A Julia toolkit for species distribution data

Timothée Poisot¹, Ariane Bussières-Fournel¹, Gabriel Dansereau¹ and Michael D. Catchen¹

¹ Université de Montréal, Département de Sciences Biologiques, Montréal QC, Canada

Correspondence to Timothée Poisot — timothee.poisot@umontreal.ca

Abstract: (1) Species distribution modeling requires to handle varied types of data, and benefits from an integrated approach to programming. (2) We introduce

SpeciesDistributionToolkit, a Julia package aiming to facilitate the production of species distribution models. It covers various steps of the data collection and analysis process, extending to the development of interfaces for integration of additional functionalities. (3) By relying on semantic versioning and strong design choices on modularity, we expect that this package will lead to improved reproducibility and long-term maintainability. (4) We illustrate the functionalities of the package through several case studies, accompanied by reproducible code.

Keywords: species distribution models, biogeography, occurrence data, land use, climatic data, pseudo-absences

1 Introduction

2 Species Distribution Models [SDMs; Elith and Leathwick (2009)], in addition to being key tools 3 to further our knowledge of biodiversity, are key components of effective conservation deci-4 sions (Guisan et al. 2013), planning (McShea 2014), and ecological impact assesment (Baker et 5 al. 2021). The training and evaluation of a SDM is a complex process, with key decisions to 6 make on design and reporting (Zurell et al. 2020). The ability to use the correct data format of 7 representation at of these steps is central to support the correct interpretation of these models 8 (Araújo et al. 2019). This is particularly true since the choice of data source can affect the 9 prediction significantly (Booth 2022, Arenas-Castro et al. 2022, Merkenschlager et al. 2023), 10 suggesting that there is a need for flexible pipelines in which data sources can be conveniently 11 swapped. In recent years, there has been an increase in the number of software packages and 12 tools to assist ecologists with various steps of the development of species distribution models. 13 As Kass et al. (2024) point out, this increase in the diversity of software tools (most of them 14 in the **R** language) is a good thing. Because the SDMs are a general-purpose methodology, a 15 varied software offers increases the chances that specific decisions can be chained together in 16 the way that best support a specific use case. By making code available for all users, package 17 developers reduce the need for custom implementation of analytical steps, and contribute to 18 the adoption of good practices in the field. However, because building, validating, and apply-19 ing SDMs requires a diversity of data types, from different sources, many existing packages have been designed independently. Therefore, they may suffer from low interoperability, 20 21 which can create friction when using multiple tools together. As an illustration, Kellner et al. 22 (2025) highlight that, out of publications on abundance or distribution models that share code 23 and data, about 20% are not reproducible because of issues in package dependencies. To promote interoperability and improve reproductibility, tools that provide an integrated 24 25 environment are important. In this manuscript, we present SpeciesDistributionToolkit 26 (abbreviated as SDT), a meta-package for the Julia programming language, offering an 27 integrated environment for the retrieval, formatting, and interpretation of data relevant to 28 the modeling of species distributions. SDT was in part designed to work within the BON-29 in-a-Box project (Gonzalez et al. 2023, Griffith et al. 2024), a GEO BON initiative to facilitate 30 the calculation and reporting of biodiversity indicators supporting the Kunming-Montréal 31 Global Biodiversity Framework. A leading design consideration for SDT was therefore to 32 maximize interoperability between components and functionalities from the ground up. This

- 33 is achieved through three mechanisms. First, by relying on strict semantic versioning: package
- releases provide information about the compatibility of existing code. Second, through the
- 35 use of interfaces: separate software components (including ones external to the package)
- 36 can interact without prior knowledge of either implementation, and without dependencies
- between the components of **SDT**. Finally, through the use of **Julia**'s extension mechanism.
- 38 These are detailed in Box 1.
- 39 In this manuscript, we describe provide a high-level overview of the functionalities of the
- 40 package(s) forming **SDT**. We then discuss design principles that facilitate long-term mainte-
- 41 nance, development, and integration. We finish by presenting four illustrative case studies:
- 42 extraction of data at known species occurrences, manipulation of multiple geospatial layers,
- 43 training and explanation of a SDM, and creation of virtual communities to simulate the
- 44 spatial distribution of ecological uniqueness. This later case study is intended to provide an
- 45 impression of what using **SDT** as a support for the development of novel analyses feels like. All
- of the case studies are available as supplementary material, in the form of fully reproducible,
- 47 self-contained Jupyter notebooks.

