

Reconstructing colonization dynamics to establish how human activities transformed island biodiversity

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Abstract

Aim: The drivers and dynamics of initial human migrations across individual islands and archipelagos are poorly understood, affecting assessments of human-modification of island biodiversity. Here, we describe and test a process-explicit approach for reconstructing human arrival and expansion on islands, which combines archaeological and climate records with high-resolution spatial population models. Using Polynesian colonisation of New Zealand as an example, we show that our new method can generate information crucial for assessing how humans affected biodiversity on islands.

Innovation: The transition of islands from prehuman to human dominated ecosystems has typically been assessed by comparing biodiversity before and after time of first arrival, without considering the potential importance of the spatiotemporal dynamics of the human expansion event. Our new approach, which uses pattern-oriented modelling methods to combine inferences of human colonisation dynamics from dated archaeological material with spatially explicit population models, produces validated reconstructions of the pattern and pace of human migration across islands at high spatiotemporal resolutions. From these reconstructions, demographic and environmental drivers of human colonization can be identified, and the role that people had on biodiversity established. Using this technique, we show that closely reconciling inferences of Polynesian colonisation of New Zealand requires there to have been a single founding population of approximately 500 people, arriving between 1233 and 1257 AD, settling multiple areas, and expanding quickly over both North and South islands. The resultant maps of Māori colonisation dynamics provide new opportunities to better determine how human activities transformed biodiversity of New Zealand in space and time.

Main conclusions: Process-explicit models can reconstruct human migration across large islands, producing validated, high resolution spatiotemporal projections of human occupancy and abundance that account for dispersal and population dynamics. This modelling framework should prove effective across any islands and archipelagos where climate and archaeological records are available.

Keywords: biogeography, colonisation, cultural ecology, distribution, human migration, mechanistic model, Pacific, Polynesia, spatially explicit population models

1 **Introduction**

2 The emergence of hominids and their sequential dispersal away from an African evolutionary cradle
3 has always been an intriguing topic for biogeographers, ecologists and conservation biologists
4 ([Diamond, 1997](#); [Finlayson, 2005](#); [Wallace, 1876](#)). However, key questions remain concerning the
5 timing, rate and mechanisms influencing the rapid expansions of our species ([Mellars, 2006](#); [Nielsen](#)
6 [et al., 2017](#)) and the broader ecological consequences of human colonization on biodiversity ([Burney](#)
7 [& Flannery, 2005](#); [Ellis, 2021](#)). This is particularly true for the colonisation of remote oceanic islands
8 ([Channell & Lomolino, 2000](#); [Russell & Kueffer, 2019](#); [Wood, 2008](#)), which are among the last areas
9 on Earth to have been settled and transformed by people ([Nogué et al., 2021](#)).

10 While several potential pathways for the global expansion of modern humans have been
11 proposed ([Beyer, Krapp, Eriksson, & Manica, 2021](#); [Eriksson et al., 2012](#); [Timmermann & Friedrich,](#)
12 [2016](#)), simulations of these colonisation dynamics have, to date, been done at relatively coarse
13 spatiotemporal scales, often underpinned by an assumed positive correlation between net primary
14 productivity and population growth in pre-agricultural societies ([Zhu, Galbraith, Reyes-García, &](#)
15 [Ciais, 2021](#)). Consequently, knowledge of drivers of human migration and their fine-scale dynamics
16 are unclear, particularly for those that operated at spatial and temporal scales relevant to individual
17 islands and archipelagos ([Douglass et al., 2019](#); [Wilmshurst, Anderson, Higham, & Worthy, 2008](#)).

18 Human arrival dates on many islands and archipelagos have been established archeologically
19 with reasonable certainty ([Wilmshurst, Hunt, Lipo, & Anderson, 2011](#)). While these dates have often
20 been used to speculate on the role and impact of human activities on island biodiversity ([Duncan &](#)
21 [Blackburn, 2004](#); [Nogué et al., 2021](#); [Wood et al., 2017](#)), this has typically been done without
22 considering the additional and important roles that founding population size and location, and rate
23 and pace of expansion could have had on the spatiotemporal pattern of biodiversity. This oversight
24 has not been intentional, but rather has occurred because of an absence of high-resolution
25 reconstructions of human migrations across islands, which is difficult to establish, and remains
26 heavily contested for most islands ([Hansford, Lister, Weston, & Turvey, 2021](#); [Rieth, Hunt, Lipo, &](#)
27 [Wilmshurst, 2011](#); [Walter, Buckley, Jacomb, & Matisoo-Smith, 2017](#)).

28 Improving knowledge of the processes responsible for the transformation of native insular biotas
29 following human arrival and expansion requires new methods that can reconstruct human
30 colonization dynamics at spatiotemporal resolutions required for biodiversity assessments. These
31 include assessments of the causal role of people on extinctions of island endemics, and resultant
32 changes in the ecological function of islands across the Pacific Ocean ([Boyer & Jetz, 2014](#)), Indian
33 Ocean ([Anderson et al., 2018](#); [Hixon et al., 2021](#); [Wood et al., 2017](#)), the Mediterranean ([Wood et](#)
34 [al., 2017](#)), and the Caribbean ([Cooke, Dávalos, Mychajliw, Turvey, & Upham, 2017](#); [Locatelli, Due,](#)
35 [van den Bergh, & van den Hoek Ostende, 2012](#)). New methods in macroecology that synthesize

36 disparate evidence from archaeological records have the potential to reconstruct human events at
37 spatiotemporal resolutions requisite for establishing human-mediated biodiversity change on islands
38 ([Fordham et al., 2020](#)). However, their application to island systems has yet to be tested.

39 Part of the challenge with spatiotemporally reconstructing the dynamics of initial human
40 migration across individual islands and archipelagos is that most remote islands were settled rapidly
41 and relatively recently, when climates were similar to current conditions ([Nogu e et al., 2021](#)).
42 Consequently, these events cannot be reconstructed adequately in space and time using existing
43 correlative techniques ([Giampoudakis et al., 2017](#)), or climate proxies ([Beyer et al., 2021](#)). A
44 potential solution could be to integrate archaeological information with spatially explicit population
45 models (SEPM) that can reconstruct fine-scale dispersal and population dynamics using process-
46 explicit approaches and pattern-oriented methods ([Fordham, Haythorne, Brown, Buettel, & Brook,
47 2021](#)). Process-explicit approaches simulate the dynamics of a biological system as explicit functions
48 of the events that drive changes in that system ([Pilowsky, Colwell, Rahbek, & Fordham, 2022](#)). When
49 coupled with pattern-oriented modelling (POM) approaches ([Grimm & Railsback, 2012](#)) — an
50 emerging and powerful tool in macroecology and biogeography ([Honkaniemi, Rammer, & Seidl,
51 2021](#)) — process-explicit models can establish chains of causality responsible for colonisation and
52 extinction dynamics ([Fordham et al., 2022](#)), and resultant biodiversity change ([Rangel et al., 2018](#)).
53 Critically, the approach has substantial potential for reconstructing rapid human expansion at
54 relatively fine spatial scales, including those across oceanic islands and archipelagos during periods
55 of climatic stasis ([Fordham et al., 2021](#)).

