



Integrated modelling reveals widespread distribution of invasive wild pigs across Australia

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ABSTRACT

Invasive wild pigs *Sus scrofa* are globally recognised as one of the most damaging invasive species: they harm ecosystems, agriculture, cultural heritage and transmit significant diseases. However, in Australia effective management of wild pigs is hindered by outdated and non-quantitative estimates of broadscale wild pig distribution. This is partly due to fragmented and disparate data held by many stakeholders across jurisdictions and institutions. Here we produced a contemporary map of wild pig relative abundance for Australia using a continental-scale integrated species distribution model fit to 51,444 presence-only, 11,176 presence-absence, and 34,981 abundance-absence records from 30 data sources. We used five ecological covariates and a spatial random effect to estimate wild pig distribution across Australia, as well as two spatial layers to correct for search effort bias in presence-only observations. Our model showed wild pigs to be more widespread across northern, eastern and southwestern mainland Australia than previously appreciated, and largely absent from the arid interior. The full model had high predictive performance when tested against an independent presence-absence dataset (>0.85 AUC_{ROC}) everywhere except for northern Australia, which was also the only region in which predictive performance did not improve with the addition of spatial random effects. Our study demonstrates that integrated species distribution models can be successfully applied to non-equilibrium species over broad spatial scales using fragmented data sources. However, in addition to computational challenges, data integration at this scale requires complex stakeholder coordination across different jurisdictions and institutions to ensure fair and accurate distribution modelling.

1. Introduction

Invasive wild pigs (hereafter ‘pigs’) *Sus scrofa* are globally widespread and recognised as one of the most damaging invasive species (Lowe et al., 2000). Outside of their natural range, pigs harm ecosystem integrity by preying on and competing with native species (Risch et al., 2021; McClure et al., 2018), as well as extensively degrading vegetation, soil and water bodies (Barrios-Garcia and Ballari, 2012; Cole and Litton, 2014). Pigs also threaten cultural heritage, are a severe

economic burden in agricultural cropping systems, and known carrier of significant endemic and exotic diseases that threaten native wildlife, domestic livestock and human health (Bengsen et al., 2014; Bevins et al., 2014). In Australia, pigs were first introduced as livestock by European colonisers in 1788, with wild populations establishing shortly afterwards. Pigs are now considered widespread in many states and territories; they continue to invade new areas through dispersal and illegal translocation (NSW Government, 2023; Spencer and Hampton, 2005). Quantitative estimates of pig distribution and abundance are of

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importance to policy makers, land managers and the public, but should be based on data and reproducible models which can be updated transparently as distributions change.

A national scale mapping effort based on expert surveys indicated that approximately 45% of Australia's land mass is inhabited by pigs (West, 2008). This map has been used widely in many different applications, such as estimates of national and global absolute pig abundance (Hone, 2019; Lewis et al., 2017), disease transmission risk (Bradhurst et al., 2021), biodiversity impacts (Risch et al., 2021) and greenhouse gas emissions (O'Bryan et al., 2022). However, this map was created at a coarse resolution and provides qualitative rather than quantitative estimates of relative abundance, distribution and uncertainty. Furthermore, it has not been updated since its publication, likely due to difficulties in properly (a) collating and standardising available sources of invasive species population data, and (b) integrating different survey methods and data types in statistical distribution models.

Estimating the distribution of species is a central focus of ecology, necessitated by the fact that we cannot survey everywhere (Elith and Leathwick, 2009). However, limited and disparate data often prevent empirical modelling of species populations over broad spatial scales. Accordingly, integrated models have been developed to make use of all available information, maximising benefits and minimising limitations of different data types to improve estimates. Integrated species distribution models (hereafter ISDMs) typically supplement high quality presence-absence and abundance-absence data with geographically expansive presence-only data to improve accuracy and precision of estimates (Fletcher Jr. et al., 2019; Isaac et al., 2020; Miller et al., 2019).

Invasive species are a priority for both distribution modelling and land management as they are a key threatening process to environmental, agricultural and socio-economic sectors (Elith, 2017; Paine et al., 2016; Pyšek et al., 2020). However invasive species present additional modelling challenges, as their distributions are often not at equilibrium with the environment due to ongoing spread and perhaps also the effects of active population control (Gallien et al., 2012). Spatially-explicit random effects (e.g., Lindgren et al., 2011) offer a partial solution for correlative models as they can account for non-equilibrium distributions. Spatial random effects are commonly used in ISDMs, but are computationally intensive and may result in overfitting to observational data (Dambly et al., 2023; Hodges and Reich, 2010). It remains unclear in what circumstances the benefits of spatial random effects outweigh potential challenges.

Here we applied newly developed ISDM methods to predict the current distribution of pigs in Australia and generate a contemporary national map based on up-to-date (as of 2024) empirical data. We compiled a comprehensive dataset containing presence-only, presence-absence and abundance-absence observations from both publicly-available and privately-held sources. We used five ecological predictor variables as fixed effects, as well as a spatial random effect to predict pig distribution and relative abundance. We included model terms to correct for spatial sampling bias in presence-only observations (Hughes et al., 2021), as well as sampling artefact terms for variation induced from different survey methods in the presence-absence and abundance-absence data (fixed-wing plane, helicopter, or camera-trap; Foster et al., 2024). We assessed model predictive performance using an independent landholder questionnaire, and compared performance with and without spatial random effects. Our model outputs were also reviewed by species experts, and our workflow from data collation to expert review was developed as a framework for modelling the distribution of other priority invasive species and supporting future updates.

2. Methods

We modelled the current distribution of pigs on Australia's mainland and included adjacent islands only where they contained known established populations of national importance. This included Flinders Island, the southernmost population, and Tiwi Islands, whose pig population

poses a significant exotic disease incursion risk for Australia. The Tasmanian mainland was excluded because pigs have not established there. We excluded all other islands because sparse data, natural barriers to dispersion, and ongoing eradication efforts introduced significant uncertainty about data currency.

