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Pattern-oriented population modelling

1 *poems: R package for simulating species' range dynamics using pattern-oriented*
2 *validation*

3 Damien A. Fordham^{1*}, Sean Haythorne^{1,2*}, Stuart C. Brown^{1,3}, Jessie C. Buettel²,
4 Barry W. Brook²

5 ¹The Environment Institute and School of Biological Sciences, University of
6 Adelaide, South Australia 5005, Australia.

7 ²School of Natural Sciences and ARC Centre of Excellence for Australian
8 Biodiversity and Heritage, University of Tasmania, Hobart, Tasmania 7001, Australia

9 ³GLOBE Institute, University of Copenhagen, 1350, Copenhagen K, Denmark

10 [*damien.fordham@adelaide.edu.au](mailto:damien.fordham@adelaide.edu.au); sean.haythorne@unimelb.edu.au

11 **Abstract**

- 12 1. Spatially explicit population models (SEPMs) can simulate spatio-temporal
13 changes in species' range dynamics in response to variation in climatic and
14 environmental conditions, and anthropogenic activities. When combined with
15 pattern-oriented modelling methods, ecological processes and drivers of range
16 shifts and extinctions can be identified, and plausible chains of causality revealed.
- 17 2. The open-source multi-platform R package `poems` provides functionality for
18 simulating and validating projections of species' range dynamics using
19 stochastic, lattice-based population models. Built-in modules allow parameter
20 uncertainty to propagate through to model simulations, with their effects on
21 species' range dynamics evaluated using Approximate Bayesian Computation.
22 These validation procedures identify models with the structural complexity and
23 parameterisation needed to simulate the effects of past changes in climate,
24 environment and human activities on species' range shifts and extinction risk.
- 25 3. We illustrate the features and versatility of `poems` by simulating the historical
26 decline and extinction of the Thylacine (*Thylacinus cynocephalus*), an icon of
27 recent extinctions in Australia. We show that `poems` can reveal likely ecological
28 pathways to extinction using pattern-oriented methods, providing validated
29 projections of the range collapse and population decline of threatened species.
- 30 4. By providing flexible and extendable modules for building and validating SEPMs
31 of species' range dynamics, `poems` allows the effects of past and future threats
32 on species' populations to be quantified using well-parameterised, structurally
33 realistic models, with important generative mechanisms. Since `poems` can
34 directly unravel ecological processes of species responses to global change, and
35 strengthen predictions of range shifts and extinction risk—within a flexible, R-
36 based environment—we anticipate that `poems` will be of significant value to
37 ecologists, conservation managers and biogeographers.
- 38 **Key words:** distribution, extinction risk, metapopulation, pattern-oriented
39 modelling, population dynamics, population viability analysis, range shift,
40 spatially explicit population model

41 **Introduction**

42 Spatially explicit population models (SEPMs) simulate movement, mortality and
43 reproduction in networks of populations across time (Hanski 1998), improving
44 knowledge on, and forecasting of, species' distributions and populations (Holt *et al.*
45 2005; Fordham *et al.* 2013a). They find their roots in matrix population models
46 (Caswell 2001) and population viability analysis (Boyce 1992), and are today used
47 frequently to simulate the effects of human-driven threats to species range dynamics
48 (Briscoe *et al.* 2019), and explore and rank the cost effectiveness of regional
49 conservation alternatives and demographically oriented management interventions
50 (Fordham *et al.* 2013a). SEPMs do this by capturing generative mechanisms
51 responsible for the distributions and abundances of species in space and time
52 (Wiegand *et al.* 1999).

53 SEPMs simulate species' range shifts and extinction pathways by explicitly modelling
54 responses of demographic processes (including dispersal and metapopulation
55 dynamics) to climate and environmental change, and human activities (Fordham *et al.*
56 2013a). While SEPMs have been used to test ecological and evolutionary theories
57 (Hanski *et al.* 2013; Hanski *et al.* 2017), and to inform conservation actions and
58 policy with respect to extinction risk from climate and environmental change
59 (Fordham *et al.* 2013b; Pearson *et al.* 2014), their predictions are rarely tested (but
60 see, Fordham *et al.* 2018), and important model-based (structural and parameter)
61 uncertainties are frequently ignored (Fordham, Haythorne & Brook 2016). This is
62 partly because, until now, open-source software for doing uncertainty analysis and
63 validating SEPMs did not exist (Table 1).

