

A curated list of R packages for ecological niche modelling

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ABSTRACT

The R language provides most applications (packages) currently available for ecological niche modelling. In the last few years, these packages have increased substantially. There are now numerous packages for computing ecological niche models (ENMs) with different algorithms, comparing species niches and niche models, creating virtual species, getting and preparing species and related environmental data, filtering species records, and evaluating models, amongst other tasks. This profusion of package options may be daunting for both beginners and more experienced R users. Here we provide an organised and annotated list of available packages for each task. We present a concise history of the creation of these packages, we briefly describe what each package does, and we discuss whether the current set of R packages covers all the necessities for modelling species' ecological niches. This list will be accessible and updated over time on a dedicated website.

1. Introduction

Ecological niche models (ENMs), which are closely related to species distribution models (SDM), are empirical or mathematical estimations of a species' ecological niche (Sillero et al., 2021). ENMs are statistical methods or theoretically derived response surfaces that relate physiological or distribution data to environmental variables, to describe and/or predict species distributions (Franklin, 2010; Peterson et al., 2011; Sillero, 2011; Guisan et al., 2017; Sillero et al., 2021). ENMs can be calculated with statistical software (e.g. SPSS, Statistica), geographical information systems (e.g. ArcGIS, QGIS, DIVA-GIS), or with dedicated graphical user interface (GUI) software (e.g. OpenModeller, ModEco, Maxent, Biomapper, Wallace, ShinyBiomod). Traditional statistical software with a GUI can run an ENM (for example, GLM or GAM) if the species and environmental data are compiled as a table. Some modelling algorithms purely designed for ENMs, such as Maximum Entropy (Phillips et al., 2006, 2017) or Ecological Niche Factor Analysis (ENFA; Hirzel et al., 2002), are not available in traditional statistical programs but in dedicated ones.

Some dedicated programs offer modelling solutions with all stages of the modelling process. ModEco (Guo and Liu, 2010) and OpenModeller (Enrique et al., 2009) are stand-alone programs available for some

operating systems such as Microsoft Windows. ModEco integrates several modelling tools within a GIS framework: algorithms (Support Vector Machines, Bioclim, Domain, Generalised Linear Model, Maximum Likelihood Classification, Artificial Neural Network, Rough Set, Maximum Entropy, Classification Trees, Ensemble Model), data management and visualisation, feature analysis, model training and prediction, and accuracy assessment. OpenModeller includes tools for sampling points, modelling, evaluating and projecting models into different environmental scenarios. Several algorithms are available as plugins: Bioclim, Domain, Mahalanobis Distance, GARP, Maxent, ENFA and Support Vector Machines.

Maxent is the java software that runs the Maximum Entropy algorithm (Phillips et al., 2017). Biomapper is the software that runs ENFA (Hirzel et al., 2002). Wallace (Kass et al., 2018) is a modular Shiny platform that guides the user through a complete modelling process, making parameter choices explicit, from data acquisition to plotting model predictions on an interactive map. ShinyBiomod (Ondo et al., 2019) is another user-friendly Shiny application that uses the R modelling package *biomod2* (Thuiller et al., 2009, 2012). Some applications are built as plugins for other programs. For example, SDMtoolbox is a Python-based toolbox for ArcGIS that includes functions for modelling pre and post-processing tasks (Brown, 2014; Brown et al.,

Abbreviations: ENM, Ecological niche model; GUI, Graphical user interface; ENFA, Ecological Niche Factor Analysis; SDM, Species distribution model; GIS, Geographical Information System; FOSS, Free Open Source Software; CRAN, Comprehensive R Archive Network.

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2017; <http://www.sdmtoolbox.org/>), or Maxent Model, a QGIS plugin to preprocess input data in Maxent (<https://geoinnova.org/plugin/maxent/>). Maxent, Wallace, SDMTToolBox and ShinyBiomod are updated regularly.

ENMs can be also calculated with programming languages, such as Python and R. Python is a high-level, interpreted, general-purpose programming language (Van Rossum and Drake, 1995). It supports multiple programming paradigms, including structured, object-orientated and functional programming. R is a programming language for statistical computing with graphical capacities (R Core Team, 2022). R is widely used amongst data scientists and statisticians to analyse data and develop statistical software (Kabacoff, 2015). Both Python and R are free and open-source software (FOSS), allowing users to create packages that augment or complement existing functions.

R is one of the most used FOSS, thanks to its ease of use, versatility, and object-orientated framework. Indeed, users have created thousands of packages. On 28/10/2022, CRAN, the main repository of R packages, hosted 18,761 packages (<https://cran.r-project.org/web/packages/>), a number that continues to increase over the years. The field of biodiversity modelling is not an exception. Many packages can be directly or indirectly used for modelling species' ecological niches and all related pre- and post-processing tasks.

Here we provide an organised list of R packages for ecological niche models. We divided the list according to the four main stages of the modelling process (Sillero et al., 2021): (1) data collection and preparation; (2) model calculation; (3) model evaluation and validation; and (4) model application. We start our review with a brief description of the development of R packages for ENMs over time, followed by the organised list. Finally, we discuss the current state of the universe of R packages for ENMs.

2. Methods

We searched Google Scholar and Web of Science for R packages for ENMs, using the words 'ecological niche model package', 'species distribution package', and 'species distribution model package'. Therefore, we searched for packages whose main aim was to provide functions for one or more of the four steps of the modelling process. We verified that all packages found in these searches were directly related to ENMs. We checked whether each package was available through CRAN and if the package had a development site on GitHub or another similar platform. We considered as release year the first year of the package publication in CRAN, or GitHub if the package is not on CRAN. After obtaining a list of R packages for ENMs, we searched in Google Scholar for the number of citations for each package or paper presenting that package.

3. Results

Our search allowed us to compile a total of 60 R packages for ENMs (Table 1) published since 2007 (Fig. 1). We found 39 packages available through CRAN and 21 currently in development for different purposes (see Table 1). These packages were cited 9664 times, with eighteen cited more than 100 times each, and two (ENMeval and biomod2) more than 1000 times (see Table 2).

Table 1
Summary of R packages for ecological niche models (last search performed at 28/10/2022).

