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Temporal validation plots: quantifying how well correlative species distribution models predict species' range changes over time

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SUMMARY

1. The use of data documenting how species' distributions have changed over time is crucial for testing how well correlative species distribution models (SDMs) predict species' range changes. So far, however, little attention has been given to developing a reliable methodological framework for using such data.
2. We develop a new tool – the temporal validation (TV) plot – specifically aimed at making use of species' distribution records at two times for a comprehensive assessment of the prediction accuracy of SDMs over time.
3. We extend existing presence-absence calibration plots to make use of distribution records from two time periods. TV plots visualise the agreement between change in modelled probabilities of presence and the probability of observing sites gained or lost between time periods. We then present three measures of prediction accuracy that can be easily calculated from TV plots.
4. We present our methodological framework using a virtual species in a simplified landscape, and then provide a real-world case study using distribution records for two species of breeding birds from two time periods of intensive recording effort across Great Britain.
5. Together with existing approaches, TV plots and their associated measures offer a simple tool for testing of how well SDMs model species' observed range changes – perhaps the best way available to assess their ability to predict likely future changes.

Keywords: species distribution models, temporal validation, prediction accuracy, range change, calibration plots, historic surveys

INTRODUCTION

Correlative species distribution models (SDMs) are increasingly used to project likely future changes in species' distributions under ongoing global environmental change (Elith & Leathwick 2009). As a result, assessing how well these approaches can predict species' geographic range changes over time is of increasing importance.

Repeated surveys that document species' distributions at multiple time periods represent invaluable opportunities for testing SDM predictions over time (Araújo *et al.* 2005a; b; Kharouba *et al.* 2009; Tingley *et al.* 2009; Rubidge *et al.* 2010; Dobrowski *et al.* 2011; Rapacciuolo *et al.* 2012; Smith *et al.* 2013). A growing number of temporal datasets are emerging from efforts to rescue and digitize natural history museum collections and other historical data sources such as field notes and photographs (Tingley & Beissinger 2009; Pyke & Ehrlich 2010; Drew 2011). So far, however, little attention has been given to how these data should best be used for testing the prediction accuracy of SDMs over time. In this paper, we develop a new type of diagnostic plot, the *temporal validation* (TV) plot, and an associated set of measures, which make use of distribution data at two time periods within a given area to evaluate how well SDMs can predict species' range changes over time.

Although tests of SDM predictions through time are still relatively rare, existing studies have primarily tested how well models built using species distribution data from a first time period (i.e., calibration data) discriminate between the species' observed presences and absences in a second time period (i.e., validation data) using common measures based on a single probability threshold (e.g., Cohen's Kappa, sensitivity, specificity; Araújo *et al.* 2005a; Rapacciuolo *et al.*

2012; Smith *et al.* 2013) or a range of possible thresholds (e.g., AUC; Kharouba *et al.* 2009; Rubidge *et al.* 2010; Dobrowski *et al.* 2011; Smith *et al.* 2013). Such tests of SDM predictions through time are generally used to estimate how well models are likely to predict species' range changes in the future (Araújo *et al.* 2005a; b; Kharouba *et al.* 2009; Tingley *et al.* 2009; Rubidge *et al.* 2010; Dobrowski *et al.* 2011; Rapacciuolo *et al.* 2012; Smith *et al.* 2013). In this context, however, this widely-used approach to temporal validation suffers from two main issues.

The first issue is that converting continuous probabilities of presence to binary presence-absence predictions using a single or multiple thresholds may not alone provide an exhaustive estimate of model prediction accuracy over time. The practice ignores a lot of information generated by the models: all predicted probabilities above the chosen threshold are considered equal, as are all those below, however near or far they are from it. As a result, slight but important changes in the environment may not be captured by binary-converted predictions and prediction accuracy measures based on these converted model predictions may wrongly infer range stability despite the probability of presence being predicted to change.

The second issue is that using calibration and validation datasets collected in different time periods across the same region does not enable fully independent model validation. This is because many modelled factors that correlate with a species' distribution across that region will remain unchanged through the entire study period. As a result, models with high explanatory power in one time period are likely to retain that power in another time period across areas where both observations and model predictions indicate no change in the species' range, regardless of whether the models have captured fundamental drivers of range change over time (Araújo *et al.*

2005a; Rapacciuolo *et al.* 2012). Importantly, spurious species-environment correlations identified during model calibration may not be revealed by temporal validation across these unchanged areas. Therefore, measuring prediction accuracy over the entire study area in a second time period – including unchanged areas – may be a misleading measure of how well models are likely to predict to a third time period (e.g., future environmental scenario). This approach should be complemented with measures that focus on how well models predict to areas where species' range changes have actually been observed and/or predicted (Rapacciuolo *et al.* 2012). The issue of examining spatial processes of change with global measures that do not incorporate spatial variation in prediction accuracy within the study region (e.g., Kappa) has been the subject of much scrutiny in the remote-sensing and map comparison literatures (Csillag & Boots 2005; Pontius & Millones 2011; Robertson *et al.* 2014), yet it has been rarely considered in the SDM literature.

TV plots aim to overcome both issues with existing approaches. First, we extend the method of presence-absence calibration plots – originally developed in the context of statistical medicine (Miller *et al.* 1991; Harrell *et al.* 1996; Harrell 2001) but repeatedly used to quantify the calibration of SDMs (Pearce & Ferrier 2000; Boyce *et al.* 2002; Hirzel *et al.* 2006; Phillips & Elith 2010) – for use with empirical distribution and environmental data from two time periods. Presence-absence calibration plots fit observed presence-absence directly as a function of continuous modelled probabilities, without converting to binary predictions based on any threshold (Phillips & Elith 2010). Thus, our method makes full use of the information generated by the modelling process without ignoring the probabilistic nature of SDM predictions. Second, we focus on assessing model performance only on grid cells where either or both observed data and model predictions indicate range change over time, whilst disregarding model performance on grid cells where both observations and predictions indicate no range change. TV plots model how well changes in modelled probability of presence between time periods reflect species' observed gains and losses separately, thus incorporating spatial variation in prediction accuracy within the study area. Building on the existing literature, we then present three measures of the agreement between modelled and observed changes that can be easily calculated from TV plots – Acc$_{\text{TV}}$, Cor$_{\text{TV}}$, and Bias$_{\text{TV}}$. Together with existing approaches to temporal validation, these measures provide a comprehensive assessment of how well a model predicts observed range changes and, thus, the fullest available picture of how likely the model is to predict future changes. We present our methodological framework using a virtual species in a simplified landscape, then provide a real-world case study using distribution records for two breeding bird species from two time periods of intensive recording effort across Great Britain (Sharrock 1976; Gibbons *et al.* 1993).

VIRTUAL CASE STUDY

Simulated environment

We consider an artificial landscape of 30 x 30 grid cells and generate environmental variation within this grid in an initial time period *t* using three 'climate' variables – *temperature*, *precipitation* and *covar* – each taking values in the range 0–1. Temperature and covar both exhibit a linear latitudinal gradient and are highly intercorrelated (Pearson's $r = 0.88$), whilst precipitation exhibits a linear longitudinal gradient (Fig. 1). We then simulate change in the environment in a second time period $t + 1$ by updating the values of the three environmental variables across the landscape. We specify alternative change scenarios for each variable – mean temperature increase, mean precipitation decrease and no change in mean covar – by sampling change values from three different normal distributions (temperature: mean ± standard deviation = 0.3 ± 0.25; precipitation: -0.15 ± 0.5; covar: 0 ± 0.5) and summing sampled values with initial environmental values (Fig. S1).

Environmental functional relationships

We simulate the distribution of a simple virtual species across this landscape by specifying four alternative functional relationships between the species' probability of presence and the environment – a *true* functional relationship and three potential misspecifications of the truth (Fig. 1). This approach, based on simulations by Phillips & Elith (2010) and Pagel & Schurr (2012), enables us to quantify the effects of alternative model misspecifications on how well models predict the species' true distribution over time. First, we specify the true probability of presence for our virtual species conditional on temperature and precipitation only, but not covar, as: 0.5 x temperature + 0.5 x precipitation. Thus, the variable covar does not bear any functional relationship with the species' probability of presence, although it significantly covaries with the species' presence-absence because of its strong correlation with temperature. We then consider three potential models of our virtual species' probability of presence, which we parameterise statistically based on subsets of the three environmental variables (see Fig. 1).