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64 Pattern-oriented modelling (POM) is a method for evaluating whether an ecological
65 model is adequate in its structure and parameterisation to simulate biological
66 processes, based on observed patterns of biodiversity or population dynamics (Grimm
67 *et al.* 2005). When applied to SEPMs, and related agent-based models, POM methods
68 provide rigorous techniques for identifying ecological models that closely simulate
69 independent validation targets (Eriksson *et al.* 2012; van der Vaart *et al.* 2015). They
70 also allow model uncertainty to be measured and integrated explicitly into simulations
71 of species' range dynamics (Dominguez Almela *et al.* 2020). By identifying
72 structurally realistic SEPMs, parameterised to capture a system's generative
73 mechanisms, probable chains of causality responsible for species' range shifts and
74 population changes can be inferred and quantified, and robust projections of future
75 range dynamics made (Grimm *et al.* 2005).

76 Configuring a SEPM in a POM framework (Figure 1) requires: (i) gridded projections
77 of species' habitat suitability through time (typically derived using ecological niche
78 modelling; Fordham *et al.* 2013a); (ii) a population model that simulates dynamic
79 interactions between demographic processes and this habitat; (iii) estimates of model
80 parameter and/or structural uncertainty; and (iv) observed (or estimated/hypothesized)
81 patterns for testing what scales, variables and processes the model needs to simulate
82 these patterns. Existing software can be used to combine aspects of environments with
83 information on dispersal capacity, vital rates, and source-sink dynamics, using
84 stochastic population models (Akçakaya & Root 2005; Nenzén *et al.* 2012; Keyel,
85 Gerstenlauer & Wiegand 2016; Visintin *et al.* 2020). However, prior to the
86 development of `poems`, no SEPM software had the functionality to simultaneously

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87 simulate model uncertainty and use Approximate Bayesian Computation (ABC;
88 Csilléry *et al.* 2010) to determine which models (i.e., parameter estimates and
89 combinations) do best at simulating observed patterns.

90 The R package `poems` (pattern-oriented ensemble model system) combines
91 functionality equivalent to existing SEPM software with new POM functionality,
92 thereby providing open-source and readily implementable software for unravelling the
93 possible drivers and processes of species' range dynamics, and for permitting
94 uncertainty in spatiotemporal projections of abundance to be explored and quantified.
95 Here we illustrate the features and versatility of `poems` by simulating the historical
96 decline and extinction of the Thylacine (*Thylacinus cynocephalus*), an icon case of a
97 recent mammal extinction in Australia.

98 **Software Overview**

99 The R package `poems` provides functions for building and simulating lattice-type
100 SEPMs of species' range dynamics with parameter uncertainty. The package allows
101 model simulations to be tested against independent validation targets using ABC in a
102 POM framework, with the goal of improving model parameterisation and predictions.
103 Patterns used as validation targets can vary greatly in complexity and underlying
104 information content, ranging from last sightings in locales or regions, to molecular
105 inferences of population decline, with data derived from targeted field and laboratory
106 studies, databases and literature reviews (Grimm *et al.* 2005; Fordham *et al.* 2016).

107 Population models in `poems` can have demographic parameters that define age- or
108 stage-based growth (or can be specified more simply as a scalar population growth

109 rate), along with density dependence, stochasticity, dispersal, and other optional user-
110 defined processes, including vital rates that are spatiotemporally variant. The spatial
111 aspect of the models are constructed using a grid-lattice-type spatial structure of
112 habitat suitability, accounting for climatic and other environmental disturbances
113 (Fordham *et al.* 2018). Uncertainties in habitat suitability and demographic processes
114 are modelled using plausible ranges for ecological parameters. For species' habitat
115 suitability, plausible bounds of niche specialisation and breadth (Dolédec, Chessel &
116 Gimaret-Carpentier 2000) can be used to address uncertainty in ecological niche
117 projections. Many potential SEPMs, each with alternative parameterisations, are then
118 generated using Latin hypercube sampling (LHS) of a multidimensional distribution
119 of possible parameter values. These SEPMs are run in parallel (multi-core in R), and
120 the effects of parameter uncertainty and model sensitivity examined using POM
121 methods, or alternative procedures outside of `poems` (described below).