We aimed to estimate the current broadscale distribution of pigs across Australia, i.e., distributions which do not fluctuate with weather or specific local contexts. We selected a model resolution of 25 km² grid cells (in which data and predictor variables were summarised, and the model predicted). This resolution offered a compromise between capturing ecological relationships at an appropriate scale (less than the size of an average pig home range) and this aim to capture broadscale patterns, as well as computational efficiency.

We applied several processing steps to transform spatial predictor variables into a consistent format, namely averaging measurements of two temporally-varying predictor variables to remove the impact of short-term fluctuations in these values for a static ISDM and aggregating spatial layer up to the 25 km² resolution. All analyses were conducted in R (v.4.3.3, R Core Team, 2024). We used 'sf' (v1.0.16, Pebesma, 2018), 'terra' (v.1.7.71, Hijmans et al., 2022) and 'rasterVis' (v0.51.6, Lamigueiro et al., 2023) R-packages for spatial data processing and visualization.

Our dataset spanned 1911–2024 (Table A1.1). We retained older records because pig distribution in Australia is unlikely to have contracted over this period - populations have historically expanded their range rather than contracted (except on some offshore islands subject to eradication, which were excluded from our analysis). While there is a temporal mismatch between these data and predictor variables, we chose variables representing climatic or largely permanent landscape features (considering the broad resolution and continental-scale of this analysis).

2.1. Observation data

We collated 168,357 presence-only records from 21 data sources (biodiversity atlases comprising state and Australia-wide observations, as well as opportunistic observations and targeted control operations from government and Indigenous land managers), 46,653 presence-absence records from 6 data sources (camera-trap surveys across national and state parks in eastern Australia and aerial surveys of magpie geese in northern floodplains), and 34,981 abundance-absence records from 3 data sources (large-macropod aerial surveys in Queensland, New South Wales and Western Australia; Fig. 1). These data were collected by diverse government, academic and private stakeholders on private and public land during aerial and camera-trap surveys, targeted control operations as well as through opportunistic observations (Table A1.1). A steering committee was also formed from these parties which helped facilitate sharing of agency knowledge about non-public datasets, and regional knowledge about pig ecology and distribution. Few of these surveys specifically targeted pigs, instead aimed at surveying species such as large macropods, magpie goose *Anseranas semipalmata*, as well as the broader invasive and native mammalian communities - meaning data were not skewed to sites where pigs were expected to occur or have impact. Some datasets were singular standardised surveys, while others were collations of multiple surveys, control operations or incidental observations. These datasets ranged from publicly available to highly sensitive, closed sources.

As an initial step, we downloaded data from state and territory biodiversity atlases (i.e. publicly-accessible repositories or aggregators of biodiversity data). These atlases typically provide some information about the project from which a record was sourced and the data collection methodology, but rarely include absence data. We additionally aggregated large amounts of control program data and landholder reported data on private and parks estates which are confidential for numerous reasons. These data covered broad regions where survey data were absent from public repositories, such as the Kimberley and inland

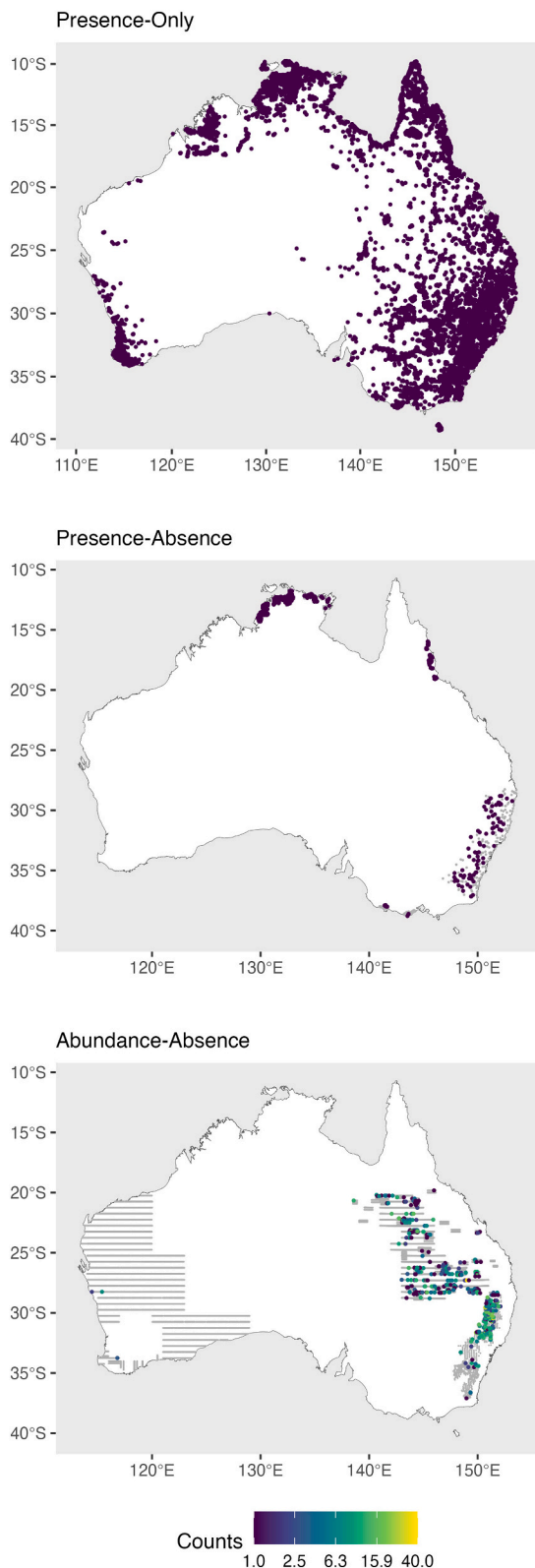


Fig. 1. Map of the spatially thinned invasive wild pig observation data used to fit the ISDM, separated by data type. Counts refers to number of wild pigs recorded; presence-only and presence-absence data types have a maximum count of 1 (dark purple). Grey dots represent non-detections in the presence-absence and grey transects represent non-detections in the abundance-absence data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

NSW. We also identified records within the atlases from projects with structured survey designs and approached the data custodians separately to obtain full data (with absence and abundance information) and detailed metadata about study design and methods. Additional survey datasets were identified through consultation with steering committee members and other stakeholders. We withheld from the model a government questionnaire of landholders about the presence of invasive species on their properties as an additional presence-absence dataset to be used as an independent testing dataset of model predictive performance (see Section 2.5 below).