1) The *Incomplete* model estimates probability of presence conditional only on temperature, ignoring precipitation, as: 0.26 + 0.51 x temperature. This model may arise if relevant predictors – in this case precipitation – were unavailable, overlooked, or wrongly excluded during model selection.

2) The *Collinear* model estimates the species' probability of presence conditional on precipitation and covar, ignoring temperature, as: 0.03 + 0.5 x precipitation + 0.5 x covar. This model may arise if irrelevant predictors are naively entered into a model selection algorithm and erroneously selected through their apparent correlation with probability of presence.
3) The *Incomplete and Collinear* model estimates the probability of presence conditional only on covar, ignoring the true predictors temperature and precipitation, as: 0.28 + 0.52 x covar. This model combines both types of misspecification included in the previous two models: it is incomplete, as it only considers a single variable instead of two, and collinear, as it includes a variable correlated but not functionally-related to the species' true probability of presence.

We predict the probability of presence of our virtual species across the landscape in period *t* and *t + 1* based on each of the four environmental functional relationships. To define the true presence-absence of the species across the landscape in both time periods, we convert each grid square's probability of presence to either presence or absence by conducting a Bernoulli trial according to the species' true probability of presence in each grid square.

Temporal validation plots

We extend the approach of presence-absence calibration plots (reviewed by Pearce & Ferrier 2000; Boyce *et al.* 2002; Hirzel *et al.* 2006; Phillips & Elith 2010 in the context of SDMs) to make use of data from two time periods and develop a new plot, the *temporal validation* (TV) plot, for assessing the prediction accuracy of SDMs over time. TV plots show the agreement between changes in observed presence-absence and changes in modelled probability of presence between *t* and *t + 1*. This is done in three steps: (i) calculating observed and modelled changes, (ii) estimating gain and loss functions, and (iii) combining gain and loss functions to visualise the agreement between observed and modelled changes.

Step 1: Calculating observed and modelled changes

First, the species' presence-absence (*y*) across the study area is compared between *t* and *t + 1* to identify observed gains (instances where $y_t = 0$ and $y_{t+1} = 1$), losses ($y_t = 1$ and $y_{t+1} = 0$), stable presences ($y_t = 1$ and $y_{t+1} = 1$), and stable absences ($y_t = 0$ and $y_{t+1} = 0$). Figure 2a shows observed changes in the presence-absence of our virtual species between *t* and *t + 1*. Overall, the species' presence across the landscape has increased: the species has experienced most gains in areas that have become warm enough for the species to expand into and have also remained wet enough for it to occur despite overall decrease in precipitation (i.e., northwest of the landscape). Additionally, there have been localised gains and losses across the entire landscape.

Second, values of change in modelled probability of presence (Δm) are calculated by subtracting modelled probability of presence in *t* (m_t) from modelled probability of presence in *t + 1* (m_{t+1}). Importantly, Δm values are not linearly related to the probability that gains or losses are actually observed, even if we assume that a model has captured perfectly a species' environmental functional relationship. For example, consider two absence sites with different m_t: for an equal increase in modelled probability of presence in *t + 1* ($\Delta m > 0$), the site with a higher m_t will exhibit an inherently higher probability of gain because it already presents a higher probability of finding the species. Similarly, for equal decreases in modelled probability of presence ($\Delta m < 0$), a presence site with a higher initial probability of absence (1 - m_t) has an inherently higher probability of loss. Therefore, weighted, instead of absolute, changes in modelled probability of presence ($\Delta m_{weighted}$) are used in TV plots. $\Delta m_{weighted}$ are calculated by weighting Δm values by m_t, using the following function:

$$\Delta m_{weighted} = f(\Delta m,\ m_t) = \begin{cases} \dfrac{\Delta m}{1 - m_t}, & if\ \Delta m > 0 \\ 0, & if\ \Delta m = 0 \\ \dfrac{\Delta m}{m_t}, & if\ \Delta m < 0 \end{cases} \qquad \text{(eqn 1)}$$

Figure 2b shows the species' weighted changes in modelled probability of presence between *t* and *t + 1*. Most increases are predicted in the west and most decreases are predicted in the northeast of the simulated landscape.

Step 2: Estimating gain and loss functions

Two separate functions – a *gain* and a *loss* function – are fitted to subsets of the values calculated in step 1. Gain and loss functions (blue and red curves of Fig. 2c, respectively) indicate the probability that gains and losses, respectively, are observed for any given value of $\Delta m_{weighted}$ by interpolating from observed instances. Each of these two functions is generated in a manner analogous to the presence-absence calibration plots of Phillips & Elith (2010): binary 1-0 observations are statistically modelled as a function of continuous modelled probabilities using natural splines (Ridgeway 2013). For the gain function, the binary response is calculated by contrasting observed gains (1; the blue tick marks in the top rug plot of Fig. 2c) with observed losses and stable absences (0; the grey tick marks in the top rug plot of Fig. 2c). Notably, stable presences are excluded from the estimation of gain functions since they are uninformative of how well a model predicts *change*: although $\Delta m_{weighted}$ may well increase at these sites, a species cannot gain sites it already occupies. Similarly, for the loss function, the binary response is calculated by contrasting observed losses (1; the red tick marks in the bottom rug plot of Fig. 2c) with gains and stable presences (0; the grey tick marks in the bottom rug plot of Fig. 2c). Stable absences are not used in the estimation of loss functions since a species cannot lose sites from which it is already absent. For both functions, responses are modelled as a function of values of $\Delta m_{weighted}$ at each site corresponding to a response value. In order to aid visualisation, the loss function is multiplied by -1 before being plotted in TV plots, so that it appears in the negative range of the *y*-axis and can be better contrasted to the gain function (Fig. 2c).

Step 3: Combining gain and loss functions to visualise the agreement between observed and modelled changes

A model that perfectly predicts range change through time should predict a probability of gain of 1 and a probability of loss of 0 in areas where there are no losses and all possible gains are made. Similarly, it should predict a probability of gain of 0 and a probability of loss of 1 where no gains are made and every presence is lost. To verify these expectations, gain and loss functions are combined into a temporal validation curve that quantifies how well a model predicts the probability of observing a given overall change in presence-absence between *t* and *t + 1*. For any given $\Delta m_{weighted}$, the temporal validation curve (thick black curve of Fig. 2c) equals the gain function minus the loss function. Note that, because probabilities of loss are plotted with a negative sign in TV plots, the model temporal validation curve is actually the sum, not the difference, of plotted gain and loss functions. Using this approach, an ideal model results in an ideal straight line going from (-1,-1) – where every presence is lost and there are no gains – to (1, 1) – where every empty cell is filled and no cell is lost (dashed line of Fig. 2c). The ideal line also passes through the origin (0, 0) – where probability of observing gains and probability of observing losses are equal. It should be noted that, even for an ideal model, the probabilities of observing gains and losses at (0, 0) are not necessarily zero: some grid cells may be gained or lost due to stochastic population processes, even after accounting for all deterministic environmental processes.

We generate TV plots of the true functional response (Fig. 2c) and the three models (Fig. 2d-f); these visualise the ability of each alternative functional response to model change in the observed distribution of our virtual species between *t* and *t + 1*. The modelled temporal validation curve can be visually compared to the ideal expectation using ± 2 standard error confidence intervals (orange lines of Fig. 2c). Predictions from the true functional response show near-perfect agreement with observed changes in presence-absence: the ideal curve almost entirely falls within the ± 2 standard error confidence intervals of the model curve and the model curve approaches both (-1, -1) and (1, 1) (Fig. 2c). On the other hand, TV plots of all three alternative models of the species' distribution indicate some level of misprediction (Fig. 2d-f). In particular, the *Incomplete and Collinear* model appears to lack any understanding of the species' drivers of range change: gains and losses are observed with comparable frequencies across the entire range of $\Delta m_{weighted}$ (Fig. 2f).

