

# Habitat suitability models based on opportunistic citizen science data: Evaluating forecasts from alternative methods versus an individual-based model

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## Funding information

Norges Forskningsråd, Grant/Award Number: 295767; Svenska Forskningsrådet Formas, Grant/Award Number: 2016-00557 and 2016-01949; Universität Zürich; Vetenskapsrådet; Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 31BD30\_172465, PP00P3\_150752 and PPOOP3\_123520

Editor: Juliano Sarmento Cabral

## Abstract

**Aim:** To evaluate the utility of opportunistic data from citizen science programmes for forecasting species distributions against forecasts with a model of individual-based population dynamics.

**Location:** Sweden.

**Methods:** We evaluated whether alternative methods for building habitat suitability models (HSMs) based on opportunistic data from citizen science programmes produced forecasts that were consistent with forecasts from two benchmark models: (1) a HSM based on data from systematic monitoring and (2) an individual-based model for spatially explicit population dynamics based on empirical demographic and movement data. We forecasted population numbers and habitat suitability for three realistic, future forest landscapes for a forest bird, the Siberian jay (*Perisoreus infaustus*). We ranked simulated forest landscapes with respect to their benefits to Siberian jays for each modelling method and compared the agreement of the rankings among methods.

**Results:** Forecasts based on our two benchmark models were consistent with each other and with expectations based on the species' ecology. Forecasts from logistic regression models based on opportunistic data were consistent with the benchmark models if species detections were combined with high-quality inferred absences derived via retrospective interviews with experienced "super-reporters." In contrast, forecasts with three other widely used methods were inconsistent with the benchmark models, sometimes with misleading rankings of future scenarios.

**Main conclusions:** Our critical evaluation of alternative HSMs against a spatially explicit IBM demonstrates that information on species absences critically improves forecasts of species distributions using opportunistic data from citizen science programmes. Moreover, high-quality information on species absences can be retrospectively inferred from surveys of the consistency of reporting of individual species and

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the identification skills of participating reporters. We recommend that citizen science projects incorporate procedures to evaluate reporting behaviour. Inferred absences may be especially useful for improving forecasts for species and regions poorly covered by systematic monitoring schemes.

#### KEYWORDS

citizen science, forecast, habitat suitability, individual-based model, inferred absence, opportunistically collected, presence-only, Siberian jay

## 1 | INTRODUCTION

Climate change, habitat loss and other global environmental changes have had detrimental effects on biodiversity and led to an increased interest in anticipating future changes in species' distributions and abundances (Mouquet et al., 2015). Forecasts can facilitate a better understanding of future effects of environmental changes on biodiversity, or of the potential value of alternative management interventions. Opportunistic data from citizen science programmes are a rapidly growing and valuable source of information for modelling organismal responses (Amano et al., 2016). A recent policy direction paper argued for the need of applying adequate modelling frameworks to opportunistic data that account for biases in the raw data to improve how opportunistic data are used in order to better support ecological impact assessments (Baker et al., 2021). Opportunistic data may be similarly important in forecasts, but assessments of their utility for making forecasts and guidelines for modelling are an emerging field.

Process-based models, such as *individual-based models* (IBMs), explicitly account for demographic processes, such as survival, reproduction and dispersal (Guisan & Zimmermann, 2000; Singer et al., 2016). Patterns of species distributions and abundances emerge from the underlying processes, which are influenced by environmental variation (Grimm et al., 2006). Despite the power of process-based models for modelling species dynamics, their use has been relatively limited because the comprehensive ecological knowledge and population data needed to parameterize ecological processes are only available for few well-studied species (Urban et al., 2016).

*Habitat suitability models* (HSM), also known as species distribution or niche models, can be constructed from more widely available occurrence data (Franklin, 2009). HSMs are pattern-based and establish relationships between the occurrence of a species versus environmental conditions at sampling locations. Species–habitat relationships can then be used to predict the current or future occurrence of the species at unsurveyed locations. However, HSMs are based on the assumption that species are in equilibrium with their environment, which may be unrealistic especially in landscapes with large, recent anthropogenic or natural disturbances. If the assumption of equilibrium is violated or if HSMs do not appropriately capture the underlying ecological processes, misleading predictions for other areas or forecasts for future times (extrapolation) may be the result (Elith et al., 2010; Urban et al., 2016).

IBMs and other process-based models require more data but improve upon HSMs because they relax the assumption that species are at equilibrium with their environment and may better represent ecological processes (Urban et al., 2016). Thus, forecasts from dynamic process-based models are expected to be more accurate than with HSMs (Zurell et al., 2016). One challenge for extrapolation with both pattern and process-based models is that environmental space in new locations or times may not be adequately represented in the sample data (Bahn & McGill, 2013; Dormann et al., 2012; Elith et al., 2010). A second challenge is that species adaptations and interspecific interactions (such as competition and predation) are often not considered or may change during the extrapolation period (Dormann, 2007; Urban et al., 2016; Zurell, 2017). Importantly, Mouquet et al. (2015) argue that the purpose of “anticipatory” forecasts is to guide present action and that they do not need to accurately forecast the future to be useful.

Different sources of data can be used to parameterize habitat suitability models, including systematic and opportunistic data. Systematic monitoring data, such as the Swedish Bird Survey (SBS, [www.fageltaxering.lu.se](http://www.fageltaxering.lu.se)), are a common source for developing HSMs. Unfortunately, in many countries, systematic monitoring programmes do not exist (Isaac et al., 2014). Even if systematic sampling is available, fewer observations may be recorded for species that are rare, active outside the main survey periods or restricted to localized habitats (Snäll et al., 2011).

Alternatively, species observations opportunistically collected by citizen scientists are a rapidly growing source of new data (Amano et al., 2016). One example is eBird (<https://ebird.org>), a global database for bird observations currently receiving over 100 million records per year. Citizen scientists also contribute to the Global Biodiversity Information Facility ([www.gbif.org](http://www.gbif.org), >1.8 billion records), and national databases, such as the Swedish Species Observation System (SSOS, [www.artportalen.se](http://www.artportalen.se), >85 million records). Citizen scientists are often particularly interested in the rare species that are less well represented in systematic monitoring programmes and thus opportunistic observations can potentially fill current data gaps (Bradter et al., 2018; Isaac et al., 2014; Snäll et al., 2011).

Despite their potential advantages, models based on opportunistic data need to overcome a number of specific challenges. In contrast to systematic surveys, reporters choose where, when and for how long to look for species, if and how to report measures of survey effort, and which of their species observations to report. Observers

may also range in experience from novices to expert naturalists. Such variation in survey and reporting effort can lead to temporal and spatial biases in occurrence and abundance records (Isaac et al., 2014). Some platforms, such as eBird, encourage the submission of “complete lists,” where reporters specify that they report all bird species found. Species that were not reported then imply non-detections. Without protocols based on complete lists, natural history records are detection-only data (frequently called presence-only) because reporters may selectively report only a subset of their observations, for example a subset of species. Thus, detection-only data are often analysed by pairing them with locations without records of a species or with a sample of locations in the study area (pseudo-absences or background, Phillips et al., 2009). Pseudo-absences or background data represent habitats that can be occupied or unoccupied, and this approach can lead to predicted species distributions that are less accurate compared to distributions based on high-quality non-detection data (Bradter et al., 2018; Johnston et al., 2021). Nevertheless, detection-only data are widespread in many platforms such as GBIF, and SSOS until 2018, and are often the only information available for many study systems. Thus, it is critical to find and test solutions for the use of opportunistic detection-only citizen science data to develop improved forecasts.

One possible solution to the problem of incomplete lists can be to obtain non-detections retrospectively using “partial lists,” at least for uncommon or charismatic species (Bradter et al., 2018; Henckel et al., 2020; Mair et al., 2017). Many highly engaged reporters (“super-reporters,” henceforth) consistently report all records of unusual species. For each candidate species, super-reporters can be asked if they always report the species if found, if they can identify the species, including by sound if the species is vocal, and if their skills and reporting decisions have been consistent since they started reporting. Non-detections (“inferred absences” henceforth) can then be inferred for locations where these reporters have reported other species, but not the focal species (Bradter et al., 2018; Henckel et al., 2020; Mair et al., 2017). Using absences from partial or complete lists, current bird species distributions have been predicted well with opportunistic, albeit spatially biased, data (Bradter et al., 2018; Henckel et al., 2020; Johnston et al., 2020).

The challenges of modelling opportunistic data have been addressed by several alternative methods. *MaxEnt* was developed specifically for detection-only data and has been a widely used software tool (Phillips et al., 2006). *Logistic regression* is more robust to sample selection (spatial and temporal) bias than other methods (Zadrozny, 2004) but requires detection and non-detection data. *Point process models* integrate opportunistic and systematic data, and explicitly model a possible sample selection bias (Fithian et al., 2015). In contrast to the previous three methods, *occupancy models* use repeated sampling to account for imperfect detection of species (MacKenzie et al., 2003) and can reduce problems due to uneven survey effort in opportunistic data (Johnston et al., 2021; Kéry et al., 2010). In our previous work, we established that these four methods with models based on opportunistic data could successfully produce species distributions that were similar to results

from systematic monitoring data (Bradter et al., 2018). However, distributions were most similar using logistic regressions with inferred absences, especially at more local scales. Our previous analysis demonstrated the usefulness of opportunistic data for predicting current distributions of species.