2.1.1. Presence-only (PO) data

We collated pig presence records from 9 biodiversity atlases as well as 12 stand-alone government and community data sources (Table A1.1). In total, there were 168,357 presence records. Atlases aggregated records from a range of sources on both public and private land; many are from state government control and monitoring programs, others include citizen science programs and community group surveys. The seven non-atlas data sources were generally highly targeted surveys and control interventions (largely aerial and ground shooting) of pigs and other pests in regions and/or tenures that are relevant to the data source. We removed records in which the reliability of species identification or spatial location was uncertain. We included all data from 1911 to 2024, as pig distribution is unlikely to have contracted over time in the long-term (except in some offshore islands subject to eradication, which we remove from the modelling frame). We removed PO data which was also present in PA or AA datasets to avoid double counting. We applied spatial filtering to the PO data so that only one observation per 0.5 km was preserved to improve computational stability as well as reduce model overdispersion and overfitting.

2.1.2. Presence-absence (PA) data

One aerial survey (fixed-wing planes) targeting magpie geese in northern floodplains and five camera-trap data sources across eastern Australia provided PA data (Table A1.1). To reduce overdispersion in the model, we clustered camera-traps within 1 km - grouping repeat visits across survey years into a single presence/absence observation per site. Most camera-trap sites were resurveyed annually for three or more years, and targeted the broader mammalian community within national and state parks. The 1 km clustering of camera-traps differs from the 0.5 km thinning applied to PO data. We were more stringent in discarding detections here as we were confident repeat detections of individuals were very likely given both high spatial precision and short survey range for camera-trap datasets (maximum survey length was 10 years relative to 113 years for a PO dataset). We discretised flight paths from the magpie goose survey into 1 km transects by segmenting the flight path, taking the central coordinate of each 1 km segment, 'snapping' records of pigs to the nearest central coordinate and calculating the presence or absence of pigs in each segment. Although group sizes were recorded for each pig observation, the data collection tool used made it challenging to enter exact abundance values for large groups, and so we included this as PA rather than AA data.

2.1.3. Abundance-absence (AA) data

We included aerial transect survey data sources which targeted large macropods in Queensland (using helicopters and fixed-wing planes), New South Wales (helicopter), and Western Australia (fixed-wing) as AA data for pigs. The Queensland macropod surveys were situated to cover major bioregions (central QLD) and local government areas (southern QLD), and featured both aircraft types. The spatial scale at which each dataset was collected and supplied for use in this modelling. For the QLD surveys, we discretised flight paths into 1 km transects by taking the central coordinate, 'snapping' counts of pigs to the nearest central coordinate and summing the group sizes. In the WA dataset, counts of animals were already aggregated to evenly spaced 5 km cells before the

dataset was supplied for this analysis. In the NSW dataset, the number of sightings per transect was recorded, with transect lengths being 5 km, 7.5 km, or 10 km.

2.2. Predictor variables of PO spatial sampling bias

Spatial sampling bias in presence-only data, introduced through systematic variation in the way which pigs have been searched for combined with unknown search effort, is difficult but important to account for (Hughes et al., 2021). Here we included two spatial layers (Fig. A1.1) as fixed linear predictors on the presence-only model error term to estimate potential spatial sampling bias in pig presence-only data (i.e., estimated separately from the ecological process model shared among all data types). This PO spatial sampling bias term specification is similar to Warton et al. (2013), further explained in Foster et al. (2024). We derived a spatial layer for invasive mammal PO search effort to account for multispecies surveys, and used an index of pig control difficulty to account for more targeted pig surveys, detailed below.

2.2.1. Invasive mammal PO records

To derive where pigs were likely to have been recorded if they were present, we created a raster layer using all counts of PO records of invasive mammals (excluding rodents as they are typically observed differently to pigs) in each cell. We hypothesized cells with many presence-only records of invasive mammals to be indicative of positive bias in pig presence-only observations. We used all invasive mammals (except rodents) rather than a specific functional group (e.g., herbivores) as these species span a diverse range of habitat preferences across Australia, meaning this layer is more likely to reflect search effort rather than suitable pig habitat. These records of the invasive mammal community came from our PO data sources which recorded multiple species, and several additional datasets which would have reliably recorded pigs if present. We spatially thinned these records by 500 m for consistency with pig PO data, and then $\log(x + 0.5)$ transformed the count in each cell. This transformation increased sensitivity to low rather than high values (particularly over 20), reflecting our belief that the distinctions between no, few and many records is likely to be more reflective of pig survey effort than linear or other transformations (further teasing apart search effort from pig habitat suitability).

2.2.2. Feral pig control difficulty index

The second predictor was the feral pig control difficulty index (Hoskins and Perry, 2020). As many of our presence-only records came from aerial and ground lethal control operations, we hypothesized a negative bias in such observations in areas of higher difficulty (e.g. due to accessibility constraints). The feral pig control difficulty index (Hoskins and Perry, 2020) is a weighted combination of landscape friction (estimated travel time across each cell), accessibility (travel time to nearest population centre), terrain ruggedness (fine-scale changes in elevation within the cell) and canopy visibility (tree cover percentage). The weightings account for the assumption that ground control is more difficult than aerial control operations through up-weighting friction and accessibility (Hoskins and Perry, 2020).

2.3. Predictor variables of pig distribution

We identified five key explanatory variables that influence four fundamental resource requirements for pigs: food (above and below ground), water, shelter and heat refuge (Froese et al., 2017). We chose the best available remotely sensed or mapped spatial data proxies for each resource requirement. These predictor variables were: (1) amount of green vegetation as a proxy for above-ground food resources available to pigs, (2) maximum temperature of the warmest month reflecting possible heat stress conditions, (3) amount of woody cover reflecting available shelter, (4) volume of soil moisture in the root zone which

affects accessibility of below-ground food resources to pigs, and (5) distance to surface freshwater used by pigs for consumption and heat regulation.