Application description

- 49 **SpeciesDistributionToolkit** is released as a package for the **Julia** programming language
- 50 (Bezanson et al. 2017). It is licensed under the open-source initiative approved MIT license. It
- 51 has evolved from a previous collection of packages to handle GBIF and raster data (Dansereau
- and Poisot 2021), and now provides extended functionalities as well as improved performance.
- The package is registered in the **Julia** package repository and can be downloaded and installed
- anonymously. It is compatible with the current long-term support (LTS) release of **Julia**. The
- 55 full source code, complete commit history, plans for future development, and a forum, are
- 56 available at https://qithub.com/PoisotLab/SpeciesDistributionToolkit.jl. This page additionally
- 57 has a link to the documentation, containing a full reference for the package functions, a series
- of briefs how-to examples, and longer vignettes showcasing more integrative tutorials.
- 59 An overview of the SDT package is given in Figure 1. The project is organized as a
- 60 "monorepo", in which separate but interoperable packages (meaning that they can be installed
- 61 independently, but are designed to work cohesively) reside. This allows expanding the scope
- of the package by moving functionalities into new component packages, without requiring
- 63 interventions from users. As **SDT** is registered in the **Julia** package repository, it can be
- installed by using add SpeciesDistributionToolkit when in package mode at the **Julia** prompt.

When loading the **SDT** package with using SpeciesDistributionToolkit, all component packages are automatically and transparently loaded. Therefore, users do not need to know where a specific method or function resides to use it. The monorepo structure has an important advantage for users: the code of all component packages can be found in the same location, and it makes inspecting the internal implementation of any package easier. In addition, users can open an issue describing a problem or desired feature within the monorepo, without needing to understand which component package is the right target for this issue. This both decreases barriers to interact with the software, while also facilitating the work of contributors who can look at all the issues to address in a centralized way. Similarly, monorepo lend themselves to integrated documentation, which is the approach we have chosen with the online **SDT** manual.

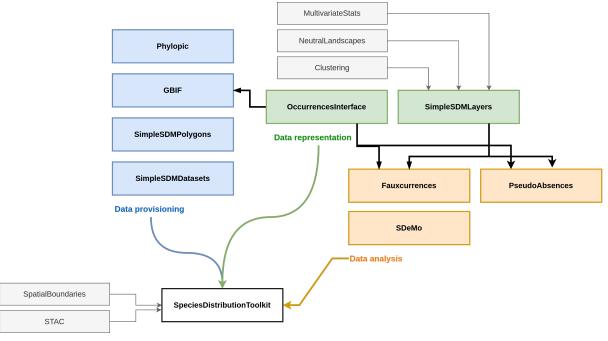


Figure 1: Overview of the packages included in **SpeciesDistributionToolkit**. The packages are color-coded by intended use (acquisition, representation, and analysis of data). The specific content of each package is presented in the main text. Note that because the package relies on *interfaces* to facilitate code interoperability, there are only three dependency relationships (black arrows). Some packages can interact with data sources, represented on the left side of the figure. When loading **SpeciesDistributionToolkit**, all public methods from the package are accessible to the user. Packages that are supported through extensions are in dashed boxes.

SDT uses the built-in **Julia** package manager to keep all dependencies up to date. Furthermore, we use strict semantic versioning: major versions correspond to changes that would break user-developped code; minor versions represent additional functionalities; patch releases cover minor bug fixes or documentation changes. All component packages are versioned independently, and have their own *CHANGELOG* file documenting each release. This strict reliance on semantic versioning removes the issues of maintaining compatibility when

- 89 new functionalities are added: all releases in the *v1.x.x* branch of **SDT** depend on component
- 90 packages in their respective *v1.x.x* branch, and users can benefit from new functionalities
- 91 without needing to adapt existing code. This behavior is extensively tested, both through unit
- tests and through integration testing generated as part of the online documentation.