56 The M ori expansion across New Zealand provides an intriguing and insightful model system to
57 demonstrate how the colonisation and subsequent expansion dynamics of humans across islands
58 can be reconstructed using an approach that combines SEPMs ([Wiegand, Moloney, Naves, & Knauer,
59 1999](#)) with POM methods ([Grimm & Railsback, 2012](#)). This is because there is a wealth of precisely
60 dated archaeological evidence of M ori activity ([S. J. Holdaway et al., 2019](#)), existing models of
61 human population growth ([Brown & Crema, 2019](#); [R. N. Holdaway et al., 2014](#); [R. N. Holdaway &
62 Jacomb, 2000](#)), and 18th century estimates of population size ([Pool, 1991](#)). Just as importantly, there
63 is an immediate need for a more detailed understanding of the pattern and pace of M ori migration
64 across New Zealand to better understand the role past human activities had on the dynamics and
65 extinctions of New Zealand's native biotas. This is because current assessments of biodiversity
66 change following the peopling of New Zealand have rarely considered the consequences of founding
67 location, or rate and pattern of human expansion across the archipelago ([R. N. Holdaway & Jacomb,
68 2000](#); [G. L. W. Perry, Wilmshurst, McGlone, & Napier, 2012](#)).

69 The East Polynesian expansion in the Pacific Ocean was the final phase of global human
70 settlement (Wilmshurst et al., 2008). It included the colonisation of the New Zealand archipelago by
71 Polynesians known subsequently as Māori. Archaeological evidence suggests an expansion that was
72 so rapid as to appear highly synchronous across the entire archipelago (Anderson, 1991; Walter et
73 al., 2017). Consequently, there remains little consensus on the location of first arrival, migration
74 routes and whether colonisation resulted from a series of small founding populations or a single,
75 concerted migration (Anderson, 2017; Walter et al., 2017; Wilmshurst et al., 2008): information
76 urgently needed to better understand the human dimension of biodiversity change in New Zealand.

77 These colonization dynamics cannot be resolved using existing human-migration models, partly
78 because they rely on climatic change (and derived changes in net primary productivity) as the
79 principal drivers of colonisation and expansion (Eriksson et al., 2012; Zhu et al., 2021). However,
80 climatic conditions in New Zealand during the period of colonisation (1200 – 1300 AD) were
81 relatively stable (Wanner et al., 2008), providing no insights into the establishment and spread of
82 people across New Zealand, nor their subsequent spatiotemporal impacts on native biotas.
83 Moreover, Polynesian colonists brought with them horticulture (but see Anderson and Petchey
84 (2020)) and, thus, were not entirely dependent on hunting and gathering (Anderson, 2016; Brown &
85 Crema, 2019; Furey, 2006), for which net primary productivity is a proxy (Zhu et al., 2021). It is likely,
86 however, that these limitations can be overcome using process-explicit models, archaeological
87 records and climate and environmental data (Fordham et al., 2020).

88 The process-explicit, pattern-oriented modelling framework that we develop and test here,
89 simulating the colonization of New Zealand, has great potential for understanding how Māori
90 transformed island biodiversity. More generally, it can be used to reconstruct the initial waves of
91 human colonisation across other remote large islands and archipelagos, potentially providing novel
92 insights into fine-resolution drivers of biodiversity change following human arrival.

93

94 **Methods**

95 Our new spatially explicit population modelling (SEPM) approach for reconstructing human
96 colonisation dynamics on islands at high spatiotemporal resolutions integrates archaeological data
97 with population growth and dispersal models to produce dynamic simulations of changing
98 populations, distributions and migration routes of people at fine spatiotemporal resolutions (Figure
99 1). Archaeological records matched with climate and environmental data are used to reconstruct
100 habitat suitability for humans on islands, and relative density patterns at spatial resolutions required
101 to capture local orographic influences (Supplementary Figure 1). This information is integrated into
102 SEPMs that simulate population growth and dispersal dynamics. Uncertainty is captured directly in
103 simulations by varying model parameters (demographic, dispersal, suitability, and density

104 parameters), producing thousands of conceivable models of human arrival and establishment
105 (Figure 1). Pattern-oriented modelling (POM) methods are used to optimise parameter values using
106 inferences of demographic change from archaeological and historical records. Models that validate
107 well are used to reconstruct human colonisation and establishment, and to identify causative
108 processes responsible for spatiotemporal patterns, generating information needed to determine
109 past influences of people on biodiversity (Fordham et al., 2022). Resultant conclusions can be tested
110 using counterfactual scenarios that modify the effects of these parameters (G. L. Perry, Wainwright,
111 Etherington, & Wilmshurst, 2016).

112 Below we describe the application of this approach to the colonization of New Zealand by Māori.
113 Models are coded in Program R version 4.0.4 (R Core Team, 2021) and are described in detail in the
114 Supporting Methods, and example simulations which are available here:

115 <https://figshare.com/s/02c292e2386633546e2e>.

116

117 *Modelling Māori relative population density*

118 Spatial models of relative density of Māori populations prior to European first contact
119 (conventionally 1769 C.E.) can be constructed using the density of archaeological finds as a proxy for
120 human density (Goldberg, Mychajliw, & Hadly, 2016). Specifically, we trained boosted regression
121 tree models (BRT; Elith, Leathwick, and Hastie (2008)) using radiocarbon (^{14}C) dated Māori
122 archaeological sites from the New Zealand Radiocarbon database (Figure 2), which we intersected
123 with paleoclimate data generated using PaleoView v1.5.1 (Fordham et al., 2017), and
124 geomorphometric data. We used a decomposed hurdle approach for BRT models (Ridout, Demétrio,
125 & Hinde, 1998). This allowed the occurrence and abundance of ^{14}C data to be trained on different
126 environmental factors (Potts and Elith (2006); Ridout et al. (1998); Supplementary Figure 2), and
127 addressed zero inflation in the archaeological database (Mellin, Russell, Connell, Brook, & Fordham,
128 2012). Zero inflation in the database resulted from both a spatial absence of archaeological finds,
129 and from a lack of ^{14}C dated artefacts at some archaeological sites. The BRT model was used to
130 project mean relative population abundance and its standard deviation across New Zealand at a grid
131 cell resolution of $0.25^\circ \times 0.25^\circ$ (Figure 2). These projections were used as a spatial template for the
132 SEPM. The BRT model and its validation are described in detail in the Supporting Methods.

