapshots were downscaled to annual estimates using bilinear interpolation. Carrying capacity, estimated through time based on habitat suitability, was multiplied by the resulting land use conversion layers to capture the impact of land use change in improving habitat suitability for foxes. We applied a lower land use threshold that conditioned the positive relationship between land use and habitat suitability. The percentage of areas of land use falling below this threshold had no positive effect on habitat suitability.

2.3 | Spatially Explicit Population Model

We used the spatiotemporal estimates of habitat suitability as inputs to SEPMs that simulated landscape-level population processes (including dispersal and source-sink dynamics) that are likely to have driven the spread of foxes across Australia. SEPMs simulate movement, mortality and reproduction in networks of populations across time, improving knowledge of species' distributions and population dynamics, including for invasive species (Botterill-James et al. 2024). Each grid cell was modelled with a single scalar population model that simulated density-dependent population growth (Dunham et al. 2006). The approach has previously been used to reconstruct range and extinction dynamics (Canteri et al. 2022; Fordham et al. 2022; Pilowsky, Haythorne, et al. 2022), including for species that suffered rapid declines in distribution and abundance in Australia (Fordham et al. 2021; Tomlinson et al. 2022), and to model the colonisation and expansion of humans on islands (Tomlinson et al. 2024). The SEPM was run at annual time steps from 1870 (time of first introduction) to 2020.

Carrying capacity: The carrying capacity in each grid cell was based on habitat suitability conditioned by land use (see above) and maximum fox density (Fordham et al. 2018). It was calculated for each grid cell (using the '*max_dens*' function in poems) by multiplying habitat suitability at each time step with maximum non-urban density. Maximum density was a variable parameter ranging from 0.5-10 foxes per km^2 (300–6250 individuals per grid square), which is based on empirically derived estimates from a wide range of habitats (Saunders et al. 1995).

2.4 | Population Growth

The maximum rate of population increase (λ_{max}) varied between 1.10 and 3.00 based on upper and lower limits for foxes in Australia (Harding et al. 2001; Hone 1999; McLeod and Saunders 2001). These values of λ_{max} aligned closely with values calculated using time series data from Stobo-Wilson et al. (2022). Since population growth rates of foxes vary climatically in Australia (Devenish-Nelson et al. 2013; Hone 1999), we allowed λ_{max} to vary spatially according to Koppen-Geiger climate regions (Köppen and Geiger 1939). More climatically arid regions had higher λ_{max} values (Hone 1999). Population growth rate varied between 0.00 (no variation) and 0.7 (high variation), enabling potentially large population fluctuations in response to environmental stochasticity (Fordham et al. 2018). We set the upper limit for variation in population growth based on the standard deviation in growth rate for foxes at carrying capacity at Roxby Downs (Read and Bowen 2001).

Density dependence was modeled using a Ricker logistic density-dependent response (Ricker 1954), where increasing population abundance in a cell reduces the available resources per individual, slowing population growth as populations reach carrying capacity.

2.5 | Natal Dispersal

Dispersal rates between populations (m_{ij}) were modelled using a distance-based function.

$$m_{ij} = \begin{cases} p^{\left(\frac{-D_{ij}}{b}\right)}, & D \le r \\ 0, & D > r \end{cases} \quad (1)$$

where p is the proportion of the population dispersing, b is the average dispersal distance and r is the maximum dispersal distance. This approach prevents large dispersal rates to closely neighbouring cells (i.e., the drainage effect) by pre-calculating a fixed proportion of individuals that should move to a given cell based on p, r and D_{ij}.

We set the maximum post-natal dispersal distance to 200km, reflecting the largest annual movements observed for foxes (G. Saunders et al. 1995; Trewhella et al. 1988). We allowed the mean dispersal distance to vary between 5km (no dispersal, since 5km falls within the natal grid square) and 40km, capturing the wide range of postnatal dispersal distances reported in the literature (Trewhella et al. 1988), including for foxes in Australia (Coman et al. 1991). The proportion of the population dispersing varied between 0.05 and 0.40 based on mark-recapture studies (Allen

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and Sargeant 1993) and the dispersal rates used in other models for foxes in Australia (Hradsky et al. 2019). Importantly, our parameter ranges for proportions of dispersers and dispersal distance replicate the relationship between dispersal distance and the proportion of dispersers seen in Storm et al. (1976) (Figure S2).

Dispersal was also modelled as a density-dependent process, where emigration increased and immigration decreased as cell abundance approached carrying capacity, reflecting competition for den sites and other resources, which is common in Australia (Hradsky et al. 2019). Thus, dispersal in the model varied across landscapes in response to habitat and density. We allowed emigration to increase linearly above an abundance threshold, set at between 70% and 100% of carrying capacity, using the '*dispersal_n_k_threshold*' function. We modelled immigration as slowing when abundance exceeded 50% of carrying capacity and prevented dispersal to cells with abundances > 90% of carrying capacity. This simulated the constraint of territory size on population abundance (Cavallini 1996). We treated dispersal thresholds as variable parameters in the model (Table 1), with lower thresholds in arid regions, where territory sizes of foxes are larger (Saunders et al. 1995).

