Comparing analytical protocols for identifying causes of population changes

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Abstract

1. Understanding the factors driving population dynamics is critical for conservation efforts, enabling e.g. the implementation of effective recovery strategies. However, selecting the most effective method for identifying drivers of population change can be challenging, given the wide range of models available for this purpose.
2. In this study, we employed a virtual ecologist approach to compare three methods: time-series (TS), species distribution model (SDM), and process-oriented model (POM), in terms of their ability to correctly identify factors contributing to population changes. While the first two approaches are commonly used in ecological studies in the presented context, the process-oriented method is a novel

approach that integrates mechanistic components with correlative approach to identify drivers of population changes.

3. We show that POM outperforms the other methods on all performance measures used, as it has the highest accuracy (0.88), sensitivity (0.84), and specificity (0.93). SDM has the medium (0.68), while TS has the lowest accuracy (0.50). Moreover, our results suggest that variable selection slightly improve the performance of suboptimal models (TS), while it significantly reduces the accuracy of other approaches (SDM and POM).
4. *Policy implications:* Our results highlight the importance of incorporating more mechanistic aspects into species distribution modelling to better identify the causes of population changes. These findings may be applicable to a range of ecological and conservation studies.

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

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 a fundamental prerequisite for the formulation of effective responses and determines our capacity to prevent detrimental changes.

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 impossible to even attempt 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). Finally, SDM have difficulty in fitting data outside the input range and in extrapolating models to a novel environment (Briscoe et al., 2019).

In this study, we compare two widely used protocols for the identification of factors influencing population abundance and hence the causes of population change, namely time series (TS), and species distribution models (SDM), with a process-oriented modelling (POM) approach, which, to our knowledge, has rarely been applied in this context. POM is our proposal for an easily implemented spatio-temporal model that also incorporates mechanistic elements: density dependence, spatial and temporal autocorrelation (acting as a proxy for both dispersal and large-scale environmental gradients), random effects for space and time (absorbing environmental noise), and random effects for observers (mimicking the observational process). We tested the effectiveness of these methods in identifying both biotic and abiotic factors responsible for shaping population abundance. To do this, we use long-term and large-scale bird monitoring data to create a virtual species that serves as a known reference. We hypothesise that POM will allow for a better identification of the factors driving population dynamics as its additional components will increase the overall effectiveness of the models. From a practical perspective, our goal is to provide recommendations for selecting the most effective modelling approach to accurately infer the causes of population changes.

2. Material and Methods

Study design

The aim of our work was to compare the performance of analytical approaches typically used to identify factors influencing population change from abundance data. One is based on 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 demonstrate its advantages over the above 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.

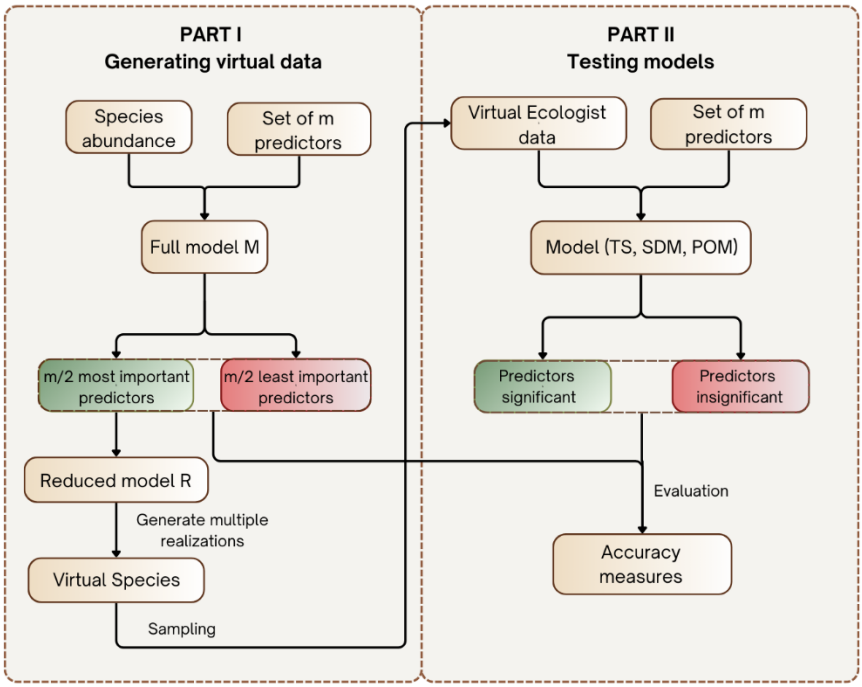

Figure 1. The study design. First, we fitted a model to the spatio-temporal bird abundance data using full set of predictors. We then selected half of the most important predictors from the full model to fit a reduced model. Multiple predictions were then generated from this reduced model, forming many 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.