133

134 *Spatially Explicit Population Model (SEPM)*

135 To reconstruct the colonisation dynamics of Māori from 1230 – 1850 AD, spatial projections of
136 potential relative population abundance and its standard deviation (described above) can be
137 coupled with a population growth model and a dispersal simulator (Figure 3). This is done using a

138 lattice-based SEPM framework (Fordham et al., 2021) that models range expansion annually as a
139 function of population size (Supplementary Figure 3) and habitable neighbourhoods (Figure 3). To do
140 this for Māori, we used an existing exponential population growth model (R. N. Holdaway et al.,
141 2014; R. N. Holdaway & Jacomb, 2000), colonising neighbourhoods sequentially. Neighbourhoods
142 with the highest potential relative abundances (those in the most suitable areas) were colonised
143 first. To do this, grid cells were grouped into spatial neighbourhoods using foraging radii. This
144 allowed dispersal of the Māori population across New Zealand to be simulated as the total
145 population grew (Figure 3).

146 To account for parameter uncertainty, we generated 25,000 potential simulations. We did this by
147 varying five parameters in the SEPM across large but plausible ranges (Table 1) using a robust
148 coverage of multi-dimensional parameter space (Fordham, Haythorne, & Brook, 2016). Variable
149 parameters were time of arrival, founding population, population growth rate, neighbourhood size,
150 and foraging distance. The SEPM was built using the ‘*poems*’ version 1.0.1 Program R package
151 (Haythorne, Fordham, Brown, Buettel, & Brook, 2021). A detailed description of the mechanics of
152 the model is provided in the Supporting Methods.

153

154 *Pattern oriented Model Validation*

155 POM methods can be used to optimise parameters in SEPMs (Haythorne et al., 2021). This is done by
156 comparing model simulations with independent validation targets and selecting models that have
157 the mechanisms to most closely replicate these targets (Grimm & Railsback, 2012), often using
158 Approximate Bayesian Computation (ABC; Csilléry, Blum, Gaggiotti, and François (2010)).

159 Model simulations of Māori arrival and expansion in New Zealand were assessed against two
160 targets: (i) Spatiotemporal occurrence, measured as modelled presence in grid cells at a time and
161 place where ¹⁴C-dated archaeological evidence indicated that that the grid cells should have been
162 occupied; and (ii) Population size, measured as a population of between 100,000 and 150,000
163 people across the archipelago in 1769 C.E. based on the earliest estimate made by the British
164 explorer Captain James Cook, including its likely uncertainty (Pool, 1991). The best 1 % of simulations
165 were selected using the rejection algorithm in the ‘*abc*’ package (Csilléry, François, & Blum, 2012).
166 The parameter ranges identified by ABC as most accurately matching the validation targets were
167 used to build additional simulation models (n = 25,000), using the posteriors of previous model runs
168 as informed priors (Pilowsky et al., 2022). This POM process was stopped when Bayes factors
169 indicated that the selected posteriors no longer differed from the informed priors (Gelman, Hwang,
170 & Vehtari, 2014). Posterior predictive checks were used to determine whether the posterior

171 distributions generated strong resemblance between the simulation results and observed data
172 ([Gelman et al., 2014](#)). See the Supporting Methods for further details.

173

174 *Model output and Sensitivity analysis*

175 To reconstruct human colonization patterns, we calculated credible intervals for model parameters
176 from the 'best' 1 % of optimised simulations and then generated multi-model averaged projections
177 of time and location of first arrival of Māori in New Zealand, founding population size, and
178 population growth and migration through space and time. Projections were weighted by ABC model
179 weights ([Fordham et al., 2022](#)).

180 We determined the sensitivity of the results to two common model-based structural assumptions
181 ([Saltelli, Tarantola, & Campolongo, 2000](#)): the form of the population growth model; and the
182 number of founding events. To do this, 25,000 simulations were generated using a robust coverage
183 of the posterior parameter space identified by the POM, altering human growth so that it followed a
184 logistic, rather than exponential, function ([Brown & Crema, 2019](#)); and by making founding events >
185 1 (i.e., multiple rather than a single fleet). Where multiple founding events were simulated, founding
186 populations were spread over multiple time steps. Model outputs were compared to simulations
187 without these structural changes. See Supporting information for further details.

188

189 **Results**

190 *Māori relative population density*

191 The likelihood of the occurrence of Māori was higher in areas with fewer steep slopes (i.e. > 20°) and
192 those closer to navigable waters (Figure 2; Supplementary Figure 2). Higher relative densities of
193 Māori were projected to occur in areas where average temperatures during the warmest three
194 months of the year exceeded 18 °C, temperatures in the coldest three months exceeded 10 °C,
195 where evapotranspiration (and thus horticultural productivity) was high, and where rainfall was
196 limited, preventing water logging of crops (Figure 2; Supplementary Figure 2). The reconstructed
197 pattern of Māori density strongly replicated the distribution of archaeological sites, with 90% of
198 archaeological sites having > 0.75 likelihood of Māori occupancy.

199

200 *Colonisation dynamics*

201 Reconstructing validation targets for human colonisation of New Zealand required a constrained set
202 of ecological parameters: a founding population size of 517 (min: 435 to max: 582), a colonisation
203 year of 1244 C.E. (1233-1257), a minimum community size of 28 individuals (23-36), a
204 neighbourhood radius of 66 km (63-68), and a population growth rate of 1.010 per annum (1.010-

205 1.011) (Table 1, Figure 4). While the first iteration of POM (with broad uniform priors) resulted in
206 selected models that replicated colonisation patterns reasonably well (Figure 4), the second and
207 third iterations of POM did better, placing colonists at nearly all known settlements prior to the
208 earliest radiocarbon dated evidence of their presence there (Figure 4). The best models of the third
209 iteration yielded estimates of population size in 1769 [119,900 (88,750-159,197)] that most closely
210 matched the target (Figure 4).

211 The best 1 % of SEPMS (from the third POM iteration) consistently simulated the North Island
212 being colonised prior to the South Island (Figure 5). They simulated the colonisation of New Zealand
213 as occurring rapidly, with the entirety of habitable regions colonised by approximately 1400 C.E.; i.e.,
214 within 200 years of arrival (Figure 5; Supplementary animation 1). On the South Island, present day
215 Otago, Canterbury, Marlborough and Nelson were projected to have been settled as early as the
216 mid-1200s C.E. in some selected simulations (Figure 5; Supplementary Figure 1). While small
217 differences in settlement and dispersal parameters between selected simulations caused some
218 variation in reconstructions of occupancy and abundance, there was substantial spatiotemporal
219 agreement between the best 1 % of simulations for the pattern of Māori establishment of New
220 Zealand (Supplementary animation 2). Based on the multi-model average of selected models,
221 approximately 63% of the Māori population lived in areas of present-day Northland, Auckland,
222 Waikato, Taranaki and Bay of Plenty during the colonising period, a finding consistent with earlier
223 suggestions that these regions harboured the largest Māori populations (Brown & Crema, 2019; M.
224 McGlone, Anderson, & Holdaway, 1994). Areas of fastest population growth occurred across the
225 North Island, especially in present day Wairarapa, Manawatu and Wellington, and in Nelson and
226 Canterbury on the South Island (Figure 5; Supplementary Figure 1).

