Comparing analytical protocols for identifying causes of population changes

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Abstract

Understanding the factors driving population dynamics is critical for conservation efforts, enabling e.g. the implementation of effective recovery strategies. In this study, we analysed common methods for their ability to correctly identify factors contributing to population changes. We compared time series (TS) and species distribution models (SDM), alongside process-oriented models (POM), which integrate mechanistic components with a correlative approach. To achieve this, we used a virtual ecologist approach to generate synthetic data where the true underlying drivers were known. We then fitted all three models to the data, mimicking the TS and SDM by aggregating the data within a specific domain (spatial or temporal). Our results show that POM outperforms the other methods in all performance

measures used, exhibiting the highest accuracy (0.88), sensitivity (0.84), and specificity (0.93) in terms of identifying factors that contribute to population changes. SDM demonstrated medium (0.68), while TS had the lowest accuracy (0.50). Furthermore, our results indicate that variable selection marginally improved the performance of suboptimal models (TS) but significantly reduced the accuracy of alternative methods (SDM and POM). Our findings highlight the importance of incorporating mechanistic aspects into species distribution modelling to more accurately identify the causes of population changes. These results have the potential to be applicable to a range of ecological and conservation studies and would facilitate the selection of analytical protocol for developing specific indicators to monitor population changes.

Key words: population change, time-series models, species distribution models, process-oriented models, generalized additive modelling, simulation study, virtual species.

1. Introduction

Identifying the causes of population change is a central issue in ecology and conservation biology. This problem is particularly relevant today, as anthropogenic environmental impacts are causing rapid changes in the populations of many species (Hutchings & Reynolds, 2004; Rigal et al., 2023). This leads to dramatic declines in some species, often culminating in extinction and irreversible loss of biodiversity (Ceballos et al., 2017). At the same time, biological invasions lead to human-nature conflicts, with measurable economic losses

(Knowler, 2005; Nentwig et al., 2018; Perrings et al., 2002). Accurate identification of the underlying causes is essential in order to create specific indicators for reporting population change. These can then be used in an indicator-based monitoring framework, thus enabling the formulation of effective responses and enhancing our ability to prevent harmful change.

A broad range of analytical approaches could be used to identify the causes of population changes (Green, 1995; T. F. Johnson et al., 2024; Rhodes et al., 2011; Zachariah Peery et al., 2004). For example, demographic modelling can provide profound insights into the intrapopulation dynamics that contribute to population declines (Allen et al., 2022; Chiquet et al., 2013; Enneson & Litzgus, 2008; H. E. Johnson et al., 2010). However, such models require specific biological data that are difficult to obtain and often unavailable. Consequently, when only abundance data are accessible, ecologists typically rely on statistical methods based on the correlative approach (Green, 1995; Zachariah Peery et al., 2004). Two of the most commonly used statistical modelling approaches for this purpose are time series (Shumway & Stoffer, 2005; Wauchope et al., 2021) and species distribution modelling (Elith & Leathwick, 2009; Guisan & Thuiller, 2005).

Time series modelling is used for census and survey data to analyse trends and seasonal variations over time. Numerous ecological studies have been conducted using temporal data across a wide range of taxa, including predictors such as weather or environmental variables (Di Fonzo et al., 2016; Kölzsch et al., 2007). Conventional time series analysis, at least in the context of identifying factors influencing population changes, does not utilise spatially explicit abundance data. Instead, population size and the corresponding environmental data are aggregated to the specific spatial scale at which the analysis is conducted (Hsieh et al.,

2005; Huthings 2000; Knape & de Valpine, 2011). Importantly, time series analysis inherently treats a single unit of time (usually a year) as a single data point. As a result, it is challenging to make inferences with this approach using typical ecological datasets (multi-year time series). In the case of 'gold standard' datasets (time series >20 years), such spatiotemporal compression, together with the lack of spatial replication, reduces statistical power and makes it significantly more difficult to detect multidimensional or non-linear relationships.

Species distribution models are very popular and have demonstrated remarkable versatility in ecological applications, serving as valuable tools for understanding species-environment relationships, predicting potential distributions, and informing conservation strategies (Zurell et al., 2020). Typically, they combine environmental predictors with information on the species occurrence or abundance, without considering the temporal dimension (Elith & Leathwick, 2009; Guisan & Thuiller, 2005), which leads to several limitations. Firstly, they assume that populations are in a state of equilibrium with their environment, which is not usually the case (Araújo & Guisan, 2006; Guisan & Thuiller, 2005; Pagel & Schurr, 2012; Zurell et al., 2009). Secondly, this approach ignores ecological dynamism such as density-dependent demographic processes, biotic interactions, dispersal, and other fundamental range-shaping phenomena that lead to forecast mismatches (Franklin, 2010; Holt, 2009; Normand et al., 2014; Zurell et al., 2009), and have difficulty in extrapolating models to a novel environment (Briscoe et al., 2019). However, it is worth mentioning that classical SDMs are undergoing extensive development with several novel approaches integrating temporal aspects, such as phenology, with these models (Zurell et al., 2024). Furthermore, there is considerable potential in the application of demographic SDM, which incorporates demographic processes

89 or multi-species models (joint-SDM) that facilitate the modelling of species communities
90 (Zurell, 2017).

