APPLICATION

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DYNAMICSDM: An R package for species geographical distribution and abundance modelling at high spatiotemporal resolution

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Abstract

1. Species distribution models (SDM) are widely applied to understand changing species geographical distribution and abundance patterns. However, existing SDM tools are inherently static and inadequate for modelling species distributions that are driven by dynamic environmental conditions.

2. DYNAMICSDM provides novel tools that explicitly consider the temporal dimension at key SDM stages, including functions for: (a) Cleaning and filtering species occurrence records by spatial and temporal qualities; (b) Generating pseudo-absence records through space and time; (c) Extracting spatiotemporally buffered explanatory variables; (d) Fitting SDMs whilst accounting for temporal biases and autocorrelation and (e) Projecting intra- and inter- annual geographical distributions and abundances at high spatiotemporal resolution.

3. Package functions have been designed to be: flexible for targeting specific study species; compatible with other SDM tools; and, by utilising Google Earth Engine and Google Drive, to have low computing power and storage needs. We illustrate DYNAMICSDM functions with an example of a nomadic bird in southern Africa, the red-billed quelea *Quelea quelea*.

4. As DYNAMICSDM functions are flexible and easily applied, we suggest that these tools could be readily applied to other taxa and systems globally.

KEYWORDS
dynamic ecological niche modelling, dynamic species abundance modelling, dynamic species distribution modelling, R package, spatial ecology, statistics: spatial or time-series

1 | INTRODUCTION

Simulating changing species geographical distributions (henceforth abbreviated to 'distributions') is usually carried out via species distribution modelling (SDM), in which species occurrence records are statistically related to environmental conditions (Guisan & Thuiller, 2005). Such conditions are typically represented in SDMs by readily available remote sensing datasets, or from heavily

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extrapolated field data (Baker et al., 2017), which usually represent annual or longer-term averages, and sometimes are poorly temporally matched with species occurrence records. From static SDMs, the drivers of species occurrence can be inferred, and it is assumed that by applying these relationships over space and time, patterns of distribution suitability can be projected, and some have even used this information to project distribution changes (Elith et al., 2010). Therefore, SDMs have become fundamental tools for, amongst other topics, biogeographic, evolutionary and applied-ecological research to inform biodiversity and species management (Zimmermann et al., 2010).

To predict sedentary species distributions, ecological theory and empirical data support the use of long-term (e.g. multi-decade), averaged climate variables (Elith & Leathwick, 2009). However, these data have been shown to be inadequate for simulating rapidly changing species distributions that are driven by short-term (e.g. annual and even sub-annual) ecoclimatic conditions (Bateman et al., 2012; Fernandez et al., 2017). Moreover, recent studies have demonstrated an improvement in SDM accuracy and precision by incorporating temporally dynamic explanatory variables when modelling distributions of mobile species (Abrahms et al., 2019; Reside et al., 2010) and in landscapes with high inter-annual environmental variability (Andrew & Fox, 2020; Fernandez et al., 2017).

Yet, to date, examples of dynamic SDMs remain scarce. Static or long-term average explanatory variables continue to be employed, even when modelling distributions of species that are highly mobile and responsive to short-term conditions, including birds (Williams et al., 2017), mammals (Wieringa et al., 2021) and insects (Kimathi et al., 2020). This is despite the availability of high spatiotemporal resolution, remote-sensed datasets for numerous environmental variables, from which dynamic explanatory variables can be derived. Utilisation of such datasets is rare probably due to a combination of the more ready-availability of static datasets, the associated analytical packages available, and the perceived added computational overheads of dynamic modelling with high resolution datasets.

Moreover, these barriers are likely to be exacerbated by existing SDM tools that are not optimised for incorporating temporally dynamic explanatory variables. Many SDM functions in R packages lack functionality for explicit consideration of the temporal dimension at key modelling stages. For instance, when modelling with temporally dynamic explanatory variables, temporal biases in occurrence datasets could over- or under- represent conditions at a given time and impact SDM performance. However, existing R package functions typically only account for spatial biases, offering tools to spatially thin records (Aiello-Lammens et al., 2015) or generate spatial buffered background points (Thuiller et al., 2016). Without appropriate tools, our ability to generate spatiotemporally dynamic SDMs is limited. The Spatiotemporal Observation Annotation Tool's RSTOAT package (https://mol.org) can extract spatiotemporally buffered data for species occurrence records, but lacks the functions for developing and projecting dynamic SDMs with these data. Here, we present DYNAMICSDM, an R package that includes user-friendly and flexible functions for extracting and incorporating dynamic explanatory variables into species distribution models and projecting distribution patterns at high spatiotemporal resolution.