Component packages

- 94 The SDT package primarily provides integration between the other packages via method
- overloading (reusing method names for intuitive and concise code), allowing to efficiently
- 96 join packages together (Roesch et al. 2023). Additional functionalities that reside in the top-
- 97 level package are the generation of pseudo-absences (Barbet-Massin et al. 2012), access to the
- 98 gadm.org database, handling of polygon data and zonal statistics, and various quality of life
- 99 methods. Because of the modular nature of the code, any of these functions can be transpar-
- ently moved to their own packages without affecting reproducibility. Note that all packages
- can still be installed (and would be fully functional) independently.
- The **SimpleSDMLayers** package offers a series of types to represent raster data in arbitrary
- projections defined by a projections (Evenden et al. 2024). This package provides the main
- data representation for most spatial functionalities that **SDT** supports, and handles saving and
- loading data. It also contains utility functions to deal with raster data, including interpolation
- to different spatial grids and CRS, rescaling and quantization of data, masking, and most
- mathematical operations that can be applied to rasters.
- 108 OccurrencesInterface is a light-weight package to provide a common interface for occur-
- rence data. It implements abstract and concrete types to define a single occurrence and a
- 110 collection thereof, and a series of methods allowing any occurrence data provider (e.g. GBIF)
- or data representation to become fully interoperable with the rest of **SDT**. All **SDT** methods
- that handle occurrence data do so through the interface provided by the **OccurrencesInter**-
- face package, allowing future data sources to be integrated without the need for new code.
- 114 The **GBIF** package offers access to the qbif.org streaming API (GBIF: The Global Biodiversity
- 115 Information Facility 2025), including the ability to retrieve, filter, and restart downloads.
- Although this package provides a rich data representation for occurrence data when access to
- the full GBIF data schema is required, all the objects it returns adhere to the **OccurrencesIn-**
- terface interface. The package also offers the functionality to download datasets from GBIF
- using their DOI.
- 120 **SimpleSDMDatasets** implements an interface to retrieve and locally store raster data, which
- can be extended by users to support additional data sources. Tt offers access to a series of

- 122 common data sources for spatial biodiversity modeling, including the biodiversity mapping
- project (Jenkins et al. 2013), the EarthEnv collection for land cover (Tuanmu and Jetz 2014) and
- habitat heterogeneity (Tuanmu and Jetz 2015), Copernicus land cover 100m data (Buchhorn
- et al. 2020), PaleoClim (Brown et al. 2018) data, WorldClim 1 and 2 (Fick and Hijmans 2017)
- and CHELSA 1 and 2 (Karger et al. 2017) and their projections under various RCPs and SSPs.
- 127 **SimpleSDMPolygons** uses the interface from **SimpleSDMDatasets** to offer access to
- geospatial polygons, including the GADM database, the OpenStreetMap polygon API, as well
- as several providers for georegions, ecoregions, and ecoprovinces (Olson et al. 2001, Diner-
- 130 stein et al. 2017).
- 131 **Phylopic** offers a wrapper around the phylopic.org API to download silhouettes for taxonomic
- entities. It also provides utilities for citation of the downloaded images. Its functionalities are
- similar to the **rphylopic** package (Gearty and Jones 2023).
- 134 **Fauxcurrences** is inspired by the work of Osborne et al. (2022), and allows generating a series
- of simulated occurrence data that have the same statistical structure as observed ones. The
- package supports multi-species data, with user-specified weights for conserving intra and
- inter-specific occurrence distances.
- 138 **PseudoAbsences** offers functions to place pseudo-absences points on layers, under various
- constraint on range and distance to existing observations (Barbet-Massin et al. 2012).
- 140 Finally, **SDeMo** provides a high-level interface to the training, validation, and interpretation
- of species distribution modeling. The package is built around a series of data transformation
- steps (PCA, Whitening, z-score, which can be chained together) and several classifiers, cur-
- rently including BIOCLIM (Booth et al. 2014), Naive Bayes, logistic regression, and decision
- trees. **SDeMo** offers functions to demonstrate training and evaluation of SDMs, as well
- as techniques related to heterogeneous ensembles and bagging with support for arbitrary
- 146 consensus (Marmion et al. 2009) and voting (Drake 2014) functions. **SDeMo** promotes the
- use of interpretable techniques: the package supports regular (Elith et al. 2005) and inflated
- 148 (Zurell et al. 2012) partial responses, as well as the calculation and mapping of Shapley values
- (Mesgaran et al. 2014, Wadoux et al. 2023) using the standard Monte-Carlo approach (Mitchell
- et al. 2021). Counterfactuals (Karimi et al. 2019, Van Looveren and Klaise 2019), representing
- perturbation of the input data leading to the opposite prediction (i.e. "what environmental
- 152 conditions would lead to the species being absent") can also be generated. The API of **SDeMo**
- has been designed to (i) enforce the use of best practices, and (ii) be consistent across analyses,
- so that the package can be used for educational material. Despite the focus on education,

SDeMo has been thoroughly tested and may be used for research. As it implements a generic interface to any predictive model, users can expand it by adding additional classifiers or transformers. This can be done either through a contribution to the SDT repository, or as part of the code written by users for a specific analysis.