2.3.1. Green vegetation

Pigs' omnivorous diet is difficult to capture directly in spatial data as pigs can use a range of above-ground food resources. In the absence of spatial layers which represent the above-ground protein derived from animal material, we used a spatial proxy for vegetation productivity. We used the satellite-derived fraction of photosynthetic vegetation ('fPV'), measured as percentage of total cover (also including non-photosynthetic vegetation and bare soil), which is a useful proxy indicator for overall vegetative productivity in natural and modified landscapes, such as crop fields (Guerschman, 2019). We took the mean value of photosynthetic vegetation layers for all months (2001–2023), replaced inland NAs with 0, and used a square root transformation to reduce data skew to help with model fitting.

2.3.2. Maximum temperature

Without sweat glands, pigs are vulnerable to overheating under high daytime temperatures. We used the 'bio5 - Max Temperature of Warmest Month' bioclimatic variable (Noce et al., 2020) as a direct proxy indicator for heat stress in pigs. Maximum temperature ranged from 17 to 42 degrees in our study area.

2.3.3. Woody cover

Pigs avoid overheating by seeking shelter in shaded microclimates. We used satellite derived woody-vegetation cover of Australia for the decade from 2000 to 2010 (the only currently available decade), measured as foliage projective cover (Gill, 2021), as a proxy indicator for thermoregulation provided by vegetation canopies. Pigs may also use woody areas as shelter from predators (mostly humans). We used a cube root transformation of this layer to reduce data skew to help with model fitting.

2.3.4. Soil moisture

Pigs use a range of below-ground food resources, such as roots, tubers, fungi and invertebrates, which they access through digging and rooting. The accessibility of these below-ground food sources depend on the 'diggability' of soils, largely influenced by soil moisture. Pigs can also obtain water for consumption through roots and tubers in the soil, and wallow in moist soils for thermoregulation, potentially reducing their reliance on free-standing freshwater. We therefore used daily total volume of soil moisture in the root zone (0–100 cm depth), which accounts for soil properties, precipitation and potential evapotranspiration (Stenson et al., 2021). We took the mean value of all available daily soil moisture layers (2005–2022). We used a cube root transformation of this layer to reduce data skew to help with model fitting.

2.3.5. Distance to water

Pigs require surface freshwater (non-salty or brackish) for consumption and in some cases to wallow for thermoregulation. We created a new spatial layer which combined mapped locations of standing water which occur in the landscape most of the time. This aggregated selected permanent features ('AHGFNetworkStream: Perennial', 'AHGFWaterbody', 'AHGFDam', 'AHGFHydroPoint: Waterhole; Spring') of the Australian Hydrological Geospatial Fabric (Bureau of Meteorology, 2020). We created a raster which recorded the presence or absence of water from any of these sources in each 1 km² cell. To remove water too brackish for consumption, we masked out brackish water bodies using an estuarine layer (Dyall et al., 2005). We then calculated the distance to the nearest cell with water present and used a cube root transformation of this layer to reduce data skew to help with model fitting.

2.4. Model specification

We fit the ISDM in INLA (v23.09.09, Rue et al., 2009, Lindgren et al., 2011) using the 'RISDM' R-package (v.1.2.21, Foster et al., 2024). We predicted the model on a raster grid at a cell resolution of 25 km², using 10,000 draw samples from the posterior distribution. We used the intercept of the abundance-absence helicopter surveys, because these were relatively well spread throughout the continent with reasonably high detection probabilities (detailed in the sections below). Here, we present median point intensity and associated 95% credible interval values. Predictions from integrated models are typically described in the terms of the dataset with the highest information content (Kéry and Royle, 2020), which in our case is an abundance pattern. As we did not incorporate imperfect detection, our predictions should only be interpreted as abundance on a relative rather than absolute scale (Guillera-Arroita et al., 2015). The outputs we present here could therefore be interpreted as the median relative abundance of pigs, to be expected using a helicopter survey.

We included model offset terms, a linear covariate with a fixed coefficient of 1, to scale the response variables by search area (Table 1). For the PO sub-model, the offset contained the proportion of each cell covered by land to not overestimate pig relative abundance along coastlines. For aerial PA and AA surveys, the offset reflected the transect length in metres, multiplied by the maximum observation distance on either side of the aircraft (transect width). For camera-trap surveys (which are deployed for multiple days at a time), we estimated the search area at 25 m² and multiplied this value by the number of deployment days to calculate the offset.

The collated PA and AA datasets surveyed pigs with multiple known survey methodologies. We mitigate the chance that these sources of variation in observation are confused with the distribution of pigs by adding fixed effects into the relevant sub-models for each data type (i.e., additional intercepts estimated separately from the shared process model), termed sampling artefacts in Foster et al., 2024. We included separate intercepts for data from each of the following survey methods: camera-traps, fixed-wing plane and helicopter (Table 1).

We specified priors for fixed effects (intercepts and covariate effects) to have a mean of 0 with a standard deviation of 10. We included polynomial terms for selected predictors of pig distribution to allow for nonlinear relationships (Table 1). For example, pig use of woody cover may decline at high cover densities (Wilson et al., 2023), while temperature and distance to water are likely to exhibit upper thresholds

beyond which pig abundance decreases due to thermoregulatory constraints. All other predictor variables were fit with linear terms.

We fit two models: one without and one with a spatial random effect that explains spatially smooth variation that is not correlated with covariates. The random effects are defined on an analysis mesh with a likely effective range of 25 km and a maximum of 96,000 nodes in the inner area. We used penalised complexity priors for the spatial random effect in the form of probability statements (Simpson et al., 2017). We set a prior of the effective range of the random effect (i.e., the distance at which two points are independent) to have a 10% chance of being less than 25 km, as this is approximately the median home range size for males (Wilson et al., 2023). We set a prior for the standard deviation of the range to have 10% chance of being greater than 2.

2.5. Model evaluation

We held out one presence-absence dataset as an independent testing dataset for independent model evaluation, partly as it represents a fundamentally different type of observation process. Evaluating models using internal (cross-validation) or otherwise non-independent data is problematic as they contain the same biases present in the training data, causing overestimation of predictive performance (Araújo et al., 2005). Testing models against independent datasets generated through a different observation process (e.g., Matutini et al., 2021) is critical for robust assessment (Baker et al., 2024).