Package main purpose	N	CRAN	In development
Data collection and preparation	18	14	4
Model calculation	24	14	10
Model evaluation and validation	7	6	1
Model application	11	5	6
Total	60	39	21

3.1. A brief history of the development of R packages for ecological niche models

To the best of our knowledge, the first R package with functions for ENMs was *PresenceAbsence* (Freeman and Moisen, 2008), released in 2007. It does not compute models but provides functions for evaluating presence-absence analysis, either ENMs or diagnostic tests. The package calculates the optimal threshold for translating a probability surface into presence-absence maps, such as percentage correctly classified, sensitivity, specificity, and kappa. It also computes the Receiver Operator Characteristic (ROC) curve and the area under the curve (AUC). However, the first R package developed specifically for the field of ENMs was *BIOMOD*, released in 2009 (Thuiller et al., 2003, 2009). A second version, *biomod2*, replaced it in 2012 (Thuiller et al., 2021). Both versions provided several ensemble forecasting methods for ENM algorithms: generalised linear models, generalised additive models, multivariate adaptive regression splines (MARS), classification tree analysis, mixture discriminant analysis, artificial neural networks, generalised boosted models, random forests, and maximum entropy (through java, a method used posteriorly by other R packages). *biomod2* also included a rectilinear envelope algorithm similar to BIOCLIM (Booth et al., 2014).

The *dismo* package, released in 2010 (Hijmans et al., 2021), provides tools for the complete modelling process, from downloading and preparing data to evaluating the models. This package implements presence-only modelling algorithms (Bioclim, Domain, Mahalanobis distance) and a presence-absence algorithm (boosted regression trees). It can also run Maxent by calling Java.

maxlike (Royle et al., 2012), a package released in 2011, implements a maximum likelihood algorithm as an alternative method to the Maximum Entropy (Maxent) algorithm. The *maxlike* algorithm endeavoured to estimate the probability of occurrence from presence-only data (Royle et al., 2012), instead of habitat suitability (but see Osorio-Olvera et al. 2019).

In 2012, besides *biomod2* (Thuiller et al., 2021), several packages were released for obtaining species records (*rgbif*, Chamberlain et al., 2022), calculating distribution and abundance (*Latimer et al., 2006*), analysing model uncertainties (*usdm*; Naimi et al., 2014), and modelling species dispersal (*MigClim*; Engler et al., 2012). *usdm* includes methods from spatial statistics to analyse positional uncertainty (Naimi et al., 2014); it also implemented the Variance Inflation Factor (VIF) to analyse collinearity between variables (Naimi et al., 2014).

Several packages released in 2014 implemented important, often novel additional tasks. These included spatially filtering species records (*spThin*; Aiello-Lammens et al. 2015), generating virtual species (*sdmvspecies*, Duan et al. 2015; *virtualspecies*, Leroy et al. 2016), modelling species range dynamics (*RangeShifter*, Bocedi et al., 2014, G. 2021), and automatically fine-tuning and validating models to determine optimal levels of complexity (*ENMeval*; Muscarella et al., 2014). A new version of *ENMeval* was released in 2021 (Kass et al., 2021). It provides functions for results visualisation, data partition with spatial criteria, model evaluation with cross-validation and null models, and niche overlap from model predictions. The package was originally built for Maxent models, but the current version allows possible extensions for any modelling algorithm. Two other packages released in the same year provided tools for estimating species' ecological niches using kernel interpolators instead of regression-based and machine-learning algorithms: *ecospat* (Di Cola et al., 2017) and *hypervolume* (Blonder et al., 2014) *ecospat* also provides other model-related functions, such as statistical comparison of species niches (using the methods proposed by Warren et al., 2008, 2010), computing ensembles of small models (Breiner et al., 2018), analysing non-analogue climates (Elith et al., 2010, 2011; Mesgaran et al., 2014), and evaluating model performance.

zoon and *SDMTTools* were released in 2015. *zoon* (Golding et al., 2018) provides functions for comparing and diagnosing models. The results can be shared from an online repository. *SDMTTools* (VanderWal et al.,

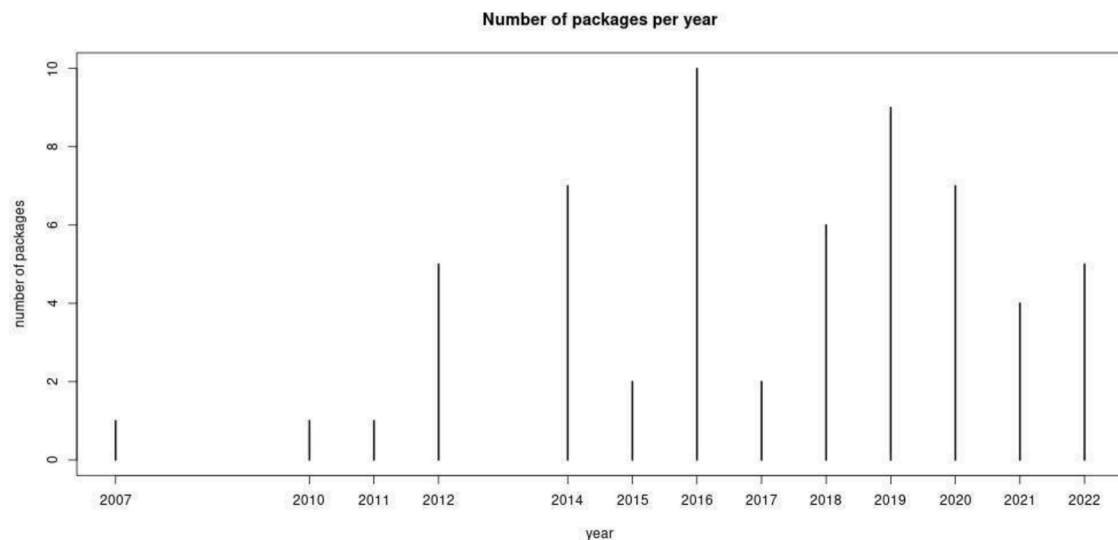


Fig. 1. Increment over time in the number of R packages for ecological niche models.

2015) has tools for post-processing models, including threshold selection, calculating validation and landscape metrics, and tracking distribution changes over time.