Case studies

159

166

- 160 In this section, we provide a series of case studies to illustrate the use of the package. The
- on-line manual offers longer tutorials, as well as a series of how-to vignettes to illustrate the
- full scope of what the package allows. As the notebooks accompanying this article cover the
- full code required to run these case studies, we do not present code snippets in the main
- text (as they are presented with detailed explanations in the Supp. Mat.), but rather focus on
- explaining how the component packages work together in each example.

Landcover consensus map

- In this case study (Supp. Mat. 1), we retrieve the land cover data from Tuanmu and Jetz (2014),
- clip them to a GeoJSON polygon describing the country of Paraguay (**SDT** can download data
- directly from gadm.org), and apply the mosaic operation to figure out which class is the most
- locally abundant. This case study uses the **SimpleSDMDatasets** package to download (and
- locally cache) the raster data, as well as the **SimpleSDMLayers** package to provide basic
- utility functions on raster data. The results are presented in Figure 2.

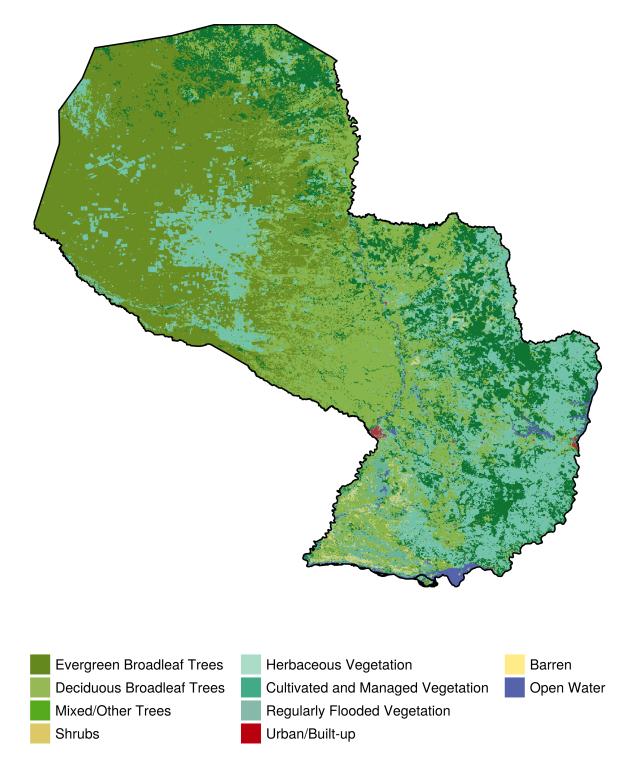


Figure 2: Land cover consensus (defined as the class with the strongest local representation) in the country of Paraguay. Only the classes that were most abundant in at least one pixel are represented. The code to produce this figure is available as Supp. Mat. 2.

173174

175

177 **SimpleSDMDatasets** uses local storage of raster data for future use, to avoid re-downloading 178 data upon repeated use. The location of the data is (i) standardized by the package itself, 179 making the file findable to humans, and (ii) changeable by the user to, e.g., store the data 180 within the project folder rather than in a central location. As much as possible, **SDT** will only 181 read the part of the raster data that is required given the region of interest to the user. This 182 is done by providing additional context in the form of a bounding box (in WGS84, regardless 183 of the underlying raster data projection, in line with the GeoJSON specification). SDT has 184 methods to calculate the bounding box for all the objects it supports.

Using data from GBIF

185

186 SDT provides strong integration between data on species occurrences and source of geospatial 187 information. To illustrate this, we will collect data on the distribution of Akodon montensis 188 (Rodentia, family Cricetidae), a known host of orthohantaviruses (Owen et al. 2010, Burgos et 189 al. 2021), in Paraguay. In Supp. Mat. 2 we (i) request occurrence data using the GBIF package, 190 (ii) download the silhouette of the species through **Phylopic**, and (iii) extract temperature and precipitation data at the points of occurrence based on bioclimatic data layers. The results 191 192 are presented in Figure 3. The full notebook includes information about basic operations on 193 raster data, as well as extraction of data based on occurrence records.

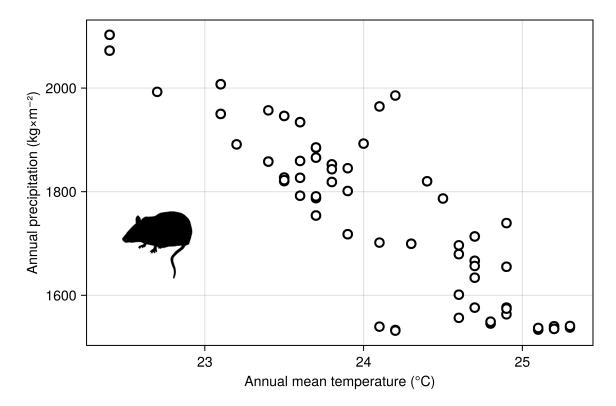


Figure 3: Relationship between temperature and precipitation (BIO1 and BIO12) at each georeferenced occurrence known to GBIF for *Akodon montensis*. The code to produce this figure is available as Supp. Mat. 1.