Prediction accuracy measures from TV plots

Visual inspection of TV plots is useful and may be all that is needed for a number of applications, but often repeatable and quantitative measures of predictive accuracy through time are required. This is especially true in studies where many models are used for comparative purposes and visual inspection is impractical (e.g., Araújo *et al.* 2005a; Kharouba *et al.* 2009; Dobrowski *et al.* 2011; Rapacciuolo *et al.* 2012; Smith *et al.* 2013). How can a model's prediction accuracy be calculated from TV plots? In the context of SDMs, a number of measures have been generated from presence-absence calibration plots; however, few of them offer a comprehensive assessment, as they generally either assume linear model curves (e.g. calibration bias and spread; Pearce & Ferrier 2000) or focus on a single aspect of model calibration whilst ignoring others (e.g., point biserial correlation; Phillips & Elith 2010). Here, we build on the work of Harrell (2001), Pearce & Ferrier (2000) and Phillips & Elith (2010), but also the work of Boyce *et al.* (2002) and Hirzel *et al.* (2006), to develop three simple measures of the agreement between the model and the ideal temporal validation curves – Acc_{TV}, Cor_{TV}, and $Bias_{TV}$. Together, these measures offer a comprehensive assessment of how well a model predicts range change through time. Figure 3 provides visual representations of the three measures, exemplified using the TV plot of the Collinear model of our virtual species.

The first measure, temporal validation accuracy ($\mathrm{Acc}_{\mathrm{TV}}$; Fig. 3a), is a measure of the weighted mean distance between the ideal and model temporal validation curves at each observation, subtracted from 1. $\mathrm{Acc}_{\mathrm{TV}}$ can be calculated using the following equation:

$$\mathrm{Acc}_{\mathrm{TV}} = 1 - \frac{\sum_{q=1}^{n} \Delta m_{weighted,q} \left| y_{model,q} - y_{ideal,q} \right|}{\sum_{q=1}^{n} \Delta m_{weighted,q}} \qquad \text{(eqn 2)}$$

where y_{model} and y_{ideal} are the y values of the model curve and ideal curve, respectively, at each observed site q, and $\Delta m_{weighted}$ are the weighted changes in modelled probability of presence at each site q. We use a weighted mean to give more importance to large changes in modelled probability of presence and less importance to minor changes, so as to provide a more rigorous measure of agreement when substantial changes are predicted. Acc$_{\mathrm{TV}}$ ranges from a minimum value of 0 – indicating a model whose predictions are on average as distant as possible from probabilities of observing change – to a maximum value of 1 – indicating a perfectly-predictive model whose weighted changes in modelled probability of presence can be taken at face value.

The second measure, temporal validation correlation (Cor$_{\mathrm{TV}}$; Fig. 3b), is the weighted Pearson's *r* correlation coefficient between y_{model} and y_{ideal} at each observed site q, whereby the weights equal $\Delta m_{weighted,\,q}$. Cor$_{\mathrm{TV}}$ can be calculated using the following equation:

$$\mathrm{Cor_{TV}} = \frac{cov(y_{model}, y_{ideal};\ \Delta m_{weighted,q})}{\sqrt{cov(y_{model}, y_{model};\ \Delta m_{weighted,q})cov(y_{ideal}, y_{ideal};\ \Delta m_{weighted,q})}} \qquad \text{(eqn 3)}$$

where *cov* is the covariance. Our Cor$_{\mathrm{TV}}$ measure is similar to the point biserial correlation (COR; Elith *et al.* 2006; Phillips & Elith 2010), except that it correlates predicted probabilities with continuous probability values fitted using natural splines, instead of observed binary values; for this reason, Cor$_{\mathrm{TV}}$ values are expected to be considerably higher than corresponding COR values.

The third measure, temporal validation bias (Bias$_{\mathrm{TV}}$; Fig. 3c), quantifies the systematic deviation between the ideal and the model curves. Unlike Acc$_{\mathrm{TV}}$ and Cor$_{\mathrm{TV}}$, Bias$_{\mathrm{TV}}$ is not simply calculated at each observed site. Instead, it is estimated over the entire interval between minimum and maximum $\Delta m_{weighted}$ values – respectively $min(\Delta m_{weighted})$ and $max(\Delta m_{weighted})$ – using definite integrals evaluating the area between the *ideal* and *model* functions and the *x*-axis. Bias$_{\mathrm{TV}}$ can be calculated as:

$$Bias_{TV} = \int_{\min(\Delta m_{weighted})}^{\max(\Delta m_{weighted})} ideal(x)dx - \int_{\min(\Delta m_{weighted})}^{\max(\Delta m_{weighted})} model(x)dx \qquad \text{(eqn 4)}$$

A model has a Bias$_{TV}$ of 0 if it perfectly predicts overall change in the probability of observing a species across the entire range of $\Delta m_{weighted}$. A negative Bias$_{TV}$ indicates the model tends to underestimate species' overall presence across the landscape in $t + 1$ by underestimating observed gains and/or overestimating observed losses. A positive Bias$_{TV}$ indicates the model tends to overestimate the species' overall presence in $t + 1$ by overestimating observed gains and/or underestimating observed losses. Importantly, a model may have a Bias$_{TV}$ of 0 despite substantial deviations from the ideal curve at given $\Delta m_{weighted}$ values. This may occur if overestimates and underestimates of gains are balanced by equal overestimates and underestimates of losses, respectively, and overall change in modelled probability averages out to overall probability of observing change in the species' presence.

Table 1 shows how the three measures derived from TV plots vary across the four environmental functional responses of our virtual species. Unsurprisingly, the true environmental functional response has the highest Acc$_{TV}$ and Cor$_{TV}$ – both close to 1 – and the lowest Bias$_{TV}$ – nearly 0. Amongst the three models, the *Incomplete* model appears to be the best, with a similar Cor$_{TV}$ to the Truth but a lower Acc$_{TV}$ and a large negative Bias$_{TV}$, whilst the *Incomplete and Collinear* model is clearly the least able to predict observed change, with a very low Acc$_{TV}$ and negative Cor$_{TV}$ and Bias$_{TV}$ values. The *Collinear* model has intermediate prediction accuracy, with a Cor$_{TV}$ comparable to the *Truth* but a lower Acc$_{TV}$ than the *Incomplete* model.

What aspects of species and their environment affect measures from TV plots?

The calculation of many commonly-used measures of SDM prediction accuracy is affected by the prevalence (i.e., proportion of observed presences) of the modelled species within the study area (McPherson *et al.* 2004; Santika 2011; Lawson *et al.* 2014). In addition, there are indications that the magnitude and extent of environmental change may also affect the assessment of SDM prediction accuracy over time (Fitzpatrick & Hargrove 2009; Elith *et al.* 2010). For these reasons, we carried out a sensitivity analysis to test whether temporal prediction accuracy measures from TV plots are sensitive to various aspects of our virtual species and simplified landscape. We investigated the effect of varying three main factors: species' initial prevalence (i.e., number of presences over total number of grid cells), magnitude of environmental change and spatial extent over which environmental change takes place. For the purposes of this sensitivity analysis, we used the same four functional responses and initial environmental values we used in our main virtual case study (see Fig. 1). However, we simplified our environmental change scenario by sampling values of change from a normal distribution with a mean of 0 and a standard deviation of 0.4 for all three variables, unless otherwise specified. First, given the linear relationship between our species' probability of presence and both temperature and precipitation, we varied the species' initial prevalence across the landscape by progressively increasing initial values of temperature and precipitation, with initial *covar* values varying accordingly (25 alternative scenarios). Second, we varied the magnitude of environmental change between time periods by progressively increasing the standard deviation – from 0.01 to 1 – of the normal distribution from which we sampled values of environmental change, concurrently for all three variables (25 alternative scenarios). Finally, we varied the spatial extent over which environmental change occurred by varying the extent of the grid over which we sampled environmental change – from a 1 x 1 grid to the entire 30 x 30 grid (30 alternative scenarios). We ran 100 repeats of each alternative scenario for each factor and present mean values of prediction accuracy measures across those 100 repeats.