122 POM is done using ABC, which is a computationally efficient method for rejecting
123 inaccurate models, and for providing credible values for parameters (Csilléry *et al.*
124 2010). Models identified as having sufficient structural complexity and adequate
125 parametrisation to match validation targets are then selected, and thereafter used to
126 simulate species' range dynamics.

127 **Package Features**

128 The R package `poems` is based on *R6* object-oriented modules (Chang 2020) for building SEPMs,
129 generating model parameters with uncertainty, managing large numbers of model simulations and
130 outputs, and applying POM techniques (Figure 2). This *R6* framework promotes flexibility and

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131 computational efficiency, making poems suitable for generating and simulating hundreds of thousands of
132 SEPMs in parallel, and testing their outputs against independent validation targets. Its dependent R
133 libraries are listed in Table S1.

134 SEPMs are built in the population-model module of `poems` (*PopulationModel*;
135 Figure 2). Population models have Leslie or Lefkovitch matrix operations (Caswell
136 2001), with or without stochasticity (demographic and environmental), and/or density
137 dependence (Burgman, Ferson & Akcakaya 1993). They are made spatially explicit
138 using a lattice-grid of relative habitat suitability. Dispersal is configured using
139 distance-based functions (Akcakaya & Root 2005) and a dispersal generator.
140 Resistance (friction) or barriers to dispersal are simulated using distance-equivalence
141 multipliers (Etherington 2016) calculated using a cost-surface generator. Correlation
142 among vital rates of different populations (Akcakaya & Root 2005) is simulated using
143 a correlation generator. Both the dispersal and correlation functions are optimised for
144 large spatial regions with many grid-cells. User-defined functions enable
145 customisable SEPMs, allowing complex demographic processes to be parametrised
146 and management actions simulated. These management actions include introductions,
147 translocations and harvesting (Visintin *et al.* 2020). The order of demographic
148 processes within the model simulator can be customized (via the *PopulationModel*
149 module).

150 After configuring the SEPM, large numbers of plausible models are generated using
151 the Latin-hypercube module (*LatinHypercube sampler*) using pre-defined ranges and
152 distributions (uniform, normal, lognormal, beta, and triangular) of parameters
153 (Fordham, Haythorne & Brook 2016). Models are run in parallel batches (if the

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154 computational resources are available) using the simulation-manager module
155 (*SimulationManager*). The results-manager module (*ResultsManager*) is used to
156 calculate and collate range and extinction dynamics simulated with variable input
157 factors, enabling sensitivity-type analysis (Pianosi *et al.* 2016). Parameters with the
158 largest relative influence on model output are identified in `poems` using comparisons
159 of posterior and prior distributions (Figure 1); or outside `poems` using regression
160 and /or statistical learning analysis (Pearson *et al.* 2014; Fordham, Haythorne &
161 Brook 2016). Both simulation- and result-manager modules have functionality for
162 checking the completeness and consistency of model runs and for managing errors,
163 which is imperative when large numbers of models are generated and simulated.

164 POM is done using ABC in the validator module (*Validator*), returning a user-
165 specified subset (a small fraction of all possible models) that best match a univariate
166 or multivariate user-defined validation target, along with weights signifying their
167 congruence (Csilléry *et al.* 2010). This approach relies on validation targets that
168 accurately capture vital aspects of species' range dynamics. Comparisons of posterior
169 and prior parameter distributions is done to identify parameter bounds (credible
170 intervals) needed to simulate validation targets, while visual posterior predictive
171 checks ensure that these new input parameter distributions result in a sufficient
172 resemblance between simulated and observed data (Gelmen *et al.* 2014). Together this
173 allows complex and often uncertain information to be integrated into SEPMs.