Ten packages were published in 2016. *sdm* (Naimi and Araújo, 2016) was the third package, together with *dismo* (Hijmans et al., 2021) and *biomod2* (Thuiller et al., 2012, Thuiller et al., 2021), providing a full set of tools for the four stages of modelling: data preparation, model calculation with several algorithms (GAM, GLM, MARS, SVM, RF, and Maximum Entropy), model evaluation, and model projection. *SDMPlay* (Charlene et al., 2021) also offers functions for the four modelling stages, but only for maximum entropy and boosted regression trees. Another package (*maxnet*) provided a direct R implementation of the maximum entropy algorithm, without the need for calling Java to run the Maxent software outside R. This package, written by the main author of Maxent, uses the package *glmnet* to fit an inhomogeneous Poisson process model, which is equivalent to the maximum entropy algorithm (Phillips et al., 2017). The package *rmaxent* (Baumgartner and Wilson, 2022), which is also Java-free, includes additional functionalities for projecting Maxent models, calculating information criteria (AIC, AICc, BIC) as implemented in Warren et al. (2010), parsing Maxent .lambda files, and estimating MESS (multivariate environmental similarity surface; Elith et al., 2010, 2011). The package *MIAMaxent* (Vollering et al., 2019) provides pre-processing (e.g., variable selection) and evaluation functions for maxent and logistic regression models. *ENIRG* (Cánovas et al., 2016) is an interface for R and GRASS GIS and implements ENFA. *modEva* (Barbosa et al., 2016) provides a varied set of tools for evaluating ENMs, including discrimination and calibration metrics, optimising classification thresholds, and analysing model extrapolation with MESS on data frames (Elith et al., 2010, 2011). *sdmpredictors* (Bosch and Fernandez, 2022) downloads environmental data from different climatic datasets, including terrestrial, marine and freshwater environments: currently WorldClim (Fick and Hijmans, 2017), ENVIREM (Title and Bemmels, 2018), Bio-ORACLE (Tyberghein et al., 2012), MARSPEC (Sbrocco and Barber, 2013) and Freshwater (Domisch et al., 2015). *biogeo* (Robertson et al., 2016) was the first package developed for automatically detecting and correcting errors in species occurrence datasets. It includes functions for assessing data quality of occurrence records, identifying potentially erroneous records in geographical and environmental space, and providing possible alternative positions for those records. Another package focused on the analysis of species occurrences is *red* (Cardoso, 2017), which calculates the Extent of Occurrence, Area of Occupancy, and Red List Index for groups of species. *red* also downloads and pre-processes species occurrences (e.g. thinning and

moving occurrences to the closest non-NA pixel), maps species ranges and calculates Maxent models with *dismo* (Hijmans et al., 2021) package.

Until 2016, R packages related to ENMs focused mainly on correlative algorithms, although *dismo* provides some simple functions for mechanistic models. In contrast, *NicheMapR* was designed specifically for mechanistic niche models, including datasets of micro-climate (Kearney and Porter, 2017, 2020). In addition, *SPEDInstabR* (Guisande et al., 2017) selects environmental variables based on a fluctuation index, which identifies the environmental factors that better discriminate between the conditions in the species' area and those in the background area.

Six packages were released on CRAN in 2018, providing some more interesting functionalities. For instance, *CENFA* (Rinnan and Lawler, 2019) presented a new implementation of ENFA: it includes algorithms for climate- and ecological-niche factor analyses and for visualisation of spatial variability of species sensitivity, exposure, and vulnerability to climate change. Three other packages provided different tools for supporting the modelling process. Here, *rangeModelMetadata* (Merow et al., 2019) catalogues ENMs with hierarchical structures through dictionaries. In this way, communicating and sharing the algorithms and parameters used to compute the models is easier and more accurate. *mopa* (Iturbide et al., 2018) provides functions for transferable models, pseudo-absence data generation, and factor contribution quantification. *fuzzySim* (Barbosa, 2015) includes functions to compute fuzzy versions of species occurrence patterns based on presence-absence data (inverse distance interpolation, trend surface analysis, and prevalence-independent favorability), and pairwise fuzzy similarity amongst species' potential distributions. *fuzzySim* currently has additional functions for data preparation, model consensus and comparison, such as unique abbreviations of species names, gridding (thinning) point occurrence data onto raster maps, converting species lists to presence-absence tables, transposing part of a data frame, selecting relevant variables for models, assessing the false discovery rate, or analysing and dealing with multicollinearity. Finally, *Metrics* (Hammer and Frasco, 2018) provides several metrics for evaluating models calculated with machine learning algorithms, while *bdclean* (Gueta et al., 2018), like *biogeo* (Guisande et al., 2017), provides functions for cleaning and validating species occurrence data.

kuenm (Cobos et al., 2019b) was released in 2019. It is a package for calibrating Maxent models by selecting optimal parameterisations for each study. Therefore, the user can run multiple Maxent models with different conditions and choose the best one. *ESDM* (Woodman et al.,

2019), also released in 2019, is a package for ensemble modelling of species distribution and abundance models. *ESDM* includes a graphical user interface (GUI) built with an R Shiny app. The *MinBAR* package (Rotllan-Puig and Traveset, 2021) estimates the minimum background area by calculating several maxent models with different parameters until determining the best one. *SDMtune* (Vignali et al., 2020) and *sdbenchmark* (Angelov, 2018) provide functions for calculating, selecting and validating models, with several algorithms of machine learning. *SDMselect* includes functions for the selection of covariates and model specifications. *ellipsenm* (Cobos et al., 2019b) and *humboldt* (Brown and Carnaval, 2019) provide advanced functions for running analyses in the environmental space: *ellipsenm* (Cobos et al., 2019a) calculates ellipsoid envelopes, calibrates and selects models, replicates models and projections, and assesses niche overlaps; and *humboldt* (Brown and Carnaval, 2019) analyses the amount of the species' observed environmental space that is truncated by the available environmental space, providing also tools for analysing niche overlap and divergence, and rarefying species occurrence records to reduce survey bias. *CoordinateCleaner* (Zizka et al., 2019) cleans occurrence datasets, similar to *bioge* (Guisande et al., 2017) and *bdclean* (Gueta et al., 2018): it detects geo-referencing and dating imprecisions in a standardised and reproducible way, based on geographical gazetteers and a global database of georeferenced biodiversity institutions to identify records from e.g. horticulture or captivity.

In 2020, the R version of *ENMTTools* (Warren et al., 2010) was finally released (Warren et al., 2021). The *ENMTTools* R package not only provides tools and statistical tests for comparing species niches but also offers a full set of tools for the four modelling stages. *ENMTTools* includes algorithms for presence-background (Maxent, Poisson point process) and presence-absence (GAM, GLM) models, and unique evaluation tools, such as Monte Carlo tests and null models. *ENMTTools* is the only package, to our knowledge, where null models are calculated at the same time as the empirical models, as a parameter of the algorithm function. One important difference with other full-set packages, such as *biomod2* (Thuiller et al., 2021) or *sdm* (Naimi and Araújo, 2016), is that *ENMTTools* has independent functions for each algorithm (similarly to *dismo*, Hijmans et al., 2021), instead of one main model computing function where all algorithms are included as parameters.