Figure 4 shows the effect of varying species' initial prevalence, magnitude and spatial extent of environmental change on temporal validation for the four alternative functional responses of our virtual species. Overall, the three prediction accuracy measures derived from TV plots were not particularly sensitive to any of the three factors: the four alternative functional responses generally maintained their relative rank and values of each measure remained relatively stable across most alternative environmental scenarios of each factor. However, there were two main noteworthy results. First, all models had higher Acc_{TV} than expected compared to the truth at particularly low magnitudes and extents of environmental change (Fig. 4a, second and third columns), suggesting that the reliability of certain measures from TV plots may increase with the amount of environmental change experienced across the study area. Considering alternative measures such as Cor_{TV} and Bias_{TV}, which were less sensitive to the magnitude and extent of environmental change, appears to be particularly important for a more consistent picture of temporal validation at low magnitudes and extents of change. Second, all three measures were somewhat sensitive to our virtual species' initial prevalence: at low and high extremes of initial prevalence, Bias_{TV} values were positive and negative, respectively, and Acc_{TV} and Cor_{TV} values were slightly lower than expected (Fig. 4a-c, first column). We suspect these results may be partially explained by the lack of ecological realism in our simulations. In fact, identifying cells as observed gains or losses from given increases or decreases in probability of presence within a Bernouilli trial is less likely when initial probabilities of presence are either extremely low (i.e. low prevalence) or extremely high (i.e. high prevalence), respectively. As a result, mismatches between observed and modelled changes in our virtual case study are more likely at extremes of prevalence. Nevertheless, it should be noted that the species' initial prevalence, through its effects on the relative probability of observing gains or losses, may have an effect on measures of prediction accuracy from TV plots when using real data.

REAL DATA CASE STUDY

We tested the method of TV plots using observed distribution records for two species of breeding birds – the Pied Wagtail and the Turtle Dove – across Great Britain in two time periods between the 1960s and the 1990s. For those two species, we asked: (1) Does model fit in one time period indicate prediction accuracy over time? (2) Can measures from TV plots – which focus on instances of range change – identify aspects of prediction accuracy over time not apparent from commonly-used range-wide measures?

Species distribution data

We used distribution records for the Pied Wagtail (*Motacilla alba*) and the Turtle Dove (*Streptopelia turtur*) in 2603 British 10-km grid squares at two time periods (*t*: 1968–1972; *t + 1*: 1988–1991), corresponding to the periods of intensive recording effort leading to the publication of two national atlases of breeding birds (Sharrock 1976; Gibbons *et al.* 1993). Although the absence of these species from each 10-km grid square could not be definitively recorded during sampling, most grid squares in Great Britain were meticulously sampled, with high levels of duplicate recording and under-recorded areas being targeted by extra recording schemes (Sharrock 1976; Gibbons *et al.* 1993). Thus, we assumed that each surveyed grid square in which a species was not recorded (i.e., non-detection) represented a true absence.

Climate predictors

We used six climate variables: mean temperature of the coldest month (°C), mean temperature of the warmest month (°C), ratio of actual to potential evapotranspiration (standard moisture index), potential sunshine (hours), total annual precipitation (mm), and the difference between total winter precipitation and total summer precipitation (mm). These were calculated from monthly values of temperature, precipitation and cloud cover for periods *t* and *t + 1* from the Climate Research Unit ts2.1 (Mitchell & Jones 2005) and the Climate Research Unit 61-90 (New *et al.* 1999) and did not show strong multicollinearity (i.e., all pairwise Spearman's $\rho < 0.85$).

Species distribution models

We modelled the presence-absence of the two bird species in period *t* as a function of climate for the corresponding period using generalised boosted models (GBMs; Ridgeway 1999); we built these using the gbm package (Ridgeway 2013) in R version 2.15.2 (R Core Team 2012), and code provided by Elith *et al.* (2008). We used the species-climate associations identified in period *t* to generate modelled estimates of probability of presence in *t* and *t + 1*, based on observed climate for the corresponding periods.

Measures of model performance

We measured how well SDMs fitted species' distributions in the calibration period *t* using the area under the receiver operating characteristic (ROC) curve (AUC; Hanley & McNeil 1982) and the point biserial correlation (COR; Elith et al. 2006) – defined as the Pearson correlation between model values and binary values of observed presence-absence. We measured how well models predicted change between *t* and *t + 1* using $\mathrm{Acc}_{\mathrm{TV}}$, $\mathrm{Cor}_{\mathrm{TV}}$, and $\mathrm{Bias}_{\mathrm{TV}}$ derived from TV plots. In addition to these, we also quantified how well models discriminated between presences and absences across the entire study area in *t + 1* using AUC and COR.

Results

Climate-based SDMs provided an excellent fit to observed distribution records for both bird species in the calibration period *t* (Pied Wagtail: AUC = 0.992, COR = 0.809; Turtle dove: AUC = 0.976, COR = 0.875). However, these two models showed different patterns of prediction accuracy over time. Discrimination across the species' entire range in period *t + 1* indicated a much higher prediction accuracy for the Turtle Dove model (AUC = 0.924; COR = 0.670) than the Pied Wagtail model (AUC = 0.691; COR = 0.335), suggesting that climate models may accurately explain the distribution over time of the Turtle Dove but not the Pied Wagtail. Furthermore, these results also indicate that model fit within one time period may not necessarily indicate a model's ability to predict change over time. Nonetheless, generating TV plots revealed additional aspects of these models and their predictions that could not be identified through focusing on the species' entire ranges.

The Pied Wagtail has expanded in areas of the Northern coast and Islands of Scotland, as well as a few localised areas of Eastern England in period *t + 1* (Fig. 5a), with gains in many of these areas being modelled accurately by our climate-based SDM (Fig. 5b). As a result, the TV plot for this model indicates a near perfect prediction of the species' gains (i.e., the positive range of the *x*-axis), leading to a very high overall precision and correlation (Fig. 5c). This suggests that expansion of the Pied Wagtail's breeding range in these areas may be linked to climate – particularly to an increase in minimum temperature of the coldest month (data not presented).

These findings are consistent with previous studies indicating that higher spring temperatures advance first egg dates in this species (Mason & Lyczynski 1980; Crick & Sparks 1999), potentially leading to higher clutch size and juvenile survival rates (Mason & Lyczynski 1980). However, the Pied Wagtail has also experienced localised losses in areas of Northern Scotland and Central and Western England (Fig. 5a). These losses do not appear to be linked to climate – or at least the climatic variables we considered – since they were not predicted by our climate-based model, which instead predicted stable or even increasing probability of presence in these areas (Fig. 5b). Losses in the Pied Wagtail may be due to loss of suitable breeding habitat (e.g. reed beds) – a driver which our climate-based model could not have captured.

Contrary to the Pied Wagtail, the Turtle Dove model appears to completely lack any understanding of the factors driving both gains and losses in the species (Fig. 6). Despite an overall increase in climatic suitability (Fig. 6b), the Turtle Dove has experienced many losses along the Northern and Western edges of its range (Fig. 6a). This inconsistency between predictions and observations is reflected in the model's TV plot and measures, which indicate a substantial lack of agreement between the ideal and the model curve (Fig. 6c). Previous studies have indicated that range contraction of the Turtle Dove in Great Britain may be a consequence of agricultural intensification (Fuller *et al.* 1995) and changes in farming practice (Browne *et al.* 2004) – drivers that are missing from our climate-based model.

In summary, our real-data case study shows that model fit in one time period does not necessarily indicate a model's ability to predict change over time. The use of empirical data on observed range changes can be used for a more reliable estimate of a model's prediction accuracy over time. TV plots, which focus on instances of change over time, revealed aspects of the relationship between species' range changes and climate that could not be identified through range-wide measures. Therefore, a comprehensive assessment of prediction accuracy over time should include both measures of model fit across the species' entire range and measures that focus on instances where range changes have been observed and/or predicted. Such an integrated approach should provide a better assessment of how useful models are likely to be in predicting to a third time period (e.g., future scenario).