In practice, although the data are retrieved using the **GBIF** package, they are used internally by **SDT** through the **OccurrencesInterface** package. This package defines a small convention to handle georeferenced occurrence data, and allows to transparently integrate additional occurrence sources. By defining a handful of methods for a custom data type, or by using the convertes built into the package, users can plug-in any occurrence data source or csv file, and enjoy full compatibility with the entire **SDT** functionalities.

The **GBIF** package also supports download of archived GBIF datasets; in the following example, we have generated a dataset from this query, which can be accessed online (GBIF.org 2025).

Training a species distribution model

In this case study, we illustrate the integration of **SDeMo** and **SimpleSDMLayers** to train a species distribution model. Specifically, we re-use the data from Figure 3, with additional layers of bioclimatic variables. We train a rotation forest (Bagnall et al. 2018), an homogeneous ensemble of PCA followed by decision trees where each model has a subset of features and training data. The results are presented in Figure 4. The model is built by selecting an optimal suite of BioClim variables, then predicted in space, and the resulting predicted species

213 range is finally clipped by the elevational range observed in the occurrence data. The data 214 transformations in **SDeMo** are always applied in a way that prevents the possibility of data 215 leakage (Stock et al. 2023). Because **SDeMo** works through generic functions, these methods can be applied to any model specified by the user. In practice, generic purpose ML frameworks 216 217 Julia, notably MLJ (Blaom et al. 2020), can also be used and interfaced with SDT by using the 218 classifier and transformer interface. 219 By default, SDeMo will always split data for cross-validation in a way that respect class 220 balance; in other words, the prevalence of the species is always the same in the validation 221 and training set (this is also true when bootstrapping observations to construct homogeneous 222 ensembles). This behavior can be adjusted, or the user may design their own training and 223 validation sets. In the future, PseudoAbsences will be extended to introduce stratified cross-224 validation (Roberts et al. 2017).

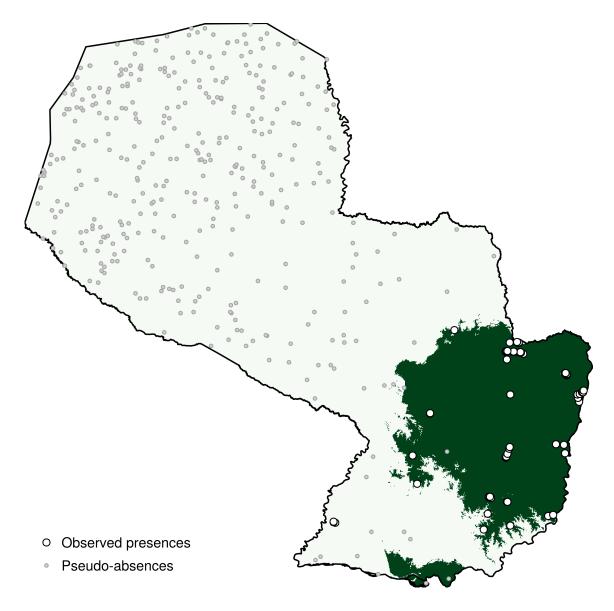


Figure 4: Predicted range of *Akodon montensis* in Paraguay based on a rotation forest trained on GBIF occurrences and the BioClim variables. The predicted range is clipped to the elevational range of the species. The code to produce this figure is available as Supp. Mat. 3.

The full notebook (Supp. Mat. 3) has additional information on routines for variable selection, stratified cross-validation, as well as the construction of the ensemble from a single PCA and decision tree. In addition, we report in Figure 5 the partial and inflated partial responses to the most important variable (highlighting an interpretable effect of the variable in the model), as well as the (Monte-Carlo) Shapley values (Mitchell et al. 2021, Wadoux et al. 2023) for each prediction in the training set. Checking the partial responses, in particular in space, is an important step, as some bioclimatic variables are known to have discontinuities stemming from their interpolation that can bias the predicted range of a species (Booth 2022).