2.6 | Founding Population

The number of individuals in founding populations was sampled as a variable parameter ranging between 10 and 100. We used release dates and locations from Fairfax (2019). These encompassed three initial wild introduction locations at Werribee, Corio and Ballarat in Victoria in 1870 (Figure 2), with subsequent additional releases in Goulburn in New South Wales (1895) and on the Yorke (1901) and Eyre Peninsulas (1902) in South Australia (Abbott et al. 2014; Rolls 1969).

2.7 | Simulations

Spatially explicit demographic models for foxes were built using 'best estimates' for demographic parameters and environmental

TABLE 1 | Parameter values used in the process-based model of fox invasion in Australia. Fixed values were consistent across all simulations, while variable parameters varied randomly across the parameter space (Type). Prior and posterior parameter ranges are shown for variable parameters.

Parameter		Type	Prior values	Posterior values	Citation
Habitat suitability parameters					
q_thresh	Habitat suitability threshold	Variable	0.9–1.0	0.91–0.99	
lu_thres	Land use threshold	Variable	0–1.0	0.63–0.98	
Demographic parameters					
initial_abundance		Fixed	Generated		
Rmax_quantile	Maximum population growth rate	Variable	0–1	0.15–0.95	(Harding et al. 2001; Hone 1999; McLeod and Saunders 2001)
standard_deviation	Variance in R_{max}	Variable	0.00–0.70	0.15–0.65	(Read and Bowen 2001)
max_dens	Maximum population density per grid cell	Variable	300–6250	4999–6131	(G. Saunders et al. 1995)
Dispersal parameters					
dispersal_max	Maximum dispersal distance	Fixed	200 km	200 km	(Storm et al. 1976)
dispersal_p	Proportion of individuals dispersing in each timestep	Variable	0.05–0.40	0.12–0.27	(Allen and Sargeant 1993; Storm et al. 1976)
dispersal_b	Mean dispersal distance	Variable	5–40 km	24–37 km	(Coman et al. 1991)
dispersal_n_k_threshold	Source and sink thresholds for dispersing individuals	Variable	0.7–1.0	0.71–0.98	(Cavallini 1996; Hradsky et al. 2019)
Introduction parameters					
trans_n	The number of founders released to establish new populations	Variable	10–100	15–96	

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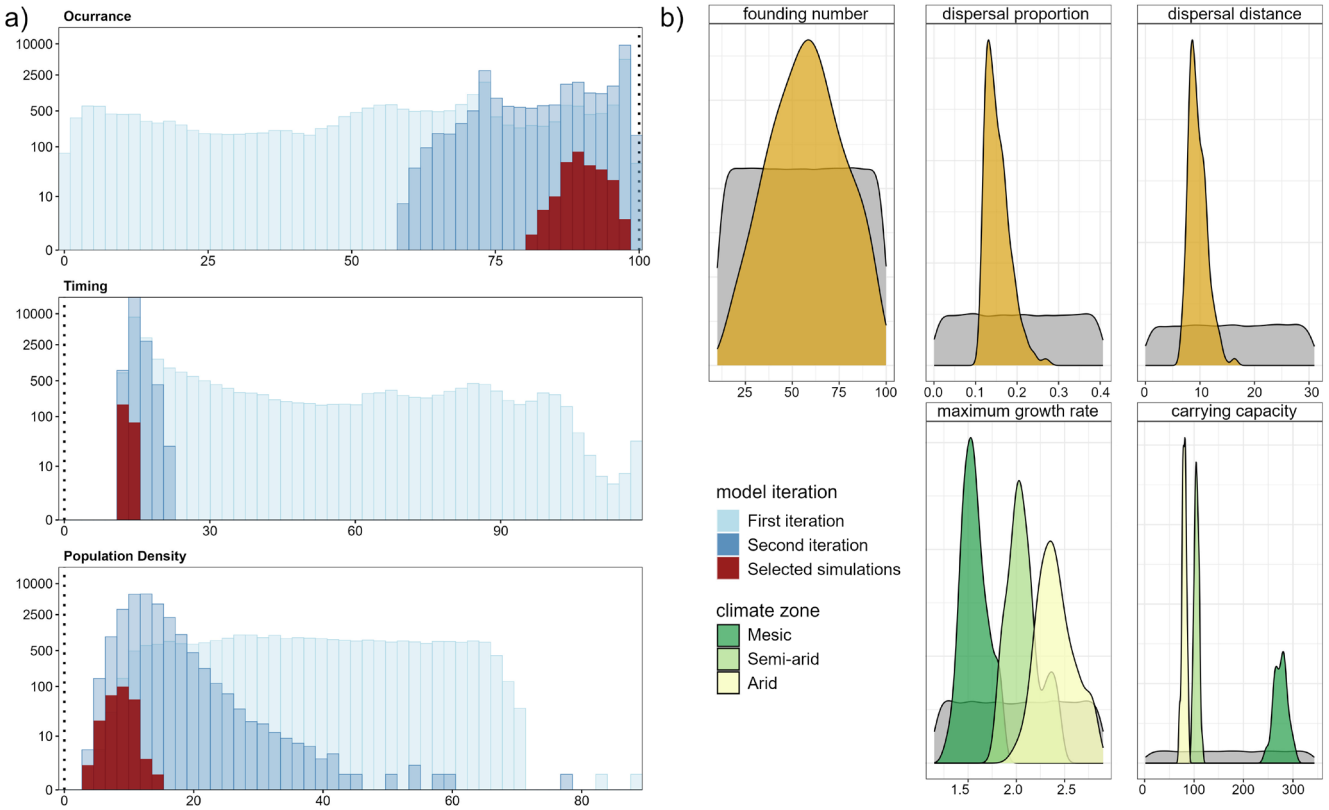