DISCUSSION

We have developed a new tool that makes full use of species' distribution records at two time periods over the same geographical area to quantify how well SDMs predict range changes over time. Our TV plots and their associated measures overcome the limitations of current approaches by using all the information generated by SDMs and focusing on predictive accuracy across areas where range changes have actually been observed and/or predicted over time. The approach we developed directly relates the redistribution of a species' suitable environment to the probability of observing it expanding or retracting from a given area. As a result, high predictive accuracy from TV plots can only be achieved by models that accurately capture drivers of *change* in species distributions.

Here, we have assumed that temporally-replicated survey data include perfect knowledge of both species' presence and absence across a study area; in reality, this assumption never entirely holds and may potentially affect the results of temporal validation tests. In principle, TV plots could be extended to alternative, more common types of temporal distribution data. Often, temporal distribution datasets only hold information on species' presence. Incorporating these data in TV plots could be done through an approach similar to that used by Phillips & Elith (2010) for presence-only calibration plots: background data (i.e., a random sample of sites in the study area) could be used in place of species' absences and a transformation employed to correct for the distortion in the model's gain and loss curves obtained this way. In some cases, including our real data case study, survey data hold more information than just species' presence: they include a list of surveyed sites in which the species of interest was not detected (i.e., non-detections). This additional information can be used to calculate a probability of false absence (PFA) for each recorded non-detection (Tingley & Beissinger 2009). Examples of statistical approaches for doing so are occupancy modelling (MacKenzie *et al.* 2002, 2011; Altwegg *et al.* 2008), if repeat samples at each site within each longer time period are available, or list-based methods (Roberts *et al.* 2007; Szabo *et al.* 2010), if repeat samples are unavailable. Estimates of PFA could be integrated in TV plots in a number of ways. First, absences could be weighted by their certainty (1 – PFA) within the estimation of gain and loss functions in TV plots. Second, hypothesised true absences could be identified from a Bernouilli trial according to absence certainty. Third, PFA estimates could be integrated directly within the response of TV plots so that the new response is no longer binary (i.e., gain vs no-gain or loss vs no-loss) but continuous, incorporating the probability of observing true gains/losses over time given absence certainty. Extending TV plots for use with presence-only and presence-non-detection data would enable taking full advantage of unsystematic historical data sources – such as natural history museum collections, field notes and photographs – for a more exhaustive and taxonomically-broader temporal validation of SDMs aimed at predicting likely future changes.

Although the three measures we developed in this paper represent an exhaustive summary of the principal information contained in TV plots, many other measures could be derived from these plots. The choice of predictive accuracy measure should depend on the particular application for which SDMs are being built. Additional measures that we can foresee being useful are measures that contrast how well models predict gains (i.e., the positive range of the *x*-axis) versus losses (i.e., the negative range of the *x*-axis). Indeed, species' gains and losses may not necessarily be driven by the same predictors and models may capture drivers of gain but not loss, or vice versa, as shown by our Pied Wagtail example. The variety of prediction accuracy measures that can be derived from TV plots should enable users to assess model performance in a manner that is better suited to their particular question. Nevertheless, different measures derived from the same TV plot are likely to be correlated to some degree; assessing the level of dependence amongst these will be a necessary step to prevent duplication of information.

We suggest that TV plots are a useful tool for assessing how well SDMs predict species' range changes over time, and thus provide R source code and a simple tutorial for their use (see Supporting Information). Our method complements current range-wide approaches to quantify the prediction accuracy of SDMs over time by focusing on instances where range changes have been observed and/or predicted. Taken together, these approaches should enable a much fuller evaluation of how well SDMs predict species' observed range changes, perhaps the best way available to assess their ability to predict the future.

DATA ACCESSIBILITY

The bird distribution data used in these analyses can be accessed via the National Biodiversity Network Gateway (1968–1972 records: https://data.nbn.org.uk/Datasets/GA000600; 1988–1991 records: https://data.nbn.org.uk/Datasets/GA000147), whilst the climate data can be accessed via the Climate Research Unit (http://www.cru.uea.ac.uk/cru/data/hrg/).

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Tables

Table 1: Prediction accuracy measures derived from temporal validation plots of the four environmental functional responses of our virtual species

Prediction accuracy measures			
	Acc$_{TV}$	**Cor$_{TV}$**	**Bias$_{TV}$**
Truth	0.930	0.996	-0.004
Incomplete	0.789	0.976	0.213
Collinear	0.603	0.993	-0.424
Incomplete and Collinear	0.424	-0.187	-0.271

Figures

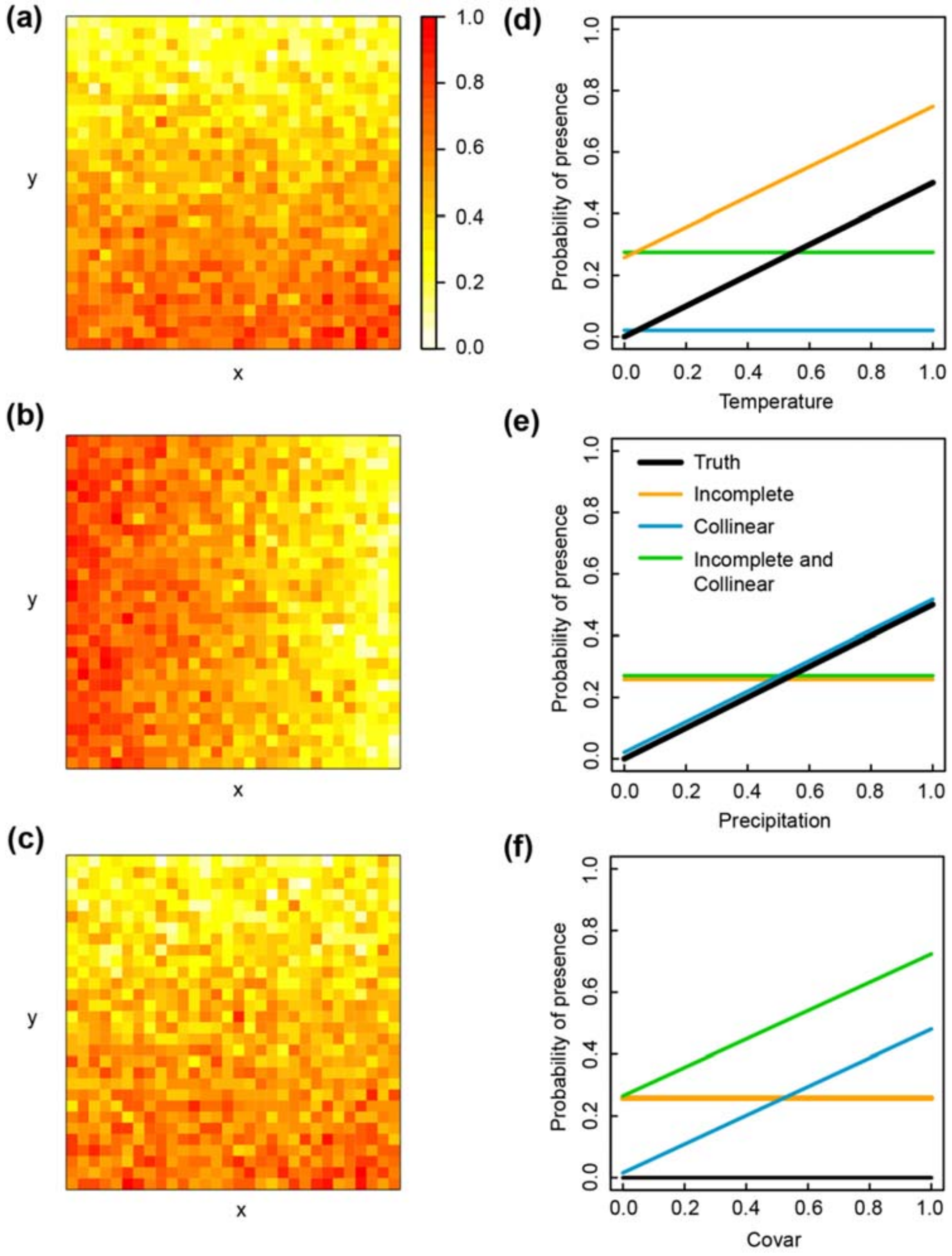
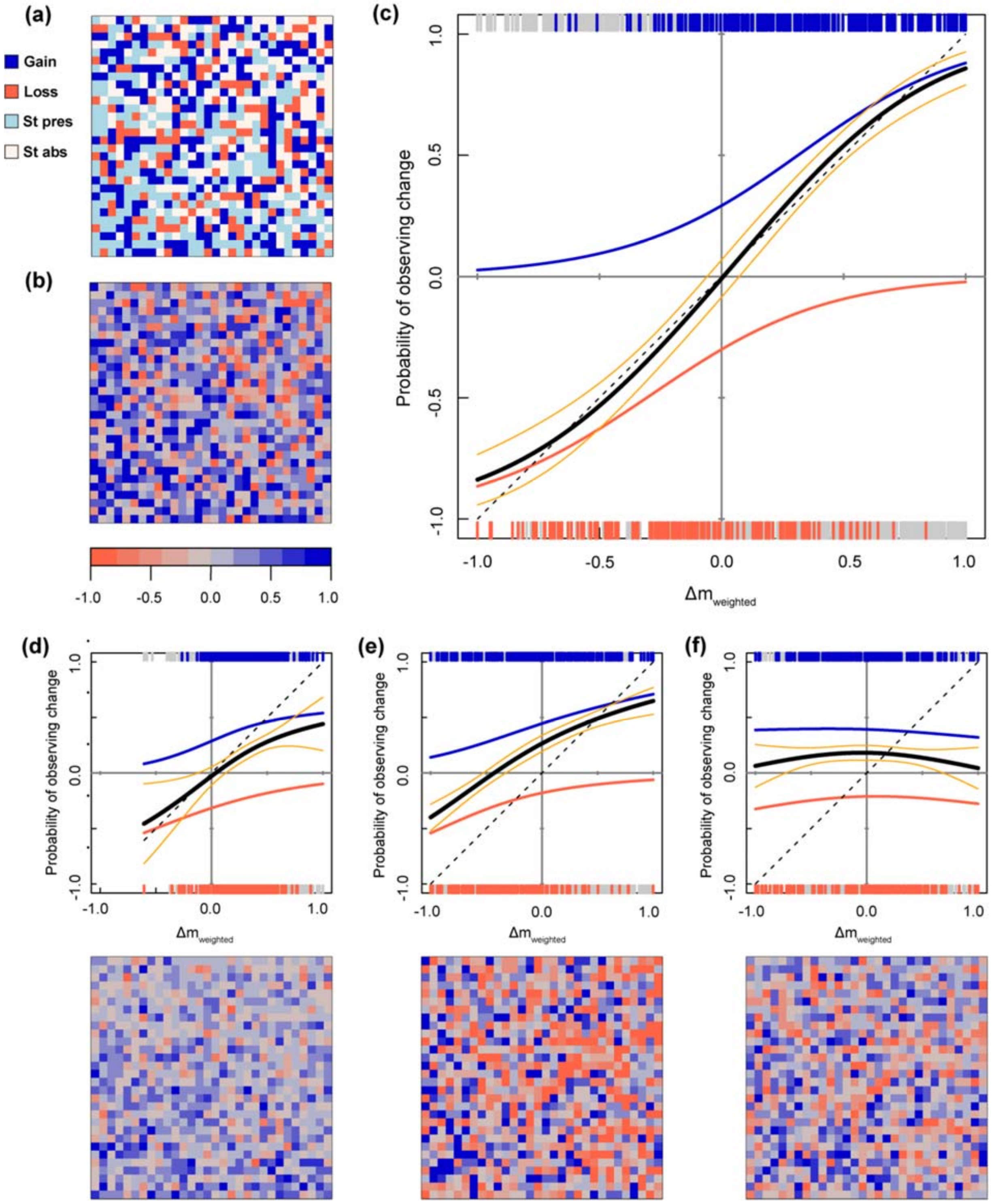