2 | PACKAGE OVERVIEW

The main features of DYNAMICSDM functions are:

- **Dynamism**: Fill gaps in existing static SDM package tools to account for both spatial and temporal dimensions at key modelling stages.
- **Flexibility**: Function arguments are highly flexible to target methods to the species and environment of interest.
- **Computer-friendly**: Explanatory variable extraction functions utilise Google Earth Engine and Google Drive to minimise computing power and storage demands.
- **Compatibility**: Function inputs and outputs can be used interchangeably with other SDM packages.

The DYNAMICSDM package workflow is presented in Figure 1 and the included functions are detailed in the following section. Table 1 outlines the novel functionality of DYNAMICSDM functions for generating high spatiotemporal resolution SDMs compared to existing SDM R packages.

3 | RESPONSE DATA

3.1 | Clean and filter species occurrence data

We provide three functions that encompass the spatial and temporal dimension when checking that species occurrence records match the study's scope and quality requirements. First, *spatiotemp_check* checks the formatting, completeness and validity of record coordinates and dates, with optional use of package COORDINATECLEANER for additional spatial checks (Zizka et al., 2019). Second, *spatiotemp_extent* excludes records outside a given spatial and temporal extent, typically dictated by the study's scope or the coverage of environmental datasets. Third, *spatiotemp_resolution* filters records by a specified spatial and temporal resolution (e.g. dates must be given to daily resolution). As DYNAMICSDM functions require occurrence data in a standardised format, *convert_gbif* transforms records from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/) into this format.

3.2 | Assess and account for spatial and temporal biases

spatiotemp_bias assesses spatial and temporal biases in occurrence records, which are prevalent due to various factors including
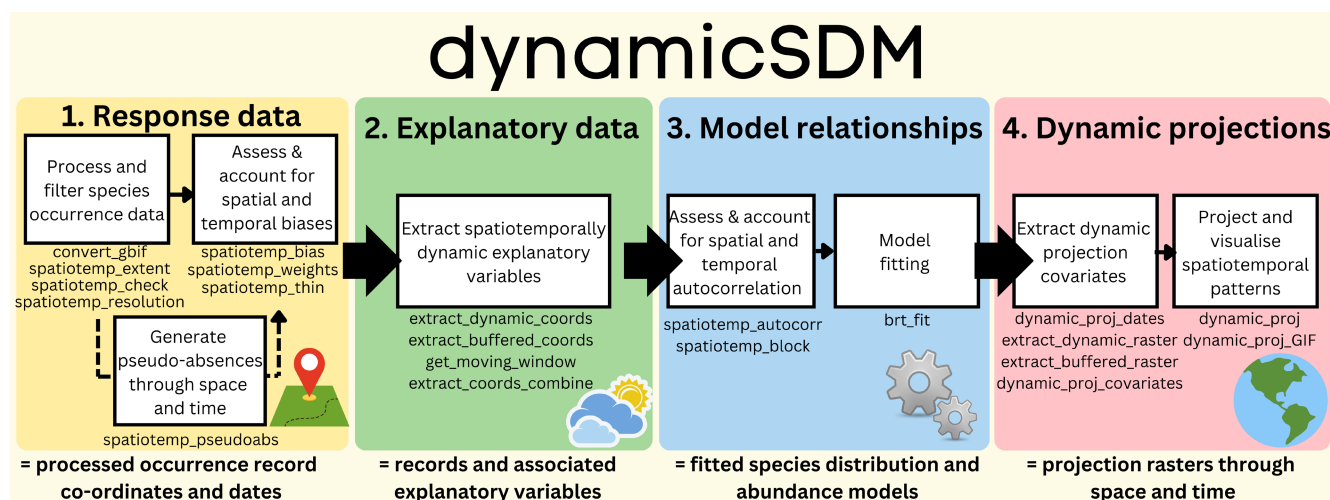
FIGURE 1 Overview of DYNAMICSDM package functions across species distribution modelling (SDM) stages. (1) Response data; functions for filtering species occurrence records by spatiotemporal quality, extent and resolution, generating pseudo-absence dates and co-ordinates, and exploring spatiotemporal biases in response data. (2) Explanatory data; functions for extracting spatiotemporally buffered explanatory variables using Google Earth Engine. (3) Model relationships; functions for fitting SDMs whilst accounting for spatial and temporal autocorrelation. (4) Dynamic projections; functions for generating high resolution projection covariates and projecting dynamic species distribution and abundance patterns.

temporal variation in sampling effort or species detectability. For temporal biases, *spatiotemp_bias* returns a histogram plot of record frequency over time, and performs a chi-squared test for significant difference between the observed temporal distribution of records compared to random. For spatial biases, *spatiotemp_bias* returns a scatter plot of record co-ordinates for visual assessment of clustering and performs a t-test for significant difference between observed nearest neighbour distance and that of random points simulated at the same density. Users can limit *spatiotemp_bias* to a specific area. This may improve the reliability of bias assessments for range-shifting species where uneven record distribution at range peripheries may be underpinned by ecological process and not sampling bias.