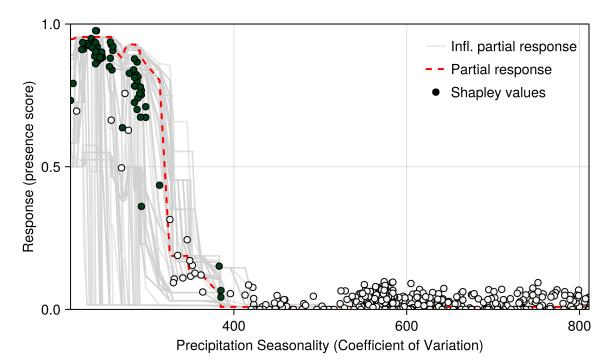


Figure 5: Partial responses (red) and inflated partial responses (grey) to the most important variable. In addition, the Shapley values for all training data are presented in the same figure; green points are presences, and pale points are pseudo-absences. Shapley values were added to the average model prediction to be comparable to partial responses. The code to produce this figure is available as Supp. Mat. 3.

Species and location contribution to beta diversity

In the final case study (Supp. Mat. 4), we simulate the distribution of virtual species (Hirzel et al. 2001) with a logistic response to two environmental covariate (Leroy et al. 2016). We then use this simulated sample to perform the decomposition of β -diversity introduced by Legendre and De Cáceres (2013) and applied by Dansereau et al. (2022) to spatially continuous data. This simulates the potential distribution of hotspots and coldspots of ecological uniqueness. The results are presented in Figure 6.

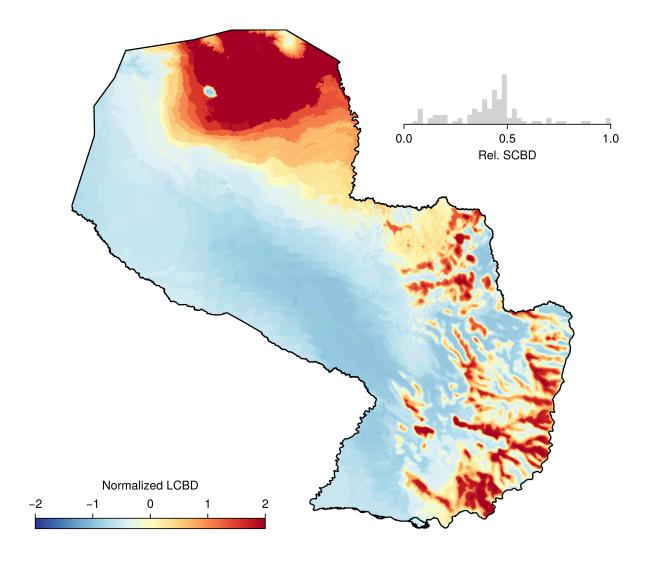


Figure 6: Virtual distribution of normalized (mean of 0 and unit variance) locality contribution to beta-diversity (Legendre and De Cáceres 2013), based on a pool of 100 virtual species. The inset histogram represents the standardized species contribution to beta-diversity. Red areas represent comparatively more unique areas in terms of simulated species composition. The code to produce this figure is available as Supp. Mat. 4.

Because the layers used by **SDT** are broadcastable, we can rapidly apply a function (here, the logistic response to the environmental covariate) to each layer, and then multiply the suitabilities together. The last step is facilitated by the fact that most basic arithmetic operations are defined for layers, allowing for example to add, multiply, substract, and divide them by one another.