Fig. 1

Figure 1: Four alternative environmental functional responses of a virtual species to three simulated variables over a simplified landscape of 30 x 30 grid cells. Right panels show

simulated values for (a) temperature, (b) precipitation, (c) covar across the simplified landscape; hotter colours indicate higher values (see figure legend). Right panels show how probability of presence varies with (d) temperature, (e) precipitation, (f) covar (whilst keeping all other variables constant at 0) according to each functional response – the Truth (thick black), the Incomplete model (orange), the Collinear model (blue), and the Incomplete and Collinear model (green).



(a)
Gain
Loss
St pres
St abs
(b)
-1.0
-0.5
0.0
0.5
1.0
(c)
Probability of observing change
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
$\Delta m_{weighted}$
(d)
(e)
(f)
Probability of observing change
1.0
0.0
-1.0
-1.0
0.0
1.0
$\Delta m_{weighted}$

726

727 **Fig. 2**

Figure 2: Quantifying the agreement between observed distribution changes and weighted changes in modelled probabilities of presence ($\Delta m_{weighted}$) between time periods *t* and *t + 1* for the four functional responses of our virtual species using TV plots. (a) Observed distributional changes in simulated space of our virtual species (gains, losses, stable presences and stable absences) between time periods. (b) $\Delta m_{weighted}$ values across the landscape according to the true functional response of our virtual species. Bluer and redder colours indicate increases and decreases in probability of presence, respectively. (c) TV plot for the true functional response of our virtual species. Shown are the model temporal validation curve (thick black) – the sum of the plotted gain function (blue curve) and loss function (red curve) – and confidence intervals of ± 2 standard errors of the mean (orange). The dashed black line represents the expectation for an ideal temporal validation curve. The rug plots show model values at observed gain sites (blue, top of the plot), loss sites (red, bottom of the plot) and stable absences/losses (grey, top of the plot) and stable presences/gains (grey, bottom of the plot). (d-f) TV plots (top panels) and $\Delta m_{weighted}$ (bottom panels) for (d) the Incomplete model, (e) the Collinear model, and (f) the Incomplete and Collinear model.

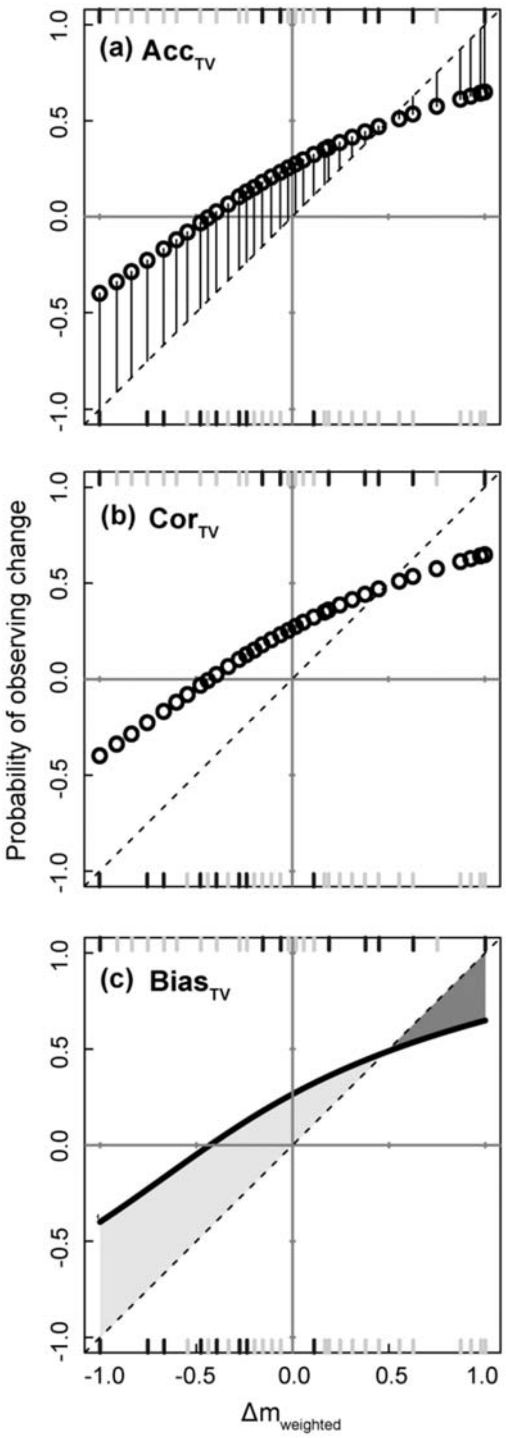

(a) Acc$_{TV}$
(b) Cor$_{TV}$
(c) Bias$_{TV}$
Probability of observing change
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
Δm$_{weighted}$