Multiple correction methods exist for spatial bias, including spatial thinning of records (Aiello-Lammens et al., 2015) or weighting by sampling effort (Stolar & Nielsen, 2015). We adapted these methods for temporal biases. *spatiotemp_thin* temporally thins occurrence records by removing records within a temporal distance of each other. Temporal distance between records can be measured by two methods: absolute number of days, or days apart within the annual cycle. For instance, temporally thinning two records with dates "2010-01-01" and "2015-01-04" by 10 days through the "absolute" method would retain both records, but the "annual cycle" method would remove one. To prevent spatially distant but temporally close records from being excluded, only records within a set grid cell size are temporally thinned. Then, *spatiotemp_thin* thins remaining records by a spatial distance using SPTHIN package functions (Aiello-Lammens et al., 2015). Alternatively, we include the *spatiotemp_weights* function that calculates total sampling events (input data) across a spatial and temporal buffer from each occurrence record.

3.3 | Generate pseudo-absences through space and time

Paucity of species absence records may necessitate the generation of pseudo-absence records or "background" points, which are inferred absences based upon known presence sites. We provide *spatiotemp_pseudoabs* that generates pseudo-absence co-ordinates and dates, either randomly within a spatiotemporal extent or buffer from occurrence records. Following pseudo-absence spatial buffering theory (VanDerWal et al., 2009), temporal buffering could reveal more fine-scale temporal drivers because presence-absence comparisons are at short time scales. Moreover, buffered pseudo-absences may be more suitable because randomly generated pseudo-absences have been shown to inflate SDM performance metrics (Acevedo et al., 2012).

4 | EXPLANATORY DATA

4.1 | Extract spatiotemporally dynamic explanatory variables

Within DYNAMICSDM there are two functions for extracting dynamic explanatory variables using Google Earth Engine (GEE). GEE is a cloud platform developed for remotely processing remote sensing datasets (Figure 2). These functions require the installation of the GEE API R package RGEE (Aybar et al., 2020) and an associated Google Drive account. By utilising GEE and Google Drive, we minimise computing power and storage demands.

extract_dynamic_coords extracts temporally dynamic explanatory variables. Users must input species occurrence records and

TABLE 1 Limitations of existing species distribution modelling R package functions for generating spatiotemporally dynamic SDMs and *DYNAMICSDM* functions to overcome these.