We evaluated model predictive performance by calculating the area under the receiver operating characteristic curve (AUC_{ROC}) with associated 95% credible intervals using an independent presence-absence test dataset with the 'pROC' r-package (Robin et al., 2011). The AUC_{ROC} metric assesses the model's ability to discriminate presences and absences at sites (Pearce and Ferrier, 2000). This discrimination metric ranges from 0 to 1, with 1 showing perfect discrimination and 0.5 commonly interpreted as indicating no better discrimination than a random classification. To understand spatial variation in predictive performance across different ecosystem types, we also calculated the AUC_{ROC} separately in each terrestrial ecoregion (Olson et al., 2001). We compared the two models' (with and without spatial random effect) AUC_{ROC} scores to determine how beneficial the added complexity of the spatial random effect was and identify regions where this term may be overfitting to the observation data.

The independent test dataset was a questionnaire survey of private landholders about the presence and impact of invasive species including

Table 1

Summary of Integrated Species Distribution Model structure. All three sub-models for each data type share the same ecological process distribution model (fixed effects and spatial random effect). We fit two models: one with and one without this spatial random effect. We included categorical fixed effects in the presence-absence and abundance-absence observation submodels to account for variable detection rates of pigs across different survey methods (i.e., "sampling artefacts"), and linear predictors on the error term to account for spatial sampling bias in pig presence-only data.

Sub-model	Data sources	Model formula			
		Observation	Spatial bias	Area offset	Distribution
Presence-only (PO) (Poisson point process)	51,444 records (after 0.5 km spatial thin) from: <ul style="list-style-type: none"> Biodiversity atlases (n = 9) Government and community data sources (n = 12) 		<ul style="list-style-type: none"> Invasive mammal PO records Feral pig control difficulty index 	<ul style="list-style-type: none"> Proportion of land area per cell 	<ul style="list-style-type: none"> Green vegetation (average) Maximum temperature (polynomial term) Woody cover (polynomial term)
Presence-absence (PA) (Binomial)	11,176 records from: <ul style="list-style-type: none"> Mammal community camera-trap surveys (after 1 km spatial clustering; n = 5) Macropod aerial surveys (n = 1) 	Survey method: <ul style="list-style-type: none"> Camera-trap Fixed-wing plane 		<ul style="list-style-type: none"> Camera: estimated detection area * survey days Aerial transect length * width; 	<ul style="list-style-type: none"> Soil moisture (average) Distance to water (polynomial term) Spatial random effect
Abundance-absence (AA) (Negative binomial)	34,981 records from macropod aerial surveys (n = 3)	Survey method: <ul style="list-style-type: none"> Helicopter Fixed-wing plane 		<ul style="list-style-type: none"> Aerial transect length * width 	

pigs on their properties, included 1463 recorded presences and 3722 absences of pigs (Stenekes et al., 2023). The proportion of surveyed landholders detecting pigs on their properties ranged from 0.08 to 0.8 per ecoregion. Many of the surveyed properties, especially in Australia's north and arid interior, were larger than our 25 km² analysis cells. To minimize the effects of this possible spatial mismatch on AUC_{ROC} evaluation, we averaged values predicted by the integrated model across the central and four adjacent cells before comparing to the test data.

3. Results

We collated 168,357 PO records spanning 1911–2024 across 21 sources, 46,653 PA records spanning 2012–2023 across 6 sources, and 34,981 AA records spanning 2013–2023 from 3 sources. PO records were distributed across all mainland states and territories, with higher densities in eastern and northern Australia. PA records were concentrated in eastern Australia (camera traps) and the northern floodplains (aerial survey). AA records covered Queensland, New South Wales and Western Australia. Together these datasets represent a broad range of survey methodologies, habitat types and land tenures. Following spatial thinning and clustering, we fit the model to 51,444 PO records, 11,176 PA records, 34,981 AA records, and tested predictions against an independent PA dataset comprising 5185 records.

The full model had good predictive performance overall (AUC_{ROC} 0.85, 95% CI: 0.83–0.86) when assessed against the hold-out test data.

Relative abundance of pigs was predicted to be highest across northern Australia, much of Queensland and New South Wales as well as south-western Western Australia (Fig. 2). The lowest abundance of pigs was predicted in central parts of Western Australia (except for where pigs have been recorded in the south-west and Pilbara), southern parts of the Northern Territory and much of South Australia (Fig. 2). However, the Bayesian credible intervals revealed that in these regions the actual value may still be quite high (Fig. 2). This high uncertainty was largely caused by the spatial random effect (compare Fig. 2 to Fig. A1.3).

The addition of a spatial random effect considerably improved model predictive performance overall by an AUC_{ROC} score of 0.16. Within ecoregions AUC_{ROC} scores increased by 0.11–0.34 (mean 0.21), except for the Tropical and Subtropical Grasslands, Savannas and Shrublands ecoregion. Here the already relatively poor AUC_{ROC} score declined further by –0.03 with high uncertainty when spatial random effects were included (Fig. 3). This ecoregion also had the highest proportion (0.8) of landholders reporting pig presence on their properties (Fig. 3). The most notable changes in predictions caused by the spatial random effects were a reduction in relative abundance across much of the states of Victoria, South Australia and Western Australia (compare Fig. 2 to Fig. A1.3).