Importantly, the ability of models to produce reliable forecasts needs to be assessed even if they reliably predict current species distributions, because models that predict well for the current periods and locations may fail when the model is used to extrapolate to future times or new areas (Bahn & McGill, 2013; Dormann, 2007; Randin et al., 2006). Independent data to validate the reliability of models for forecasting or hindcasting are rarely available. Alternatively, forecasts can be assessed against forecasts from independent models that explicitly address the temporal aspect, and preferably also the spatial aspect, to increase confidence in their reliability. Of particular value are thus validations against forecasts from dynamic, spatially explicit population models, which are assumed to be more realistic because they are based on demographic processes and do not rely on the equilibrium assumption, which can be unrealistic, particularly over time (Zurell et al., 2016). However, such validations are only rarely possible due to the scarcity of the comprehensive data on demography or population dynamics needed to parameterize these models.

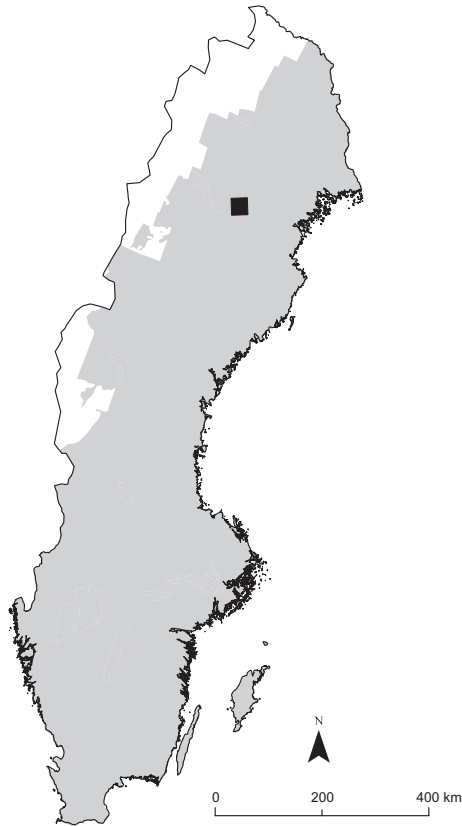
The aim of our current study was to test whether models based on opportunistic data and four different HSM methods (MaxEnt, logistic regression, occupancy and point process model) could produce forecasts that would rank benefits of different forest management scenarios in the same order as independent forecasts from two benchmark models: (1) a dynamic, spatially explicit IBM based on demographic data, and (2) a HSM based on systematic monitoring data. The dynamic, spatially explicit IBM therefore served as a benchmark model for all pattern-based HSMs, including the HSM developed with systematic data.

We chose the Siberian jay (*Perisoreus infaustus*), a group-living forest specialist as our study system, because (1) the availability of long-term, large-extent life-history data and detailed knowledge of the species ecology allowed us to develop a dynamic, spatially explicit demographic model, and (2) absences can be inferred via partial lists from citizen science data because several super-reporters were motivated to consistently report jays as an uncommon and charismatic species.

## 2 | METHODS

### 2.1 | Overview

We used life-history data from a long-term population study of Siberian jays at a field site in the boreal forest near Arvidsjaur, northern Sweden (Figure 1). The study population has been followed from 1989 onwards, and the monitoring area is currently 74 km<sup>2</sup>. Using the long-term demographic data, we developed and parameterized a new IBM with 13 sub-models that capture different life-history



**FIGURE 1** Location of the study areas within Sweden (solid black line): HSMs were created for the area covered by remotely sensed forest data (grey area). Empirical life-history data were collected in a long-term study population in the boreal forest of northern Sweden (black square), 2000–2017

processes. In previous work, Bradter et al. (2018) developed HSMs (detailed below) for Siberian jays in Sweden (Figure 1) with opportunistic data, and also a benchmark HSM with systematic data from the Swedish Bird Survey. Here, we projected the distribution of Siberian jays with the IBM and all HSMs in a virtual, realistic forest landscape (1,033 km<sup>2</sup>), for which 105 years of forest growth and management had previously been simulated by Eggers et al. (2020; see their Figure 1) according to management preferences of stakeholders. All analyses, including the coding of the IBM, were conducted in R (R Core Team, 2020).

## 2.2 | Life-history data

Siberian jays are sedentary forest birds, which live in stable groups consisting of a breeding pair and up to five non-breeders. Juveniles in the group are either offspring that delayed dispersal (retained juveniles) or unrelated individuals that immigrated from another group (dispersed juveniles) (Ekman et al., 2001; Griesser et al., 2008). Long-term data on survival, reproductive success and group composition were available for an 18-year period from 2000–2017 (5,535 sightings of 1,388 Siberian jays in 75 groups with 812 reproductive outcomes). The life-history models were fitted using these data (“empirical life-history

data” henceforth). The study population is located in two areas, one in managed forests and one in near-pristine forests (Griesser et al., 2014). All groups were visited twice a year in March and September to record all individuals and to uniquely mark any unringed group members (Layton-Matthews et al., 2018). The age (juvenile or older) was established at ringing via the shape of the outermost tail feathers (Griesser et al., 2014). Kinship (retained or dispersed juvenile) was established by locating nests and ringing nestlings, assessed with molecular methods (Griesser et al., 2015), or by assessing social interactions between breeders and non-breeders on feeders (Griesser et al., 2014). Reproductive success was recorded in September as the number of retained juveniles per group (Layton-Matthews et al., 2018).

## 2.3 | Environmental data

Environmental covariates were based on existing knowledge of the species ecology and divided into three categories (Appendix S1): Forest, Climate and Biotic (Table 1; Appendix S2).

*Forest covariates* were calculated from the nationwide forest raster data in Sweden (25 m resolution), available at 5-year intervals (2000, 2005 and 2010). The raster data are based on Landsat imagery and field measurements from the repeat National Forest Inventory (Reese et al., 2003). Forest harvest in Sweden is predominantly via clear-cutting, and the rasters were corrected for yearly clear-cuts using field observations and the Global Forest Change v1.5 dataset (Hansen et al., 2013). Mature forest was characterized using total forest age and volume. We expected that forest age is a good indicator for resources such as arboreal lichen, in which Siberian jays cache food (Cramp & Perrins, 1994). Alternatively, forest volume is a direct indicator of dense forest, which may visually shield nests from predators (Griesser & Lagerberg, 2012; Pukkala et al., 2012). *Forest covariates* (Table 1) were calculated as the mean or percentage value within squares (covariate units henceforth) centred on the average nest location per territory.

Siberian jays are affected by environmental variation within the territory. Thus, we used covariate units of 1 × 1 km to approximate territory sizes of our empirical live-history population (Nystrand et al., 2010). For models of recruitment, we additionally evaluated smaller covariate units of 0.3 and 0.66 km<sup>2</sup>, which capture much of the core habitat used during the breeding season (Griesser & Lagerberg, 2012; Nystrand et al., 2010).

In the social system of Siberian jays, vacant breeding positions are usually filled by non-breeders from the same or a neighbouring territory (Griesser et al., 2008). Thus, vacant breeder positions surrounded by neighbours may be more likely to be occupied. We quantified the age of mature forest patches as an index of suitable nesting habitat within 10 × 10 km moving windows as a proxy for the presence of occupied territories in the neighbourhood (Table 1).

*Climate covariates* were calculated from monthly mean temperature and precipitation sum and daily minimum temperatures obtained for the three weather stations nearest the empirical

**TABLE 1** Environmental covariates tested in life-history models of Siberian jay

| Category | Description  | Unit               | Abbreviation         |
|----------|--|--------------------|----------------------|
| Forest   | <b>Percentage mature forest (<math>\geq 50</math> years &amp; <math>\geq 100</math> m<sup>3</sup>/ha)</b>                          | %                  | <b>PercMature</b>    |
|          | Mean forest age  | years              | MeanAge              |
|          | Mean forest volume   | m <sup>3</sup> /ha | MeanVol              |
|          | <b>Mean age of patches (<math>\geq 50</math> years &amp; <math>\geq 100</math> m<sup>3</sup>/ha &amp; <math>&gt; 30</math> ha)</b> | years              | <b>Neighbourhood</b> |
|          | Percentage spruce volume of total volume   | %                  | PercSpruce           |
|          | Percentage pine volume of total volume   | %                  | PercPine             |
| Climate  | <b>Winter temperature (January–February)</b>   | °C                 | <b>WinterTemp</b>    |
|          | Winter precipitation (January–February)  | mm                 | WinterPrec           |
|          | <b>Spring temperature (April–May)</b>  | °C                 | <b>SpringTemp</b>    |
|          | Spring precipitation (April–May)   | mm                 | SpringPrec           |
|          | Number of days above freezing (October–March)  | days               | PlusDays             |
| Biotic   | Territory group size   | Individuals        | GrSizeTerr           |
|          | Siberian jay density   | Individuals        | PopDens              |
|          | Number of breeders remaining from one time step to the next  | Individuals        | BreedsRemain         |

Note: For details of calculations and data sources, see Appendix S2. Covariates in **bold** were previously included in the HSMs (Bradter et al., 2018).

life-history population. As *biotic covariates*, we quantified Siberian jay density at both the territory and  $10 \times 10$  km scale to evaluate density-dependent effects on demographic parameters within and among groups, as previously reported by Layton-Matthews et al. (2018). For full details on the calculation of covariates, see Appendix S2.