227 Our projections of Māori arrival and expansion in New Zealand were not sensitive to the
228 population growth function (i.e., logistic versus exponential; Supplementary Figure 6). However, the
229 number of founding events substantially altered the pattern and timing of colonisation, and these
230 differences were magnified with increasing numbers of founding events (Supplementary Figure 7).
231 Total population size in the year 1769 C.E. was sensitive to both the type of population growth
232 function and number of founding events (Supplementary Figures 6 and 7). The implications of these
233 observations are discussed below.

234

235 Discussion

236 Given the integral role that human population growth and expansion has had on biodiversity
237 declines during the Holocene (Burney & Flannery, 2005; Channell & Lomolino, 2000), understanding
238 how humans colonised different islands and archipelagos in response to their unique environments

239 is key to understanding the ecological consequences of these events, including globally-significant
240 declines in biodiversity (Nogué et al., 2021). However, absence of high-resolution reconstructions of
241 patterns and paces of human migrations across islands continues to hinder the extent to which
242 islands can be used as replicated model systems to establish processes of human transformation of
243 biodiversity. We show that process-explicit models that are informed by the archaeological record
244 and spatiotemporal reconstructions of past climates and environments can provide new and
245 important insights into the patterns and drivers of colonisation and establishment of people on
246 islands, generating spatiotemporal reconstructions of human abundance at resolutions needed for
247 biodiversity assessments.

248 Our SEPM projections of the arrival and expansion of Māori in New Zealand closely reconciled
249 inferences of demographic change from the archaeological record, and more recent historical
250 observations, revealing the importance of topography, proximity to navigable water bodies, and the
251 geography of climatic conditions and habitats on colonisation dynamics. These validated simulations
252 provide new opportunities to explore more extensively the potential ecological impacts of human
253 colonisation on New Zealand's native biota and ecosystems in space and time (Greig & Rawlence,
254 2021; M. S. McGlone & Wilmshurst, 1999; G. L. Perry, Wheeler, Wood, & Wilmshurst, 2014),
255 including the roles people have had on species distributions and changes in species richness and
256 ecological function (Figure 3). More generally, the framework developed for reconstructing the
257 colonization of New Zealand by Māori, is directly transferrable to other islands and archipelagos,
258 where climate and archaeological records are available.

259

260 *Spatially Explicit Insights on Māori Colonisation*

261 While Polynesian expansion across the Pacific is hypothesised to have resulted from carefully
262 planned, specific colonial intentions (Diamond, 1985), others have argued otherwise (Anderson,
263 Binney, & Harris, 2015; Walter et al., 2017). Our modelling supports the assertion of Diamond
264 (1985), showing that Polynesian colonisation of New Zealand was highly synchronous, with early
265 settlements arising nearly simultaneously in multiple locations, probably connected by coastal
266 navigation routes. Parameter values in our models, chosen through pattern-oriented methods, are
267 highly congruent with established estimates, including timing of arrival in New Zealand (G. L. Perry et
268 al., 2014; Wilmshurst et al., 2008), number of colonisers (Anderson, 2017; Walter et al., 2017;
269 Whyte, Marshall, & Chambers, 2005), and spatial variation in population growth rates (Brown &
270 Crema, 2019). The areas projected by our models as the most likely sites of Māori first settlement
271 also encompass sites with the oldest archaeological evidence of Māori presence, such as Wairau Bar,

272 Houhora and Tairua ([R. N. Holdaway et al., 2014](#); [Kinaston et al., 2013](#); [Wilmshurst, Higham, Allen,](#)
273 [Johns, & Phillips, 2004](#))

274 Sensitivity analysis indicated that increasing the number of independent founding events above
275 one substantially altered the projected colonisation dynamics, resulting in a poorer match between
276 model simulations and inferences of demographic change from the archaeological record. This
277 suggests that New Zealand was likely to have been founded by a single colonisation event. However,
278 this result must be viewed cautiously since the parameters of models with founding events greater
279 than one were not optimised using POM approaches ([Pilowsky et al., 2022](#)). Nevertheless, a very
280 high (and perhaps unrealistic) population growth rate would be needed to reproduce the
281 archaeological record under a scenario of multiple founding events.

282 An element of the Māori colonisation of New Zealand that we could not replicate was the
283 putative abandonment of the South Island following the extinction of the moa, which has been
284 inferred from the fossil record ([Rawlence et al., 2015](#); [Walter et al., 2017](#)). Some authors have
285 suggested that the South Island was never densely populated by Māori ([Diamond, 1997](#)), as
286 indicated by our SEPM, and that sparse populations persisted following the depletion of wild food
287 resources such as moa ([Brown & Crema, 2019](#); [Hamel, 1982](#)). However, this runs contrary to the
288 prevailing view that the South Island initially harboured large Māori populations who then shifted to
289 the North Island when wild food sources were depleted ([Rawlence et al., 2015](#); [Walter et al., 2017](#)).

290

291 *Ecological Implications of Rapid Colonisation*

292 The arrival and spread of humans across the world's islands had substantial ecological
293 consequences ([Russell & Kueffer, 2019](#)), and the Polynesian colonisation of New Zealand was no
294 different. The colonisation of New Zealand resulted in widespread deforestation ([G. L. W. Perry et](#)
295 [al., 2012](#)), wholesale extinctions of the terrestrial megafauna ([R. N. Holdaway & Jacomb, 2000](#); [G. L.](#)
296 [Perry et al., 2014](#)), and serious declines in marine mammal populations ([Smith, 2013](#)). However, until
297 now, the timing, rate and magnitude of these anthropogenic impacts have been difficult to resolve
298 because of the absence of a detailed spatiotemporal understanding of how Māori expanded across
299 the archipelago.

300 Our new macroecological modelling approach for reconstructing the peopling of islands shows
301 strong spatiotemporal variation in colonisation patterns of New Zealand and subsequent densities of
302 people. We project that colonisation happened more rapidly on the North Island, spreading from the
303 northwest of the island to the southeast. On the South Island the colonisation and spread of people
304 is likely to have happened more slowly, spreading from the east of the island to the west. Given that
305 human density and environmental change are strongly correlated at local-to-regional scales ([Ellis,](#)

306 [2021](#)), this fresh perspective on Māori colonisation dynamics is likely to provide important new
307 insights into the ecological impacts of this rapid migration of humans across New Zealand.