91 In this study, we compare two widely used protocols for the identification of factors
92 influencing population abundance and, consequently, the causes of population change,
93 namely time series (TS), and species distribution model (SDM), with a process-oriented
94 model (POM). The latter constitutes our proposal for an easily implementable spatio-
95 temporal model incorporating mechanistic elements such as, density dependence, spatial
96 and temporal autocorrelation (acting as a proxy for both dispersal and large-scale
97 environmental gradients), random effects for space and time (absorbing environmental
98 noise), and random effects for observers (mimicking the observational process). In order to
99 achieve this objective, a virtual species was generated using large-scale and long-term bird
100 monitoring data, thereby providing a known reference. The effectiveness of TS, SDM and the
101 proposed POM in identifying the biotic and abiotic factors responsible for shaping population
102 dynamics was then tested. We hypothesise that POM will outperform both TS and SDM in
103 identification of the factors driving population dynamics as its additional components will
104 increase the overall effectiveness of the models.

105 2. Material and Methods

106 2.1 Study design

107 The aim of our work was to compare the performance of analytical approaches typically used
108 to identify factors influencing population change from abundance data. One is based on
109 inference from time series correlations, while the other is based on the use of spatial data

and the construction of species distribution models. In addition, we propose a more sophisticated approach, which we call 'process-oriented', and test its performance against other methods.

Comparing different methods requires knowledge of the reference. Therefore, we employed an approach to generate a virtual species (VS) based on predefined relationships between environmental factors and population abundance, and then test the effectiveness of the selection of variables actually used in VS generation (Fig. 1) (Malinowska et al., 2023).

To test the effectiveness of the analytical methods, we used abundance data for 10 pairs of western Palearctic passerine bird species (Supplementary File 1, Table S1). For each pair, 100 virtual instances of the species were generated, resulting in a total of 1000 replications in this computational experiment. For detailed algorithm of the study design see Supplementary File 2.

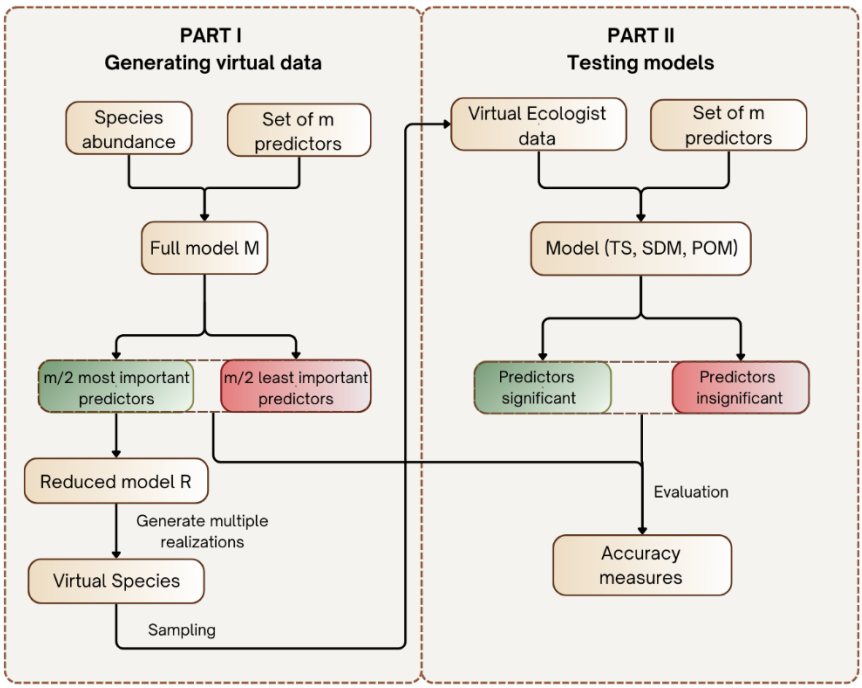

Figure 1. The study design. First, we fitted a model to the spatio-temporal bird abundance data using full set of predictors. We then selected half of the most important predictors from the full model to fit a reduced model. Multiple predictions were then generated from this reduced model, forming many instances of a virtual species. By introducing a realistic level of randomness at this stage, each virtual species was different, even though it was generated from the same model. The sampling procedure, which mimicked data collection, produced virtual ecologist data. These data, which provided a known reference, were then used as input to test the three analytical approaches – time series (TS), species distribution model (SDM) and process oriented approach (POM). Each of these models was fitted with the full set of predictors and then the variables were classified as "significant" using the $p<0.05$ criterion. As the true relevance of the predictors was known, it was possible to evaluate the three methods in terms of their effectiveness in identifying the real factors influencing population change.