FIGURE 2 | Model performance and structure. (a) Histograms show accuracy of simulations assessed against a multivariate target of percentage of simulations that accurately modelled the occurrence of foxes in Australia (occurrence) on or before first sighting, timing of arrival in a region (timing) and regional population abundance in 2020 (population density). The dashed vertical lines indicate the model targets. Pale blue bars represent the first simulations and darker bars represent later iterations. Red bars represent the selected simulations. (b) Prior (grey) and posterior (coloured) distributions for five variable parameters generated during the simulation process. For parameters that did not vary with Koppen Geiger climate zone, the posterior parameter distributions are shown in gold. Posterior ranges for climatically variable parameters are shown in colours ranging from green (mesic) to yellow (arid).

attributes that were varied across wide but plausible ranges using Latin hypercube sampling (McKay et al. 1979). This procedure produced 50,000 conceivable models (25,000 each across two iterations of POM; see below), with different combinations of variable parameters (Table 1). SEPMs were run at an annual time step for the period 1870–2020 C.E. We ran each model for a single replicate (Tomlinson et al. 2022). From each model we extracted information on annual population abundance in each grid cell. These data allowed us to calculate the timing of arrival and annual total population size (and consequently density) in each region.

All the simulations and code underpinning them can be found online (10.6084/m9.figshare.28720223.v1). This includes temporal sequences of all the spatial projections of our simulations, representing open-access resources of our grid-cell outputs for best models and their model-averaged values.

2.8 | Pattern-Oriented Modelling

POM was used to identify SEPMs that closely simulated independent validation targets (Eriksson et al. 2012; van der Vaart et al. 2015), providing important insights into likely causal drivers of observed patterns of range dynamics (Fordham et al. 2020; Grimm and Railsback 2012).

We used Approximate Bayesian Computation (ABC; Csilléry et al. 2012) to identify the 1% of models (250 simulations) that most accurately reconstructed the validation targets. Model simulations were assessed against a three-dimensional target (Figure 2) that tested the ability of our models to accurately project: (i) timing of arrival in a region; (ii) timing of occurrence at sites within regions (local pattern of spread); (iii) current-day population sizes of foxes in different regions. Eco-climatic regions were derived by aggregating the Interim Biogeographical Regionalisation of Australia regions (Thackway and Cresswell 1997) into six coarser regions that categorised the fox distribution by aridity, with the most mesic in the south-east, followed by the north-east and southwest, and increasing aridity in the central south, north-west and central north (Figure S1 and Table S1). Contemporary fox population sizes were calculated using estimates from Stobo-Wilson et al. (2022). Simulations were penalised as the years between the estimated and simulated time of arrival in each region increased (assuming an equal penalty for simulations populating regions too early or too late). Local occurrence was correct if foxes were simulated to have occurred at or before the earliest site-based record (Fairfax 2019), but after the region was colonised by foxes. Simulations were penalised as the percentage of correct reconstructions of local occurrence declined, and as population abundance in each region deviated

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from best estimates. Deviation in timing of arrival and population abundance was estimated by calculating the root mean square error (RMSE) between the modelled parameters and the empirical targets across all grid cells where target data were available.

We retained the 1% of models (250 simulations) that most accurately reconstructed this multivariate target, using the rejection algorithm in the abc package (Csilléry et al. 2012). Variable parameter ranges for these most accurate models were used to inform prior distributions for a further 25,000 simulations, which we again simulated and tested using POM methods. At each round, we calculated Bayes factors and ceased further model generation when these indicated that the posterior distributions had converged (Berger and Pericchi 1996). We assess the accuracy of these simulations using a goodness-of-fit test with the *'gfit'* function in the abc package (Csilléry et al. 2012).

The most accurate simulations of fox invasion across Australia were used to generate a multi-model averaged projection of colonisation and expansion across Australia, weighted by the inverse of the Euclidean distance of the model from the validation targets (Fordham et al. 2022). This gives higher weights to models that best reproduce the multivariate target.