## 2.4 | Individual-based model

We present a new individual-based model that integrated our long-term demographic data for Siberian jays with variation in environmental conditions by estimating response functions relating variation in environmental conditions with demographic processes determining population size, such as births, deaths, emigration and immigration (Schurr et al., 2012). An alternative to our models would be to mechanistically model fitness components, such as survival or reproduction as physiological processes interacting with environmental conditions, such as energy balance interacting with environmental conditions (Kearney & Porter, 2009). However, data to produce the required eco-physiological equations are not available for Siberian jay. Here, we give a brief overview of our IBM. A complete description of the model protocol is provided in Appendix S3.

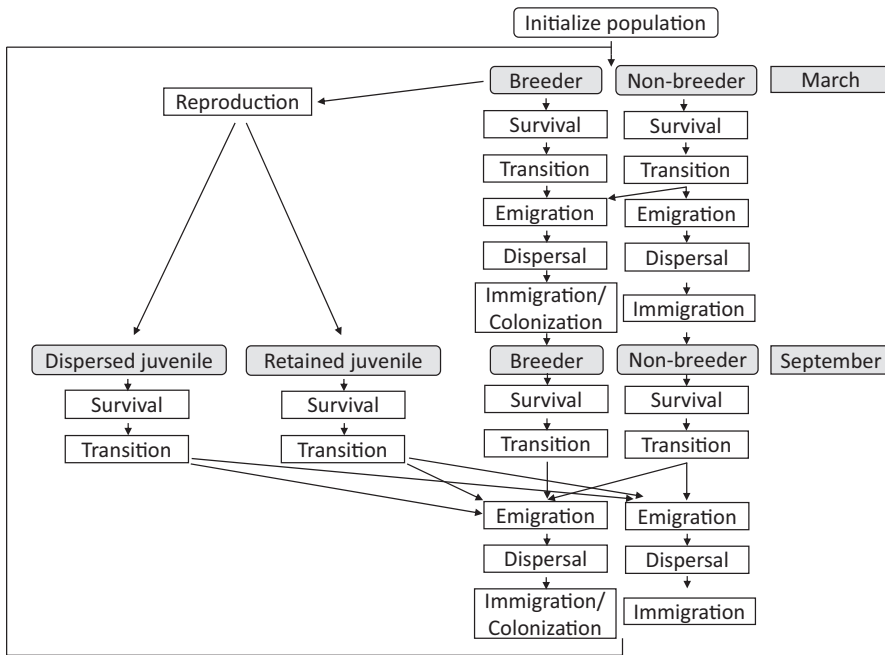
The IBM modelled the six-stage life cycle of individuals (Figure 2; Layton-Matthews et al., 2018): summer breeders, summer non-breeders, winter breeders, winter non-breeders, retained and dispersed juveniles. Individuals occurred in groups of different sizes and lived in a gridded forest landscape. Grid cells had the assigned

features centroid coordinate, climate covariates and the forest covariates from the management scenarios (Table 1).

Projections proceeded in six-month time steps (summer, winter). The following processes were executed for each individual and at each time step in this order: reproduction (summer breeders only), survival, stage-to-stage transition, emigration (decision to leave a cell), dispersal (movement between cells), immigration (at cells occupied by an existing group) or colonization (of unoccupied cells). Environmental conditions affected the processes (Table 2), and the number of individuals per stage and per cell emerged from the IBM. The four processes of reproduction, survival, stage-to-stage transition and emigration were based on empirical sub-models parameterized with our long-term demographic data. Despite the availability of a large and long-term dataset, data on dispersal, immigration and colonization were limited. The movement processes were based on sub-models parameterized with the empirical data and on expert-based rules informed by the long-term monitoring of this population. We investigated if conclusions from the IBM were robust despite these uncertainties in movement processes by evaluating forecasts from key sub-models.

## 2.5 | Habitat suitability models

In previous work predicting current distributions, we tested four HSM methods with opportunistic data versus an HSM with systematic data based on data recorded between 2000 and 2013 (Bradter et al., 2018). The goal in this work was to evaluate forecasts of future distributions, and we developed forecasts for the same set of HSMs to facilitate a



**FIGURE 2** Progress of individuals in the individual-based model through life-history processes and stages. The grey rectangular boxes (March, September) represent the times when the six life-history stages of Siberian jay (grey boxes with round edges) are observed: summer breeder, summer non-breeder (March), winter breeder, winter non-breeder, dispersed juvenile, retained juvenile (September). Life-history processes are represented by white rectangles with dispersal, immigration or colonization only applied to individuals that emigrate

direct comparison of performance in forecasts versus predicting the current distribution. All forest covariates used in the IBM were also included in the HSMs (see Table 1 and Bradter et al., 2018). A detailed description of the HSMs is provided in Appendix S4.

### 2.5.1 | HSM fitted with systematic data

Siberian jay detection/non-detection data from the Swedish Bird Survey (SBS) (679 detections, 5,683 non-detections) had been modelled with a generalized linear mixed model using a Binomial distribution and a logit link, and survey route as a random effect to account for repeated measurements of the same route.

### 2.5.2 | HSMs fitted with opportunistic data

#### MaxEnt

MaxEnt models species distributions by comparing the environmental information between detection and available (background) locations (Phillips et al., 2006). Two models had been evaluated: 2,865 detections with 10,000 background cells randomly selected from either (1) the study area (MaxEnt-Random) or (2) the target-group background (MaxEnt-TGB). The use of a target-group background aims to decrease the effect of spatial bias and consists of locations impacted by a similar spatial bias as the detection data (Phillips et al., 2009).

#### Logistic regression with inferred absences

Detections and inferred absences of Siberian jays had been modelled using a Binomial distribution and a logit link. Two models were evaluated: 4,758 absences inferred from 2,003,193 records of 38 super-reporters paired with (1) 2,865 detections from all reporters

(PresAbs-all) to facilitate a comparison with MaxEnt models using the same detections, or (2) a subset of 960 detections from the same 38 super-reporters (PresAbs-38) to facilitate a comparison with the point process model using the same detection and inferred absence data. Forecasts were produced with these models and after resampling the data to the same prevalence of detections as in the systematically collected data (0.107) with the following expression:

$$\text{Prevalence} = \left( \frac{\text{number of detections}}{\text{number of detections} + \text{number of non-detections}} \right)$$

#### Point process model

The multispecies point process model jointly models systematic detection/non-detection data with opportunistic detection-only data of multiple species, while accounting for the spatial bias of detection-only data through covariates describing area choice of reporters (Fithian et al., 2015). Seven additional species of forest birds had been used for joint modelling: Siberian tit (*Poecile cinctus*), long-tailed tit (*Aegithalos caudatus*), red-breasted flycatcher (*Ficedula parva*), three-toed woodpecker (*Picoides tridactylus*), grey-headed woodpecker (*Picus canus*), hazel grouse (*Tetrastes bonasia*) and lesser spotted woodpecker (*Dryobates minor*). In contrast to the original implementation of the method, the model was evaluated for situations when systematic data were not available and the detection and inferred absence data from super-reporters were used instead.

#### Occupancy model

Occupancy models account for imperfect detection of the species by estimating both the observation and ecological processes in one model (Kéry, Gardner, et al., 2010; Kéry, Royle, et al., 2010). Occupancy probability was modelled using a Bernoulli distribution and a logit link. Detection probability was modelled using a Binomial