Conclusion

260

261 We have presented **SpeciesDistributionToolkit**, a package for the **Julia** programming 262 language aiming to facilitate the collection, curation, analysis, and visualisation of data 263 commonly used in species distribution modeling. Through the use of interfaces and a modular 264 design, we have made this package robust to changes, easy to add functionalities to, and well 265 integrated to the rest of the **Julia** ecosystem. All code for the case studies can be found in Supp. 266 Mat. 1-4. Plans for active development of the package are focused on (i) additional techniques 267 for pseudo-absence generations, to be incorporated in the **PseudoAbsences** package, (ii) 268 full compatibility with the MultivariateStatistics for transformation, and (iii) additional 269 **SDeMo** functionalities to allow cross-validation techniques with biologically relevant struc-270 ture (Roberts et al. 2017). 271 The **SDT** package benefits from close integration with other packages in the **Julia** universe. 272 Notably, this includes Makie [including GeoMakie; Danisch and Krumbiegel (2021)] for 273 plotting and interactive data visualisation: all relevant plot types are overloaded for layer 274 and occurrence data. Most data handled by **SDT** can be exported using the **Tables** interface, 275 which allows data to be consumed by other packages like **DataFrames** (Bouchet-Valat and 276 Kamiński 2023) and MLJ (Blaom et al. 2020), or directly saved as csv files. Interfaces to 277 internal Julia methods are implemented whenever they are pertinent. SimpleSDMLayers 278 and OccurrencesInterface objects behave like arrays, are iterable, and broadcastable. The 279 **SDeMo** package relies in part on the **StatsAPI** interface, allowing to easily define new data 280 transformation and classifier types to support additional features. Achieving integration with 281 other packages through method overloading and the adherence to well-established interfaces 282 is important, as it increases the chances that additional functionalities external to **SDT** can be 283 used directly or fully supported with minimal addition of code. For situations where interfaces 284 are not sufficient to link with other packages, we rely on **Julia**'s extension mechanism. For 285 instance, SimpleSDMLayers objects can be used with Clustering, MultivariateStats, as 286 well as **SpatialBoundaries** (Strydom and Poisot 2023), with strict version bounds, ensuring 287 that this integration will remain usable regardless of possible changes in external packages. 288 A key advantage of **Julia** for species distribution modeling is its emphasis on extensibility 289 and composability. In developing SDT, we leveraged these strengths by ensuring that each 290 component package operates independently, while the top-level package provides additional 291 methods to integrate their functionalities. Through method overloading, we minimize the

292 number of unique function names users must learn—core operations such as arithmetic, 293 dimension queries, and statistical summaries are consistently available across relevant data 294 types. This unified approach not only streamlines the user experience but also makes the code 295 more readable and accessible, which is particularly beneficial in educational settings. SDT is 296 intentionally structured to promote best practices and long-term sustainability. The unified 297 interface for occurrence, raster, and polygon data allows new data sources or representations 298 to be incorporated with minimal changes to existing workflows. Strict adherence to semantic 299 versioning and interface-based design ensures that updates do not compromise reproducibil-300 ity. Advanced model interpretation tools—including Shapley values and counterfactuals—are 301 built in, which will help with their adoption, and users can extend the modeling pipeline with 302 custom classifiers or data transformations via Julia's multiple dispatch. 303 **Acknowledgements**: TP is funded by an NSERC Discovery grant, a Discovery Acceleration 304 Supplement grant, and a Wellcome Trust grant (223764/Z/21/Z). MDC is funded by an IVADO 305 Postdoctoral Fellowship.

Bibliography

- Araújo MB, Anderson RP, Márcia Barbosa A, et al (2019) Standards for distribution models in biodiversity assessments. Science advances 5:eaat4858. https://doi.org/10.1126/sciadv.
- 309 aat4858

- Arenas-Castro S, Regos A, Martins I, et al (2022) Effects of input data sources on species distribution model predictions across species with different distributional ranges. Journal
- of biogeography 49:1299–1312. https://doi.org/10.1111/jbi.14382
- Bagnall A, Flynn M, Large J, et al (2018) Is rotation forest the best classifier for problems with
- 314 continuous features?. arXiv [csLG]
- 315 Baker DJ, Maclean IMD, Goodall M, Gaston KJ (2021) Species distribution modelling is needed
- $316 \qquad \qquad to support \ ecological \ impact \ assessments. \ The journal \ of \ applied \ ecology \ 58:21-26. \ https://$
- 317 doi.org/10.1111/1365-2664.13782
- 318 Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species
- distribution models: how, where and how many?: How to use pseudo-absences in niche
- modelling?. Methods in ecology and evolution 3:327–338. https://doi.org/10.1111/j.2041-
- 321 210x.2011.00172.x