3 | Sensitivity Analysis

We did a sensitivity test using a Bayesian linear method in the rstanarm package for R (Muth et al. 2018), applied to the parameter bounds optimised through two rounds of POM (i.e., that range which described our final model set). This approach regresses the model parameters against an idealised model to assess which model parameters most strongly reduce the Euclidean distance between simulated and inferred demographic change (Si et al. 2020). We ensured model convergence using Gelman–Rubin statistics (where values less than or equal to 1.1 were considered acceptable), along with testing for effective sample size, and visually examining trace plots (Fordham et al. 2024).

3.1 | Counterfactual Introduction Scenarios

Fairfax (2019) indicates that foxes were deliberately introduced to three locations across Australia (1895 in Goulburn, 1901 on the Yorke Peninsular and 1902 on the Eyre Peninsular) following their initial introduction in 1870. We used our validated simulation models and counterfactual scenarios to test the importance of these additional introductions. We did this by running simulations where these subsequent introductions were not implemented and calculating the difference in timing of arrival across Australia. These *in silico* experiments tested the hypothesis that fox invasion across Australia was rapid enough that additional fox releases were not needed to speed up their spread across Australia. Specifically, differences between our baseline simulation (with subsequent releases) and the counterfactual scenario were assessed by comparing the difference in timing of arrival in different regions and the time to reach carrying capacity in a region.

3.2 | Post-Simulation Analysis

Biogeographical patterns in our simulated fox abundances were interrogated by comparing patterns of population growth and timing of arrival in our target eco-climatic regions, aggregated from the Interim Biogeographical Regionalisation of Australia regions (Thackway and Cresswell 1997) by aridity. This was done by extracting abundance data from each simulation and calculating year of first arrival, annual population increase and the number of years between first arrival and the year in which the population reached the 90th percentile of maximum abundance.

To gain greater insights into rates of population expansion, we calculated gradient-based velocities of population abundance (Brito-Morales et al. 2018). We did this using our multi-model averaged estimate of fox spatiotemporal and the VoCC package (García Molinos et al. 2019).

4 | Results

4.1 | Pattern-Oriented Modelling

The fit of our models improved through re-iterations of POM (Figure 2). The second (and final) iteration of POM resulted in models that: (i) colonised different eco-climatic regions within 15 years of empirical estimates; (ii) populated approximately 90% of known location records at or before the timing of first sighting; and (iii) closely estimated current-day regional population sizes and densities.

Closely simulating this multivariate target required specific demographic parameters in our SEPMs (Figures 2, S3). These included an average founding population size of 58 ± 19.5 (1 S.D.) individuals, a dispersal rate of $15 \pm 2.9\%$ of the population moving each year at an average natal dispersal distance of 30 ± 2.9 km. It also required maximum population growth rates of $\lambda = 1.6 \pm 0.13$ in mesic Koppen-Geiger regions, increasing to $\lambda = 2.4 \pm 0.19$ in arid Koppen–Geiger regions, and carrying capacities ranging from 0.20 ± 0.01 foxes per km^2 in arid Koppen–Geiger regions to 0.69 ± 0.03 foxes per km^2 in mesic Koppen-Geiger regions (Figure 2; Table 1).

4.2 | Invasion Dynamics

The multi-model average of the best SEPMs—those that best reconstructed the multivariate target (best 0.5% of all 50,000 models)—showed a rapid invasion pattern for foxes, with expansion occurring across Australia in approximately 60 years following their initial release (Figure 3). We show that it is likely that the carrying capacity of foxes in Australia was reached shortly after the middle of the 20th century, after which time population growth plateaued (Figure 3). This coincided with foxes expanding to the northern limit of their distribution (Figure 3).

Specifically, our modelling indicates that foxes quickly expanded their distribution throughout the southeastern corner of Australia between 1870 and 1895, before rapidly spreading in northerly