TABLE 2 Parameters of the IBM sub-models including the link functions for empirical sub-models and references

| Sub-model   | Link   | Linear predictor or expert-based rule   |
|---|--------|---|
| 1-2: Reproduction                                 |        |   |
| retained juvenile                                 | log    | $-0.59 + 0.14 * \text{Neighbourhood} - 0.12 * \text{PercSpruce} - 0.15 * \text{PlusDays} + 0.12 * \text{GrSizeTerr} - 0.09 * \text{GrSizeTerr}^2$   |
| dispersed juvenile <sup>1</sup>                   |        | $1.6 * \text{Number of retained juveniles}$   |
| 3: Survival                                       |        |   |
| retained juvenile (rj)                            | logit  | $-6.12 + 0.07 * \text{Neighbourhood}$   |
| dispersed juvenile (dj)                           | logit  | $-8.66 + 0.07 * \text{Neighbourhood} + 0.11 * \text{PlusDays} + 0.01 * \text{WinterPrec} + 2.79 * \text{GrSizeTerr} - 0.02 * (\text{GrSizeTerr} * \text{Neighbourhood}) - 0.04 * (\text{GrSizeTerr} * \text{PlusDays})$   |
| winter non-breeder (wn)                           | logit  | $-4.74 + 0.07 * \text{Neighbourhood} - 0.07 * \text{PlusDays} + 3.41 * \text{GrSizeTerr} - 0.03 * (\text{GrSizeTerr} * \text{Neighbourhood})$   |
| summer non-breeder (sn)                           | logit  | $-6.91 + 0.07 * \text{Neighbourhood}$   |
| winter breeder (wb)                               | logit  | $-4.87 + 0.07 * \text{Neighbourhood} - 0.03 * \text{PlusDays} + 0.98 * \text{GrSizeTerr} - 0.01 * (\text{GrSizeTerr} * \text{Neighbourhood})$   |
| summer breeder (sb)                               | logit  | $-5.48 + 0.07 * \text{Neighbourhood} - 0.13 * \text{GrSizeTerr}$  |
| 4: Transition                                     |        |   |
| rj to sb  | mlogit | $7.70 - 0.07 * \text{MeanVol} + 0.13 * \text{PlusDays} - 0.02 * \text{WinterPrec} - 2.72 * \text{PopDens} + 0.03 * (\text{PopDens} * \text{MeanVol})$   |
| dj to sb  | mlogit | $10.24 - 0.07 * \text{MeanVol} + 0.05 * \text{PlusDays} - 0.01 * \text{WinterPrec} - 2.72 * \text{PopDens} + 0.02 * (\text{PopDens} * \text{MeanVol})$  |
| wn to sb  | mlogit | $7.79 - 0.07 * \text{MeanVol} + 0.26 * \text{PlusDays} - 2.72 * \text{PopDens} + 0.03 * (\text{PopDens} * \text{MeanVol}) - 0.07 * (\text{PopDens} * \text{PlusDays})$  |
| sb to wb  | mlogit | $9.00 - 0.07 * \text{MeanVol} - 2.72 * \text{PopDens} + 0.02 * (\text{PopDens} * \text{MeanVol})$   |
| 5-7: Emigration                                   |        |   |
| wb to sb  | logit  | $-8.42 - 0.76 * \text{Neighbourhood} - 1.92 * \text{WinterTemp} + 1.50 * \text{WinterPrec}$<br>single breeders at the end of winter: 1  |
| sb to wb  | logit  | $-6.37 - 0.76 * \text{Neighbourhood} - 0.89 * \text{WinterPrec}$  |
| rj to sb  | logit  | $0.18 - 0.01 * \text{BreedsRemain}(1) + 3.21 * \text{BreedsRemain}(2)$  |
| dj to sb  | logit  | $-2.14 - 0.01 * \text{BreedsRemain}(1) + 3.21 * \text{BreedsRemain}(2)$   |
| wb to sb  | logit  | $-1.67 - 0.01 * \text{BreedsRemain}(1) + 3.21 * \text{BreedsRemain}(2)$   |
| sn to wb  | logit  | $-0.53 - 0.01 * \text{BreedsRemain}(1) + 3.21 * \text{BreedsRemain}(2)$   |
| rj to sn  | logit  | $-3.60 - 0.59 * \text{GrSizeTerr} + 0.23 * \text{GrSizeTerr}^2$   |
| dj to sn  | logit  | $-3.54 - 0.59 * \text{GrSizeTerr} + 0.23 * \text{GrSizeTerr}^2$   |
| wn to sn  | logit  | $-3.09 - 0.59 * \text{GrSizeTerr} + 0.23 * \text{GrSizeTerr}^2$   |
| sn to wn  | logit  | $-2.20 - 0.59 * \text{GrSizeTerr} + 0.23 * \text{GrSizeTerr}^2$   |
| 8: Habitat suitability <sup>2</sup>               | logit  | $-3.83 + 0.28 * \text{PercMature} + 0.44 * \text{MeanAge} + 0.27 * \text{PercOther} - 1.65 * \text{WinterTemp} - 0.51 * \text{SpringPrec} + 1.55 * \text{Elevation} - 0.46 * \text{Elevation}^2 - 0.49 * (\text{WinterTemp} * \text{SpringPrec})$   |
| 9: Dispersal                                      |        | For distances $\leq 278$ m or $\geq 13,321$ m: 0; for distances $> 278$ m and $< 1,262$ m and breeder: 1  |
|   | logit  | For distances $> 278$ m and $\leq 500$ m: $((\text{Distance} - 278) * 0.58) / 230$  |
|   | logit  | For distances $> 500$ and $< 13,321$ m: $e^{(5.351 - (0.0009 * \text{Distance})) / 230}$  |
| 10: Immigration experienced breeder <sup>3</sup>  |        | To occupied cell with $< 2$ breeder and habitat suitability $\geq$ habitat suitability of cell of origin  |
| 11: Colonization experienced breeder <sup>3</sup> |        | If no immigration possible to empty cells with habitat suitability $\geq$ habitat suitability of cell of origin.<br>Empty cells in proximity (within 750 m) of occupied cells will be colonized only if not exceeding the proportion of close neighbours observed in the empirical life-history population (0.06 within 500 m and 0.3 within 750 m) |
| 12: Immigration new breeder <sup>3,4</sup>        |        | To occupied cell with $< 2$ breeder and habitat suitability $\geq 2/3$ habitat suitability of cell of origin  |
| 13: Immigration non-breeder <sup>3</sup>          |        | To occupied cell with $\geq 1$ breeder  |

Notes: For further details on expert-based rules, see Appendix S3. PercOther: Percentage of non-mature forest; for other covariate abbreviations, see Table 1. For the calculation of covariates see Appendix S2 (IBM) and S4 (HSM). Levels for the categorical variable BreedsRemain are denoted by BreedsRemain (1): 1 breeder remaining and BreedsRemain(2): 2 breeders remaining. Interactions between factors are denoted by "x"; quadratic effects by "<sup>2</sup>". For sub-models 1 and 5-8, covariates were standardized to a mean of zero and a standard deviation of one prior to model fitting.

Note: References: <sup>1</sup>Layton-Matthews et al. (2018), <sup>2</sup>Bradter et al. (2018), <sup>3</sup>Griesser et al. (2007), <sup>4</sup>Ekman et al. (2001)

distribution and a logit link, with covariates describing search effort and abundance of Siberian jay, as detection probability may be higher where the species is more abundant.

### 2.5.3 | Forest management scenarios and Siberian jay projections

We used three possible future forest management scenarios that had previously been simulated and represented alternative perspectives of three stakeholders with different views on how to balance wood production with biodiversity conservation for a virtual, realistic 1,033 km<sup>2</sup> forest landscape in northern Sweden (Eggers et al., 2020). The spatial extent was large enough to allow for the existence of many groups of jays in the IBM (511 groups at initialization) and a diversity of forest stands. The stakeholders included the LRF Skogsägarna representing private forest owners (LRF), the Swedish Society for Nature Conservation (SSNC) and the Swedish Environmental Protection Agency (SEPA). Scenarios had been created using the Heureka forest decision support system over a 105-year period and simulated realistic forest changes due to management and slowly occurring forest growth (Wikström et al., 2011).

From the spatially explicit Heureka projections for each forest stand every five years, we used the four variables of forest age, standing wood volume, spruce and pine volume, and then calculated the same forest covariates as used in HSMs and IBM sub-models. Some predicted forest ages were higher than observed in the data used to develop the HSMs and IBM sub-models. We opted to cap age covariates to the maximum observed values. The future distribution of all Siberian jay individuals was then projected for each 5-year period and each grid cell with each HSM, and for 6-month intervals with the IBM.

## 3 | RESULTS

### 3.1 | Benchmark models

The individual-based model (IBM) projections successfully recovered the population trends observed in the long-term monitoring of the natural populations: stable in the near-pristine area and declining in the managed area (Appendix S5). Further, we confirmed that our IBM results were robust to potential uncertainties in sub-models of

the birds' dispersal behaviour (Appendix S6). The two initial validations indicate that the IBM should be suitable for rankings of forest management options.

All IBM forecasts were characterized by an initial stable population trend. Subsequently, populations were projected to decline, coinciding with an initial decline in forest ages of mature patches in all scenarios (Appendix S6). Later in the projection period, populations increased in the scenarios based on the Swedish Society for Nature Conservation (SSNC, Figure 3a) and the Swedish Environmental Protection Agency (SEPA, Figure 3b), while in the scenario from the forest owners (LRF, Figure 3c), the population size remained approximately constant over time. Under constant forest conditions, after an initial steady period, the population declined throughout the projection period (Figure 3d).

For HSM models, the three alternative forest management scenarios were ranked by the sum of habitat suitability across all cells in the simulated landscapes. Both benchmark models, the IBM (Figure 3a–c) and the HSM with systematic data (Figure 3e) ranked the SSNC (skyblue solid line) and the SEPA scenarios (dashed green line) as the two forest management plans with the greatest benefit for Siberian jay over a 105-year projection period, and the LRF scenario (dotted orange line) as having the least benefit. Thus, we proceeded with evaluations of alternative HSMs based on opportunistic data from citizen science programmes.