The direction of the fixed effect coefficients were all consistent with a priori reasoning for their inclusion, with distance to water being the strongest driver (Fig. A1.4). The model predicted pig abundance to increase with the amount of green vegetation cover and average soil

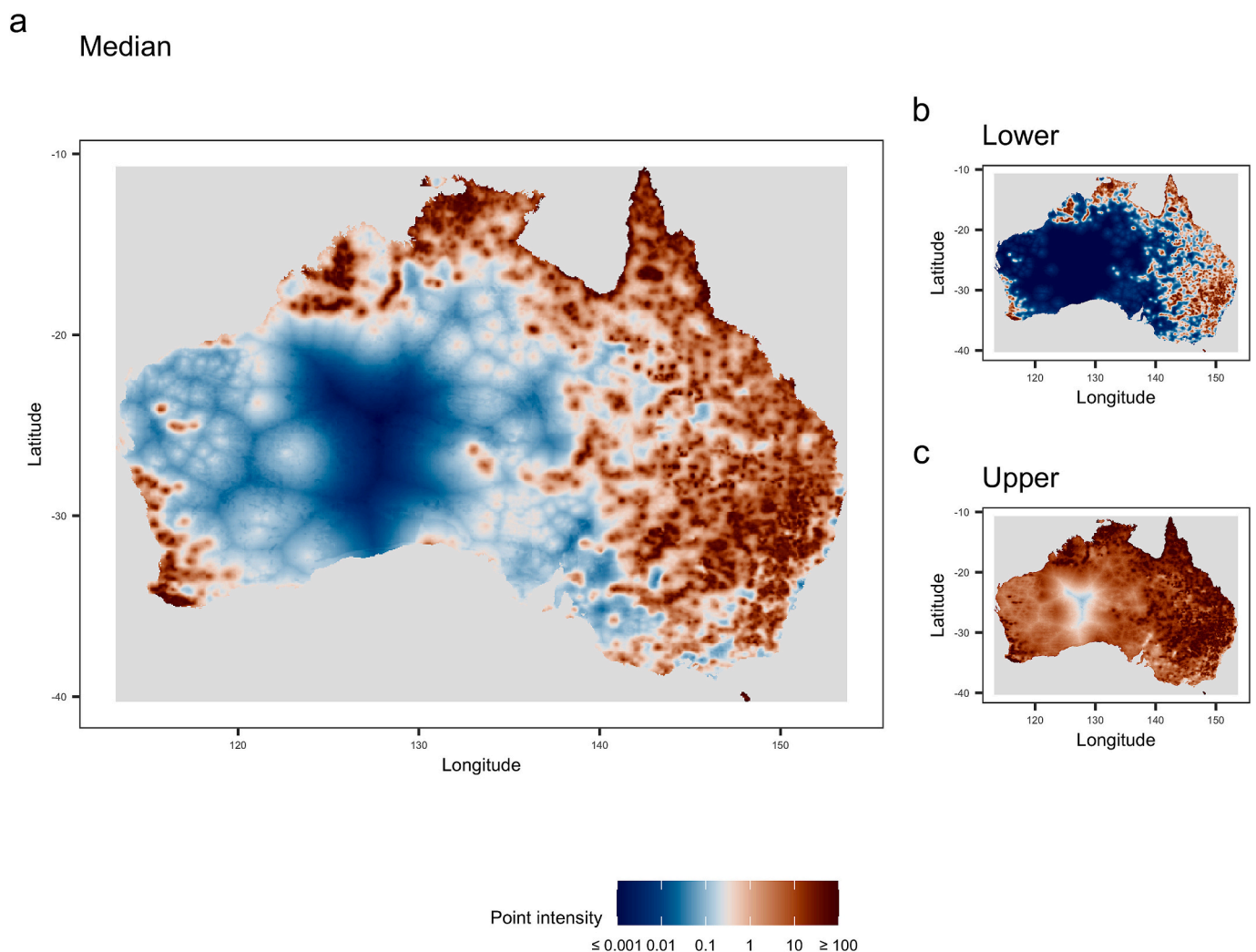


Fig. 2. Predicted posterior point intensity estimates (here interpreted as relative abundance) of the invasive wild pig integrated species distribution model incorporating spatial random effects (log-scaled; abundance-absence intercept): median intensity (a), lower (b) and upper (c) bound of the 95% credible interval.