2.2 Bird abundance data

The study uses data from 14 common western Palearctic passerine birds organised into 10 pairs (see Table S1 for details). Bird data were obtained from the Common Breeding Birds Survey in Poland (MPPL), and span 20 years (2001-2020), covering the entire area of Poland, which is more than 300 000 km^2. The monitoring programme strictly follows the methodology of the British Breeding Bird Survey (Gregory et al., 1996) and is also included in the Pan-European Common Bird Monitoring Scheme (PECBMS, Brlík et al., 2021). Specific details on data collection are presented in Supplementary File 1. The MPPL programme

144 provides counts that are used to calculate species densities (pairs/km^2) using the distance
145 sampling method (Buckland et al., 2001, 2004).

146 **2.3 Environmental data**

147 In the study we used dynamic environmental data, such as annual land cover data that were
148 derived from ESA CCI Land Cover (Defourny et al., 2017, 2021) and monthly climate data
149 from TerraClimate (Abatzoglou et al., 2018), which were obtained for each MPPL survey site
150 (see Supplementary File 1 and Table S2 for full details). The environmental variables
151 mentioned above are bionomic, which means that they are neither interacting nor
152 consumable (Soberón & Nakamura, 2009). Therefore, we also incorporated biotic interaction
153 into the model, as it can influence species-environmental relationships and species co-
154 occurrence patterns (Wisz et al., 2013). We used the example of social information transfer,
155 which is a mechanism of obtaining, using, and sharing environmental information from
156 conspecifics or heterospecifics (Szymkowiak, 2013). Social cues may provide useful
157 information during the habitat selection process, potentially leading to various population-
158 level consequences (Szymkowiak, 2013). To integrate this mechanism into models, we
159 selected a single variable representing a biotic component, which was the abundance of an
160 interacting species, defined as a species for which there is external, empirical evidence that
161 it interacts biotically with the target species. The set of potential interacting species (Table
162 S1) was restricted to positively interacting species only, due to the mechanism of information
163 use during habitat selection (Szymkowiak, 2013).

164

2.4 Virtual species and virtual ecologist

The virtual data, which serve as a known reference, were generated using a framework described in Malinowska et. al (2023), which could be summarised with the following steps:

1) **Fitting a model to the observed data**. In this step we used Generalised Additive Mixed Models (GAMM) (Wood, 2017), as they offer a range of distributions relevant to population modelling, and are capable of handling zero-inflated and overdispersed data. Flexible functions can also be used, which is important as species-environment relationships tend to be non-linear and complex. Hierarchical structures typical of biodiversity monitoring data can be incorporated via random effects, and autocorrelation structures allow for increased biological realism.

   The model was fitted with 20 variables, including the interacting species. Half of the variables were then removed by backward elimination. In this way, the final (reduced) model, which was later used to generate the VS, was built using only part of the available variables. In this way it was possible to create a scenario in which certain factors had an effect on species abundance and others did not.

2) **Generating the VS.** Predictions from the above reduced model were computed and treated as a virtual species abundance. Although they were generated from the same model, the randomness required for statistical inference was achieved by assigning random intercepts to sites and then generating random realisations from the original distribution (Malinowska et al. 2023). As a result, virtual species abundance were obtained for each site *i* and year *t*.

186 3) **Sampling**. Virtual ecologist data was obtained by simulating the observational process
187 applied to the VS. For each virtual observer, we simulated the sampling error p by
188 drawing a random value from a lognormal distribution with a mean of 1 and a variance
189 which was estimated by fitting the GAMM (this was the variance of the random intercepts
190 for the observer identifiers). The virtual ecologist data were than obtained by
191 multiplying the VS densities by a relevant p.

192 4) **Calibration**. VE data generated in this way tend to overestimate prevalence and
193 underestimate variance (Malinowska et al., 2023). Therefore, to increase ecological
194 realism, we calibrated the VE data using a procedure known as quantile mapping. The
195 virtual data were mapped so that the frequency distribution of the transformed data
196 matched the frequency distribution of the data observed. Simulations show that this
197 procedure is capable of generating virtual data with distributional properties that are
198 indistinguishable from the real data (Malinowska et al., 2023).