174 Selected “best” models are used to simulate uncertainty in species' range dynamics
175 (Dominguez Almela *et al.* 2020). Multi-model averages of spatiotemporal patterns of

176 abundance and temporal estimates of total population size can be generated and
177 weighted by ABC congruence with validation targets.

178 **Example: Thylacine range collapse and extinction**

179 Australia has a particularly woeful record of recent mammal extinction, and one of
180 the most infamous was the loss of the Thylacine, a wolf-like marsupial predator, in
181 Tasmania (Brook *et al.* 2021). The Thylacine was distributed broadly across
182 Tasmania prior to settlement by Europeans in 1803. However, threatening processes
183 of land-use change and bounty hunting led to it being extremely rare by the early 20th
184 century (Bulte, Horan & Shogren 2003). In 1931, the last Thylacine was captured (it
185 died in 1936), and the species went extinct in the wild sometime between 1940
186 (Carlson, Bond & Burgio 2018) and the late 20th century (Brook *et al.* 2021). We
187 illustrate the features and flexibility of `poems`, by simulating the historical decline
188 and extinction of the Thylacine, assuming that human-persecution was the primary
189 determinant of its extinction (Prowse *et al.* 2013).

190 *Spatially Explicit Population Model*

191 Using the population-model module of `poems`: we built a Thylacine age-based
192 stochastic demographic model (Prowse *et al.* 2013); coupled it to a bio-economic
193 harvest model (Bulte, Horan & Shogren 2003) that simulates opportunistic and
194 bounty harvesting; and made it spatially explicit using a 10 km × 10 km lattice-grid of
195 habitat suitability (the territorial range of thylacines; Guiler & Godard 1998) for
196 Tasmania (Buettel *et al.* 2021; Haythorne *et al.* 2021). The generator module
197 (*Generator*; Figure 2) was used to reconstruct the effects of land-use change on

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198 habitat suitability (Bulte, Horan & Shogren 2003), and to compute carrying
199 capacities, harvest dynamics and density dependence. Dispersal was simulated using a
200 distance-based function that suppressed movement to resource-depleted areas and
201 prevented overcrowding. Density dependence operated at a neighbourhood level,
202 accounting for the nearby density of mates and resources in calculations of
203 reproduction and survival. A Tasmanian-wide Allee effect simulated a threshold
204 below which the thylacine could not persist (Stephens & Sutherland 1999). Model
205 parameters and functionality are described in detail in the vignette that accompanies
206 the `poems` package on CRAN (Haythorne *et al.* 2021).

207 *Pattern-oriented modelling*

208 The Thylacine SEPM had fixed and variable parameters (Table S2). Variable
209 parameter ranges were sampled 100,000 times from uniform distributions (using the
210 Latin-Hypercube-Sampling module). The resulting models were run over the years
211 1888–1967 at an annual time step (using the simulation-manager module) and time of
212 extirpation, rates of bounty harvesting, and time of Tasmanian-wide extinction were
213 calculated (Haythorne *et al.* 2021). These summary statistics were identified *a priori*,
214 because they capture important spatiotemporal information on the range collapse,
215 regional extirpation and eventual range-wide extinction of Thylacine; and because
216 they can be estimated with high confidence, using harvest (pelt) records during the
217 bounty period (1888-1909) and the later (1910s to 1930s) physical evidence from
218 captured or killed specimens (Table S3). The validator module was used to compare
219 these estimates to the validation targets by: summing the root mean square error for
220 extirpation and harvest rates and calculating absolute error for extinction time; and

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221 then using ABC to select the 1% of simulations that did best at matching to the multi-
222 variate target (Haythorne *et al.* 2021). We compared differences between posterior
223 and prior distributions of parameters, calculated credible intervals, and then generated
224 multi-model averaged projections of range collapse, population decline and harvest of
225 Thylacines. These steps are described in Haythorne *et al.* (2021), with R code.