ENMTools was not the only full-set package released in 2020: *ENMTools* (de Andrade et al., 2020) provides a single function with all arguments necessary to calculate ENMs, including variable collinearity control, bias control, accessible area delimitation, pseudo-absence allocation, data partition, 13 modelling algorithms (Bioclim, Mahalanobis Distance, Domain, ENFA, GLM, GAM, BRT, Random Forests, SVM, Maximum Entropy with quadratic and linear and default features, Maximum Likelihood, and Gaussian Process), classification thresholds, model evaluation metrics, over-prediction analysis, ensemble modelling, and projections over time and space. In this way, *ENMTools* aims to simplify the entire modelling process by reducing it to a single command.

Five more packages were released in 2020. *blockCV* (Valavi et al., 2019) provides functions for generating spatially or environmentally separated folds for k-fold cross-validation of models. *blockCV* can be used to separate training and test data for other modelling packages. Similarly, *enmSdm* (Morelli et al., 2020) is a complement to *dismo* (Hijmans et al., 2021), with advanced functions for preparing data, training and evaluating *dismo* models, and comparing ecological niches. *embarcadero* (Carlson, 2020) calculates ENMs with Bayesian additive regression trees (BART), including basic model summary statistics and diagnostics, variable importance measures, and plotting. *modleR* (Sánchez-Tapia et al., 2020) provides a modelling workflow based on *dismo*. *ssdm* (Schimtt et al., 2017) calculates potential species richness from a set of stacked individual models.

Four additional packages were released in 2021. *geodata* (Hijmans et al., 2022) downloads geographic and environmental data directly into R, including species occurrences and variables like climate (from

WorldClim), elevation, land use, soil, accessibility, and administrative boundaries. The other three packages (*occAssess*, *sampbias*, and *bRacatus*) provide functions for detecting errors in species occurrence datasets. Specifically, *bRacatus* (Arlé et al., 2021) presents a method to estimate the probability of a georeferenced record being true or false and corresponding to a native or an alien occurrence. It avoids subjective thresholds of data filtering by implementing a probabilistic framework to propagate uncertainties in posterior analyses. On the other hand, *occAssess* (Boyd et al., 2021) and *sampbias* (Zizka et al., 2020) detect geographical biases in species occurrence data.

Finally, five more packages were released in 2022. *flexsdm* (Velazco et al., 2022) is another package providing functions for the four modelling stages. It includes algorithms for presence-background (Maxent) and presence-absence (GAM, GLM, GBM, SVM, RF, ANN) modelling, together with functions for survey bias correction, sampling pseudo-absences and background points, data partitioning, and reducing collinearity in predictors; fitting and evaluating models, ensembles of small models and ensemble models; and prediction, interpolation, and overprediction correction. *itsdm* (Song, 2022) provides functions for modelling presence-only records with isolation forest (iForest) and variations (extended iForest and SCiForest). *mcera5* (Klinges et al., 2022) is the second R package designed for mechanistic models: it includes functions for getting microclimate data from ERA5 climate data. *specieschrom* (Klęparski and Beaugrand, 2022) quantifies niche optimum, breadth and overlap, and identifies the most discriminant combination of environmental variables. *bdc* (Ribeiro et al., 2022) includes functions for merging biodiversity datasets; flagging and removing erroneous occurrence data; cleaning, parsing and harmonizing scientific names; and flagging and correcting inconsistent collection dates.

3.2. An organised list of packages

We present the list of packages in Table 2, organised by the four main modelling steps: data collection and preparation, model calculation, model evaluation and validation, and model application. This list will be curated and frequently updated at <https://sites.google.com/view/sblab/r-packages-for-enms>.

Many packages can tackle more than one aim, but they are placed in our table in only one of the modelling steps, according to its main purpose. We considered the following main purposes in each modelling step: (1) data collection and preparation: compilation of biodiversity and geographical data, species filtering, preprocessing data for models, creating virtual species; (2) model calculation: mechanistic models, correlative models, ensemble modelling, Bayesian models, functions complementary to other packages, Maxent specific, ENFA specific, niche estimation; (3) model evaluation and validation; (4) model application: comparison of models, dispersion, utilities. We indicate in the table the main purpose of each package, followed by a small description, main contributor(s), main reference, CRAN link, and development website (if available).

4. Discussion

The number of packages for ENMs has increased over time. Since 2010, at least one package has been released on CRAN every year, except in 2013. The number of packages will likely continue to increase. Therefore, do we have all the packages we need? Considering our organised list, some functions for ENMs may be redundant. A varied set of ENMs can be computed and validated currently through several packages: *dismo*, *biomod2*, *sdm*, *ENMeval*, *ENMTtools*, *ENMTML*, *flexsdm*, *SDMtune* and *sdmbench* provide multiple algorithms, for presence-absence, presence-background, or presence-only data. *ssdm* (Schmitt et al., 2017) also provides all the necessary functions for computing and validating ENMs, but it is designed specifically to calculate potential species richness from stacked individual ENMs. Several packages for

Table 2

Curated list of R packages for ecological niche models organised by their main purpose.