| Stage		Limitation	Examples	dynamicSDM function
1. Response data	Clean and filter species occurrence data	Focus chiefly on record co-ordinates	CoordinateCleaner (Zizka et al., 2019)	Filter by spatial and temporal features. • *spatiotemp_check* • *spatiotemp_extent* • *spatiotemp_resolution*
	Assess & account for biases	Limited to spatial bias	ENMTML (de Andrade et al., 2020). ENMeval (Kass et al., 2021)	Spatial and temporal biases. • *spatiotemp_bias* • *spatiotemp_thin*
	Generate pseudo-absences	Generate pseudo-absences co-ordinates only	biomod2 (Thuiller et al., 2016) megasdm (Shipley et al., 2022)	Generate pseudo-absence co-ordinates and dates. • *spatiotemp_pseudoabs*
2. Explanatory data	Extract explanatory variables	Static variables at record co-ordinate	dismo (Hijmans et al., 2017)	Extract across spatial and temporal buffers. • *extract_dynamic_coords* • *extract_buffered_coords*
3. Model relationships	Assess & account for autocorrelation	Limited to spatial autocorrelation	ecospat (Di Cola et al., 2017)	Spatial and temporal autocorrelation. • *spatiotemp_autocorrelation* • *spatiotemp_block*
4. Dynamic projections	Project and visualise spatiotemporal patterns	Annotate occurrence records onto spatiotemporally dynamic conditions.	rstoat by Map of Life (https://mol.org).	Project species distribution and abundance models onto dynamic conditions. • *dynamic_proj*
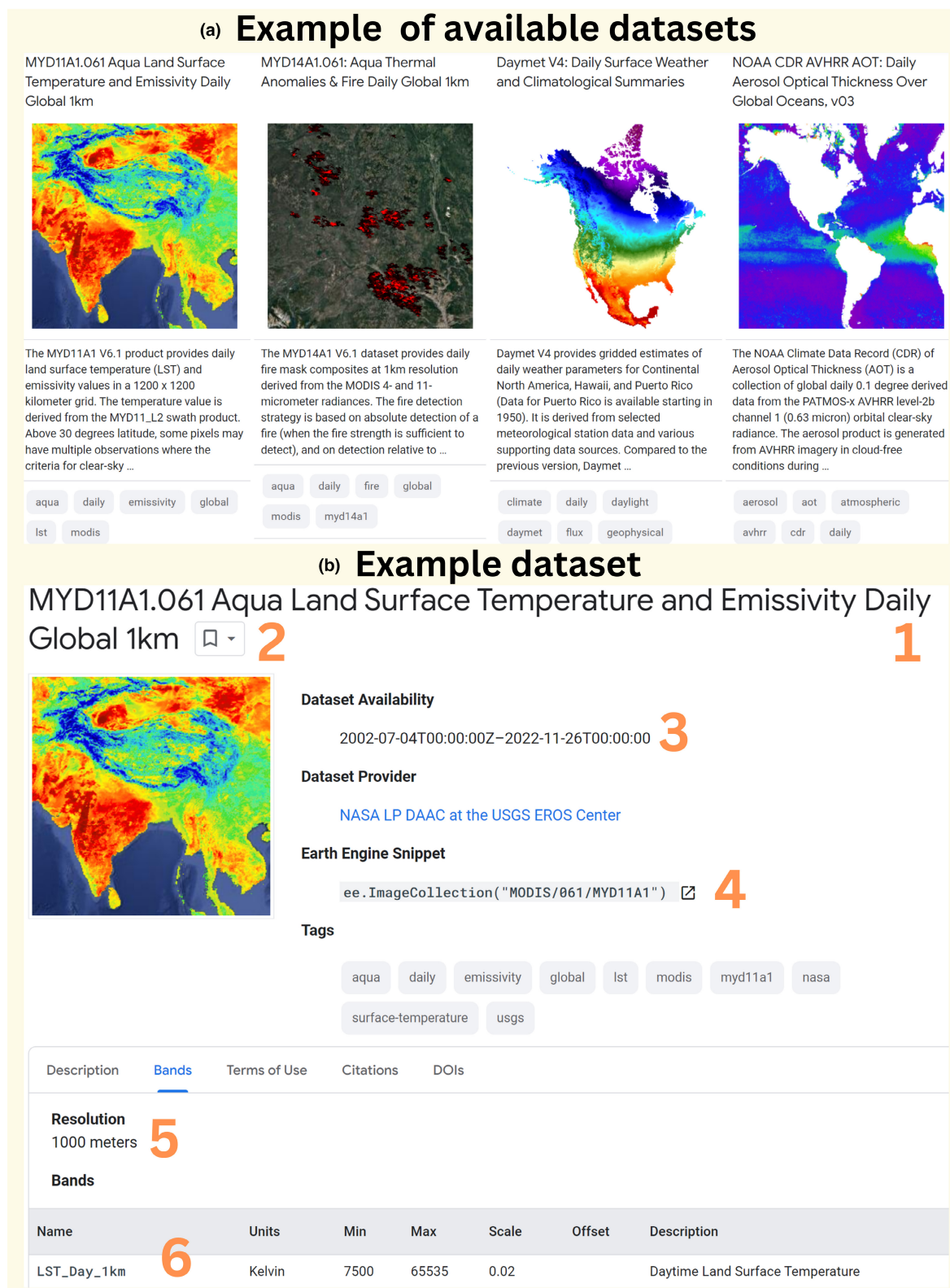
FIGURE 2 Google Earth Engine catalogue snapshots illustrating examples of remote sensing datasets available (a) and a dataset catalogue page (b). Numerical labels indicate dataset features: 1, temporal resolution; 2, spatial extent; 3, temporal extent; 4, dataset name; 5, spatial resolution; and 6, band names. See https://developers.google.com/earth-engine/datasets/catalog for available datasets.

specify the variable through highly flexible arguments (Table 2). The function iterates through each record's co-ordinate and date, submitting the request to GEE for remote processing and exporting returned data. Function speed will depend on user's internet connection, the spatiotemporal resolution of extracted data and the number of occurrence records. Output for

TABLE 2 Arguments for the *DYNAMICSDM* function *extract_dynamic_coords* to extract a temporally dynamic explanatory variable for each species occurrence record. Example input would extract MODIS mean land surface temperature across the 10 days prior to each occurrence record.