226 The top 1,000 Thylacine SEPMs simulated the observed rates of bounty harvesting,
227 timing of regional patterns of extirpation, and time of Tasmania-wide extinction, with
228 good accuracy (Figure 3a-c). Checks of differences of posterior and prior distributions
229 showed that hitting these validation targets required narrow ranges for some
230 parameters (Figure 3d), whereas other parameters had little influence on the measured
231 output. For these non-identifiable parameters it is important to consider whether the
232 summary statistics used for POM best fit the study animal and system (Gelmen *et al.*
233 2014), which they do for the Thylacine. Models with a relatively high Allee effect, a
234 relatively low initial abundance (relative to carrying capacity), low catchability of
235 Thylacines and low cost-per-effort for hunters were better able to hit validation
236 targets, indicating the importance of these parameters for reconstructing summary
237 statistics of extinction of Thylacine in Tasmania. Credible intervals for all parameters
238 are reported in Table S2.

239 *Decline and Extinction*

240 Multi-model averaged projections of the range dynamics of Thylacine (weighted by
241 simulated/observed congruence) show that its range collapsed in an east-west
242 direction (supporting the conjecture by Sleightholme & Campbell 2016), starting at

243 the end of the 19th century (Figure 4a), with the last remnant populations being
244 restricted to remote parts of northwest Tasmania. The model projects that total
245 population size of Thylacines declined substantially from 1888 to 1909 during the
246 bounty period (Figure 4b), and thereafter dwindled gradually, with extinction
247 occurring in 1944 (range = 1929–1946). While the multi-model average estimate
248 predicted well the total number of recorded bounty payments, matches to regional
249 differences in these payments were not as high (Figure 4c). This, along with the large
250 value of the Allee parameter required, points to deficiencies in the current model that
251 could be refined with further work.

252 **Conclusion**

253 SEPMs built using pattern-oriented modelling methods with `poems` produce
254 validated reconstructions of past species' range and extinction dynamics, potentially
255 improving future projections for extant species. However, ultimately the quality of the
256 outcomes will be strongly dependent on the accuracy and resolution of the
257 independent validation targets: better projections of past and future range dynamics
258 using SEPMs will be realised with `poems` only if ecologically meaningful and
259 accurate validation data are available, which capture important spatiotemporal
260 patterns of geographic and demographic change. We envisage `poems` to be
261 particularly useful to ecologists and biogeographers studying the causes of species'
262 range shifts through time, and conservation biologists focused on establishing
263 extinction risk of threatened species and prescribing remedies.

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267 **Author contributions**

268 DAF, SH and BWB developed the modelling framework. SH coded the package
269 with help from SCB. JCB generated data for the case study. All authors contributed to
270 writing the manuscript.

271 **Conflict of interest**

272 The authors report no conflicts interest.

273 **Data availability**

274 All data are available from *figshare* (<https://doi.org/10.25909/c.5458320>) and *cran*
275 (<https://cran.r-project.org/web/packages/poems/index.html>).

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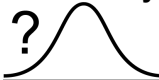