N	R package	Main purpose	Description	Data collection and preparation		CRAN link	Development site	Citations
				Main contributor(s)	Main reference			
1	sdmpredictors	Geographical data compilation	Functions for getting terrestrial and marine predictors, including WorldClim, ENVIREM, Bio-ORACLE and MARSPEC.	Samuel Bosch; Lennert Tyberghein; Olivier De Clerck; Salvador Fernandez; Lennert Schepers		https://cran.r-project.org/package=sdmpredictors	https://lifewatch.github.io/sdmpredictors/	8
2	geodata	Geographical data compilation	Functions for getting geographic data, including climate, elevation, land use, soil, species occurrence, accessibility, and administrative boundaries.	Robert J. Hijmans; Aniruddha Ghosh; Alex Mandel		https://cran.r-project.org/package=geodata		NA
3	mcera5	Geographical data compilation	Functions for getting microclimate data for mechanistic models from ERA5 climate data.	James P. Duffy Dave Klings Lydia Soifer	Klinges et al., 2022	Not in CRAN	https://github.com/dklinges9/mcera5	0
4	rgbif	Species data compilation	Interface to the Global Biodiversity Information Facility (GBIF) API.	Scott Chamberlain; Damiano Oldoni; Vijay Barve; Peter Desmet; Laurens Geffert; Dan McGlinn; Karthik Ram rOpenSci; John Waller		https://cran.r-project.org/package=rgbif		8
5	spThin	Model preparation	Functions for spatial thinning of species occurrence records.	Matthew E. Aiello-Lammens; Robert A. Boria; Aleksandar Radosavljevic; Bruno Vilela; Robert P. Anderson; Robert Bjornson; Steve Weston	Aiello-Lammens et al., 2015	https://cran.r-project.org/package=spThin		884
6	biogeo	Data preparation	Assessing and improving data quality of occurrence record datasets	Robertson, MP; Visser, V; Hui, C	Robertson et al., 2016	https://cran.r-project.org/web/packages/biogeo/index.html	https://github.com/cran/biogeo	61
7	CoordinateCleaner	Data preparation	Standardised cleaning of occurrence records from biological collection databases		Zizka et al., 2019	https://cran.r-project.org/package=CoordinateCleaner		285
8	bdc	Data preparation and cleaning	Standardising, integrating, and cleaning biodiversity data	Ribeiro, BR; Velazco, SJE; Guidoni-Martins, K; Tessarolo, G; Jardim, Lucas; Bachman, SP; Loyola, R	Ribeiro et al., 2022	https://cran.r-project.org/web/packages/bdc/index.html	https://github.com/brunobrr/bdc/issues	3
9	bRacatus	Data preparation	A method to estimate the accuracy and biogeographical status of georeferenced biological data	Arlé, E; Zizka, A; Keil, P; Winter, M; Essl, F; Knight, T; Weigelt, P; Jiménez-Muñoz, M; Meyer, C	Arlé et al., 2021	https://cran.r-project.org/web/packages/bRacatus/index.html	https://github.com/EduardoArlé/bRacatus	2
10	bdclean	Data preparation	User-friendly biodiversity data cleaning pipeline	Gueta, T; Barve, V; Nagarajah, T; Agrawal, A; Carmel, Y	Gueta et al., 2018	https://cran.r-project.org/web/packages/bdclean/index.html	https://github.com/bd-R/bdclean	17
11	SPEDInstabR	Data preparation	Selection of environmental variables based on a fluctuation index	Cástor Guisande González	Guisande et al., 2017	https://cran.r-project.org/package=SPEDInstabR		30
12	occAssess	Data preparation	Assessing potential biases in species occurrence data		Boyd et al., 2021		https://github.com/robboyd/occAssess/	5
13	sampbias	Data preparation	Quantifying geographic sampling biases in species distribution data	Zizka, A; Antonelli A; Silvestro, D	Zizka et al., 2021	Not in CRAN	https://github.com/azizka/sampbias	25
14	MinBAR	Model preparation	Functions for defining the minimum background area	Xavier Rotllan-Puig Anna Traveset		https://cran.r-project.org/package=MinBAR	https://github.com/xavi-rp/MinBAR	3
15	SDMselect					Not in CRAN		5

(continued on next page)

Table 2 (continued)

N	R package	Main purpose	Description	Data collection and preparation		CRAN link	Development site	Citations
				Main contributor(s)	Main reference			
		Model preparation	Functions for covariate selection and model specifications with cross-validation and forward model selection.	Sébastien Rochette Travis CI			https://github.com/statnmap/SDMSelect	
16	MIAMaxent	Data preparation	Functions for variable transformation and selection, model evaluation and projection training of maximum entropy and standard logistic regression algorithms.	Julien Vollerling; Sabrina Mazzoni; Rune Halvorsen Steven Phillips	Vollerling et al., 2019	https://cran.r-project.org/package=MIAMaxent	https://github.com/julienvollerling/MIAMaxent	28
17	sdmvspecies	Virtual species computation	Functions for creating virtual species	Xiaoquan Kong; Renyan Duan; Minyi Huang	Duan et al., 2015	https://cran.r-project.org/package=sdmvspecies		25
18	virtualspecies	Virtual species computation	Functions for creating virtual species	Boris Leroy; Christine N. Meynard; Celine Bellard; Franck Courchamp; Robin Delsol; Willson Gaul	Leroy et al., 2016	https://cran.r-project.org/package=virtualspecies		165
N	R package	Main purpose	Description	Main contributor(s)	Main reference	CRAN link	Development site	Citations
19	NicheMapR	Model computation	Framework for microclimate and mechanistic niche models.	Michael Kearney; Rafael Schouten; Ilya Maclean	Kearney and Porter, 2017, 2020	Not in CRAN	https://mrke.github.io/ https://github.com/mrke/NicheMapR/	222
20	dismo	Model computation	Algorithms for presence-only (Bioclim, Domain, Mahalanobis distance), presence-background (Maxent), and presence-absence (BRT). Functions for comparing models.	Robert J. Hijmans; Steven Phillips; John Leathwick; Jane Elith	Hijmans et al., 2021	https://cran.r-project.org/package=dismo	https://github.com/rspatial/dismo	564
21	enmSDM	Data preparation Model preparation Model evaluation Model comparison	Complement to dismo. Functions for preparing data, training and evaluating dismo models, and comparing ecological niches.	Adam B. Smith; Ahmed El-Gabbas		Not in CRAN	https://github.com/adamlilith/enmSdm	NA
22	biomod2	Model computation	Algorithms for presence-only (SRE), presence-background (Maxent) and presence-absence (GAM, GLM, BRT, ANN). Functions for calibration and evaluation, ensemble of models, ensemble forecasting and visualisation.	Wilfried Thuiller; Damien Georges; Maya Gueguen; Robin Engler; Frank Breiner	Thuiller et al., 2003, 2009, W 2021	https://cran.r-project.org/package=biomod2		1916
23	sdm	Model computation	Algorithms for presence-background (Maxent) and presence-absence (GAM, GLM, MARS, SVM, RF). Functions for ensemble modelling, calibration and evaluation, and projections over time and space.	Babak Naimi; Miguel B. Araujo	Naimi and Araújo, 2016	https://cran.r-project.org/package=sdm		473
24	ENMTools							68

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Table 2 (continued)