199 We repeated the described process (steps 2-4) 100 times to generate multiple instances
200 of virtual ecologist data for every 10 case studies. These virtual data were then used as a
201 known reference to test the effectiveness of variable selection for the three methods
202 considered.

203 **2.5 Models tested**

204 Many methods can be used to make inferences about the effects of environmental factors on
205 abundance, provided they allow specific properties of these data to be modelled. The obvious
206 choice seems to be Generalized Linear Models (GLM). However, the relationships between
207 environmental factors and population densities very often are non-monotonic because

208 organisms have certain optimal preferences along a gradient of environmental
209 characteristics, which are best described by unimodal functions. This implies that it is not
210 feasible to describe a species' preference for a particular environmental factor with a single
211 parameter. Consequently, it is usually not possible to ascertain unambiguously the direction
212 or magnitude of the effect. For this reason, we do not attempt to reconstruct effect sizes, but
213 rather test the effectiveness of a given statistical method in terms of a binary decision as to
214 whether or not a given variable actually affects population numbers.

215 It is evident that this creates problems of interpretation, but the solution seems relatively
216 straightforward and may involve exploratory analysis and visual evaluation of response
217 curves. Thus, the approach we propose is to first assess whether a given environmental factor
218 is important and has an effect on population densities, and then to analyse the direction and
219 strength of the effect exploratively. This can also be done formally, using methods that can
220 infer non-monotonic effects.

221 For these reasons, we used GAM as a flexible way of testing the models for their ability to
222 select the true drivers of population change. An additional advantage of this method is that it
223 not only allows non-linear relationships to be modelled, but also allows the smoothness of
224 those relationships to be reduced until linearity is achieved. Thus, if the patterns in the data
225 are linear, or the data are so sparse that more complex functions cannot be estimated, GAM
226 is reduced to GLM.

227 **2.5.1 Time series**

228 To mimic the time series data, we averaged both population density information and each of
229 the m environmental variables across space and then built a GAM model:

$$N_t \sim T_\xi(\mu_t, \phi)$$

$$\ln(\mu_t) = \alpha + \sum_{j=1}^{m} f_j\left(X_{t,j}\right)$$

Here, population density N_t, which is assumed to come from the Tweedie distribution with index parameter ξ and dispersion parameter ϕ, is indexed by the year identifier t. The natural logarithm of the expected population density is a sum of the intercept α and smooth functions f_j, each fitted to predictor X_j.

2.5.2. Species distribution model

To mimic the static spatial data, we averaged both population densities and each of the m environmental variables across time (i.e. by calculating arithmetic means for each of 1x1 km MPPL squares). Then, the following SDM was build:

$$N_i \sim T_\xi(\mu_i, \phi)$$

$$\ln(\mu_i) = \alpha + \sum_{j=1}^{m} f_j\left(X_{i,j}\right)$$

The model structure is analogous to the time series model (above) except for the population density N is varying in space, i.e. it is indexed by sampling site identifiers denoted as i.

2.5.3 Process-oriented model

In this approach both species and environmental data are dynamic, i.e. they vary in space and time. Moreover, the model was extended by explicitly embedding the following processes

into the model structure: density-dependence, temporal and spatial autocorrelation, random temporal and spatial variation and observational process.

The density dependence was modelled using Gompertz dynamics based on the following concept: for every site i, the population growth rate between time $t-1$ and time t can be expressed as $r = \ln(N_t/N_{t-1})$, which implies $\ln(N_t) = \ln(N_{t-1}) + r$. Density-dependence takes the form of self-regulation, where r is a function of N_{t-1}. Thus, we can substitute r by an arbitrary function of N_{t-1} to obtain:

$$\ln(N_t) = \ln(N_{t-1}) + f_d\big(\ln(N_{t-1})\big),$$

where f_d is a function determining how population growth rate changes with changing population density. Traditionally, this function is assumed to be monotonically decreasing, however it can take many forms, including non-monotonic (Allee effect). Here, to allow for flexibility and generality in density-dependent effects, we allowed the f_d function to be smooth and non-parametric. To do so, we fitted the following GAMM model:

$$N_{i,t} \sim T_\xi\big(\mu_{i,t}, \phi\big)$$

$$\ln\big(\mu_{i,t}\big) = \alpha + \ln\big(N_{i,t-1}\big) + f_d\left(\ln\big(N_{i,t-1}\big)\right) +$$

$$+ \sum_{j=1}^{m} f_j\left(X_{i,t,j}\right) + \mathcal{GP}\big(f_t(t), u(t,t')\big) + \mathcal{GP}\big(f_s(x), v(x,x')\big) + a_i + b_t + o_{i,t}$$

$$u(t,t') = c_0(\| t - t' \|, \rho_t), \qquad v(x,x') = c_0(\| x - x' \|, \rho_x)$$

$$c_0(d,\rho) = (1 + d/\rho)\exp(-d/\rho)$$

$$a_i \sim N(0, \sigma_a^2), \qquad b_t \sim N(0, \sigma_b^2), \qquad o_{i,t} \sim N(0, \sigma_o^2)$$