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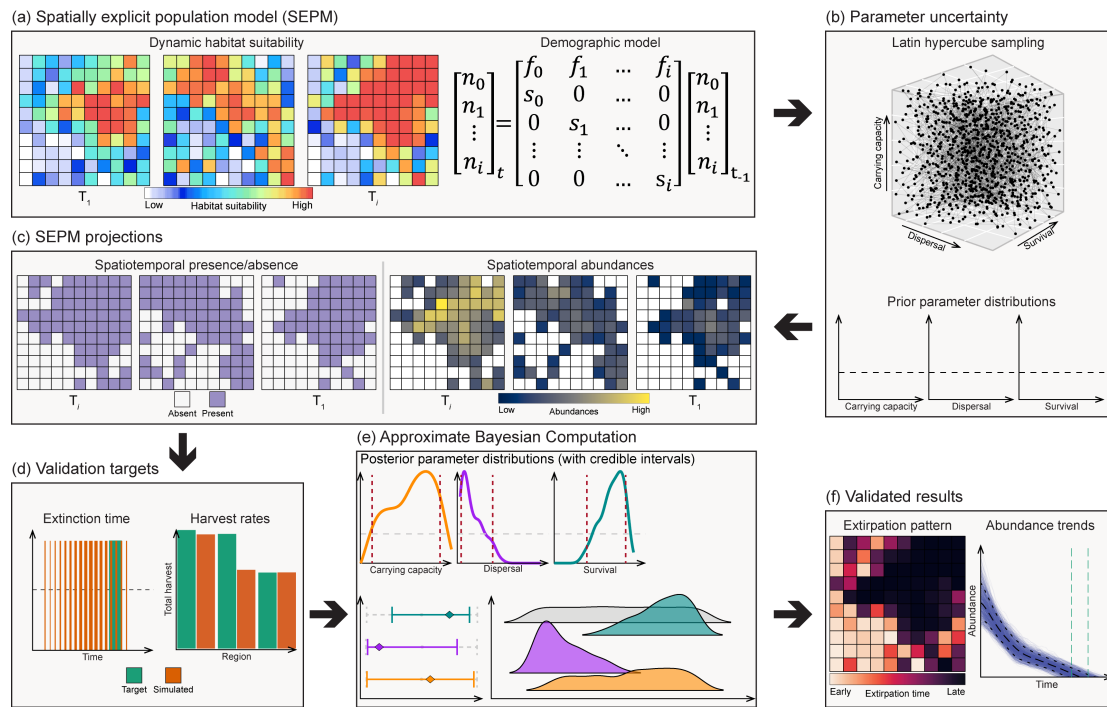
391 **Figures and tables**

Software	Open source 	Customisable 	Parameter Uncertainty 	Parameter Estimation 
<i>RAMAS + SARDM</i>	•	•	✓	•
<i>demoniche</i>	✓	•	•	•
<i>SpatialDemography</i>	✓	•	•	•
<i>STEPS</i>	✓	•	•	•
<i>poems</i>	✓	✓	✓	✓

392 **Table 1:** Common software for simulating species' range dynamics with SEPMs.
 393 SEPM software include: RAMAS (Windows operating system) and its associated
 394 analysis module SARDM (Akçakaya & Root 2005; Fordham, Haythorne & Brook
 395 2016), and the R packages (UNIX platforms, Windows and MacOS) *demoniche*
 396 (Nenzén *et al.* 2012), *SpatialDemography* (Keyel, Gerstenlauer & Wiegand
 397 2016), *STEPS* (Visintin *et al.* 2020) and *poems*. Ticks represent the presence of key
 398 software features: open source, easily customisable model structure, capability to
 399 generate and simulate parameter uncertainty, and capacity to do parameter estimation.