N	R package	Main purpose	Description	Data collection and preparation		CRAN link	Development site	Citations
				Main contributor(s)	Main reference			
		Model computation Model comparison	Algorithms for presence-background (Maxent) and presence-absence (GAM, GLM). Functions for Monte Carlo tests and null models.	Dan Warren; Nick Matzke; Marcel Cardillo; John Baumgartner; Linda Beaumont; Nicholas Huron; Marianna Simoes; Teresa Iglesias; Russell Dinnage	Warren et al., 2021	https://cran.r-project.org/package=ENMTools	https://github.com/danlwarren/ENMTools	
25	FLEXSDM	Model preparation Model computation	Algorithms for presence-background (Maxent) and presence-absence (GAM, GLM, GBM, SVM, RF, ANN). Functions for sampling bias correction, sampling pseudo-absences and background points, data partitioning, and reducing collinearity in predictors; fitting and evaluating models, ensembles of small models and ensemble models; models' predictions, interpolation and overprediction correction.	Santiago José Elías Velazco; Miranda Brooke Rose; André Felipe Alves de Andrade; Ignacio Minoli; Janet Franklin	Velazco et al., 2022	Not in CRAN		0
26	SDMtune	Model computation	Functions for training and testing of Maxent, Random Forest, neural networks, and BRT.	Sergio Vignali Arnaud Barras Veronika Braunsch		https://cran.r-project.org/package=SDMtune		43
27	sdbench	Model preparation Model computation	Functions for compiling species occurrence and environmental data; spatial data partitioning; and machine learning algorithms.	Boyan Angelov		Not in CRAN	https://github.com/boyanangelov/sdbench	5
28	kuenm	Support for Maxent	Functions for model calibration of Maxent models by selection of optimal parameterizations for each study.	Marlon E. Cobos Luis Osorio	M.E. Cobos et al., 2019	Not in CRAN	https://github.com/marloncobos/kuenm	294
29	rmaxent	Maxent implementation	Implementation of tasks related to Maxent in models R.	John Baums		Not in CRAN	https://github.com/johnbaums/rmaxent	13
30	maxnet	Maxent implementation	Fitting 'Maxent' models with 'glmnet'.	Steven Phillips		https://cran.r-project.org/package=maxnet		NA
31	ENiRG – Ecological Niche in R-GRASS – ENFA	Model computation	Interface for R and GRASS to overcome issues when working with large data sets. Functions from rgrass7 package.	Fernando Canovas; Chiara Magliozzi; Jose Antonio Palazon-Ferrando; Frederico Mestre; Mercedes Gonzalez-Wanguemert	Cánovas et al., 2016	Not in CRAN	https://rdrr.io/cran/ENiRG/man/ENiRG-pac-kage.html	12
32	maxlike	Model computation	Maxlike implementation, a likelihood-based approach for modelling with presence-only data. Maxlike yields estimates of occurrence probability.	Richard Chandler; Andy Royle; Roeland Kindt	Chandler and Royle, 2013; Fitzpatrick et al., 2013	https://cran.r-project.org/package=maxlike		3
33	SDMPlay	Model computation	Algorithms for presence-background (Maxent) and	Guillaumot Charlene; Martin Alexis; Eleaume	Guillaumot et al., 2017	https://cran.r-project.org/package=SDMPlay		2

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Table 2 (continued)

N	R package	Main purpose	Description	Data collection and preparation		CRAN link	Development site	Citations
				Main contributor(s)	Main reference			
34	hSDM – Hierarchical Bayesian Species Distribution Models	Model computation	presence-absence (BRT). Functions for calibration, evaluation, and visualisation. Designed specifically for marine environments. Functions for estimating parameters of hierarchical Bayesian distribution and abundance models.	Marc; Danis Bruno; Saucedo Thomas Ghislain Vieilledent; Matthieu Autier; Alan E. Gelfand; Jérôme Guélat; Marc Kéry Andrew M. Latimer; Cory Merow; Frédéric Mortier; John A. Silander Jr.; Adam M. Wilson; Shanshan Wurinnan	Latimer et al., 2006	https://cran.r-project.org/package=hSDM		3
35	CENFA – Climate and Ecological Niche Factor Analysis	Model computation	Algorithms for climate- and ecological-niche factor analyses. Functions for visualisation of spatial variability of species sensitivity, exposure, and vulnerability to climate change. It supports processing of large files and parallel methods.	D. Scott Rinnan	Rinnan and Lawler, 2019	https://cran.r-project.org/package=CENFA		33
36	ENMTML	Model computation	ENMTML provides a single function with all arguments necessary to calculate ENMs: variable collinearity control, bias control, accessible area delimitation, pseudo-absence allocation, data partition, several algorithms, thresholds, evaluation metrics, over-prediction, ensemble modelling, and projections over time and space.	André F.A. Andrade; Santiago J.E. Velazco; Paulo De Marco	de Andrade et al., 2020	Not in CRAN	https://andrefaa.github.io/ENMTML/	59
37	embarcadero	Model computation	Functions to calculate ENMs with Bayesian additive regression trees (BARTs), including basic model summary statistics and diagnostics, variable importance measures, and plotting.	Colin J. Carlson; Seth Musker	Carlson, 2020	Not in CRAN	https://github.com/cjcarlson/embarcadero/	34
38	modleR	Model computation	A workflow for ecological niche models based on 'dismo'.	Andrea Sánchez-Tapia, Sara Ribeiro Mortara, Diogo Souza Bezerra Rocha, Felipe Sodré Mendes Barros, Guilherme Gall, Martinez Ferreira de Siqueira	Sánchez-Tapia et al., 2020	https://cran.r-project.org/package=modleR	https://github.com/Model-R/modleR	6
39	hypervolume	Niche calculation	Functions for estimating shapes and volumes of high-dimensional niches using kernel density estimation, support vector machine delineation, and convex hulls.	Benjamin Blonder; David J. Harris	Blonder et al., 2014	Not in CRAN		482
40	ssdm	Niche calculation	Calculates potential species richness from	Sylvain Schmitt Robin Pouteau	Schmitt et al., 2017			96

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Table 2 (continued)