Population density $N_{i,t}$, which is assumed to come from the Tweedie distribution, is indexed by the site identifier i and the year identifier t. As in the previous models, the natural logarithm of expected density $\mu_{i,t}$ is the sum of smooth functions fitted to m predictors. However, in this model, all predictors vary in both space and time.

In addition to the density-dependence, this model has been extended to include the following processes:

1. Temporal autocorrelation, modelled as a Gaussian process $\mathcal{GP}$ with the expectation f_t which itself is modelled as a smooth function of time and the covariance matrix u describing temporal autocorrelation structure. The elements of matrix u are modelled as a function of a between-year distance using the Matérn correlation function c_0 with the parameter ρ_t.

2. Spatial autocorrelation, modelled as a Gaussian process $\mathcal{GP}$ with the expectation f_s which is a smooth, 2-dimensional function of geographic coordinates (denoted as x) and the covariance matrix v describing a spatial autocorrelation structure. The elements of matrix v are modelled as a function of geographic distance between sampling sites using the Matérn correlation function c_0 with the parameter ρ_x.

3. Random spatial variation, modelled as a normally distributed random intercept for each sampling site i with the mean zero and the variance σ_a^2.

4. Random temporal variation, modelled as a normally distributed random intercept for each year t with the mean zero and the variance σ_b^2.

5. Observational process, modelled as a normally distributed random intercept for each observer, with the mean zero and the variance σ_o^2.

2.6 Evaluation of models

After generating virtual data simulating population densities, we were able to make model comparisons. Since the virtual data were replicated multiple times (100 simulations for each of the 10 virtual species pairs), formal statistical inference was possible.

A commonly used approach to improve the interpretability of a model while increasing its predictive accuracy is variable selection. In the case of GAM, Marra & Wood (2011) used an extensive simulation study to demonstrate that, in terms of predictive power, shrinkage approaches to variable selection perform significantly better than competing methods. To test this in the context of our study, and identify which variables were 'significant', the models were fitted in two configurations: one in which variable selection was not applied and one in which it was. In the latter case, the double penalty shrinkage was used. In this approach, in addition to the standard penalty that controls for the shape of smooth functions and thus prevents them from overfitting, an additional penalty is constructed that penalises the size of functions. In this way, the model can effectively shrink the entire function for a variable to zero if its contribution is negligible, thus performing automatic variable selection (Marra & Wood, 2011). Technically, the double penalty is invoked by using '`gam(…, select = TRUE)`' from the `mgcv` package (Wood, 2017).

306 For each of the fitted models, we classified variables as ‘significant’ if the estimated p-value
307 was below the threshold of 0.05. This is, of course, an arbitrary criterion, but the objective of
308 this study is to provide recommendations on the use of analytical methods for their
309 subsequent application. Therefore, it seems reasonable to adopt a criterion that is commonly
310 used in the practice of ecological and conservation research.

311 After classifying variables as 'significant' or not, we compared them to the variables that were
312 actually used to generate the virtual data. We then calculated the following measures:

313 1) Accuracy (correct classification rate) - the probability of detecting an effect if there is
314 one or detecting no effect if there is none, i.e., whether the model correctly classified
315 the variable as included in the set used to generate virtual data or not.

316 2) True positive rate (sensitivity) – the power of a test, that is the probability of detecting
317 an effect if there is one. More specifically, in this study it is the probability that a
318 variable classified as significant in the model was actually included in the set used to
319 generate the virtual data.

320 3) True negative rate (specificity) – the probability of detecting no effect when there is
321 none, i.e., the probability that a variable classified as non-significant in the model was
322 actually excluded from the variable set used to generate the virtual data.

323 A binomial Generalised Linear Mixed Model using the R package “glmmTMB” (Brooks et al.,
324 2017) was used to quantitatively assess the effect of method, variable selection strategy and
325 their interaction on the above measures of classification performance. Species was entered
326 into the model as a random intercept. Estimated marginal means were used to assess
327 contrasts using the R package “emmeans” (Searle et al., 1980). The analyses were performed

using R 4.5.0 software (R Core Team, 2025). The code is available on the GitHub repository: https://github.com/popecol/Causes.