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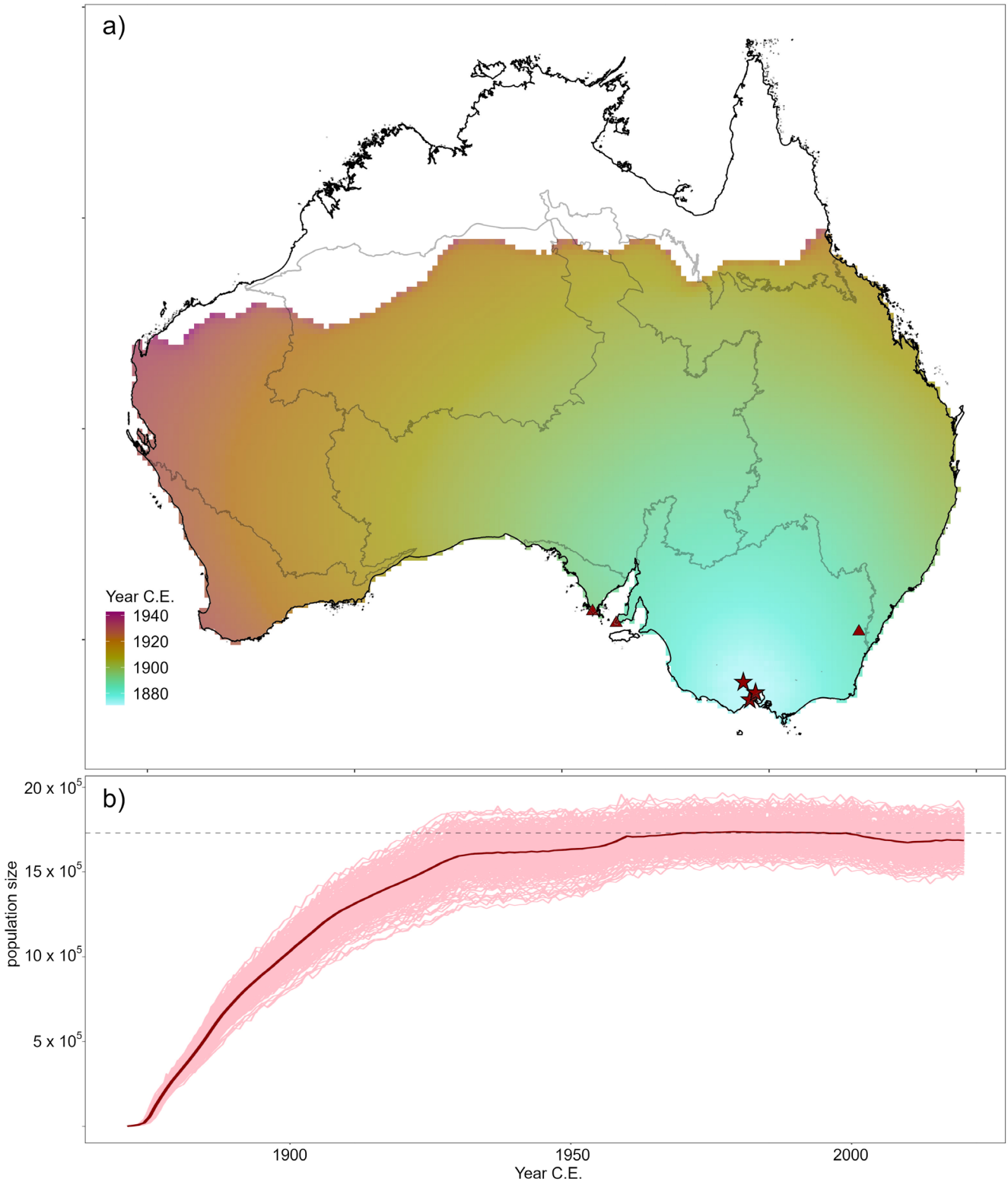


FIGURE 3 | Timing of fox invasion of Australia (a) Map shows estimated year of arrival. Stars show sites of initial introduction. Triangles show sites of later introductions. Grey polygons show eco-climatic regions used for subsequent analyses of the expansion dynamic (b) Population trajectory for foxes from time of release to the current day. Solid line shows the multi-model averaged estimate of population growth based on the best 250 SEPMs. Pale lines show estimates based on individual runs. The dashed horizontal shows the estimate of fox abundance today (Stobo-Wilson et al. 2022).

and westerly directions. By 1900, it is likely that foxes had occupied all available habitat in the south-eastern region of Australia (Figure 3). They then spread more slowly along the north-east, and across more arid central regions of Australia between 1885 and 1920 (Figure 4; Animation S1). These areas are more marginally suitable for foxes. Upon reaching the southwest of Australia

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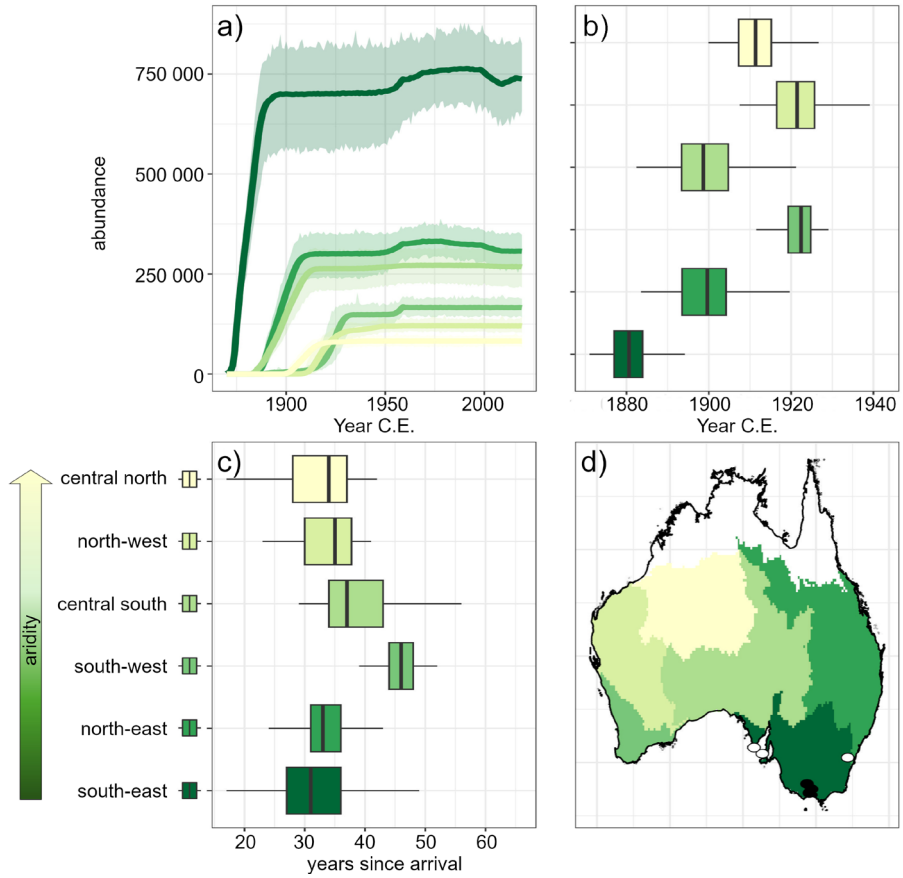