308 Although our modelling shows that Māori are likely to have had little ecological impact on the
309 forests west of the Southern Alps, the pervasive impacts of altered fire regimes ([G. L. W. Perry et al.,](#)
310 [2012](#)) and introduced commensals such as the kiore (*Rattus exulans*) or the kurī (*Canis familiaris*)
311 were significant ([Greig & Rawlence, 2021](#); [Wilmshurst et al., 2008](#)). Accordingly, future modelling
312 exercises that investigate biodiversity change following human-colonisation of New Zealand will
313 ideally need to include the likely impacts of commensals and their cascading effects on native,
314 insular biota.

315

316 *Broader application*

317 While New Zealand presents a tractable example of human colonisation and expansion, resulting in
318 a globally-significant decline in biodiversity ([Duncan & Blackburn, 2004](#); [Valente, Etienne, & Garcia-R,](#)
319 [2019](#)), it is far from unique in this regard. Human arrival and expansion in the Holocene was a major
320 event on many other islands ([Boivin et al., 2016](#); [Louys et al., 2021](#)), leading to extinctions, changes
321 in community structure of plants and animals, and wholesale shifts in the structure and function of
322 insular ecosystems ([Crowley, 2010](#); [Louys et al., 2021](#); [G. L. Perry et al., 2014](#); [Steadman, 1995](#);
323 [Wood et al., 2017](#)).

324 Islands across the Pacific Ocean were populated at different times during the Polynesian
325 expansion ([Wilmshurst et al., 2011](#)), often resulting in extreme declines in biodiversity. Among the
326 most heavily impacted islands was Rapa Nui/Easter Island, which lost its entire endemic forest cover
327 following the arrival of Polynesian colonists ([Diamond, 2007](#)). Similarly, Polynesians colonized the
328 Hawaiian archipelago in the early 1200s ([Rieth et al., 2011](#)), resulting in a greater loss of native
329 vertebrates (birds) than that following their colonization of New Zealand ([Steadman, 1995](#)). Yet each
330 of the Pacific Islands was unique, both in their endemic biodiversity, and in their capacity to support
331 human populations ([Kirch, 1980](#)). This surely resulted in different patterns of human population
332 growth and spread across the archipelagos of the Pacific, and different speeds and possibly different
333 mechanisms of biodiversity loss.

334 In the Indian Ocean, a similar scenario of human colonisation and extinction befell the ratite
335 elephant birds of Madagascar ([Hansford & Turvey, 2018](#); [Hawkins & Goodman, 2003](#)), among other
336 species. The patterns and consequences of human colonisation of Madagascar are even more
337 uncertain than those of New Zealand or Hawaii, with continuing debates over the latency between
338 human colonisation and extinctions ([Anderson et al., 2018](#); [Hixon et al., 2021](#)), along with the
339 putative driving forces ([Hansford et al., 2021](#)). Likewise, the Caribbean islands lost many endemic

340 vertebrates during the late Holocene (beginning around 6000 BP) (Cooke et al., 2017), however the
341 spatiotemporal signatures and anthropogenic contribution to these extinctions remains contested
342 (Orihuela et al., 2020).

343 In each of these cases, the process-explicit modelling approach we used to reconstruct island
344 colonisation of humans across New Zealand could help untangle the potential interdependence
345 between the dynamics of first colonists of an archipelago and the subsequent demographic,
346 geographic and ecological dynamics of its native biota. At a minimum, this would require a dated
347 archaeological record, climate data and ideally either an independent, direct estimate of population
348 size following colonisation (as used here), or one inferred from molecular data (Fordham, Brook,
349 Moritz, & Nogués-Bravo, 2014).