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

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

143 Environmental data

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

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*.

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

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

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

Models tested

Many methods can be used to make inferences about the effects of environmental factors on abundance, provided they allow specific properties of these data to be modelled. The obvious choice seems to be Generalized Linear Models (GLM). However, the relationships between

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

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

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

Time series

To mimic the time series data, we averaged both population density information and each of 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.

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.

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.

Model evaluation

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).

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

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

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

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

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

A binomial Generalised Linear Mixed Model using the R package "glmmTMB" (Brooks et al., 2017) was used to quantitatively assess the effect of method, variable selection strategy and

their interaction on the above measures of classification performance. Species was entered into the model as a random intercept. Estimated marginal means were used to assess 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 and data associated with the final results are available in the GitHub repository: https://github.com/popecol/Causes.

3. Results

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, $p<0.0001$).

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

342 variable selection improving sensitivity (odds ratio: 0.77, p<0.0001) (Table S7). In the case
343 of POM, the sensitivity was the highest of the methods tested: 0.84 (CI: 0.81-0.88), and there
344 was no difference regarding the variable selection strategy (odds ratio: 1.0, p=0.79). POM
345 outperformed SDM in both cases (odds ratio: 0.38, p<0.0001 and 0.50, p<0.0001) and TS
346 when the variable selection was applied (odds ratio: 0.03, p<0.0001) (Table S8).