400

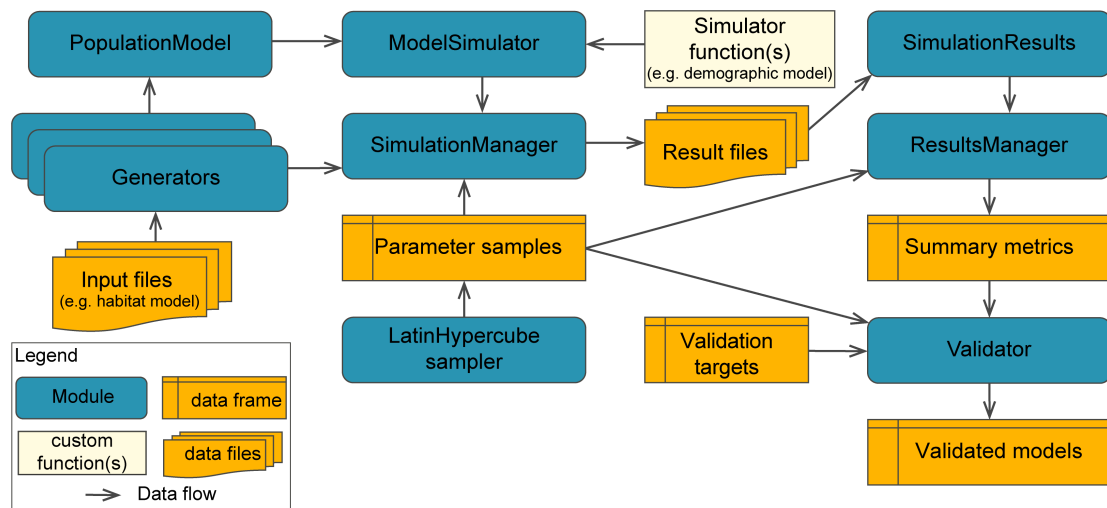
Pattern-oriented population modelling



401

402 **Figure 1:** Simulating species range dynamics using SEPMs and pattern-oriented
 403 modelling. `poems` can be used to build SEPMs (a), which account for parameter
 404 uncertainty (b), and produce spatiotemporal projections of abundance and occurrence
 405 (c). These projections can be validated against observed patterns [targets] (d), using
 406 Approximate Bayesian Computation, allowing visual comparisons of posterior and
 407 prior distributions of parameters (e), and target-validated projections to be generated
 408 for range and extinction dynamics (f).