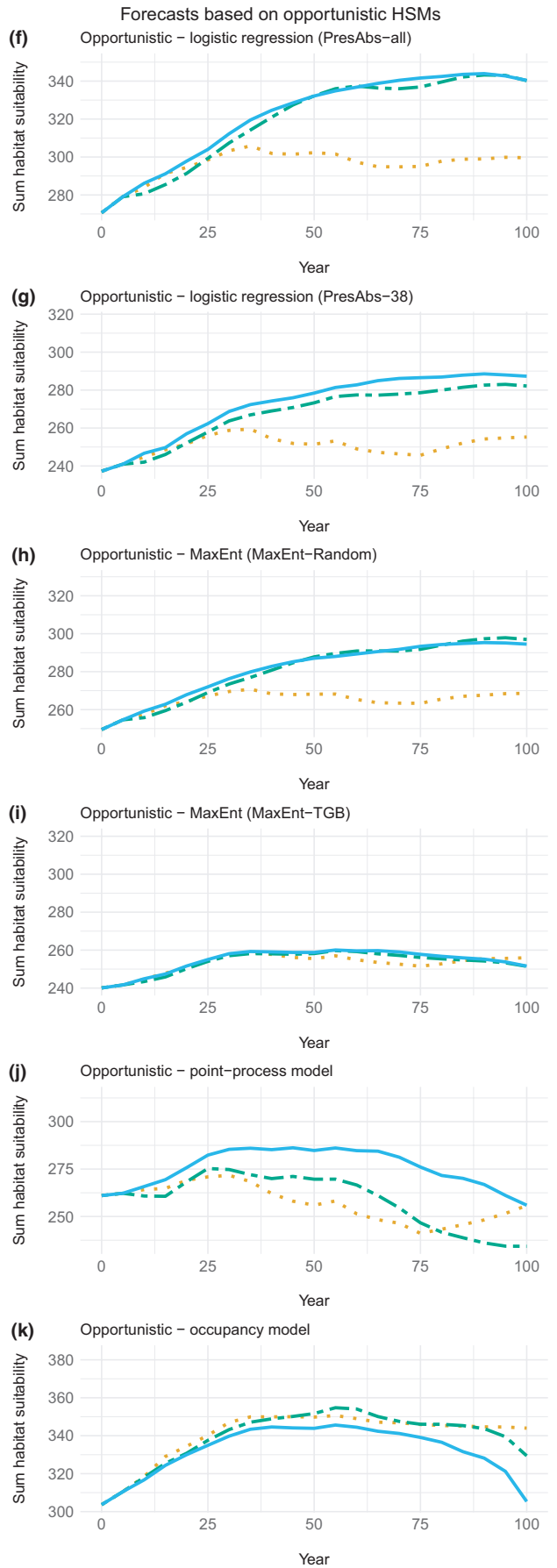
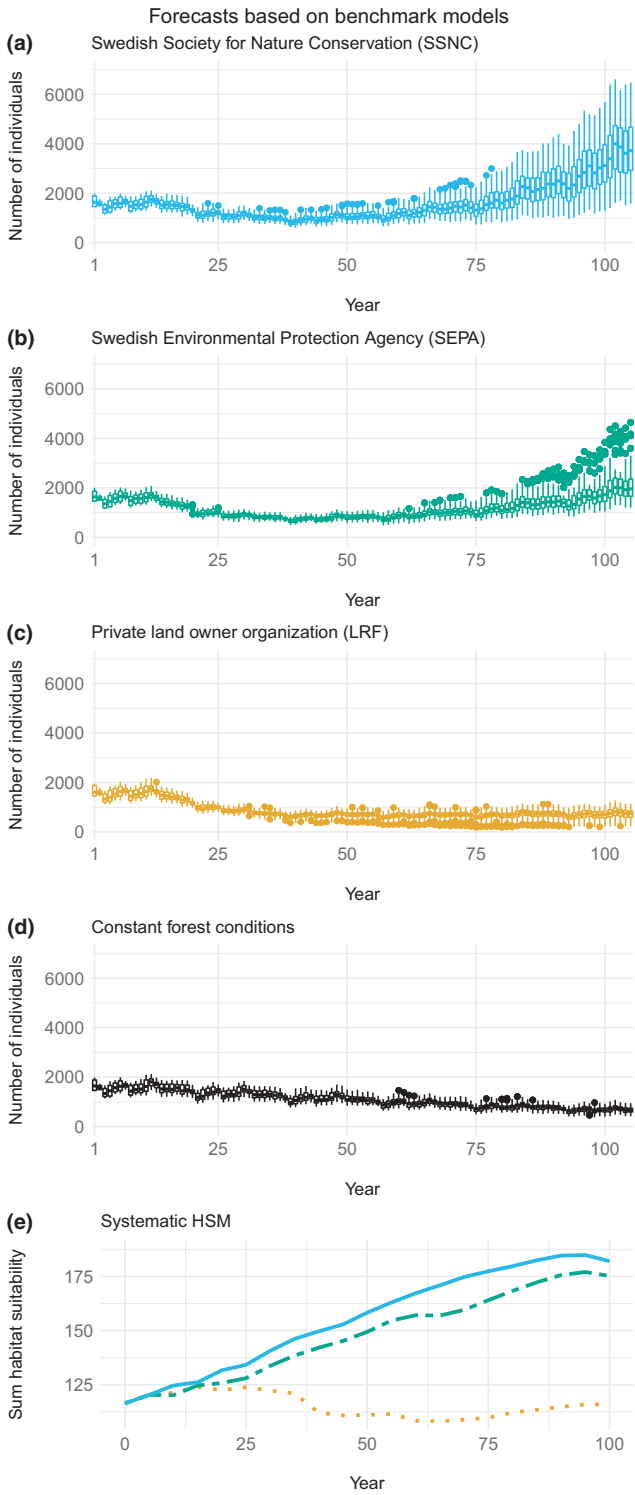
### 3.2 | HSMs based on alternative models and opportunistic data

Model performance varied dramatically among the alternative models based on opportunistic data. The best results were obtained with logistic regressions using inferred absences and MaxEnt with a random background (PresAbs-all, PresAbs-38, MaxEnt-Random, Figure 3f–h), which identified the same scenarios as beneficial for Siberian jays as our two benchmark models. In contrast, habitat suitability forecasts based on MaxEnt with a target-group background were unsuccessful at discriminating among the three alternative scenarios (MaxEnt-TGB, Figure 3i). The point process model successfully identified the SSNC scenarios as beneficial for Siberian jays but failed to identify the SEPA scenario (Figure 3j). Finally, the occupancy model ranked the worst scenario as being more beneficial than the best (Figure 3k).

The prevalence of detections was higher in the opportunistic (0.17 for PresAbs-38 and 0.38 for PresAbs-all), than in the systematic

**FIGURE 3** Forecasts from the two benchmark models (left) and from HSMs based on opportunistic data (right). Figures (a–d) show the population size of Siberian jay over 105 years with 100 repetitions of the IBM for three forest management scenarios, and for constant forest conditions throughout the forecasting period. Boxplots for each time point show the interquartile range and median; whiskers show the maximum of 1.5 \* interquartile range and dots values outside this range. Figures (e–k) show forecasts of the summed habitat suitability across all cells over 105 years with HSMs based on either e) systematic or (f–k) opportunistic data. Forest input data for HSMs are updated every five years and for the last period (100–105 years) forecasts are only shown up to the point of update (100 years). PresAbs-all was based on all detections while PresAbs-38 was based on detections from 38 super-reporters, MaxEnt-Random used a random background while MaxEnt-TGB used a target background. Note, the y-axis for HSM forecasts covers the same range (80 units) for each graph. The summed habitat suitability in year 0 differs among panels due to variation in the prevalence of detections in the different models





data (0.11). Without resampling the opportunistic data to match the lower prevalence of the systematic data, the magnitude of forecasted change of habitat suitability was smaller in the logistic regressions with inferred absences (Appendix S7). The high prevalence of detections led to a high habitat suitability sum throughout the projection period, and consequently little improvement could be made.

## 4 | DISCUSSION

We asked if anticipatory forecasts with HSMs using opportunistic data can be useful despite the challenges of modelling citizen science data. Our first major findings were that the conclusions from our two benchmark forecasts were consistent with each other and with existing knowledge of the species ecology for Siberian jays. The area of old forest increased over time in the beneficial management scenarios (Eggers et al., 2020), and the benefits of mature and old forest to the species are well known (Edenius et al., 2004; Griesser & Lagerberg, 2012). Our second finding was that HSMs based on opportunistic data could recover the same rankings of management scenarios as our benchmark models, but only for a subset of models. The best performance was obtained with two models: logistic regression based on detections combined with inferred absences and MaxEnt with a random background (but see below for our reservations on other forecasts with the latter). In contrast, three other HSM methods based on opportunistic data failed to identify the same two scenarios as beneficial (point process model, MaxEnt with target-group background), and in one case returned a completely opposite set of rankings (occupancy model). Our last finding was that previous work demonstrated that all alternative HSMs were able to predict the nationwide current distribution of Siberian jay (Bradter et al., 2018), but forecasts for three methods failed in this study. While choice of modelling method mattered greatly, with some methods we obtained forecasts based on opportunistic data that produced reliable rankings of forest management scenarios, even when challenged against forecasts from a dynamic, spatially explicit model. Thus, forecasts based on opportunistic data can have a useful role in ecology and conservation if used in an adequate modelling framework.