Arguments	Description	Example
datasetname	Google Earth Engine dataset catalogue name	"MODIS/061/MOD11A1"
bandname	Name of the dataset band	LST_Day_1km
spatial.res.metres	Spatial resolution in metres for data extraction	1000
temporal.res	Temporal resolution in days to calculate the variable across	14
temporal.direction	Direction from record date to calculate across ("**prior**" or "**post**")	Prior
GEE.math.fun	Mathematical function to compute across the period.	Mean
varname	Unique variable name.	"mean_two_week_temp"

multiple variables can be combined into one data frame using *extract_coords_combine*.

Additionally, we provide *extract_buffered_coords* for extracting temporally and spatially buffered explanatory variables. Spatial buffering allows explanatory variables to represent the suitability or connectivity of environmental variables in the area surrounding the occurrence record. Such variables could better explain distribution patterns in dynamic landscapes than variables correlated to the co-ordinate alone. Therefore, *extract_buffered_coords* requires a spatial buffer size in the form of a "moving window" matrix, which specifies the neighbourhood of cells to calculate the variable across (e.g. three by three matrix calculates the variable across the eight surrounding cells plus the cell the record falls within). The matrix is required because *extract_buffered_coords* utilises the *focal* function in package RASTER (Hijmans et al., 2015) to standardise the calculation and improve projection raster generation time. If the traditional approach of a circular buffer from record co-ordinates is used, then generating high resolution projection rasters can be computationally heavy. The "moving window" matrix size will vary with radial distance of interest and the resolution of environmental data, so we include *get_moving_window* that calculates an optimal matrix by balancing these factors.

5 | MODEL RELATIONSHIPS

5.1 | Assess and account for spatial and temporal autocorrelation

spatiotemp_autocorr tests explanatory data for spatial and temporal autocorrelation, where samples taken closer in space and time are more similar than those more distantly sampled. For temporal autocorrelation, *spatiotemp_autocorr* returns a scatterplot of the relationship between the variable at consecutive observations and tests for significant correlation. For spatial autocorrelation, the function returns Moran's *I* test statistic. To account for spatial autocorrelation in SDMs, blocking is an established method that involves splitting occurrence data into sampling units based upon non-contiguous ecoregions, and grouping these into spatially disaggregated blocks of approximately equal sample size, within which the mean and

range of covariate data are similar (Bagchi et al., 2013). Following this, blocks are left out in turn in a jack-knife approach for model fitting and testing. *spatiotemp_block* adapts this approach to account for temporal autocorrelation by splitting records into sampling units by a temporal step too (e.g. year).

5.2 | Model fitting

To model the relationships between species occurrence and dynamic conditions, we include *brt_fit* for fitting Boosted Regression Tree models using the *gbm.fit* algorithm from GBM R package (Greenwell et al., 2019). *brt_fit* takes optional arguments, including for fitting jack-knife models to spatiotemporal blocks and weighting records by spatiotemporal sampling effort. We include *brt_fit* only for completeness as an SDM package. We suggest *DYNAMICSDM* could be easily integrated with alternative modelling approaches because pre-modelling functions generate a simple response and explanatory dataset, and post-modelling functions accept various model types.

6 | DYNAMIC PROJECTIONS

6.1 | Extract dynamic projection covariates

The *dynamic_proj_dates* function generates dates at given intervals within an extent. Then *extract_dynamic_raster* and *extract_buffered_raster* functions iterate through each date and extract variable rasters at a given extent and resolution. To minimise storage demands, these rasters are stored on Google Drive. *dynamic_proj_covariates* stacks rasters for each date and exports either data frames or raster stacks.

6.2 | Project and visualise spatiotemporal patterns

The *dynamic_proj* function projects species distribution and abundance models onto each covariate data frame or stack and exports projection rasters. To visualise spatiotemporal patterns, we include *dynamic_proj_GIF* that combines projections into an animated GIF.

7 | EXAMPLE—THE RED-BILLED QUELEA *QUELEA QUELEA*

We illustrate the application of DYNAMIC*SDM* to model the highly variable intra- and inter-annual distribution and abundance of the granivorous and nomadic weaver bird, the red-billed quelea *Quelea quelea*; a major pest of small grain cereals in sub-Saharan Africa.