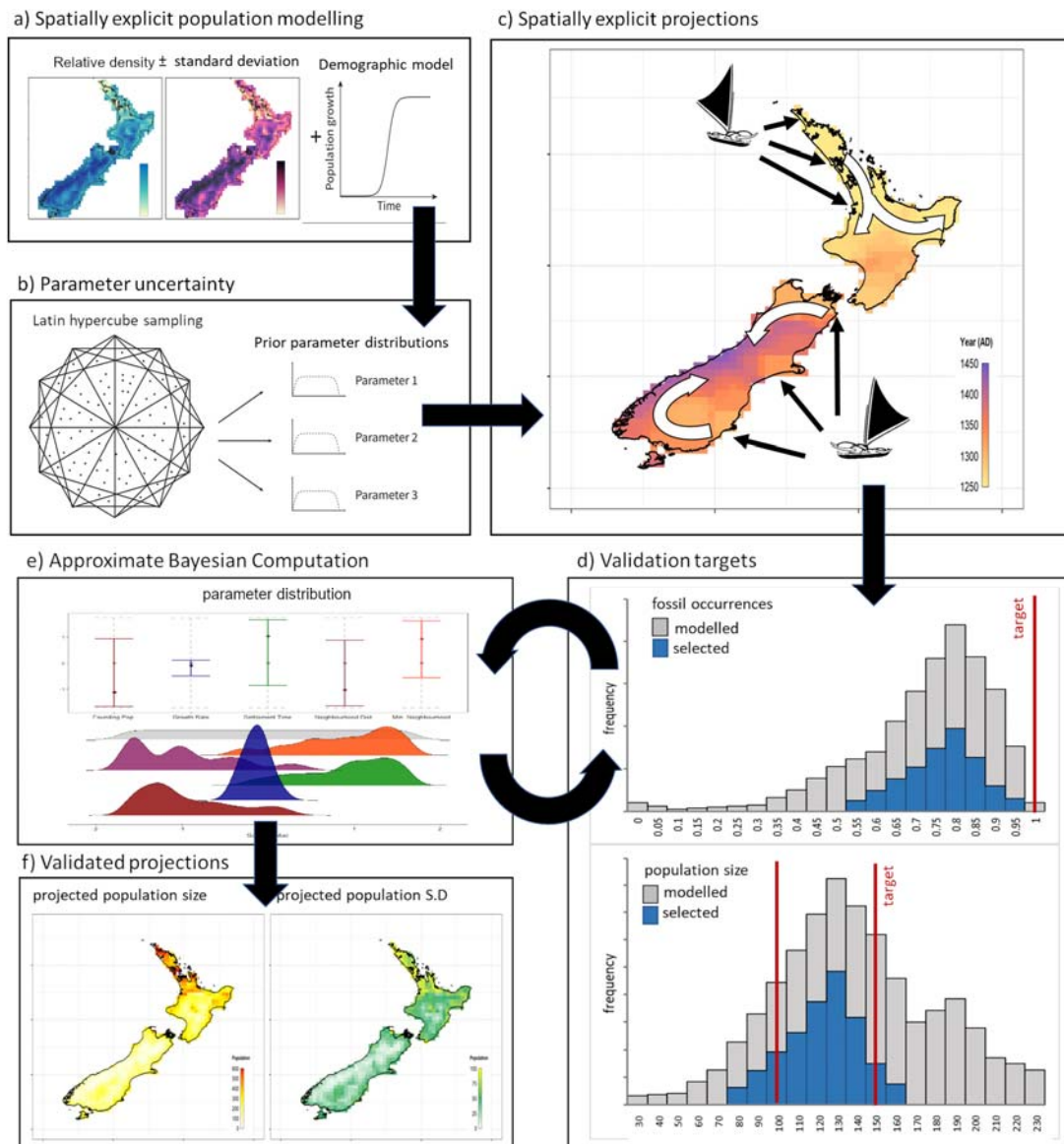
350

351 **Conclusions**

352 The integration of accurately dated archaeological evidence and spatially explicit population
353 models using a pattern-oriented paradigm enabled reliable and plausible simulations of Māori
354 colonisation and expansion across New Zealand at a fine spatiotemporal resolution. In comparison
355 to commonly used statistical approaches for reconstructing human migration, the modelling
356 protocol we implemented has an advantage in that it can identify the demographic and
357 environmental drivers of rapid colonisation events, including those that took place during periods of
358 climatic stability, producing high resolution projections of abundance patterns that pinpoint
359 migration routes. This is the very information needed to establish how human activities transformed
360 island biodiversity.

361 Our new approach for reconstructing island colonization by humans has the potential to address
362 outstanding questions concerning the spatiotemporal dynamics of humanity and their ecological
363 impacts on native insular biotas of islands across the Pacific, as well as those of the Caribbean,
364 Mediterranean, Mascarenes and Madagascar. The framework is flexible to future refinements,
365 including the addition of different population growth models, different targets based on new
366 archaeological and palaeobiological information, and different simulations of past climate and
367 environmental change.