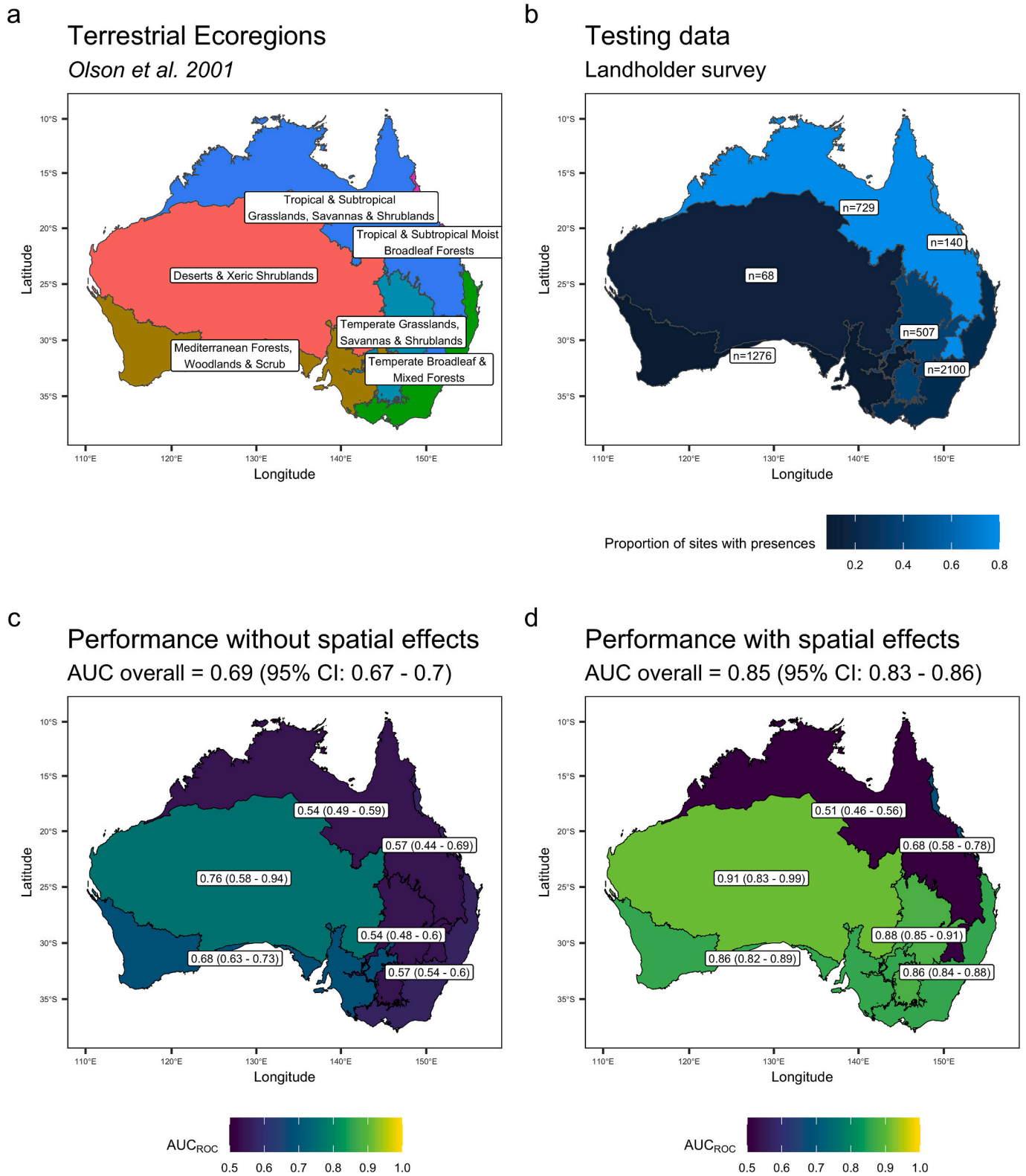


Fig. 3. Evaluation of the invasive wild pig model predictive performance with (d) and without (c) a spatial random effect on an independent presence-absence dataset, overall and within each Terrestrial Ecoregion (panel a; Olson et al., 2001). Panel b shows the independent data set (landholder questionnaire), with colour fill scale depicting the proportion of reported pig presences relative to absences in each ecoregion, with the sample size shown in the label. The colour fill scale in panels c and d show the area under the receiver operating characteristic curve (AUC_{ROC}) score in each ecoregion.

moisture (which are likely to affect availability and accessibility of above- and below-ground food sources, respectively). The effect of woody cover (i.e., shelter) was nonlinear; the positive effect of woody cover waned when cover became very dense (Fig. A1.4). Relative pig abundance declined with average maximum temperatures (i.e., heat stress) and distance to water; these effects were closer to being linear despite modelled with polynomial terms.

Sampling bias of pig presence-only records increased in areas with more invasive mammal presence-only records and decreased with pig control difficulty. The number of invasive mammal presence-only records had a substantive effect on the presence-only model bias component (coefficient 1.02, 95% CI: 1.01–1.31), whereas the relative contribution of the pig control difficulty index was modest (coefficient – 0.14, 95% CI: –0.23 - -0.06). Between abundance-absence surveys, helicopters were more effective at detecting pigs than fixed-wing aircraft (coefficient 1.35; 95% CI: 1.19–1.50). Between presence-absence surveys, aerial fixed wing surveys were considerably less effective at detecting pigs than camera-trap surveys (coefficient – 8.02; 95% CI: –8.24 - -7.81). Randomised quantile residuals showed poorest model performance at high values of abundance-absence data (Fig. A1.5).

4. Discussion

Here we have presented a data-driven map of invasive wild pig relative abundance throughout the entirety of Australia. Our map broadly agrees with previous qualitative estimates derived from an amalgamation of both data and expert opinion (West, 2008). We have advanced on this work through formal statistical integration of a more comprehensive and updated dataset, encompassing various data types and sources. Our ISDM workflow is also updatable and transparent, currently being extended to other pest species.

Model predictions show pigs to be widespread and abundant across the Australian mainland, particularly in northern and eastern Australia (with hotspots in southern and northern parts of Western Australia). The distribution and relative abundance of pigs in Victoria, South Australia and central areas of the Northern Territory and Western Australia was patchy and mostly scarce. The 95% credible intervals of our predictions highlight that our estimates of relative abundance may be much higher and more widespread, cautioning that pigs could occur across most of the country except where water is scarcest in Australia's arid interior. Efforts to limit the spread of wild pigs into new areas therefore continues to be important.

Distance to surface freshwater was the strongest environmental driver of relative abundance predictions—our ability to accurately model pig distribution therefore hinges on our ability to map water availability and determine water features that are accessible and used by pigs (Glanville et al., 2023). Here, we only included mapped permanent water features, which may underestimate pig distribution during wet climate cycles when there can be significant water availability in non-perennial sources. We chose not to include non-perennial water sources as this could have led to overestimation during average and dry climate cycles, particularly in arid and semi-arid regions where water features are isolated and only present in the landscape for a small percentage of the time, making them unlikely to support resident pig populations.

We made other similar modelling decisions to estimate where pigs are currently distributed consistently rather than transiently. We averaged all available temporal estimates of soil moisture (2005–2022) and green vegetation (2001–2023) to create a single layer for these variables. Such averaging is broadly analogous to how the other pig distribution predictor variables were derived: maximum temperature reflects the historical 1960–1999 period (Noce et al., 2020) and woody cover was measured for the 2000–2010 decade (this was the only time period available). Ultimately, we consider the model to be ecologically appropriate as pigs are highly adaptable; we expect that they can tolerate fluctuations in these variables over short-periods of time (e.g.,

individual years) – whereas prolonged exposure (e.g., decades) is more likely to affect broad patterns in their distribution (Stoklosa et al., 2015). Pigs may therefore have broader distributions than those estimated here (namely during wet weather cycles). Nonetheless, we aimed to provide a map where pigs are consistently distributed rather than transiently following extreme weather patterns or other situations.

We included a spatial random effect in our model to account for pigs' non-equilibrium distribution (caused by ongoing invasive spread and effects of active population control) rather than just environmental suitability. The spatial random effect most notably improved estimations by lowering the predicted relative abundance of pigs in productive landscapes of Victoria, South Australia and Western Australia, where pigs have not widely established. However, one downside of our data-driven and spatial random effect approach is that model-predicted current distribution hinges on data availability, particularly around new incursions. It is possible that recent range expansions may not be fully captured within the data and hence the model would underestimate pig relative abundance in these areas. Further, overfitting is an established problem with random effects (Dambly et al., 2023; Hodges and Reich, 2010) and likely contributed to the greater predictive uncertainty which was introduced with the addition of the spatial random effect.