7.1 | Response data

Species occurrence and abundance data were collated from GBIF (Gbif Occurrence Download, 2021) and pest control organisations (Table S1). Occurrence data were filtered to exclude records containing anomalous or missing values using *spatiotemp_check*. Using *spatiotemp_resolution*, records not given to a spatial resolution of four decimal places or a temporal resolution that was >1-day were excluded due to being of an inadequate resolution to study intra-annual, local-scale distribution patterns. Then *spatiotemp_extent* filtered occurrence data to 2001–2017, the temporal extent of explanatory datasets, and the spatial extent of southern Africa to

focus solely on the subspecies *Q. quelea lathamii* (Figure 3). Paucity of absence records necessitated pseudo-absence generation using *spatiotemp_pseudoabs*, which randomly generated pseudo-absence co-ordinates within a 250-500km spatial buffer and dates within a 6–12week buffer. Buffer sizes were informed by quelea movement capabilities (Elliott, 1990) and typical rates of change in their habitat (Cheke et al., 2007). Spatial and temporal biases in occurrence records were detected by *spatiotemp_bias*. Therefore, *spatiotemp_weights* summed e-Bird records (Auer et al., 2022 https://ebird.org) across a 14day buffer and 100km radius from each record. These were transformed into scaled weights for model fitting. Buffer sizes were chosen to reflect the spatiotemporal scale of avian sampling bias in southern Africa. Occurrence data were split into breeding or roosting life-cycle stages for separate modelling (Supplementary Materials 1).

7.2 | Explanatory data

For each record, explanatory variables were extracted using *extract_dynamic_coord* and *extract_buffered_coord*, which represented short-term (8-week) and longer-term (52-week) weather conditions,
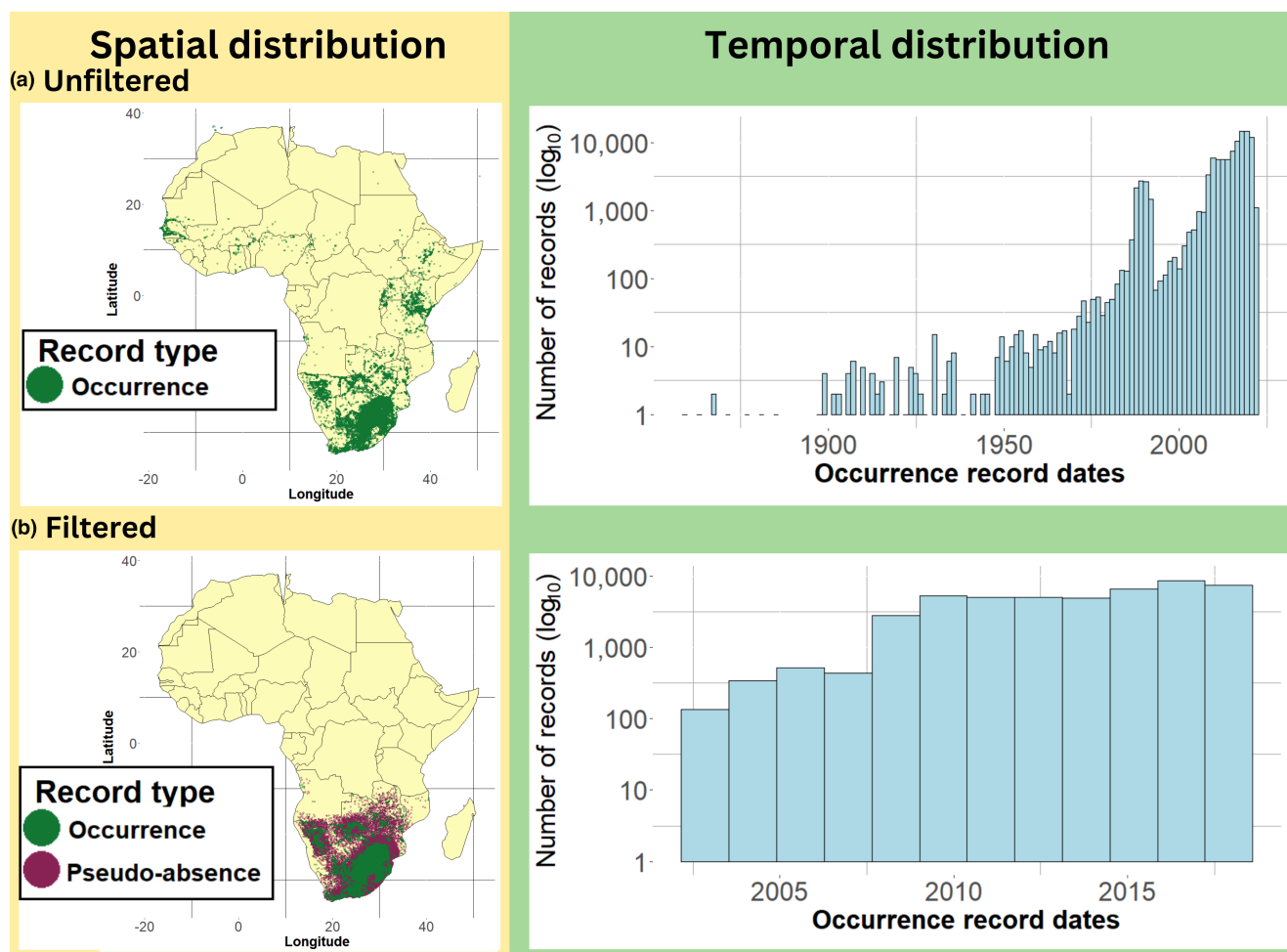