3. Results

3.1 Accuracy

TS performed most poorly of the approaches tested. Its accuracy was 0.50 (95% confidence interval: 0.48-0.53) when no variable selection was applied and 0.55 (CI: 0.52-0.57) when variable selection was used (Fig. 2, Table S3), which improved accuracy (odds ratio: 0.83, $p<0.0001$) (Table S4). SDMs performed better: the mean accuracy was 0.68 (CI: 0.66–0.70) without variable selection and 0.63 (CI: 0.61-0.65) when it was applied. Variable selection reduced the accuracy in this case (odds ratio: 1.24, $p<0.0001$). SDM was significantly more accurate than TS under both variable selection strategies (odds ratio: 0.47, $p<0.0001$ and 0.71, $p<0.0001$) (Table S5). The POM approach outperformed both TS and SDM, its accuracy was 0.88 (CI: 0.87-0.89), or 0.77 (CI:0.76-0.79) depending of the variable selection strategy (odds ratio: 2.22, $p<.0001$). POM was significantly more accurate than both SDM (odds ratio: 0.28, $p<0.0001$ and 0.50, $p<0.0001$), and TS (odds ratio: 0.13, $p<0.0001$ and 0.36, $p<0.0001$).

3.2 Sensitivity

Sensitivity (true positive rate) was zero for the TS approach with no selection (in all simulations none of the variables that actually influenced population abundance were selected as significant) and 0.14 (CI: 0.11-0.17) when variable selection was used (Table S3). For the SDM approach, it was 0.68 (CI: 0.62-0.73) and 0.73 (CI: 0.68-0.78), respectively, with variable selection improving sensitivity (odds ratio: 0.77, $p<0.0001$) (Table S7). In the case

349 of POM, the sensitivity was the highest of the methods tested: 0.84 (CI: 0.81-0.88), and there
350 was no difference regarding the variable selection strategy (odds ratio: 1.0, p=0.79). POM
351 outperformed SDM in both cases (odds ratio: 0.38, p<0.0001 and 0.50, p<0.0001) and TS
352 when the variable selection was applied (odds ratio: 0.03, p<0.0001) (Table S8).

353 **3.3 Specificity**

354 The specificity (true negative rate) for the TS approach was 1.00 (in all simulations the
355 variables identified as non-significant were correctly classified as such) in the case of no
356 variable selection, and 0.95 (CI: 0.95-0.96) in the case when it was used (Table S3). For the
357 SDM, these estimates were 0.69 (CI: 0.66-0.72) and 0.54 (CI: 0.51-0.57), respectively, and
358 variable selection reduced the specificity (odds ratio: 2.00, p<0.0001) (Table S10). For the
359 POM approach, the specificity was 0.93 (CI: 0.92-0.94) and 0.71 (CI: 0.68-0.74), depending on
360 the selection strategy. The difference between these estimates was significant, the use of
361 variable selection noticeably produced poorer results (odds ratio: 5.00, p<0.0001). POM
362 outperformed both SDM in terms of specificity, regardless of selection strategy (odds ratio
363 for both contrasts: 0.00, p<0.0001), and TS when variable selection was applied (odds ratio:
364 8.0, p<0.0001) (Table S11).