FIGURE 4 | Regional variation in arrival and population growth of foxes across Australia. Spatial variation in (a) population growth, where heavy lines represent the multi-model averaged estimate of population size, while the shading represents the upper and lower bounds. (b) Timing of arrival and (c) time needed to reach carrying capacity, calculated as the time period between arrival in a region and its population hitting carrying capacity. These model outcomes were summarised for (d) six distinct regions of Australia, described in detail in Table S1.

in c.1910, foxes rapidly spread across this region in approximately 20 years (Figure 4). Fox colonisation across the northwest of Australia was the final phase of colonisation, with the distribution of foxes being completely infilled in c.1940 (Figure 3). It is likely that foxes spread from central Australia in a north-westerly direction, colonising the last areas of suitable habitat. The rate of expansion slowed as foxes reached their northern range limits. This was most pronounced in the northwest, where habitats along the range boundary are arid (Figure S4).

The total abundance of foxes in Australia is likely to have increased sigmoidally until the late 1930s (Figure 3), reaching a stable upper population of approximately 1.7 ± 0.084 (1 S.D.) million foxes shortly after 1950. Different regions of Australia are likely to have experienced different rates of population growth, with abundances increasing most slowly in arid regions and fastest in temperate regions (Figure 4). Fox populations in each region reached carrying capacity over similar durations following the first arrival of foxes in that region (Figure 4). This is despite differences in area, timing of arrival and carrying capacity. Times to carrying capacity ranged from approximately 30 years in the southeast to approximately 45 years in the southwest.

A counterfactual scenario, testing the importance of additional reinforcing introductions done at two sites in South Australia (Yorke and Eyre Peninsulas) and one site in New South Wales (Goulburn) following initial release, found that the range and population dynamics of foxes would have remained unaltered if these additional reintroductions had not been done (Figure S5). Regional patterns of timing of arrival and population growth were identical for the baseline and counterfactual scenario with no additional releases.

4.3 | Sensitivity Analysis

A global sensitivity analysis showed that our reconstructions of inferences of fox colonisation of Australia were most sensitive to uncertainty in maximum population growth rate and density-dependent drivers of emigration and immigration ('dispersal threshold'; Figure S6). The models were least sensitive to our estimates of the proportion of the population that dispersers and dispersal distance.

5 | Discussion

Invasive predators represent a substantial threat to biodiversity globally (Doherty et al. 2016; Hogue and Breon 2022). Understanding their roles in past extinctions and the shaping of distributions of extant species requires detailed knowledge

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of the arrival and expansion of invasive predators at high spatial and temporal resolutions (Lomolino and Channell 1998). By reconstructing the invasion of Australia by European red foxes (*Vulpes vulpes*) at high resolution using process-based models and pattern-oriented methods, we show that it took just 60 years for foxes to infill their entire current-day distribution in Australia, pinpointing landscapes and environments that were more and less conducive for range expansion. These model-based findings are supported by molecular evidence of invasion routes (Sarre et al. 2024).

Reconstructing estimates of time of arrival and population densities of foxes at local and regional scales across Australia required foxes to have specific invasion dynamics (number and size of founding populations) and demographic parameters (growth rates and carrying capacities) affected by climatic conditions. We show that the invasion of Australia by foxes required only 60 animals to be released at three sites in Victoria, with foxes filling their potential distribution in Australia in just 60 years.

5.1 | Biogeography of Foxes in Australia

Our simulations show that following the introduction of foxes to Australia in 1870, they took just 30 years to colonise Australia's south-eastern corner. The colonisation routes of foxes then turned north and west, spreading across the Australian continent (Animation S1). While this pattern of spatial spread is broadly consistent with coarser scale, pattern-based estimates of the timing of fox expansion across Australia (Abbott et al. 2014; Fairfax 2019), our process-driven approach enabled population growth and expansion to be reconstructed annually across space at a high resolution. This resulted in estimates of time of arrival at a spatial scale of 25 km^2. It also allowed us to reconstruct population abundances of foxes across their broad distribution, revealing a more nuanced pattern of range expansion. For example, we show that expansion across Australia's arid zone slowed between 1900 and 1930, probably because of lower rainfall, which is associated with generally lower average population growth rates of foxes in Australia (Scroggie et al. 2018). Consequently, foxes arrived in Australia's northwest only in 1940.