### 4.1 | Static versus dynamic, spatially explicit models

Agreement in rankings of scenarios between both benchmark forecasts suggests that the IBM, built with detailed demographic data from a relatively limited area, was sufficiently general to apply to a wider area. Moreover, agreement between forecasts indicates that the pattern emerging from the processes in the dynamic, spatially explicit IBM was represented adequately with the simpler static HSM based on occurrence data from systematic monitoring. Thus, the forecasts from both benchmark models validated each other, increasing confidence in both. Disagreement between benchmark forecasts might arise due to a failure of the static HSM to adequately

capture the dynamic ecological processes or due to the IBM not being generalizable to a larger area.

A major difference between forecasts from the static HSMs and the dynamic IBM is that forest changes that affect Siberian jay will affect habitat suitability forecasts from HSMs as soon as these changes occur while effects on the forecasted population trend in the IBM may be delayed. For example, an improvement in forest conditions in cells of the IBM remote from occupied cells will only contribute to the population trend once individuals have dispersed to these cells. Delayed responses explain why habitat suitability in the well performing HSM forecasts plateaued towards the end of the projection period for the two management scenarios most beneficial for Siberian jay, while the IBM forecasted continued growth. Temporal trends in forecasts of static HSMs and dynamic IBMs can therefore not be expected to be identical apart from exceptional cases. To assess the reliability of conclusions from forecasts, we therefore compared the consistency of rankings of forest management scenarios over the entire forecast period instead of the similarity in the shape of the forecasted curve. The time-lag also implies that the benefit of land use management measures for the conservation of species may not be seen immediately.

Another major difference between forecasts from the static HSMs and the dynamic IBM is that under no environmental change, HSM forecasts are invariant while the population trend forecasted by the IBM declined under no forest change, which is the baseline against which the effect of management scenarios in the IBM had to be assessed. In contrast to the dynamic IBM, forecasts from HSMs do not account for dynamic changes in space or time caused by ecological processes such as source-sink dynamics or non-equilibrium. The population trend of Siberian jay in managed forests in the empirical life-history population was negative (Layton-Matthews et al., 2018). Therefore, the finding of a negative population trend in the IBM with no forest change in an area dominated by managed forests is realistic. However, certainty about the absolute population trend is affected by limitations. We parameterized our models using covariates derived from remotely sensed forest maps. In contrast, the virtual projection landscape was based on direct measurements from the national forest inventory (Eggers et al., 2020). The remotely sensed forest characteristics may be biased low or high relative to direct measurements leading to a corresponding bias in our forecasted values. The covariates also did not quantify some characteristics important for the species, such as the structure of the forest understorey (Klein et al., 2020). Data on long-distance dispersal and settlement decisions were limited despite a large and long-term life-history dataset, leading to uncertainties in the parameterization of the dispersal process. However, the ranking of scenarios was robust despite these uncertainties about the absolute population trend (Appendix S6) suggesting that relative differences between population trends are reliable.

Another major difference between HSMs and IBMs relates to biotic interactions, which can substantially influence species distributions (Cabral & Kreft, 2012). In conventional HSMs, biotic interactions may be indirectly accounted for because species occurrence

records are constrained by suitable environment, biotic interactions (e.g. predation or competition) and the ability to reach suitable habitats (Gallien et al., 2010; Zurell, 2017). Forecasting with conventional HSMs therefore assumes that neither the biotic interactions, nor the implicit relationships between, for example, predation risk and environmental covariates change (Dormann, 2007). In IBMs by contrast, biotic interactions can be explicitly included relaxing the assumption of constant relationships. We did not include explicit sub-models of interactions with other species in the IBM because our objective was to construct a benchmark IBM that tests the reliability of forecasts from HSMs under the assumption of no change in biotic interactions over time. While this assumption may be unrealistic for some systems, the resulting forecasts can still be regarded as useful as the aim of anticipatory forecasts is not necessarily to produce an accurate prediction of future species distributions, but of possible trajectories of species responses (Mouquet et al., 2015).

A cause of concern of models consisting of several sub-models can be circularity (Gallien et al., 2010; Zurell et al., 2016). As described above, HSMs may implicitly account for factors such as dispersal limitations or biotic interactions, and these factors may be double-accounted for with additional sub-models that explicitly account for the processes. The risk of circularity in our models should be low. For example, main predators of Siberian jay nests are corvids while main predators of post-fledging Siberian jay are birds of prey (Eggers et al., 2006; Griesser & Nystrand, 2009). Consequently, while our reproduction and survival models may both implicitly account for predation risk, for example through covariates describing forest density, which can influence the risk of detection of eggs, nestlings or post-fledging individuals, both models account for two separate predation risks. Including the two sub-models in an IBM would therefore not double-account for predation risk, but instead more explicitly account for the separate effects of predation risk.

## 4.2 | Forecasts versus predicting the current distribution

Most of the HSM methods that predicted the current distribution of Siberian jay less accurately (Bradter et al., 2018) performed even worse in forecasts of future distributions (this study). However, at least at the nationwide scale, all methods produced useful maps of the current species distribution with only relatively small differences in predictive accuracy. By contrast, the performance differences among forecasts from the different models were much larger. Some methods successfully produced correct rankings of forest management scenarios, whereas other methods produced incorrect rankings which could lead to the recommendation of forest management practices that would not be beneficial, or even detrimental, to conservation efforts for Siberian jays. Therefore, predictive performance for the current distribution of a species may be a poor indicator for the reliability of models for future forecasts. Similarly, previous work suggested that good predictive ability of models in one area and time does not necessarily indicate that the same models perform well in

other areas or future times (Bahn & McGill, 2013; Dormann, 2007; Randin et al., 2006).

In the three HSMs that produced incorrect forecasts, species–habitat relationships contrary to strong expectations based on the species ecology were found by Bradter et al. (2018). The authors also found species–habitat relationships contrary to expectations in a fourth HSM, the MaxEnt model with a random background, but nonetheless forecasts with this model were consistent with the benchmark forecasts in this study. In this MaxEnt model, habitat suitability increased with a decreasing percentage of young or sparse forest, which was contrary to the positive association found in the SBS benchmark model (Bradter et al., 2018). Further, the relationship was opposite to the species' known associations with not only particularly mature and old forest, but with a variety of forest types (Brotons et al., 2003), which are more valuable to the species than non-forested areas, such as lakes. We are sceptical that forecasts from the MaxEnt model would agree with benchmark forecasts if the scenarios would include conversions from young/sparse forest to non-forest, such as agriculture or reservoirs. Our results indicate that scepticisms is appropriate when forecasting with models containing incorrect species–habitat relationships. Conversely, a lack of species–habitat relationships that are counter to expectations may not necessarily indicate that these models will produce reliable forecasts. First, the realism of species–habitat relationships suggested by models can rarely be assessed for all relationships. Even for the well-studied Siberian jay the HSMs contained species–habitat relationships for which Bradter et al. (2018) had no strong prior expectations, such as the relationship with pine-dominated forest. Second, model selection uncertainty is widespread (Burnham & Anderson, 2004) with models with different combinations of covariates performing very similar in predicting the current distribution. Characteristics of the data and the choice of modelling method will further influence the modelled species–habitat relationships. Alternative HSMs may therefore not produce identical species–habitat relationships and consequently are unlikely to produce identical forecasts, which hampers assessing the reliability of forecasts based on species–habitat relationships in HSMs. Discrepancies in modelled species–habitat relationships were also evident among the two logistic regressions based on opportunistic data and the HSM based on systematic data in this study. They differed in the selected forest covariates (see Bradter et al., 2018) and forecasts were not identical (this study). However, they led to the same conclusions by producing the same ranking of forest management scenarios, suggesting sufficient robustness for ecological applications. Further research to identify the characteristics of opportunistic data for which different HSM methods either produce reliable or unreliable forecasts may be useful to increase confidence in forecasts based on opportunistic data.

The unexpected species–habitat relationships found by Bradter et al. (2018) for the MaxEnt, the point process and occupancy model are unlikely to be caused by the wrong choice of covariates or covariate scales, as model selection for all HSMs was performed using the same covariates and scales and the logistic regressions with inferred absences fitted expected relationships. It is likely that the other

methods were not able to account for the sample selection bias appropriately, possibly because the data did not contain enough information on the observation process to allow for successful correction of the observation bias. Successful forecasts may reflect that logistic regression is robust to common forms of sample selection bias in opportunistic data (Zadrozny, 2004). Moreover, the reduction in information content in the data through biased sampling was minimized through a selection of super-reporters by Bradter et al. (2018), which ensured widespread geographic coverage of inferred absences and therefore of environmental space.