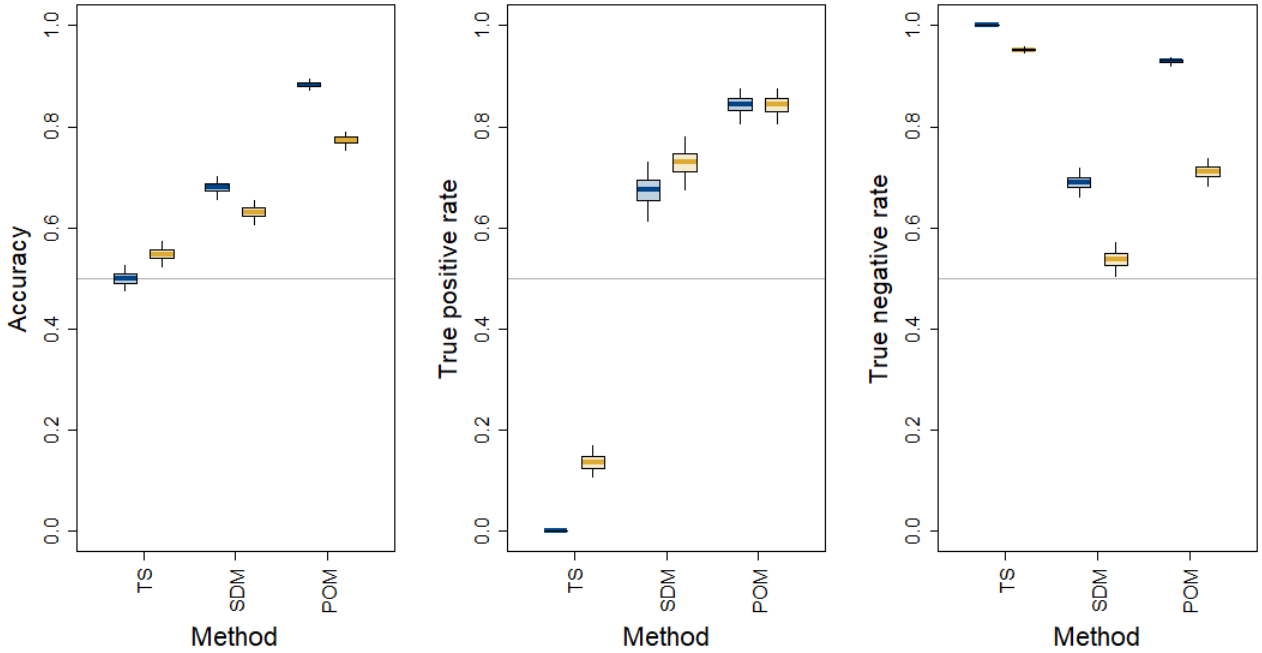

Figure 2. *Performance measures for the classification of variables using the following methods: TS - time series, SDM - species distribution model, POM – process-oriented model, with different variable selection strategies: blue indicates no variable selection, whereas yellow indicates that variable selection was applied. Box plots show the distribution of classification measures over 1000 replications. Whiskers represent 95% confidence intervals, lower and upper hinges are 50% confidence intervals and the middle line is the mean. The baseline at 1/2 indicates expected value if the variables were classified randomly.*

4. Discussion

This study compares two analytical protocols for inferring causes of population changes with a process-oriented approach. Our findings demonstrate that time series data are unable to

377 detect factors influencing population abundance. In the simulations carried out, all variables
378 were classified as non-significant, regardless of their actual impact. SDM performed
379 significantly better than TS across all performance measures and achieved satisfactory
380 accuracy (0.68) and balanced sensitivity and specificity. Finally, the most complex approach,
381 POM showed the best performance overall, with the highest accuracy (0.88) and well-
382 balanced sensitivity and specificity.

383 The choice of modelling method, although constrained by data availability and analytical
384 skills, depends first and primarily on the research question posed. The consequences of this
385 choice are generally underestimated and can drastically affect the results obtained and the
386 conclusions drawn. For example, Gould et al. (2025) show, that a single research problem,
387 when analysed using different approaches, can provide a different set of answers. When
388 examining the factors influencing population dynamics the choice of analytical approach also
389 depends on the nature of the data and the research hypotheses. For instance, when working
390 with demographic data, time series models may be a better tool to capture fluctuations in
391 apparent survival, as this parameter shows more variation across years than between sites.
392 Conversely, species distribution models may be better suited to analysing productivity,
393 which tends to vary more spatially than temporally (Morrison et al., 2022).

394 **4.1 Efficiency of time series and species distribution models**

395 Our results demonstrate that although these two popular methods are often used to identify
396 the drivers of population change, they do not always provide satisfactory results and may be
397 of limited use in conservation decision making. The main reason for their poor performance
398 appears to be data aggregation, which fundamentally alters the statistical properties of the

399 data, reducing variance and decreasing degrees of freedom. As a result, the signal-to-noise
400 ratio is lowered, reducing the validity of statistical inference and introducing the bias of
401 variable selection. This affects both sensitivity (true positive rate) and specificity (true
402 negative rate) in identifying relevant predictors. The higher the level of data aggregation, the
403 greater the loss of granularity and the greater the attenuation of effect sizes - this explains
404 the poor performance of TS, slightly better for SDM and quite satisfactory for POM, where the
405 original fine-scaled patterns are retained. Data aggregation could lead to biased results
406 across a wide range of statistical models (Abrahamowicz et al., 2004; Pollack et al., 2022;
407 Pollet et al., 2015; Schad et al., 2024), and time series tend to demonstrate a weaker covariate
408 effect if the dataset has been previously averaged over inadequate time scales (Ferguson et
409 al., 2017).