Fig. 3

Figure 3: Visualisations of the three measures of prediction accuracy from TV plots (Acc$_{\text{TV}}$, Cor$_{\text{TV}}$ and Bias$_{\text{TV}}$), exemplified using the TV plot for the Collinear model. (a) Acc$_{\text{TV}}$ equals 1 minus the mean absolute distance between the model's and the ideal *y* values (black lines), weighted by the corresponding *x* values, at each observed site (tick marks). (b) Cor$_{\text{TV}}$ is the Pearson's *r* coefficient between the model's and the ideal *y* values, weighted by the corresponding *x* values, at each observed site (tick marks). (c) Bias$_{\text{TV}}$ is the difference between the area under the model curve (thick black) and the area under the ideal curve (dashed black); it is equivalent to the dark grey minus the light grey area. Note that observed sites shown in scatter and rug plots have been subsampled to aid visualisation.

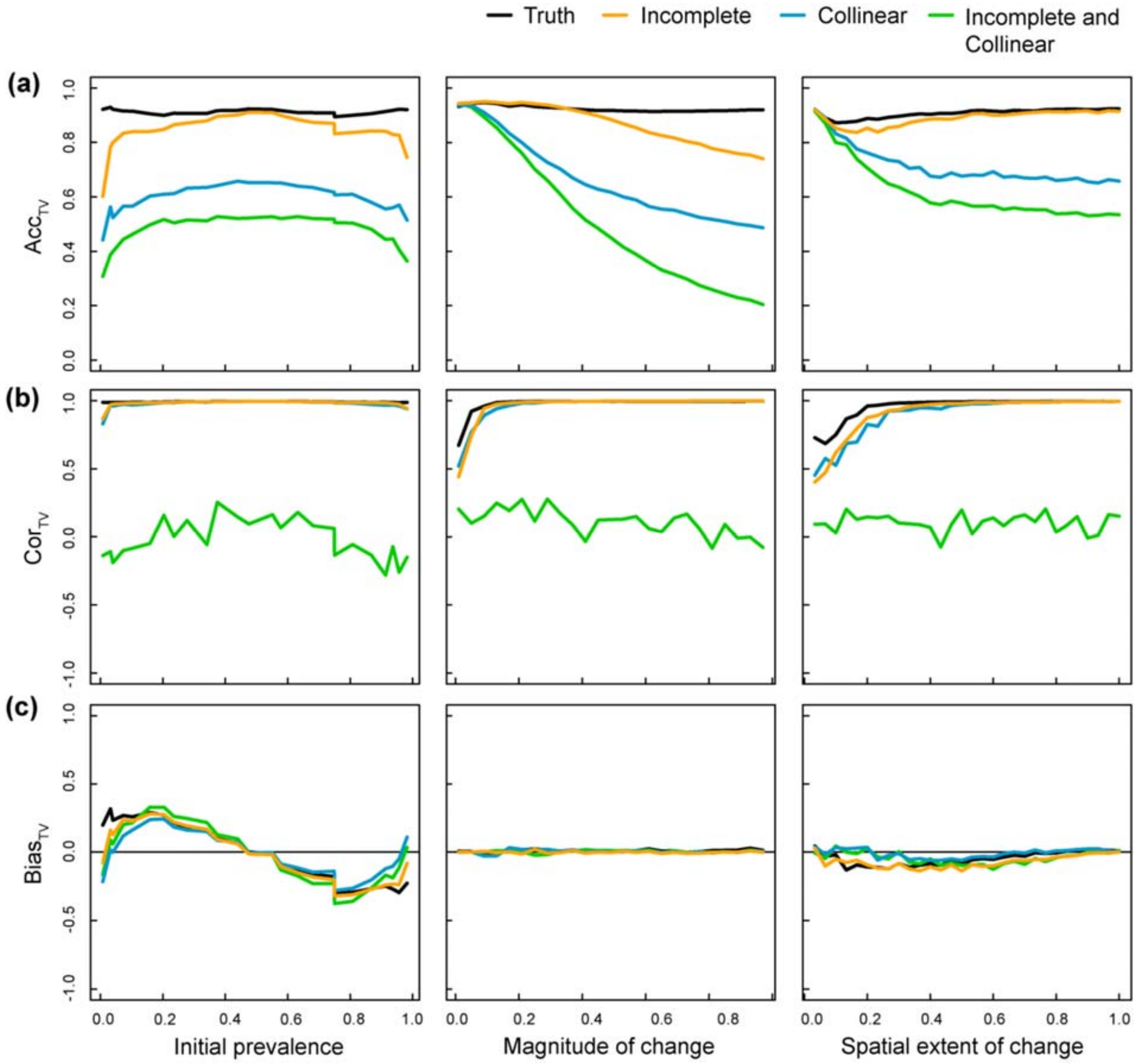

Truth
Incomplete
Collinear
Incomplete and Collinear
(a)
(b)
(c)
Acc$_{TV}$
Cor$_{TV}$
Bias$_{TV}$
0.0
0.2
0.4
0.6
0.8
1.0
-1.0
-0.5
0.0
0.5
1.0
Initial prevalence
Magnitude of change
Spatial extent of change

Fig.4

Figure 4: Sensitivity analysis of the effect of species' initial prevalence, magnitude and spatial extent of environmental change on (a) Acc_{TV}, (b) Cor_{TV}, and (c) Bias_{TV} measured from TV plots of the four functional responses of our virtual species. Initial prevalence is the number of species' presences in *t* divided by the total number of grid cells (n = 25). Magnitude of environmental change corresponds to the standard deviation of the normal distribution from which we sampled environmental change values (n = 25). Spatial extent of change is the number of grid cells over which we sampled environmental change divided by the total number of grid cells (n =30). For each measure, values shown represent the mean values of 100 randomisations of each alternative environmental scenario.