N	R package	Main purpose	Description	Data collection and preparation		CRAN link	Development site	Citations
				Main contributor(s)	Main reference			
41	itsdm	Model calculation	stacked individual ENMs. Functions for presence-only species distribution modelling with isolation forest (iForest) and its variations, such as Extended isolation forest and SCiForest.	Dimitri Justeau Florian de Boissieu Lukas Baumbach Philippe Birnbaum Lei Song; Lyndon Estes	Song, 2022	https://cran.r-project.org/package=SSDM https://cran.r-project.org/package=itsdm		NA
N	R package	Main purpose	Description	Model evaluation and validation Main contributor(s)	Main reference	CRAN link	Development site	Citations
42	PresenceAbsence	Model evaluation	Functions for evaluating presence-absence analysis, either ENMs or diagnostic tests. Functions for calculating thresholds and AUC.	Elizabeth Freeman	Freeman and Moisen, 2007	https://cran.r-project.org/web/packages/PresenceAbsence/index.html		465
43	ENMeval	Model evaluation	Functions for calculating models with all combinations of settings, partition data spatially, cross validation evaluation, model selection based on balance goodness-of-fit and model complexity, null models.	Jamie M. Kass; Robert Muscarella; Peter J. Galante; Corentin Bohl; Gonzalo E. Buitrago-Pinilla; Robert A. Boria; Mariano Soley-Guardia; Robert P. Anderson	Muscarella et al., 2014, 2020	https://cran.r-project.org/package=ENMeval		1230
44	SDMTools – Species Distribution Modelling Tools	Model evaluation	Functions for post processing and visualising model outcomes, selecting thresholds, calculating accuracy metrics and landscape fragmentation statistics, comparing models, tracking changes in distributions over time.	Jeremy VanDerWal; Lorena Falconi; Stephanie Januchowski; Luke Shoo; Collin Storie	Vanderwal et al., 2015	Not in CRAN		46
45	Metrics	Model evaluation	Functions for calculating evaluation metrics of machine learning models.	Ben Hamner; Michael Frasco; Erin LeDell	Hamner and Frasco, 2018	https://cran.r-project.org/package=Metrics		4
46	modEvA – Model evaluation and analysis	Model evaluation	Functions for performing variation partitioning, discrimination and calibration metrics, optimizing prediction thresholds, performing multivariate environmental similarity surface (MESS) analysis, and displaying analytical plots.	A. Márcia Barbosa	Barbosa et al., 2016	https://cran.r-project.org/package=modEvA	https://modtools.wordpress.com/packages/modEvA/	123
47	usdm – Uncertainty analysis for species distribution models	Model evaluation	Functions for assessing the impact of different sources of uncertainties on model performance.	Babak Naimi	Naimi et al., 2014	https://cran.r-project.org/package=usdm		792
48	blockCV	Model preparation Model evaluation	Functions for generating spatially or environmentally separated folds for k-	Roosbeh Valavi; Jane Elith; José Lahoz-Monfort; Gurutzeta Guillera-Aroita	Valavi et al., 2019	https://cran.r-project.org/package=blockCV		236

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N	R package	Main purpose	Description	Data collection and preparation		CRAN link	Development site	Citations
				Main contributor(s)	Main reference			
			fold cross-validation of models.					
N	R package	Main purpose	Description	Main contributor(s)	Main reference	CRAN link	Development site	Citations
49	ecospat	Model comparison	Functions for spatial ecology analyses on pre, core and post modelling analyses of species distribution, niche quantification and community assembly.	Olivier Broennimann; Valeria Di Cola; Blaise Petitpierre; Frank Breiner; Daniel Scherrer; Manuela D'Amen; Christophe Randin; Robin Engler; Wim Hordijk; Heidi Mod; Julien Pottier; Mirko Di Febbraro; Loic Pellissier; Dorothea Pio; Ruben Garcia Mateo; Anne Dubuis; Luigi Maiorano; Achilles Psomas; Charlotte Ndiribe; Nicolas Salamin; Niklaus Zimmermann; Flavien Collart; Antoine Guisan	Di Cola et al., 2017	https://cran.r-project.org/package=ecospat		556
50	ellipsenm	Model comparison	Functions for ellipsoid envelopes, calibrating and selecting models, replicating models and projections, and assessing niche overlap.	Marlon E. Cobos; Luis Osorio; Jorge Soberón; A. Townsend Peterson; Vijay Barve; Narayani Barve		Not in CRAN	https://github.com/marloncobos/ellipsenm	3
51	fuzzySim – Fuzzy Similarity in Species Distributions	Model combination	Functions to compute fuzzy versions of species occurrence patterns based on presence-absence data (including inverse distance interpolation, trend surface analysis, and prevalence-independent favorability), and pairwise fuzzy similarity. Additional functions for model consensus and comparison, and for data preparation: unique abbreviations of species names, gridding (thinning) point occurrence data onto raster maps, converting species lists to presence-absence tables, transposing part of a data frame, selecting relevant variables for models, assessing the false discovery rate, or analysing and dealing with multicollinearity.	A. Márcia Barbosa	Barbosa, 2015	https://cran.r-project.org/package=fuzzySim	http://fuzzySim.r-project.org/	102
52	zoon	Model comparison	Functions for reproducible and shareable analysis of models from an online repository, comparing and diagnostic models.	Tom August; Tim Lucas; Nick Golding; Emiel van Loon; Greg McNerny	Golding et al., 2018	https://cran.r-project.org/package=zoon		39
53	Mopa	Model ensemble	Functions for transferable models, pseudo-absence data generation, and factor contribution quantification.	Maialen Iturbide; Joaquín Bedia; SantanderMetGroup	Iturbide et al., 2018	Not in CRAN		19

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Table 2 (continued)

N	R package	Main purpose	Description	Data collection and preparation		CRAN link	Development site	Citations
				Main contributor(s)	Main reference			
54	MigClim	Model dispersion	Functions from implementing dispersal into models over time.	Robin Engler; Wim Hordijk; Loic Pellissier	2012 Not in CRAN	Not in CRAN		144
55	RangeShifterR	Model dispersion	Spatially-explicit, individual-based simulation platform for modelling species' range dynamics, such as expansion and shifting, and patch connectivity by linking complex local population dynamics and dispersal behaviour, while also taking into account inter-individual variability and evolutionary processes.	Anne-Kathleen Malchow; JetteReeg; Damaris Zurell	Bocedi et al., 2014 , G. 2021	Not in CRAN	https://github.com/RangeShifter/RangeShifterR-package	210
56	ESDM	Model application	Functions for ensemble modelling of species distribution and abundance models. eSDM includes a GUI (R Shiny app).	Sam Woodman	Woodman et al., 2019	https://cran.r-project.org/package=eSDM		10
57	rangeModelMetadata – Range modeling Metadata Standards	Publication of metadata	Functions for creating data dictionaries specifying a hierarchical structure to catalogue models.	Cory Merow; Brian MaitnerHannah Owens; Jamie Kass; Brian Enquist; Rob Guralnik; Damaris Zurrell; Christian Koenig	Merow et al., 2019	https://cran.r-project.org/package=rangeModelMetadata		17
58	specieschrom	Model comparison	Quantification of niche optimum and breadth, niche overlapping (index D), and identification of most discriminant combination of environmental variables.	Loïck Kléparski	Kléparski and Beaugrand, 2022	Not in CRAN	https://github.com/loick-klpr/specieschrom	1
59	humboldt	Model comparison	Functions to analyse the amount of the species' observed E-space that is truncated by the available E-space.	Jason L. Brown	Brown and Carnaval, 2019	Not in CRAN	https://jasonleebrown.github.io/humboldt/	43
60	red	Model application	Functions for performing spatial analyses using species occurrences or estimated ranges. It calculates Maxent models with dismo function.	Pedro Cardoso	Cardoso, 2017	https://cran.r-project.org/package=red		42

cleaning and filtering occurrence data are also available: *spThin*, *bdclean*, *CoordinateCleaner*, *bdcc*, *bRacatus*, *biogeo*. *occAssess* and *sambbias* are specialised in correcting geographical biases in species occurrences.