FIGURE 3 Spatiotemporal distribution of red-billed quelea *Quelea quelea* occurrence records a) before filtering (N = 342,434) and b) after filtering (N = 66,740) using DYNAMIC*SDM* response data functions. Purple points represent spatiotemporally buffered pseudo-absence records (N = 66,740) generated with function *spatiotemp_pseudoabs*.

TABLE 3 Dynamic explanatory variables in red-billed quelea *Quelea quelea* species distribution and abundance models. Accessible area is a "moving window" matrix matching quelea's 100km dispersal radius generated by DYNAMICSDM function *get_moving_window.*

Type	Variable	Description
Environmental	Precipitation	Precipitation sum in 8 and 52 weeks prior
	Temperature	Temperature mean and standard deviation in 8 and 52 weeks prior
	Productivity	Productivity mean in 8 weeks prior
Resource	Surface water	Total annual land cover '*water bodies*' cells within accessible area
	Nesting trees	Total annual land cover '*deciduous tree*' cells within accessible area
	Habitat connectivity	Total suitable habitat ('*grassland*' and '*cereal cropland*') annual land cover cells within accessible area
	Seed availability	Total grass and crop seed available within accessible area, derived from vegetation phenology

and the availability of resources governing quelea distribution and abundance (Ward, 1971; Table 3). Spatial buffer size was generated by *get_moving_window* using quelea's 100km dispersal radius to access resources (Elliott, 1990). Variable selection and extraction is detailed in Supplementary Materials 2.

7.3 | Model relationships

spatiotemp_autocorr revealed significant spatial and temporal autocorrelation in explanatory variable data. Therefore, *spatiotemp_block* split records into six blocks by record year and contiguous sections of a terrestrial ecoregion in southern Africa for jack-knife model fitting using function *brt_fit* (model details in Supplementary Materials 3).

7.4 | Dynamic projections

dynamic_proj_dates generated dates at monthly intervals for a 5 year period (2013–2017). Rasters for each variable were extracted to Google Drive using *extract_dynamic_raster* and *extract_buffered_raster*
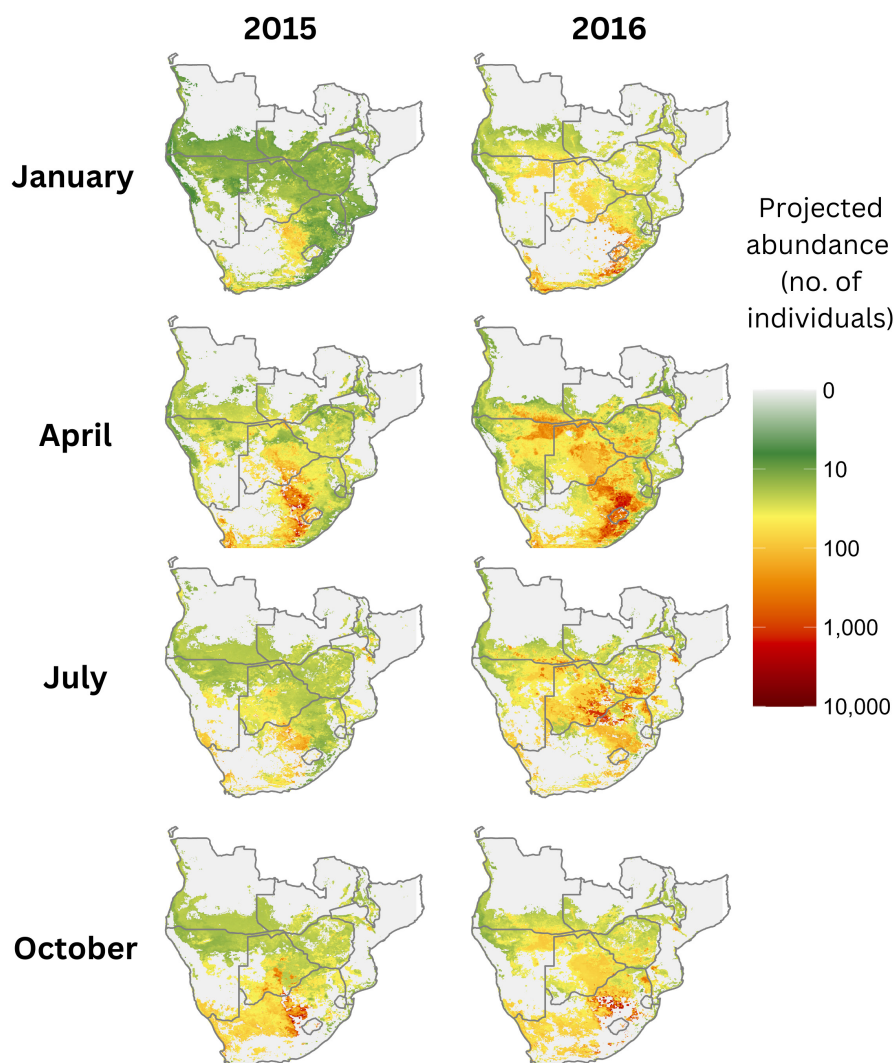