Although the spatial random effect increased predictive uncertainty, it simultaneously improved model predictive performance when evaluated against an independent test data set. By capturing residual spatial structure not explained by the fixed ecological covariates, the spatial random effect allowed the model to better distinguish presences from absences in areas where covariates alone were insufficiently informative. Increased predictive uncertainty and improved discrimination are therefore complementary outcomes rather than mutually exclusive. This improvement in discriminative performance (AUC) was seen in all ecoregions except Tropical and Subtropical Grasslands, Savannahs and Shrublands (covering northern Australia, Fig. 3). The slight worsening in performance here likely reflects greater overfitting or spatial confounding produced by the spatial random effect in areas where pigs are widespread, such as northern Australia where 80% of landholders had observed pigs in our testing dataset, and pigs are expected to reach their highest densities (Hone, 2019).

By evaluating the predictive performance of two models with and without spatial random effects, we were able to advance understanding on the general question of whether the added complexity of spatially-explicit methods is worthwhile for species distribution models (Mäkinen et al., 2022). In our case we were able to show through evaluation against an independent testing dataset that any spatial confounding was outweighed by considerable improvement overall in predictive performance. Further research to understand the contexts in which spatial effects are unlikely to provide a net-benefit to predictive performance (as was the case for northern Australia here) is warranted.

Our model evaluation results showing generally good predictive performance are encouraging, although not definitive due to several limitations. Firstly, the test data was collected only on private land (via a landholder questionnaire), so we do not know how well the model performs on public land. Secondly, there was high variability in property size among respondents. Larger properties are less likely to be searched as thoroughly as smaller ones, although may have higher chance of pig occurrence due to a greater survey area. Larger properties may also straddle multiple prediction cells producing a spatial mismatch between prediction and observation location (although we partly accounted for this by averaging model predictions on a moving focal window before evaluation). Properties tended to be considerably larger in northern Australia, which could provide another explanation for poor model predictive performance here. Lastly, our relative abundance estimates may not be linearly proportional to probability of occurrence, which would bias predictive performance scores (Guillera-Arroita et al., 2015). Nonetheless, these limitations are outweighed by the benefit of an independent testing dataset which lacks the same systematic biases

present in the training dataset, considered the most robust approach to assessing species distribution models (Guisan et al., 2017).

Integrating many disparate data sources presented technical challenges that were addressed through the modelling, but also institutional and social challenges in collating the data and coordinating stakeholders across different jurisdictions and institutions. For example, a key limitation of a recent ISDM application was the exclusion of a dataset with complicated custodianship causing underestimation of a threatened species distribution (Lacombe et al., 2025). As public exposure of pig records can be sensitive (for example, due to concerns about attracting illegal hunting activities), it was critical to ensure that the way in which data was used, stored and shared was carefully discussed with each data custodian, and appropriate data agreements put in place that outline conditions of use and particular sensitivities. Model outputs were also reviewed by a steering committee comprising members of state and territory government environment and primary industries agencies, to ensure the outputs are a reasonable reflection of the distribution and relative abundance of wild pigs at the national scale. Overall, this consultation process allowed additional avenues for model evaluation and improvement, as well as fostering stakeholder trust in the process. The proliferation of wildlife data repositories and integrated modelling methods means we are now able to rapidly assess species distributions at scale, however we caution that in-depth knowledge of both the species' ecology and each data source, regional data scarcities, as well as proper consultation with data custodians, is essential to ensure species distribution modelling provides reliable insight.

CRediT authorship contribution statement

Matthew W. Rees: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **David J. Mitchell:** Writing – review & editing, Validation, Project administration, Methodology, Data curation, Conceptualization. **Katherina Ng:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Data curation, Conceptualization. **Sandra K. Parsons:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization. **Kirstin M. Proft:** Writing – review & editing, Validation, Project administration, Methodology, Data curation, Conceptualization. **Scott D. Foster:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Conceptualization, Software. **David Peel:** Writing – review & editing, Software, Methodology, Conceptualization. **Zachary Amir:** Validation, Resources, Data curation, Conceptualization, Writing – review & editing. **Tom Bruce:** Validation, Resources, Data curation, Conceptualization, Writing – review & editing. **Matthew S. Luskin:** Writing – review & editing, Validation, Supervision, Data curation, Conceptualization. **Jens G. Froese:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Environment, Planning and Sustainable Development Directorate – Environment; Government of South Australia Department for Environment and Water; Government of South Australia Department of Primary Industries and Regions; Northern Territory Government Department of Lands, Planning and Environment; NSW Government Department of Climate Change, Energy, the Environment and Water; NSW Government Department of Primary Industries and Regional Development; Queensland Government Department of Environment, Tourism, Science and Innovation; Queensland Government Department of Primary Industries; Victoria State Government Department of Energy, Environment and Climate Action; Parks Victoria; Government of Western Australia Department of Biodiversity, Conservation and Attractions; Government of Western Australia Department of Primary Industries and Regional Development. We also thank past team members who contributed to this project: Miles Keighley, Margarita Medina and Philip Tennant (all ABARES at the time of contributing). This project was supported with funding from the Australian Government Department of Agriculture, Fisheries and Forestry's Established Pest Animals and Weeds Management Pipeline Program and Supporting Communities Manage Pest Animals and Weeds Program.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2026.111917>.

Data availability

The outputs of the full ISDM (including the spatial random effect) for pigs can be downloaded from the website of the Australian Bureau of Agricultural and Resource Economics and Sciences (Australian Bureau of Agricultural and Resource Economics and Sciences and Commonwealth Scientific and Industrial Research Organisation, 2024; <https://www.agriculture.gov.au/abares/research-topics/invasive-species/national-feral-pig-current-distribution-australia>). The pig data used to fit the model in this project were collated through an Australian Government-led process, governed by strict data sharing and use conditions. Non-public datasets that contributed to this project were used in agreement with the data custodians and are not publicly available.

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