These and other differences to existing spatial maps of the timing of fox colonisation of Australia are likely to extend from explicitly considering important demographic and ecological elements of invasion in our reconstructions. These include spatiotemporal variation in carrying capacity and reproductive and survival rates. Our reconstructions show that fox carrying capacity is highest in mesic agricultural landscapes, which is consistent with field observations (G. Saunders et al. 1995). However, maximum population growth rates in our reconstructions were higher in arid, compared to mesic, eco-climatic regions, probably reflecting high spatiotemporal variability in fox reproduction (Burrows 2018) and the propensity for fox population growth to be high in arid and semi-arid conditions (Hone 1999). More generally, our simulations suggest that fox populations in mesic regions are likley to have had high impacts on native fauna, because of earlier arrival times and higher sustained abundances.

Foxes are likely to have reached the most northerly parts of their current geographic extent in the middle of the 20th century. Although it has been suggested that foxes are potentially still expanding their distribution northwards into vacant habitat and territories (Hradsky et al. 2019), this is not supported by our modelling. Simulations reached full occupancy in all eco-climatic regions by approximately 1950, coinciding with total population size stabilising at current-day levels of around 1.7 million foxes (Stobo-Wilson et al. 2022). However, our reconstructions of spatial abundances also found population growth rates of foxes in agricultural regions to have increased notably in the 1950s, including in the south-east, south-west and north-east regions of Australia. This coincides with a period of large-scale agricultural expansion following World War II (Godden 1999) and is in agreement with current-day field-based studies showing a positive relationship between agricultural expansion and fox abundance (Sharp et al. 2001). It is also consistent with suggestions that processes of fox predation and land conversion operate synergistically to drive biodiversity loss in Australia (Woinarski et al. 2015).

Tests of whether additional reinforcing introductions were needed to speed up the invasion of Australia by foxes following their initial release in Victoria in 1870 showed that they were not needed. Modelling subsequent releases in Goulburn in New South Wales (1895) and on the Yorke (1901) and Eyre Peninsulas (1902) in South Australia did not impact the timing or pattern of range expansion or trajectory of population growth. This is consistent with molecular evidence showing that foxes in Australia expanded from a single origin near Geelong (Sarre et al. 2024).

A global sensitivity analysis showed that our simulated reconstruction of fox invasion in Australia is most sensitive to our estimates of population growth and dispersal. Fortunately, these are demographic traits that have been well studied and have robust empirical estimates, including for foxes in Australia (Harding et al. 2001; Hone 1999; McLeod and Saunders 2001; Read and Bowen 2001). Thus, our best simulations are likely to provide an accurate representation of the colonisation of Australia by foxes, providing biogeographic data needed to quantify past losses of Australia's unique fauna and to avert future extinctions.

5.2 | Conservation Value

In Australia, invasive predators are thought to have caused one of the highest rates of recent losses of terrestrial species (Woinarski et al. 2019). However, the timing, rate and magnitude of these losses have been difficult to resolve (Johnson 2006). This is at least partly due to an overly coarse understanding of how invasive predators expanded across the continent (Tomlinson et al. 2022). Thus, our high-resolution reconstructions of fox abundances provide important new open-access data that are needed to definitively establish the extent to which foxes caused range collapses and extinctions of Australia's endemic mammals (Wallach and Lundgren 2025). Our reconstructions of fox invasion of Australia also identified areas that could have provided sanctuaries from foxes due to later invasions or lower predator densities. The prevalence and spatial connectivity of these refugial areas might help to explain patterns of range collapse and current-day persistence for endemic species (Reside et al. 2019).

While we reconstructed the invasion of foxes across Australia in recognition of their critical role in driving biodiversity loss since

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European colonisation (Stobo-Wilson et al. 2022), our modelling approach provides a framework for better understanding the range dynamics of other invasive species. Introduced cats have also had devastating impacts on Australia's unique biota (Dickman 1996; Moseby et al. 2015). Like foxes, the colonisation dynamics of cats in Australia are only understood at coarse resolutions (Abbott 2008). However, the process-based modelling approach developed here for foxes could be easily adapted to cats since their demography is well understood (Baker and Bode 2016; Legge et al. 2017; Miller et al. 2014) and details on the timing of arrival at a wide variety of localities have already been extracted from newspaper articles (Abbott 2008; Abbott et al. 2014).