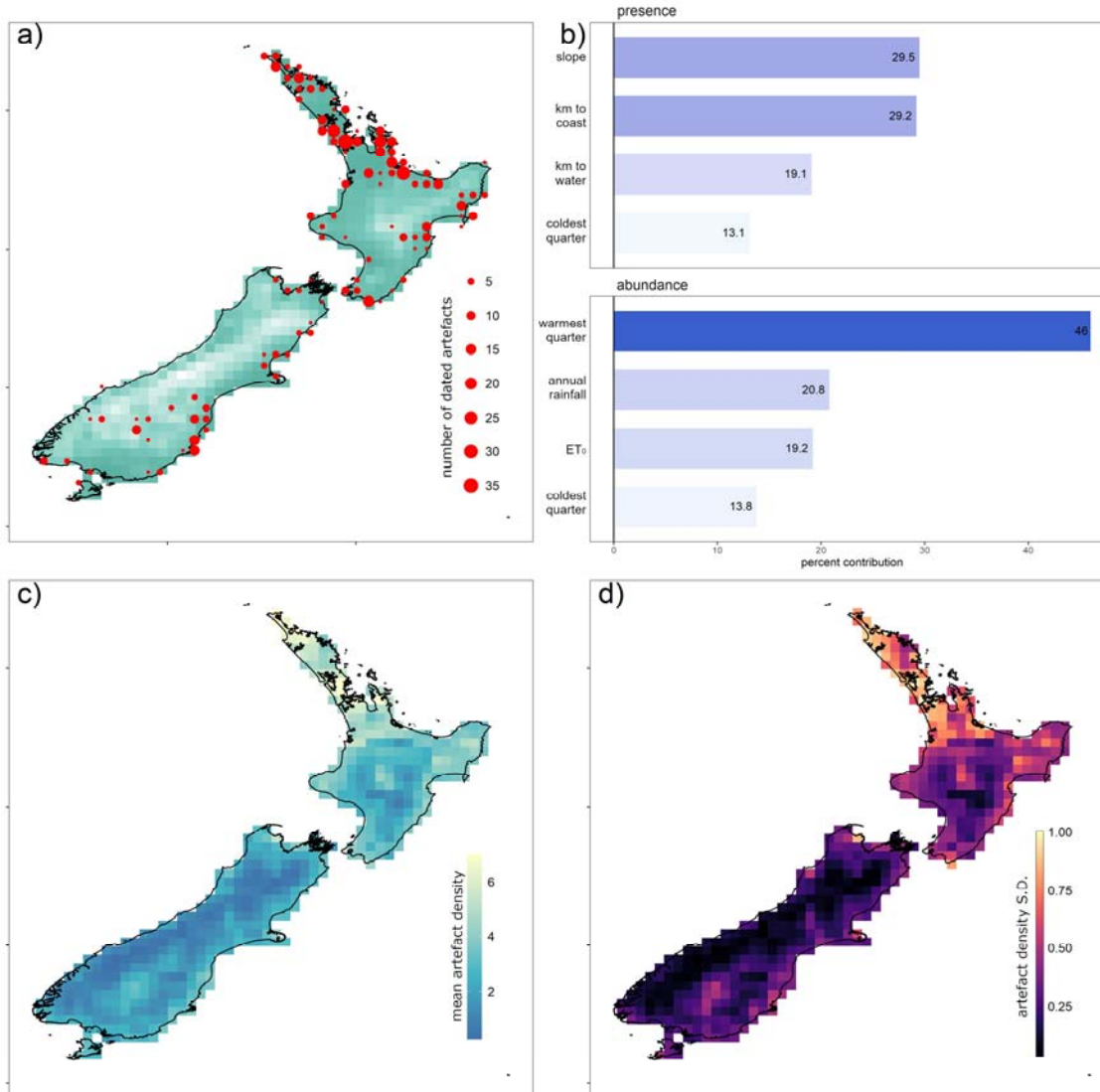
368 **FIGURES AND TABLES:**



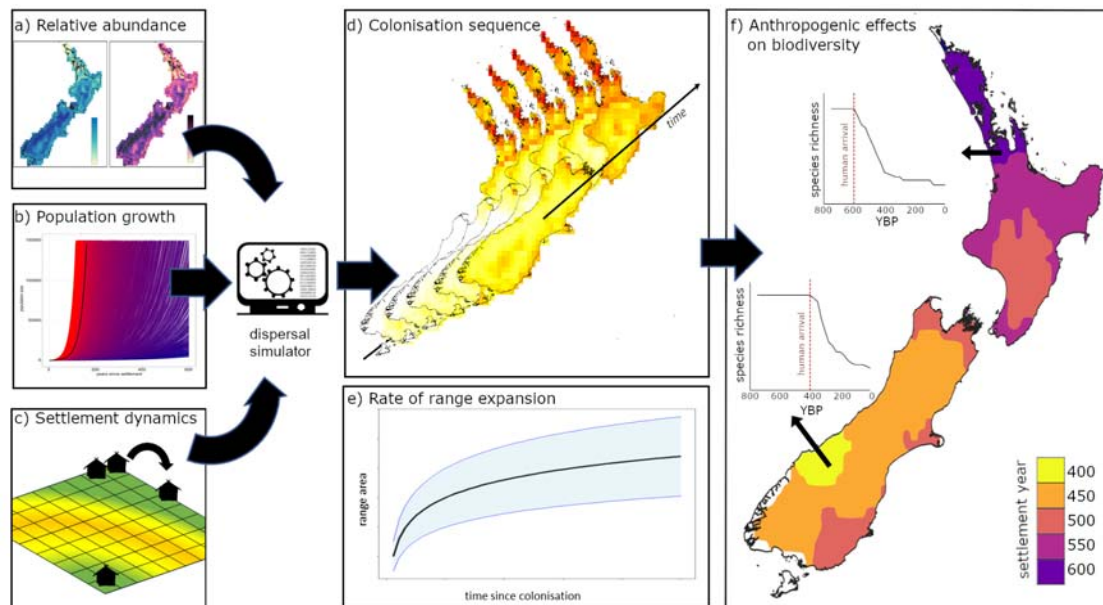
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370 **Figure 1:** Reconstructing Māori colonisation dynamics using spatially explicit population modelling (SEPM) with
371 pattern-oriented modelling (POM). **(a)** Spatiotemporal estimates of Māori relative density were combined
372 with demographic models to simulate colonisation, population growth and geographic expansion. **(b)** To
373 account for parameter uncertainty, thousands of potential models were generated using Latin hypercube
374 sampling, and **(c)** each model was simulated, providing a plausible spatiotemporal projection of arrival time,
375 range expansion and population abundance. **(d)** Model projections were validated against inferences from
376 archaeological archives, and **(e)** the 'best' projections were selected using Approximate Bayesian Computation.
377 The frequency distribution of parameters in these best models were compared to their frequency distribution
378 for all models, and if they differed the processes was repeated. **(f)** Once the parameters converged, the best
379 models were used to project population abundance in space and time

380



381
382 **Figure 2:** Reconstructing relative abundance of people using archaeological data. **(a)** ^{14}C dated archaeological
383 artefacts across New Zealand during the colonisation period (1000 to 1650 C.E.) mapped at a 0.25° resolution.
384 Lighter cells represent higher elevations. **(b)** Effect sizes for variables contributing to the probability of
385 presence and the relative abundance of human artefacts (proxies for presence and abundance of people)
386 across the period of colonisation in New Zealand (estimated using a boosted regression tree). **(c)** Map of mean
387 relative density of human artefacts and **(d)** its standard deviation. Together **(c)** and **(d)** form the spatial
388 template for the spatially explicit population models (SEPMs). Variables in **(b)** are the area of each grid cell
389 steeper than 20° (slope), the distance to the coast (km to coast), the distance to navigable water (km to
390 water), the average temperatures in the coldest quarter (coldest quarter) and the warmest quarter (warmest
391 quarter) of the year, annual rainfall, and annual evapotranspiration (ET_0)
392

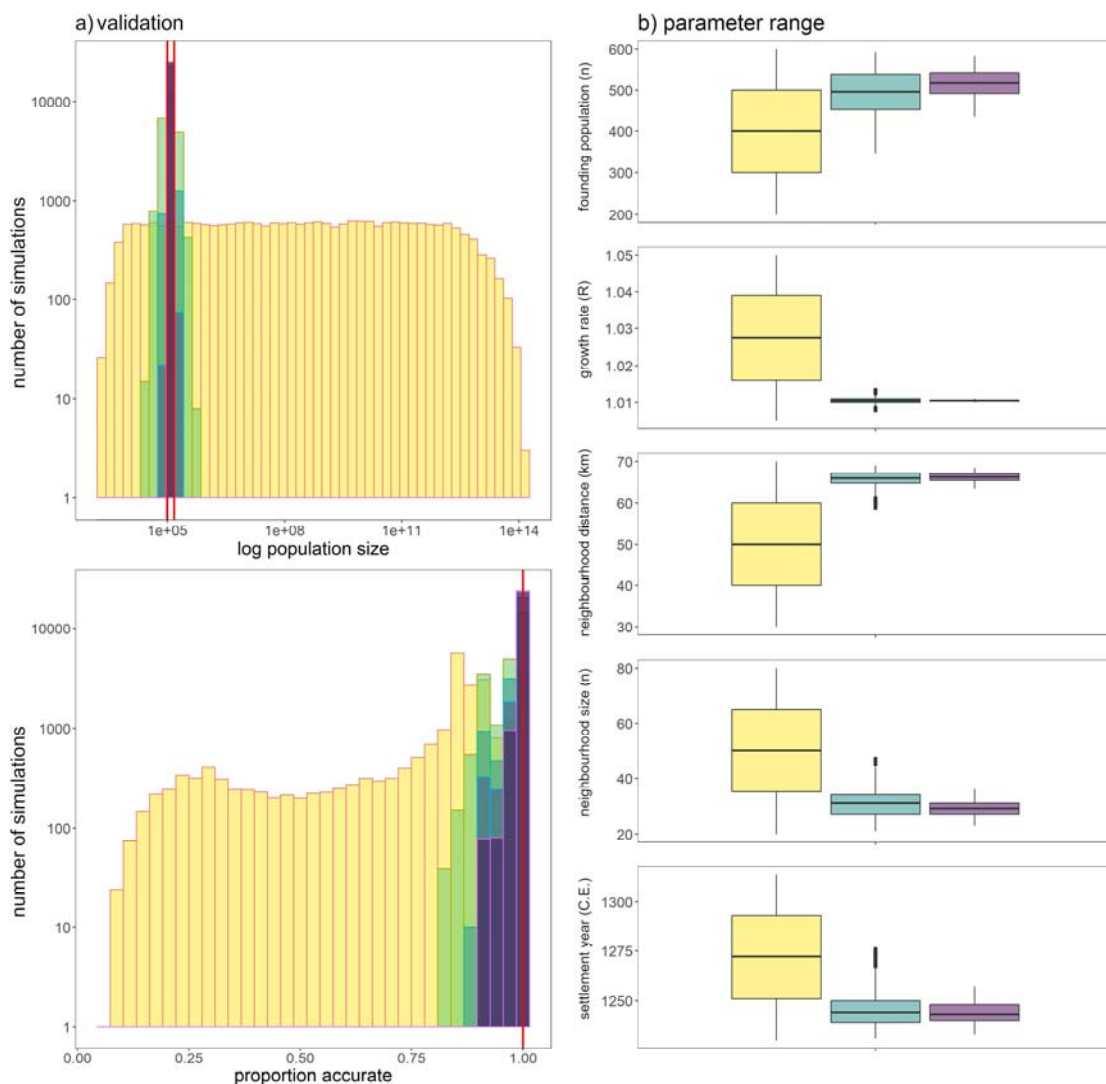


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Figure 3: Simulating range expansion using spatially explicit population model (SEPMs). Māori migration is simulated using (a) statistical estimates of relative abundance (see Figure 2), (b) demographic growth models and (c) the minimum number of people required to found a new community. This results in (d) spatiotemporal estimates of timing of colonisation and (e) temporal estimates of rate of range expansion. These results can be mapped as (f) estimates of the timing of human arrival, establishment and growth: information required to establish the role of human activities on island biodiversity change, including changes in species richness (as indicated here), ranges of species and ecosystem structure.