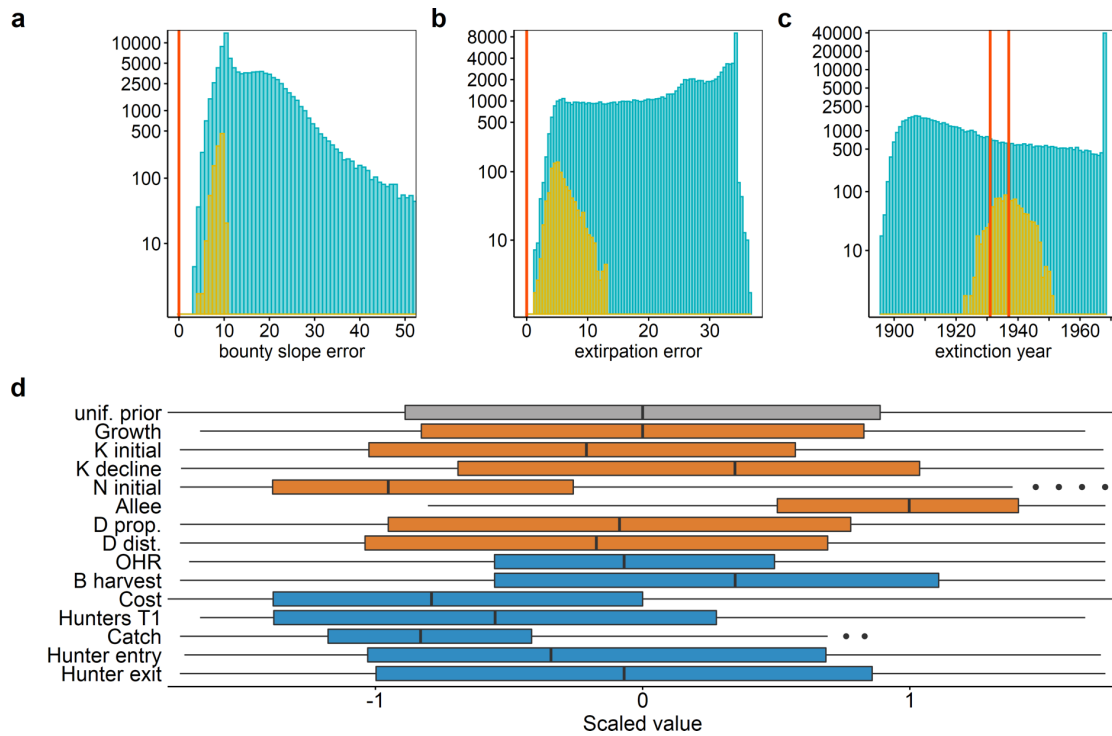
Pattern-oriented population modelling



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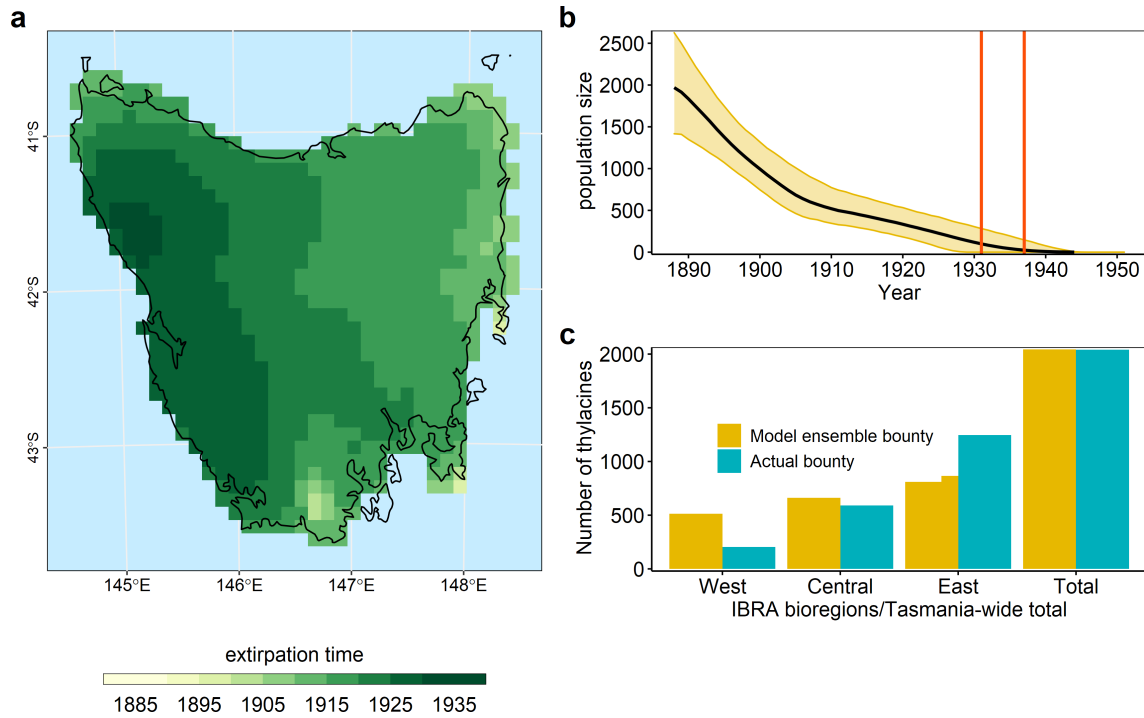
410 **Figure 2:** Modules for building SEPMS and doing pattern-oriented modelling in
 411 `poems`. The different `R6` object-oriented modules and their data inputs and outputs
 412 are detailed in Package Features.

Pattern-oriented population modelling



413

414 **Figure 3:** Model validation and parameter sensitivity for an example case study on
 415 the extinction dynamics of the Thylacine in Tasmania. Histograms show differences
 416 between simulated and observed targets for bounty harvest rate (**a**), timing of regional
 417 extirpations (**b**) and the range-wide extinction year (**c**). Note: the y-axes are on the
 418 log-scale. Yellow bars show results for the POM best 1% of models. Blue bars show
 419 results for all models. Red solid line shows validation target. Orange and blue box
 420 plots (**d**) show posterior distributions for demographic and hunting parameters,
 421 respectively. Grey box plot shows uniform prior values for comparison. Values have
 422 been centred and scaled. Parameters listed in **d** are described in Table S2.



423

424 **Figure 4: Range collapse and population decline in the Thylacine, as modelled**
 425 **with poems.** Multi-model averaged estimates of the spatio-temporal pattern of
 426 extirpation (**a**), range-wide population size (**b**) and bounty-harvest (**c**) for the best
 427 1,000 models. Estimates are weighted by ABC congruence with validation targets.
 428 Population size is shown as the mean (black line) \pm 1 standard deviation (yellow).
 429 Red lines show the estimated extinction window. Yellow and blue bars show
 430 simulated and recorded bounty estimates for all of Tasmania (Total) and Tasmania
 431 divided into three biogeographic regions (West, Central and East).