FIGURE 4 Projected intra- and inter-annual distribution and abundance of red-billed quelea *Quelea quelea* in southern Africa. Coloured cells indicate projected quelea presence (distribution suitability over 0.5) and the colour gradient represents projected quelea abundance in these cells (number of individuals, $\log_{10}$ scale).

and then combined into data frames by *dynamic_proj_covariates*. Using *dynamic_proj* a binary distribution was projected onto covariates and then projected abundance was stacked onto positive occurrence cells (Figure 4, Supplementary Materials 4). The maximum projected abundance across life-cycle stages was taken to produce a single projection for each month. *dynamic_proj_GIF* generated a GIF to visualise the intra- and inter- annual distribution suitability and abundance patterns of quelea (Supplementary Figures S1 and S2). For comparison, we also fitted and projected models using long-term average ecoclimatic variables (Supplementary Materials 5).

8 | CONCLUSION

Overall, *DYNAMICSDM* provides users with flexible and easily applied tools to model the dynamic distributions and abundances of species worldwide and advance SDM-based research.

AUTHOR CONTRIBUTIONS
Rachel Dobson wrote the R package and conducted the package tests. All authors wrote the package website and function documentations; Rachel Dobson led the manuscript writing, and all authors wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interests.

PEER REVIEW
The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14101.

DATA AVAILABILITY STATEMENT
Data and code from this manuscript's case studies are archived through Zenodo at https://doi.org/10.5281/zenodo.7670393 (Dobson et al., 2023).

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SUPPORTING INFORMATION

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

Supplementary Figure S1. GIF of projected intra- and inter-annual distribution suitability for redbilled quelea *Quelea quelea* in southern Africa at monthly intervals across a 5 year period (2013–2017), created using R package DYNAMICSDM projection functions. Distribution suitability ranges between 0, representing no suitability for quelea and 1, representing the highest projected suitability for quelea.

Supplementary Figure S2. GIF of projected intra- and inter-annual abundance for red-billed quelea *Quelea quelea* in southern Africa at monthly intervals across a 5 year period (2013–2017), created using R package DYNAMICSDM projection functions. Coloured cells indicate projected quelea presence (distribution suitability over 0.5) and the colour gradient represents projected quelea abundance (number of individuals, $\log_{10}$ scale) in these cells.

Supplementary Figure S3. Projected distribution suitability and abundance of red-billed quelea *Quelea quelea* in southern Africa onto long-term average or static ecoclimatic variables. (a) Distribution suitability, ranges between 0, representing no suitability for quelea and 1, representing the highest projected suitability for quelea. (b) Abundance, coloured cells indicate projected quelea presence (distribution suitability over 0.5) and the colour gradient represents projected quelea abundance (number of individuals, $\log_{10}$ scale) in these cells.

Supplementary Materials 1. Response data.

Supplementary Materials 2. Explanatory data.

Supplementary Materials 3. Model relationships.

Supplementary Materials 4. Dynamic projections.

Supplementary Materials 5. Static projections.