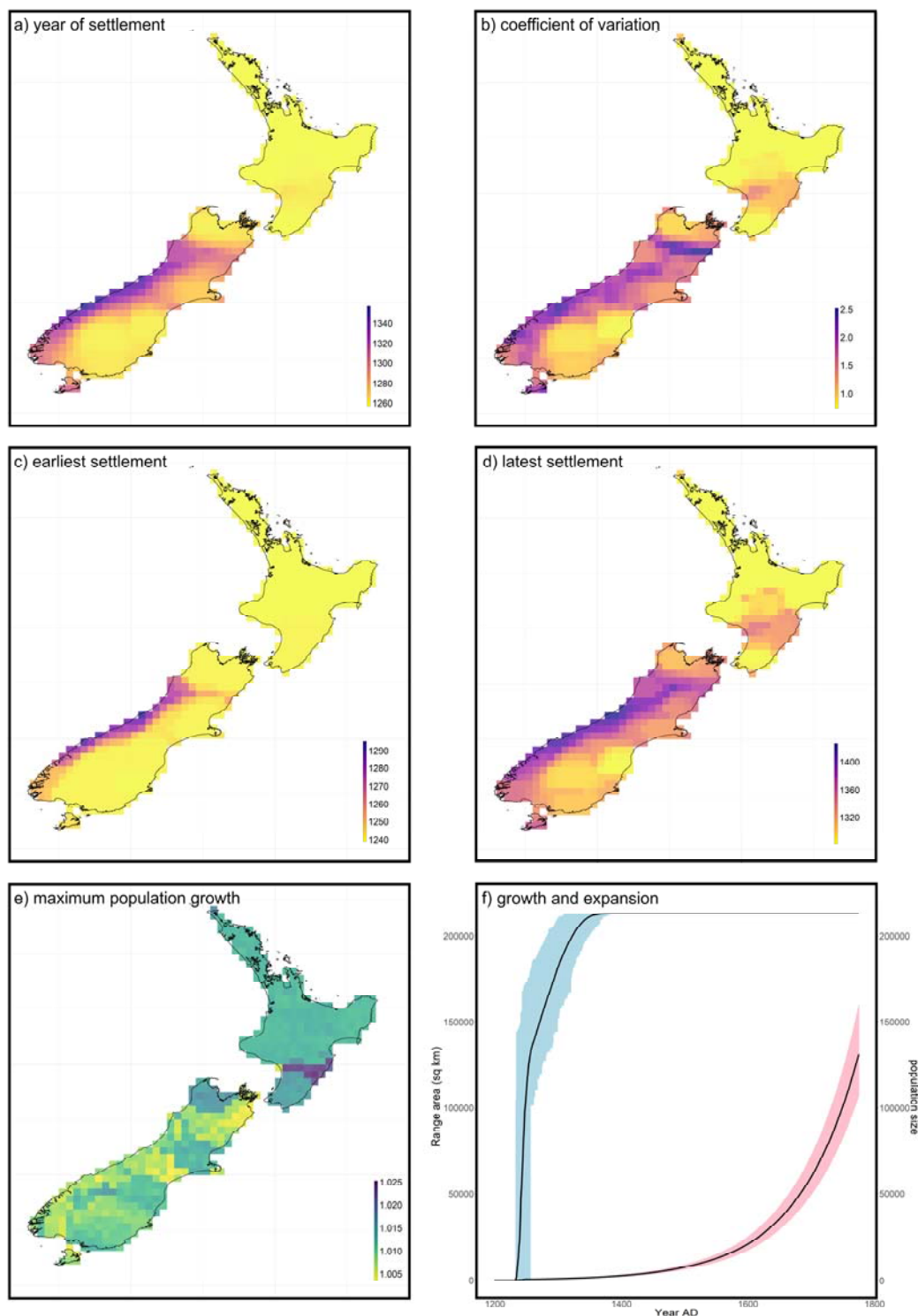
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402

403 **Figure 4:** Estimates of settlement and colonisation of New Zealand by Māori using pattern-oriented modelling
404 (POM). **(a)** Histograms show differences between simulated frequencies and observed targets for three
405 iterations of the model, refined using Approximate Bayesian Computation (ABC). Top histogram shows results
406 for population size at time of first European contact (plotted on the log scale). Bottom histogram shows the
407 proportion of archaeological records accurately modelled in space and time. Red solid lines indicate validation
408 targets. **(b)** Box plots show ranges for model parameters resulting from reiterative ABC resampling. In **(a)** and
409 **(b)**, yellow represents the first iteration, green indicates the second iteration, and purple indicates the third
410 iteration.

411



412

413 **Figure 5:** Island colonisation dynamics. Spatial estimates of **(a)** mean colonisation year and **(b)** its coefficient of
414 variation, **(c)** earliest and **(d)** latest estimate of colonisation, and **(e)** maximum population growth rate.

415 Estimates are multi-model ensemble average based on the 250 spatially explicit population models that best
416 reconciled validations targets. **(f)** Estimated rate of range expansion (blue) and population growth (pink). The

417 ensemble mean is shown in black.

420

Table 1: Parameter values used in the process-explicit model (POM) of Māori colonisation and expansion. Fixed values were consistent across all simulations, while variable parameters were allowed to vary randomly across the entire parameter space (Type). Fixed and prior values for parameters are provided (Values). Posterior values for variable parameters according to POM validation are shown (Credible Interval). Superscript letters indicate published sources for credible intervals; a = (R. N. Holdaway & Jacomb, 2000); b = (G. L. Perry et al., 2014); c = (Wilmshurst et al., 2008).

<i>poems</i> parameter	Description	Type	Values	Credible interval
<i>Spatiotemporal template</i>				
simulation_start_year	The year at which all simulations were initiated	fixed	850 AD	NA
time steps	Simulation years	fixed	1101	NA
Lattice	Number of 0.25° grid-cells	fixed	431	NA
<i>Demographic parameters</i>				
human_founding_population	The number of Polynesian colonists that first arrived in New Zealand	variable	200 - 600	435-582 ^a
human_growth_rate	The rate at which the Māori population increased following arrival in New Zealand	variable	1.005 – 1.050	1.010-1.011 ^a
<i>Settlement and expansion parameters</i>				
human_colonisation_time	The year (AD) in which Polynesians colonised New Zealand	variable	1230 - 1314	1233-1257 ^{b, c}
human_foraging_distance	The radius (km) of the foraging range of each Māori settlement	variable	30 – 70	63-68
human_min_neighbourhood	The minimum number of people required to seed a new Māori settlement	variable	20 – 80	23-36

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