Additionally, the approach could be used to reconstruct the arrival of dingoes in Australia and their expansion across the continent some 3,500 years ago (Letnic et al. 2014). As Australia's mainland apex predator, dingoes serve vital ecological functions, reducing overgrazing by macropods (Fancourt et al. 2019; Johnson and VanDerWal 2009; Letnic et al. 2012), and more recently regulating cat and fox abundances (Brook et al. 2012; Letnic et al. 2011). However, dingoes today have experienced widescale population declines following European colonisation of Australia (C. Johnson 2006). A more detailed spatiotemporal understanding of dingo abundance in Australia would provide information vital for reestablishing dingoes and their important ecosystem functions, including providing a better understanding of pre-European densities and carrying capacities.

While reconstructing inferences of past colonisation dynamics required specific life-history traits and founding population size, the posterior distributions for some parameters in our process-based models remained wide, despite multiple rounds of pattern-oriented optimisation. For these nonidentifiable parameters, it is important to consider whether the empirical targets used for pattern-oriented modelling best fit the study animal and system (Gelman et al. 2013), which they did. By using diverse types of data (historic sightings and contemporary abundance estimates) to quantify distributional and demographic changes of foxes across a hierarchy of spatial scales, our pattern-oriented modelling method allowed us to characterise the colonisation dynamics of foxes in Australia. However, our reconstructions of fox range dynamics would likely benefit from explicitly accounting for prey availability in model simulations. This is because it is thought that the availability of rabbits, particularly in drought years, influenced the pace of range expansion of foxes in Australia (Low 1984). Models of spatiotemporal variation in rabbit abundance could potentially be used to generate historic maps of rabbit abundance in space and time (Brown et al. 2020), which could be incorporated into the SEPM as a prey base (Fordham, Akçakaya, Brook, et al. 2013). Likewise, accounting for fox management in model projections would likely further improve the capability of our SEPMs to simulate current-day spatial patterns of abundance. This is because fox abundances are today heavily controlled across much of their distribution in Australia (G. R. Saunders et al. 2010).

6 | Conclusion

Halting or reversing the loss of Australia's terrestrial fauna is unlikely to be successful without understanding the landscape-scale processes that caused their post-European declines (Tomlinson et al. 2022). By reconstructing the invasion of Australia by foxes, we have generated critical data needed to disentangle the role of foxes in the demise of Australia's terrestrial fauna. These continental-wide spatiotemporal estimates of annual fox abundances from time of arrival in Australia (1870 to 2020 CE), which are downloadable (10.6084/m9.figshare.28720223.v1), will enable fox predation to be better considered in threat assessments and recovery planning. They also promise to provide opportunities to better quantify predation pressures by foxes on fauna since their release into Australia in 1870.

Author Contributions

D.A.F.: funding acquisition and project administration; D.A.F. and S.T.: conceptualisation, visualisation and investigation; S.T.: data curation, formal analysis, validation, writing – original draft; S.T., S.C.B. and S.H: methodology; S.T., D.A.F., S.C.B. and S.H.: writing, review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available on FigShare at https://figshare.com/s/26310cce90724f4e95d7.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Animation S1.** Changing spatiotemporal patterns of Europen Red Fox (*Vulpes vulpes*) abundance across Australia from 1870 to 2020 C.E. The data are presented as the number of foxes per grid cell, square root transformed to improve the visualisation of spatiotemporal change, demonstrating the weighted ensemble average of the most accurate simulation set. **Table S1:** Target regions used to define patterns of fox abundance and colonisation dynamics. Regions were derived by aggregating polygons of the Interim Bioregionalisation of Australia (IBRA; Thackway and Cresswell 1997) into six regions grouped by increasing aridity. They are shown in Figure 4. **Figure S1:** Fox simulations models were assessed against (a) the earliest records at each location reported by Fairfax (2019), and the first appearance in six eco-climatic regions, represented by the coloured regions of the map. (b) These regions were categorised by increasing aridity, represented by the boxplot of vapour pressure deficit. **Figure S2:** Dispersal functions as parameterised in the SEPMs. The grey shading represents 1000 random draws across the dispersal parameters, summarised by the mean dispersal function indicated by the blue curve. The points show the fox dispersal data reported by Storm et al. (1976). **Figure S3:** repeated approximate Bayesian computation refined the model parameter space from uniformly distributed priors to more tightly distributed posteriors. **Figure S4:** Rate of expansion of fox invasion of Australia (a) showing the rate mapped across Australia, where the polygons represent eco-climatic regions of increasing aridity. **(b)** There was a general trend of slower expansion across arid eco-climatic regions. **Figure S5:** Number of introductions needed for fox colonisation of Australia. Comparison of our baseline (optimised) reconstructions of fox invasion of Australia that included multiple release sites, with a counterfactual scenario where no subsequent introductions were permitted following initial release near Port Phillip Bay in 1870. Estimated (a) abundance, (b) year of invasion and (c) time to reach carrying capacity are shown for both scenarios. The latter two are shown for different regions across Australia. **Figure S6:** Sensitivity analysis. Relative contributions of model parameters to reconstructions of inferences of fox invasion of Australia. Parameter definitions, ranges and sources are described in Table 1.

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