410 **4.2 Properties of process-oriented models**

411 The strong performance of the process-oriented models is most likely due not only to the use
412 of spatio-temporal data, but also to the structure of the model itself. Including at least some
413 elements of the data-generating mechanism, such as density dependence, autocorrelation,
414 random effects or observer effects, is likely to significantly improve the ability to correctly
415 identify relevant factors and reject spurious ones. Similar findings are recognised in the
416 literature (Johnson et al., 2024). Ignoring the hierarchical structure of the data can lead to
417 underestimation of population trends, and complex models provide more accurate
418 inferences about ecological systems (Johnson et al., 2024). It is acknowledged that dynamic
419 and process-orientated models are highly promising tools in ecology for a better and more
420 effective understanding of population dynamics, e.g., in the light of climate change (Franklin,

2010; Zurell, 2017), especially considering that static models, such as classic SDM, are characterized by a number of drawbacks (Guisan & Thuiller, 2005).

However, POMs are subject to certain limitations. The increasing complexity of a model can have a negative impact on its feasibility and tractability, which affects its subsequent understanding. Furthermore, spatio-temporal models require large amounts of data. In addition to data availability requirements, higher complexity can lead to higher computational costs, including longer simulation times and more time spent on data preparation and analysis. Whether this approach will always be more profitable than less advanced models will therefore depend on the specific problem being addressed and the data available.

4.4 Usability of variable selection

The results of our study contribute to the ongoing debate about the validity of variable selection strategies (Tredennick et al., 2021; Whittingham et al., 2006). We have shown that in the case of TS, variable selection improves accuracy; however, the difference is without practical importance due to the method's inherent flaws. Furthermore, in our study variable selection actually reduces the efficiency of more advanced approaches, such as SDM and POM. Many variable selection strategies are now used in ecology, although each method, such as the double shrinkage penalty used here, may have potential weaknesses that limit its usefulness. Alternative approaches can therefore be used, or the full model can be fitted to obtain the best outcomes (Tredennick et al., 2021; Whittingham et al., 2006).

4.4 Practical implications

The results of this study also have practical implications for conservation ecology and management practice in terms of population and ecosystem monitoring. We emphasise the need to collect fine-grained, long-term and large-scale monitoring data, such as that from the Pan-European Common Bird Monitoring Scheme (Brlík et al., 2021). This enables the use of complex and effective analytical methods, which are crucial for identifying reliable biodiversity indicators for monitoring global change (Clavero et al., 2011).

4.5 Overall conclusions

In conclusion, our study provides a comparison of methods frequently used to infer the drivers of population change, and we acknowledge that these do not exhaust all the possibilities available. However, our aim was not to provide a detailed comparison of multiple methods or different selection strategies, but rather to show that the commonly used analytical approaches applied to the problem of identifying the causes of population change may not be very effective and may lead to erroneous conclusions. Instead, we offer an easy-to-implement method that not only accounts for ecological mechanisms (such as density dependence or the observational process), but is also much more effective at correctly identifying the factors driving population change. We hope that this will contribute to a more effective use of large-scale and long-term monitoring data in a time of biodiversity crisis.

Acknowledgements

The study was supported by the National Science Centre (NCN) in Poland (grant no. 2018/29/B/NZ8/00066). The computational resources used in this work were provided by the Poznań Supercomputing and Networking Centre (grant no. pl0090-01). We are grateful to Klaudia Szala who tested the early versions of the models. The authors gratefully acknowledge MPPL volunteers for collecting the data, Chief Inspectorate for Environmental Protection (GIOŚ) and OTOP BirdLife Poland for providing the bird data.

CRediT authorship contribution statement

Katarzyna Malinowska: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **Michał Wawrzynowicz:** Conceptualization, Writing – original draft. **Katarzyna Markowska**: Data curation. **Tomasz Chodkiewicz:** Resources, Writing - review and editing; **Simon Butler:** Methodology, Validation, Writing - review and editing; **Lechosław Kuczyński:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Visualization, Writing – original draft.

Declaration of competing interest

The authors declare no conflict of interests.

Data availability

The code and data associated with the final results are available on the GitHub repository: https://github.com/popecol/Causes. Bird population data used in the analysis are partially owned by OTOP BirdLife Poland (2000-2006) and Chief Inspectorate for Environmental Protection (GIOŚ, 2007-2021). OTOP provides the data upon request. GIOŚ provides the data at: https://monitoringptakow.gios.gov.pl/PM-GIS/?lang=en. Environmental data, such as climate data are publicly available at the page: https://www.climatologylab.org/terraclimate.html, as well as land cover data: https://maps.elie.ucl.ac.be/CCI/viewer/download.php.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplementary File 1. Specific details concerning data used in the analysis, data treatment and variable selection.

Supplementary File 2. Additional results not included in the main article.