Caution will be required when interpreting forecasts if the proportion of inferred absences differs from the true proportion. Here, the low proportion of inferred absences resulted in high habitat suitability scores, allowing for little improvement due to forest management, which underestimated the magnitude of habitat suitability change compared to the benchmark forecasts. Conversely, if both habitat suitability and true prevalence would be high while the prevalence in the data would be lower, we expect that forecasts would have suggested a larger effect of forest management scenarios compared to forecasts based on data with the true prevalence. Resampling the data to the prevalence level expected for the species better revealed this magnitude of change. However, with small sample sizes, resampling to smaller datasets can lead to model instability, where model conclusions change as data points are added or removed. Hence, we recommend comparing model conclusions from models with resampled data with conclusions of the full model, or to average over many resampled models.

Confidence in our forecasts can be higher because we produced consistent forecasts with a diversity of models: a dynamic, spatially explicit IBM and static, pattern-based HSMs with spatially biased and unbiased data. Moreover, the forecasts from the logistic regressions with inferred absences and from the benchmark models agreed with expectations based on the ecology of this well-studied species.

### 4.3 | Relevance of opportunistic data and inferred absences for forecasts

Consultation of super-reporters was an effective method for deriving high-quality inferred absences that minimized false absences. It has the added advantage that it can be applied retrospectively in situations when complete checklists were not recorded (Bradter et al., 2018). Contributions from super-reporters tend to dominate citizen science datasets across a variety of taxa (Isaac & Pocock, 2015) and inferring absences based on records from super-reporters has successfully been applied to several bird species and to other taxa such as fungi (Henckel et al., 2020; Mair et al., 2017). Thus, inferred absences can potentially be applied to the large amount of data that have already been recorded and enhance the usability of opportunistic data, which are increasingly available for species and regions for which systematic data are not available. We suggest that citizen science projects routinely survey reporters regarding their consistency of reporting of certain

species and their identification skills and make partial list information available for data collected without complete checklists. Submission of complete checklist data by reporters is preferable over retrospective construction of partial lists, but citizen science projects can enhance the usability of their detection-only data, at least for the uncommon species which some super-reporters consistently report, by providing partial list information.

Despite the current methodological limitations of forecasts and their validation, and the challenges of working with opportunistic data, the results of our study are encouraging because we have shown that HSMs with such data can result in the same conclusions as an HSM with systematic data or a dynamic, spatially explicit IBM. Anticipatory forecasts can be valuable for qualitative ranking of the relative benefits of alternative management decisions even if their forecasted absolute population numbers or species distributions may not be reliable. Appropriate monitoring needs to accompany management action to guard against unexpected effects that current forecasts cannot appropriately capture. While forecasts are only as good as the underlying data and models, our results are encouraging for study systems where baseline data from systematic monitoring are not yet available.

### ACKNOWLEDGEMENTS

We thank the reporters and coordinators of the Swedish Species Observation System and the Swedish Bird Survey. We also thank Koen van Benthem for discussions on multistate models, Olof Billinger for IT assistance and reviewers and editors for valuable comments on earlier drafts of this manuscript. The study was part of GREENFUTUREFOREST funded by the 2015–2016 BiodivERsA COFUND call for research proposals with the national funders the Swedish Research Council Formas (2016-01949) and the Swiss National Science Foundation (31BD30\_172465) and of the 2017-2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND programme, including financial support from the Research Council of Norway (Forskningrådet, 295767) and of a grant funded by the Swedish Research Council Formas (2016-00557). Data collection for the Siberian jay study population was financed by grants from the Swiss National Science Foundation (MG: PPOOP3\_123520, PP00P3\_150752), the Swedish Research Council (MG, Jan Ekman), Formas (Jan Ekman) and the University of Zurich (AO, MG).

### CONFLICT OF INTEREST

None.

### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13409>.

### DATA AVAILABILITY STATEMENT

The species data for the HSMs are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.4722kf7>. The forest raster can be downloaded from <https://www.slu.se/centrumbildning>

ar-och-projekt/riksskogstaxeringen/statistik-om-skog/slu-skogskarta/ and the climate data from <http://opendata-download-metobs.smhi.se/explore/#>. Parameter estimates from the HSMs are published in Bradter et al. (2018). The IBM can be coded following the ODD protocol in the Supporting Information and using the parameter estimates published in this study. Our own IBM code is additionally provided in the Github repository: <https://github.com/UteBradter/SiberianJayIBM/>.

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## REFERENCES

- Amano, T., Lamming, J. D. L., & Sutherland, W. J. (2016). Spatial gaps in global biodiversity information and the role of Citizen Science. *BioScience*, 66, 393–400. <https://doi.org/10.1093/biosci/biw022>
- Bahn, V., & McGill, B. J. (2013). Testing the predictive performance of distribution models. *Oikos*, 122, 321–331. <https://doi.org/10.1111/j.1600-0706.2012.00299.x>
- Baker, D. J., Maclean, I. M. D., Goodall, M., & Gaston, K. J. (2021). Species distribution modelling is needed to support ecological impact assessments. *Journal of Applied Ecology*, 58(1), 21–26. <https://doi.org/10.1111/1365-2664.13782>
- Bradter, U., Mair, L., Jönsson, M., Knape, J., Singer, A., & Snäll, T. (2018). Can opportunistically collected Citizen Science data fill a data gap for habitat suitability models of less common species? *Methods in Ecology and Evolution*, 9, 1667–1678. <https://doi.org/10.1111/2041-210X.13012>
- Brotans, L., Mönkkönen, M., Huhta, E., Nikula, A., & Rajasärkkä, A. (2003). Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland. *Landscape Ecology*, 18, 377–393.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33, 261–304. <https://doi.org/10.1177/0049124104268644>
- Cabral, J. S., & Krefl, H. (2012). Linking ecological niche, community ecology and biogeography: Insights from a mechanistic niche model. *Journal of Biogeography*, 39(12), 2212–2224. <https://doi.org/10.1111/jbi.12010>
- Cramp, S., & Perrins, C. M. (1994). *The Birds of the Western Palearctic (Vol. VIII Crows to Finches)*. Oxford University Press.
- Dormann, C. F. (2007). Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, 8, 387–397. <https://doi.org/10.1016/j.baae.2006.11.001>
- Dormann, C. F., Schymanski, S. J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B., & Singer, A. (2012). Correlation and process in species distribution models: Bridging a dichotomy. *Journal of Biogeography*, 39, 2119–2131. <https://doi.org/10.1111/j.1365-2699.2011.02659.x>
- Edenius, L., Brodin, T., & White, N. (2004). Occurrence of Siberian jay *Perisoreus infaustus* in relation to amount of old forest at landscape and home range scales. *Ecological Bulletins*, 51, 241–247.
- Eggers, J., Rätty, M., Öhman, K., & Snäll, T. (2020). How well do stakeholder-defined forest management scenarios balance economic and ecological forest values? *Forests*, 11, 86. <https://doi.org/10.3390/f11010086>
- Eggers, S., Griesser, M., Nystrand, M., & Ekman, J. (2006). Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society B*, 273, 701–706. <https://doi.org/10.1098/rspb.2005.3373>
- Ekman, J., Eggers, S., Griesser, M., & Tegelström, H. (2001). Queuing for preferred territories: Delayed dispersal of Siberian jays. *Journal of Animal Ecology*, 70, 317–324. <https://doi.org/10.1046/j.1365-2656.2001.00490.x>
- Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1, 330–342. <https://doi.org/10.1111/j.2041-210X.2010.00036.x>
- Fithian, W., Elith, J., Hastie, T., & Keith, D. A. (2015). Bias correction in species distribution models: Pooling survey and collection data for multiple species. *Methods in Ecology and Evolution*, 6, 424–438. <https://doi.org/10.1111/2041-210X.12242>
- Franklin, J. (2009). *Mapping species distributions - Spatial inference and prediction*. Cambridge University Press.
- Gallien, L., Münkemüller, T., Albert, C. H., Boulangéat, I., & Thuiller, W. (2010). Predicting potential distributions of invasive species: Where to go from here? *Diversity and Distributions*, 16(3), 331–342. <https://doi.org/10.1111/j.1472-4642.2010.00652.x>
- Griesser, M., Halvarsson, P., Drobnik, S. M., & Vila, C. (2015). Fine-scale kin recognition in the absence of social familiarity in the Siberian jay, a monogamous bird species. *Molecular Ecology*, 24(22), 5726–5738. <https://doi.org/10.1111/mec.13420>
- Griesser, M., Halvarsson, P., Sahlman, T., & Ekman, J. (2014). What are the strengths and limitations of direct and indirect assessment of dispersal? Insights from a long-term field study in a group-living bird species. *Behavioral Ecology and Sociobiology*, 68, 485–497. <https://doi.org/10.1007/s00265-013-1663-x>
- Griesser, M., & Lagerberg, S. (2012). Long-term effects of forest management on territory occupancy and breeding success of an open-nesting boreal species, the Siberian jay. *Forest Ecology and Management*, 271, 58–64. <https://doi.org/10.1016/j.foreco.2012.01.037>
- Griesser, M., & Nystrand, M. (2009). Vigilance and predation of a forest-living bird species depend on large-scale habitat structure. *Behavioral Ecology*, 20, 709–715. <https://doi.org/10.1093/beheco/arp045>
- Griesser, M., Nystrand, M., Eggers, S., & Ekman, J. (2007). Impact of forestry practices on fitness correlates and population productivity in an open-nesting bird species. *Conservation Biology*, 21, 767–774.
- Griesser, M., Nystrand, M., Eggers, S., & Ekman, J. (2008). Social constraints limit dispersal and settlement decisions in a group-living bird species. *Behavioral Ecology*, 19, 317–324. <https://doi.org/10.1093/beheco/arm131>
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S. K., Huse, G., Huth, A., Jepsen, J. U., Jørgensen, C., Mooij, W. M., Müller, B., Pe'er, G., Piou, C., Railsback, S. F., Robbins, A. M., ... DeAngelis, D. L. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, 198(1–2), 115–126. <https://doi.org/10.1016/j.ecolmodel.2006.04.023>
- Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135, 147–186. [https://doi.org/10.1016/S0304-3800\(00\)00354-9](https://doi.org/10.1016/S0304-3800(00)00354-9)
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of 21st-Century forest cover change. *Science*, 342(6160), 850–853. <https://doi.org/10.1126/science.1244693>