Some algorithms are available through specialised and generalistic packages: for example, the Maxent algorithm ([Phillips et al., 2006, 2017](#)) can be computed with *maxnet*, *kuenm*, *dismo*, *biomod2*, *sdm*, *ENMeval*, *ENMTools*, *flexsdm*, *SDMPlay*, *ENMTML*, *SSDM*, *MinBAR*, *red*, and *SDMtune*. However, many of these packages use a function included in another package (e.g. *dismo*). On the other hand, are there some missing functionalities not included in R packages for ENMs? The user has currently at least 60 available packages providing multiple functions for all modelling steps. However, not all modelling steps are represented equally: fewer packages are available for evaluating models. In general, we probably need more functions for validating models, especially for

computing null models ([Raes and ter Steege, 2007](#); [Beale et al., 2008](#); [Bohl et al., 2019](#)). Only *ENMTools* ([Warren et al., 2021](#)) has implemented the calculation of null models as a parameter of the functions for computing ENM algorithms. *ENMeval* ([Muscarella et al., 2014](#); [Kass et al., 2021](#)) also provides functions for computing null models. It is desirable that validating ENMs with null models becomes a more extended and standard practice ([Sillero et al., 2021](#)). There is also room for improvement in properly evaluating models on true presence-only data, without requiring unoccupied background localities.

If we consider the necessity to gather geographical, environmental and biodiversity data directly from within R, we will need several packages to run all modelling procedures. However, once the data are compiled, there are several packages offering all necessary functions to compute, validate and apply the models, namely *dismo*, *biomod2*, *sdm*,

ENMeval, *ENMTools*, *ENMTML*, *flexsdm*, and *SDMtune*. However, not all these packages provide the same functionalities. For example, *dismo* (Hijmans et al., 2021) does not have ensemble modelling functions, while *ENMTools* (Warren et al., 2021) does not provide tools to replicate the models. On the other hand, *ENMTools* (Warren et al., 2021) validates the models both in the environmental and geographical space, and it includes the computing of null models as part of the general calculation of the model. Recent packages have also reduced the number of steps for calculating the models. In comparison to *biomod2* (Thuiller et al., 2021), which requires formatting the data through several functions before computing the models, other packages have reduced the necessary steps to a minimum: *sdm* (Naimi and Araújo, 2016) only needs one function for this pre-modelling step, and *ENMTML* (de Andrade et al., 2020) integrates all modelling steps in one single function.

The most cited packages are *biomod2* (Thuiller et al., 2021) and *ENMeval* (Muscarella et al., 2014; Kass et al., 2021). This is likely a representation of the users' needs: most users require a package for both computing and validating models. Some packages such as *dismo* (Hijmans et al., 2021) have fewer citations, probably because they do not have a paper associated. Users frequently forget to cite R packages, or they do not know how to cite them, as their citations cannot be seamlessly uploaded to a reference manager program.

The communication between packages should also be improved. R is a free open-source software enhanced by a wide community of developers and users, and therefore it includes a huge diversity of approaches (Lovelace et al., 2020). For example, several packages provide tools for reading, importing, and exporting data, either in tabular (matrix, data frame, data table, tibble) or in spatial (vector or raster) formats (*sp*, *sf*, *raster*, *terra*, *stars*, amongst others). Different packages often require different classes of input objects and also produce output objects of these classes. This reduces the flexibility for sharing objects between functions from different packages. This is important, for example, if we want to apply spatial statistics (Baddeley et al., 2015) to the results of widely used packages, such as *dismo* (Hijmans et al., 2021) and *biomod2* (Thuiller et al., 2021). These two packages currently require input objects implemented by packages *raster* (Hijmans, 2022a) and *sp* (Pebesma and Bivand, 2005), which use the *rgdal* (Bivand et al., 2022) and *rgeos* (Bivand and Rundel, 2021) packages for importing and handling spatial data. However, *spatstat* (Baddeley and Turner, 2005) - the most complete package for spatial statistics, currently depends on *sp* (Pebesma and Bivand, 2005) and *sf* (Pebesma, 2018). Therefore, interconnection and communication amongst packages should be improved.

Most ENM packages currently use *sp* (Pebesma and Bivand, 2005) and *raster* (Hijmans, 2022a) package formats as spatial data inputs. However, support for some dependencies or suggestions of these packages (such as *rgdal*, *rgeos* and *maptools*) will end in 2023. Currently, very few ENM packages (*fuzzySim*, *modEva*, *blockCV*, *dismo* in part, and *biomod2* in the development version on GitHub) have migrated their code to newer spatial packages like *terra* (for both raster and vector data; Hijmans, 2022b) or *sf* (for vector data; Pebesma, 2018), which substitute the *raster* and *sp* packages and are actively maintained, besides being considerably faster. Future updates of R can introduce problems between versions of the packages as older spatial packages are retired. Therefore, code migration to modern spatial packages (e.g. *terra* or *stars* for raster data, *terra* or *sf* for vector data) should be a current priority for ENM package developers.

Other packages provide functions (e.g. model computation or validation) for methods rarely used in ENMs. Also, other packages use ENMs to perform phylogeographic (e.g. *phyr*, Li et al. 2020; *phylin*, Tarroso et al., 2015) and biogeographical analyses (e.g. *rangemap*; Cobos et al. 2022).

Some packages are in development and not currently on CRAN (e.g. *SDMTTools*, VanderWal et al. 2015; *MigClim*, Engler et al., 2012; *embarcadero*, Carlson 2020). More and more packages (even widely used ones) are now maintained on GitHub instead of CRAN, as it is often difficult to meet CRAN requirements. We included some packages if they were

published in a scientific journal, even if they were not on CRAN; they need to be installed following instructions on their development website.

5. Conclusions

What may be the future of R packages for ENMs? This question is not easy to answer. As indicated above, packages should implement better evaluation metrics and validating procedures such as null models, and improve their communication and integration. With the migration to modern spatial packages like *terra* (at least for raster spatial data), we hope that computing speed and stability will increase. Also, packages should facilitate the computation of replicated models for large numbers of species, without the necessity of using for-loop functions, and provide a more optimised syntax concerning the R language.

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Data availability

No data was used for the research described in the article.

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