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

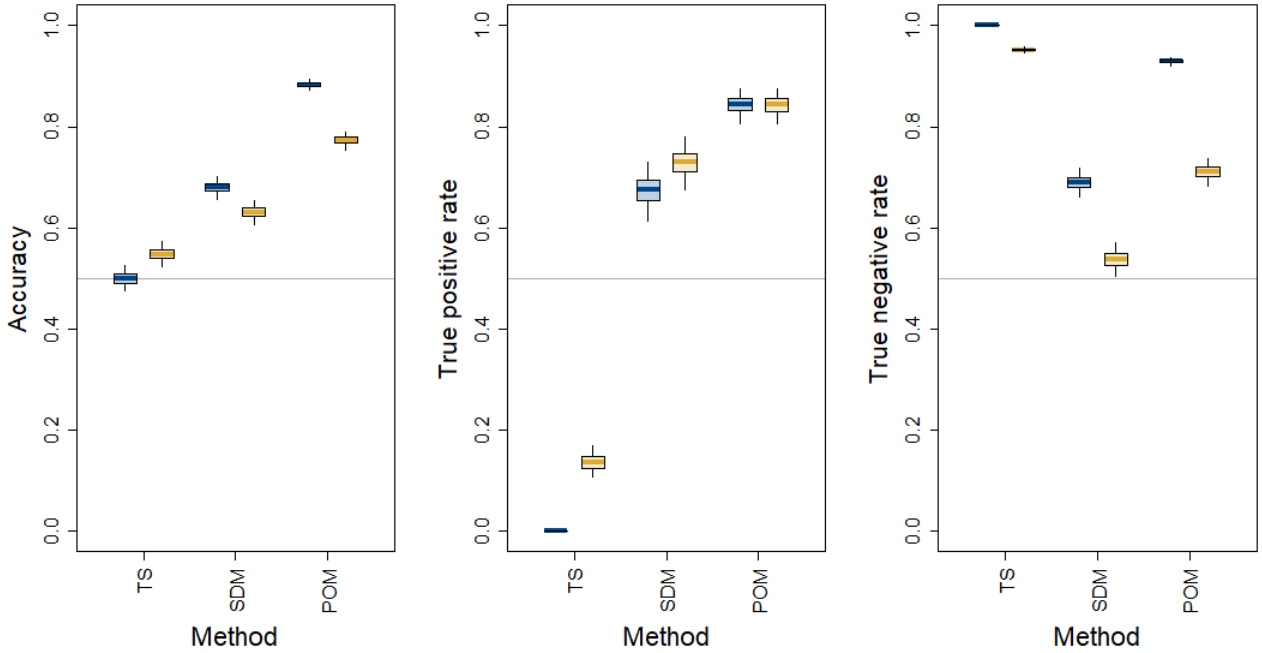

Figure 2. *Performance measures for the classification of variables using the following methods: TS - time series, SDM - species distribution model, POM – process-oriented model, with different variable selection strategies: blue indicates no variable selection, whereas yellow indicates that variable 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 aggregated over a larger spatial domain are unable to detect factors influencing population abundance. In the

371 simulations carried out, all variables were classified as non-significant, regardless of their
372 actual impact. SDM performed significantly better than TS across all performance measures
373 and achieved satisfactory accuracy (0.68) and balanced sensitivity and specificity. Finally, the
374 most complex approach, POM showed the best performance overall, with the highest
375 accuracy (0.88) and well-balanced sensitivity and specificity.

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

387 However, our results demonstrate that although these two popular methods are often used
388 to identify the drivers of population change, they do not always provide satisfactory results
389 and may be of limited use in conservation decision making. The main reason for their poor
390 performance appears to be data aggregation, which fundamentally alters the statistical
391 properties of the data, reducing variance and decreasing degrees of freedom. As a result, the
392 signal-to-noise ratio is lowered, reducing the validity of statistical inference and introducing

393 the bias of variable selection. This affects both sensitivity (true positive rate) and specificity
394 (true negative rate) in identifying relevant predictors. The higher the level of data
395 aggregation, the greater the loss of granularity and the greater the attenuation of effect sizes
396 - this explains the poor performance of TS, slightly better for SDM and quite satisfactory for
397 POM, where the original fine-scaled patterns are retained. Data aggregation could lead to
398 biased results across a wide range of statistical models (Abrahamowicz et al., 2004; Pollack
399 et al., 2022; Pollet et al., 2015; Schad et al., 2024), and time series tend to demonstrate a
400 weaker covariate effect if the dataset has been previously averaged over inadequate time
401 scales (Ferguson et al., 2017).

402 The strong performance of the process-oriented models is most likely due not only to the use
403 of non-aggregated data, but also to the structure of the model itself; including at least some
404 of the structure of the data-generating mechanism, such as density dependence,
405 autocorrelation, random effects or observer effects, is likely to significantly improve the
406 ability to correctly identify relevant factors and reject spurious ones. Similar findings are
407 recognised in the literature (Johnson et al., 2024). Ignoring the hierarchical structure of the
408 data can lead to underestimation of population trends, and complex models provide more
409 accurate inferences about ecological systems (Johnson et al., 2024). It is acknowledged that
410 dynamic and process-orientated models are highly promising tools in ecology for a better
411 and more effective understanding of population dynamics, e.g., in the light of climate change
412 (Franklin, 2010; Zurell, 2017), especially considering that static models, such as SDM, are
413 characterized by a number of drawbacks (Guisan & Thuiller, 2005).

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

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

431 The results of this study also have practical implications for conservation ecology and
432 management practice in terms of population monitoring. We emphasise the need to collect
433 fine, long-term and large scale monitoring data, such as Pan-European Common Bird
434 Monitoring Scheme (Brlík et al., 2021), that allow the use of complex and effective analytical

methods, as the conclusions drawn from them could have a crucial impact on decisions in further conservation planning.

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.

Authors' contribution

Katarzyna Malinowska conceptualised the idea, developed the methodology, performed the analysis, analysed the results and wrote the manuscript; Michał Wawrzynowicz conceptualised the idea and wrote the manuscript; Katarzyna Markowska implemented and organised the code; Tomasz Chodkiewicz obtained the bird data and wrote the supplementary file; Simon Butler provided valuable feedback, reviewed and wrote the manuscript; Lechosław Kuczyński conceived the idea, developed the methodology, designed

the models, analysed the results, wrote the manuscript, obtained funding and supervised the research. All authors gave final approval for publication.

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Conflict of interest

The authors declare no conflict of interests.

Data availability statement

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

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.