- Henckel, L., Bradter, U., Jönsson, M., Isaac, N. J. B., & Snäll, T. (2020). Assessing the usefulness of citizen science data for habitat suitability modelling: Opportunistic reporting versus sampling based on a systematic protocol. *Diversity and Distributions*, 26, 1276–1290. <https://doi.org/10.1111/ddi.13128>
- Isaac, N. J. B., & Pocock, M. J. O. (2015). Bias and information in biological records. *Biological Journal of the Linnean Society*, 115, 522–531. <https://doi.org/10.1111/bij.12532>
- Isaac, N. J. B., van Strien, A. J., August, T. A., de Zeeuw, M. P., & Roy, D. B. (2014). Statistics from citizen science: Extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, 5, 1052–1060. <https://doi.org/10.1111/2041-210X.12254>
- Johnston, A., Hochachka, W. M., Strimas-Mackey, M. E., Gutierrez, V. R., Robinson, O. J., Miller, E. T., & Fink, D. (2021). Analytical guidelines to increase the value of community citizen science data: An example using eBird data to estimate species distributions. *Diversity and Distributions*, 27, 1265–1277. <https://doi.org/10.1111/ddi.13271>
- Johnston, A., Moran, N., Musgrove, A., Fink, D., & Baillie, S. R. (2020). Estimating species distributions from spatially biased citizen science data. *Ecological Modelling*, 422, 108927. <https://doi.org/10.1016/j.ecolmodel.2019.108927>
- Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, 12(4), 334–350. <https://doi.org/10.1111/j.1461-0248.2008.01277.x>
- Kéry, M., Gardner, B., & Monnerat, C. (2010). Predicting species distributions from checklist data using site-occupancy models. *Journal of Biogeography*, 2010, 1851–1862. <https://doi.org/10.1111/j.1365-2699.2010.02345.x>
- Kéry, M., Royle, J. A., Schmid, H., Schaub, M., Volet, B., Häfliger, G., & Zbinden, N. (2010). Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. *Conservation Biology*, 24, 1388–1397. <https://doi.org/10.1111/j.1523-1739.2010.01479.x>
- Klein, J., Haverkamp, P. J., Lindberg, E., Griesser, M., & Eggers, S. (2020). Remotely sensed forest understory density and nest predator occurrence interact to predict suitable breeding habitat and the occurrence of a resident boreal bird species. *Ecology and Evolution*, 10(4), 2238–2252. <https://doi.org/10.1002/ece3.6062>
- Layton-Matthews, K., Ozgul, A., & Griesser, M. (2018). The interacting effects of forestry and climate change on the demography of a group-living bird population. *Oecologia*, 186, 907–918. <https://doi.org/10.1007/s00442-018-4100-z>
- Mackenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., & Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, 84, 2200–2207. <https://doi.org/10.1890/02-3090>
- Mair, L., Harrison, P. J., Jönsson, M., Löbel, S., Nordén, J., Siitonen, J., Lämäs, T., Lundström, A., & Snäll, T. (2017). Evaluating citizen science data for forecasting species responses to national forest management. *Ecology and Evolution*, 7, 368–378. <https://doi.org/10.1002/ece3.2601>
- Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., Faure, D., Garnier, E., Gimenez, O., Huneman, P., Jabot, F., Jarne, P., Joly, D., Julliard, R., Kéfi, S., Kergoat, G. J., Lavorel, S., Le Gall, L., Meslin, L., ... Loreau, M. (2015). Predictive ecology in a changing world. *Journal of Applied Ecology*, 52(5), 1293–1310. <https://doi.org/10.1111/1365-1248.12482>
- Nystrand, M., Griesser, M., Eggers, S., & Ekman, J. (2010). Habitat-specific demography and source-sink dynamics in a population of Siberian jays. *Journal of Animal Ecology*, 79, 266–274. <https://doi.org/10.1111/j.1365-2656.2009.01627.x>
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190(3–4), 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Phillips, S. J., Dudik, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, 19, 181–197. <https://doi.org/10.1890/07-2153.1>
- Pukkala, T., Sulkava, R., Jaakkola, L., & Lähde, E. (2012). Relationships between economic profitability and habitat quality of Siberian jay in uneven-aged Norway spruce forest. *Forest Ecology and Management*, 276, 224–230. <https://doi.org/10.1016/j.foreco.2012.04.006>
- R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org>
- Randin, C. F., Dirnböck, T., Dullinger, S., Zimmermann, N. E., Zappa, M., & Guisan, A. (2006). Are niche-based species distribution models transferable in space? *Journal of Biogeography*, 33, 1689–1703. <https://doi.org/10.1111/j.1365-2699.2006.01466.x>
- Reese, H., Nilsson, M., Pahlén, T. G., Hagner, O., Joyce, S., Tingelöf, U., Egberth, M., & Olsson, H. (2003). Countrywide estimates of forest variables using satellite data and field data from the National Forest Inventory. *Ambio*, 32, 542–548. <https://doi.org/10.1579/0044-7447-32.8.542>
- Schurr, F. M., Pagel, J., Cabral, J. S., Groeneveld, J., Bykova, O., O'Hara, R. B., Hartig, F., Kissling, W. D., Linder, H. P., Midgley, G. F., Schröder, B., Singer, A., & Zimmermann, N. E. (2012). How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, 39(12), 2146–2162. <https://doi.org/10.1111/j.1365-2699.2012.02737.x>
- Singer, A., Johst, K., Banitz, T., Fowler, M. S., Groeneveld, J., Gutiérrez, A. G., Hartig, F., Krug, R. M., Liess, M., Matlack, G., Meyer, K. M., Pe'er, G., Radchuk, V., Voinopol-Sassu, A.-J., & Travis, J. M. J. (2016). Community dynamics under environmental change: How can next generation mechanistic models improve projections of species distributions? *Ecological Modelling*, 326, 63–74. <https://doi.org/10.1016/j.ecolmodel.2015.11.007>
- Snäll, T., Kindvall, O., Nilsson, J., & Pärt, T. (2011). Evaluating citizen-based presence data for bird monitoring. *Biological Conservation*, 144, 804–810. <https://doi.org/10.1016/j.biocon.2010.11.010>
- Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., ... Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, 353, aad8466. <https://doi.org/10.1126/science.aad8466>
- Wikström, P., Edenius, L., Elfving, B., Eriksson, L. O., Lämäs, T., Sonesson, J., & Klintebäck, F. (2011). The Heureka forestry decision support system: An overview. *Mathematical and Computational Forestry & Natural-Resource Sciences*, 3, 87–94.
- Zadrozny, B. (2004). Learning and evaluating classifiers under sample selection bias. *Proceedings of the 21st International Conference on Machine Learning* (p. 114). <https://doi.org/10.1145/1015330.1015425>
- Zurell, D. (2017). Integrating demography, dispersal and interspecific interactions into bird distribution models. *Journal of Avian Biology*, 48, 1505–1516. <https://doi.org/10.1111/jav.01225>
- Zurell, D., Thuiller, W., Pagel, J., Cabral, J. S., Munkemüller, T., Gravel, D., & Zimmermann, N. E. (2016). Benchmarking novel approaches for modelling species range dynamics. *Global Change Biology*, 22(8), 2651–2664. <https://doi.org/10.1111/gcb.13251>

**BIOSKETCH**

The project was a collaboration among authors with skills in the modelling and evaluation of citizen science data, in distribution modelling and population ecology, and ecologists with expertise on Siberian jay and forest ecology. Ute Bradter is a field ecologist and ecological modeller with an interest in citizen science, birds and applied questions relevant to biodiversity conservation. The SLU Swedish Species Information Centre provides infrastructure for collection and analysis of species records for all taxa occurring in Sweden.

**How to cite this article:** Bradter, U., Ozgul, A., Griesser, M., Layton-Matthews, K., Eggers, J., Singer, A., Sandercock, B. K., Haverkamp, P. J., & Snäll, T. (2021). Habitat suitability models based on opportunistic citizen science data: Evaluating forecasts from alternative methods versus an individual-based model. *Diversity and Distributions*, 27, 2397–2411. <https://doi.org/10.1111/ddi.13409>

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Additional supporting information may be found online in the Supporting Information section.