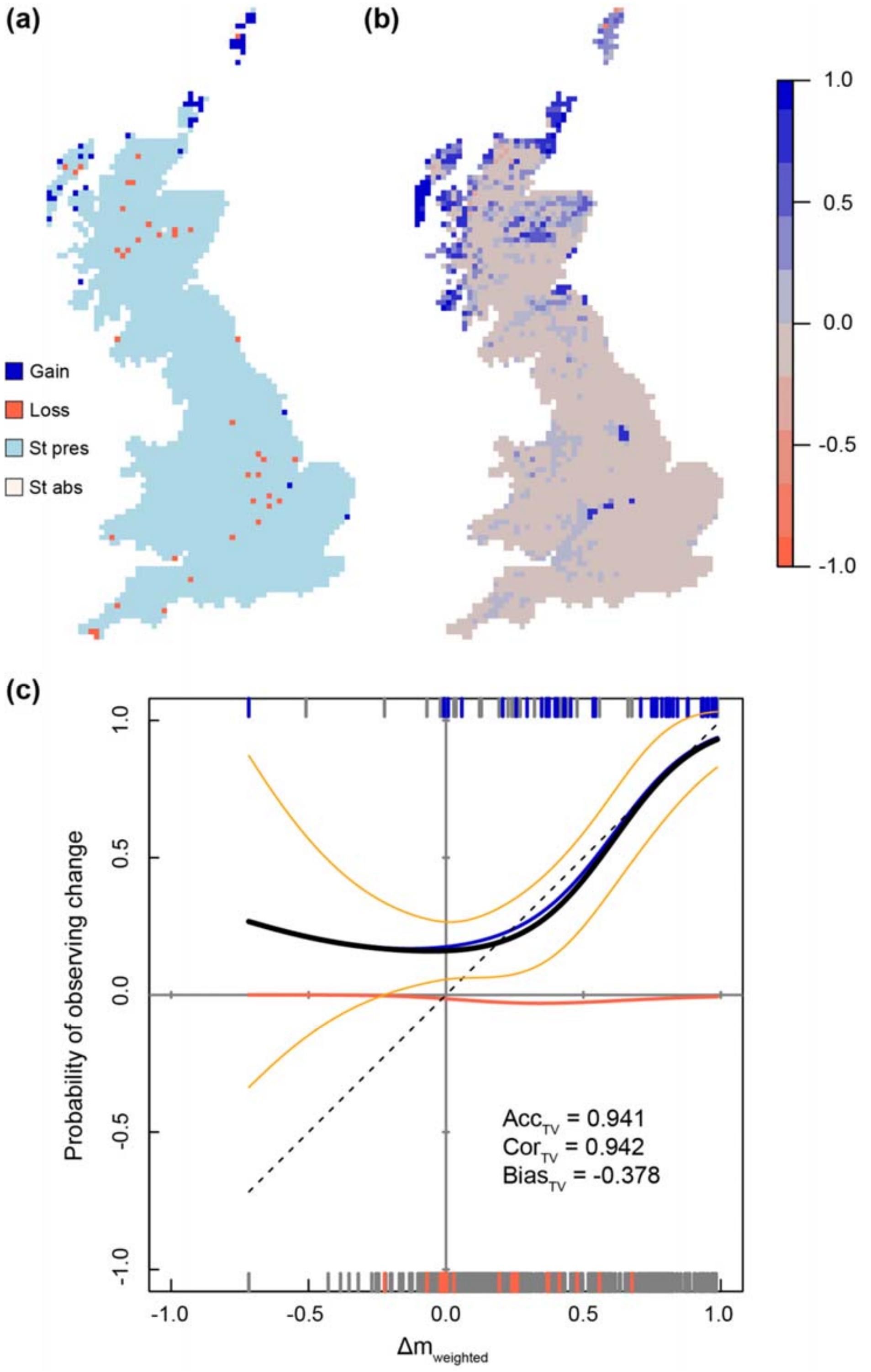

(a)
(b)
Gain
Loss
St pres
St abs
1.0
0.5
0.0
-0.5
-1.0
(c)
Probability of observing change
1.0
0.5
0.0
-0.5
-1.0
Acc$_{TV}$ = 0.941
Cor$_{TV}$ = 0.942
Bias$_{TV}$ = -0.378
-1.0
-0.5
0.0
0.5
1.0
Δm$_{weighted}$

Fig. 5

Figure 5: Temporal validation of a climate-based species distribution model of the Pied Wagtail across Great Britain between *t* and *t +1*. (a) Observed changes in the distribution of the Pied Wagtail between time periods. (b) Weighted changes in modelled probability of presence ($\Delta m_{weighted}$) from a climate-based SDM. Bluer and redder colours indicate increases and decreases in probability of presence, respectively. (c) TV plot of the climate-based SDM. Shown are the model temporal validation curve (thick black) – the sum of the plotted gain function (blue curve) and loss function (red curve) – and confidence intervals of ± 2 standard errors of the mean (orange). The dashed black line represents the expectation for an ideal temporal validation curve. The rug plots show model values at observed gain sites (blue, top of the plot), loss sites (red, bottom of the plot) and no-gain and no-loss sites (grey, top and bottom of the plot).

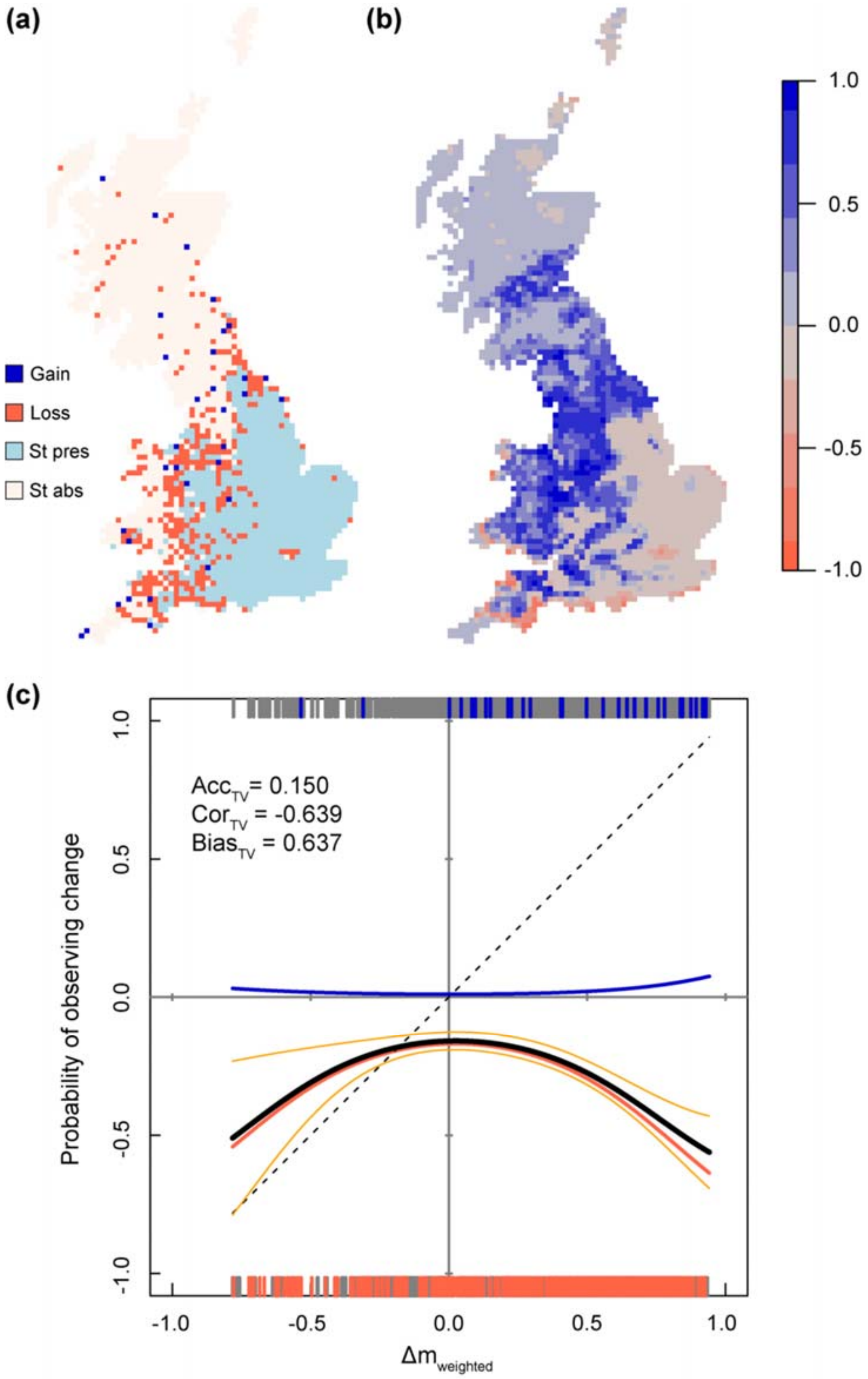

(a)
(b)
Gain
Loss
St pres
St abs
1.0
0.5
0.0
-0.5
-1.0
(c)
Acc$_{TV}$= 0.150
Cor$_{TV}$ = -0.639
Bias$_{TV}$ = 0.637
Probability of observing change
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
Δm$_{weighted}$

Fig. 6

Figure 6: Temporal validation of a climate-based species distribution model of the Turtle Dove across Great Britain between *t* and *t +1*. (a) Observed changes in the distribution of the Turtle Dove between time periods. (b) $\Delta m_{weighted}$ from a climate-based SDM. Bluer and redder colours indicate increases and decreases in probability of presence, respectively. (c) TV plot of the climate-based SDM. Shown are the model temporal validation curve (thick black) – the sum of the plotted gain function (blue curve) and loss function (red curve) – and confidence intervals of ± 2 standard errors of the mean (orange). The dashed black line represents the expectation for an ideal temporal validation curve. The rug plots show model values at observed gain sites (blue, top of the plot), loss sites (red, bottom of the plot) and no-gain and no-loss sites (grey, top and bottom of the plot).