322	Bezanson J, Edelman A, Karpinski S, Shah VB (2017) Julia: A fresh approach to numerical
323	computing. SIAM review Society for Industrial and Applied Mathematics 59:65–98.
324	https://doi.org/10.1137/141000671
325	Blaom A, Kiraly F, Lienart T, et al (2020) MLJ: A Julia package for composable machine
326	learning. Journal of open source software 5:2704. https://doi.org/10.21105/joss.02704
327	Booth TH (2022) Checking bioclimatic variables that combine temperature and precipitation
328	data before their use in species distribution models. Austral ecology 47:1506–1514. https://
329	doi.org/10.1111/aec.13234
330	Booth TH, Nix HA, Busby JR, Hutchinson MF (2014) bioclim: the first species distribution
331	modelling package, its early applications and relevance to most current MaxEnt studies.
332	Diversity & distributions 20:1–9. https://doi.org/10.1111/ddi.12144
333	Bouchet-Valat M, Kamiński B (2023) DataFrames.Jl: Flexible and fast tabular data in Ju
334	lia}. Journal of statistical software 107:. https://doi.org/10.18637/jss.v107.i04
335	Brown JL, Hill DJ, Dolan AM, et al (2018) PaleoClim, high spatial resolution paleoclimate
336	surfaces for global land areas. Scientific data 5:180254. https://doi.org/10.1038/sdata.2018
337	254
338	Buchhorn M, Smets B, Bertels L, et al (2020) Copernicus Global Land Service: Land Cover
339	100m: collection 3: epoch 2019: Globe
340	Burgos EF, Vadell MV, Bellomo CM, et al (2021) First evidence of Akodon-borne orthohan
341	tavirus in northeastern Argentina. EcoHealth 18:429–439. https://doi.org/10.1007/s10393
342	021-01564-6
343	DanischS, KrumbiegelJ(2021)Makie.jl:Flexiblehigh-performancedatavisualizationforJulian and the control of the cont
344	Journal of open source software 6:3349. https://doi.org/10.21105/joss.03349
345	Dansereau G, Legendre P, Poisot T (2022) Evaluating ecological uniqueness over broad spatial
346	extents using species distribution modelling. Oikos (Copenhagen, Denmark) 2022:e9063
347	https://doi.org/10.1111/oik.09063
348	Dansereau G, Poisot T (2021) SimpleSDMLayers.Jl and GBIF.Jl: A framework for species
349	distribution modeling in Julia. Journal of open source software 6:2872. https://doi.org/10
350	21105/joss.02872
351	Dinerstein E, Olson D, Joshi A, et al (2017) An ecoregion-based approach to protecting half
352	the terrestrial realm. Bioscience 67:534–545. https://doi.org/10.1093/biosci/bix014

353 Drake JM (2014) Ensemble algorithms for ecological niche modeling from presence-back-354 ground and presence-only data. Ecosphere (Washington, DC) 5:1–16. https://doi.org/10. 355 1890/es13-00202.1 356 Elith J, Ferrier S, Huettmann F, Leathwick J (2005) The evaluation strip: A new and robust 357 method for plotting predicted responses from species distribution models. Ecological 358 modelling 186:280–289. https://doi.org/10.1016/j.ecolmodel.2004.12.007 Elith J, Leathwick JR (2009) Species distribution models: Ecological explanation and prediction 359 360 across space and time. Annual review of ecology, evolution, and systematics 40:677-697. 361 https://doi.org/10.1146/annurev.ecolsys.110308.120159 Evenden GI, Rouault E, Warmerdam F, et al (2024) PROJ 362 Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for 363 global land areas: NEW CLIMATE SURFACES FOR GLOBAL LAND AREAS. International 364 365 journal of climatology: a journal of the Royal Meteorological Society 37:4302-4315. https://doi.org/10.1002/joc.5086 366 367 GBIF.org (2025) GBIF Occurrence Download GBIF: The Global Biodiversity Information Facility (2025) \textit{What is GBIF?} 368 369 Gearty W, Jones LA (2023) rphylopic: An R package for fetching, transforming, and visualising 370 PhyloPic silhouettes. Methods in ecology and evolution 14:2700–2708. https://doi.org/10. 371 1111/2041-210x.14221372 Gonzalez A, Vihervaara P, Balvanera P, et al (2023) A global biodiversity observing system 373 to unite monitoring and guide action. Nature ecology & evolution 1–5. https://doi.org/10. 374 1038/s41559-023-02171-0 375 Griffith J, Lord J-M, Catchen MD, et al (2024) BON in a Box: An Open and Collaborative 376 Platform for Biodiversity Monitoring, Indicator Calculation, and Reporting. https://doi. 377 org/10.32942/X2M320 378 Guisan A, Tingley R, Baumgartner JB, et al (2013) Predicting species distributions for conser-379 vation decisions. Ecology letters 16:1424–1435. https://doi.org/10.1111/ele.12189 380 Hirzel AH, Helfer V, Metral F (2001) Assessing habitat-suitability models with a virtual species. 381 Ecological modelling 145:111–121. https://doi.org/10.1016/s0304-3800(01)00396-9 382 Jenkins CN, Pimm SL, Joppa LN (2013) Global patterns of terrestrial vertebrate diversity and 383 conservation. Proceedings of the National Academy of Sciences of the United States of 384 America 110:E2602–10. https://doi.org/10.1073/pnas.1302251110

386	land surface areas. Scientific data 4:170122. https://doi.org/10.1038/sdata.2017.122
387	Karimi A-H, Barthe G, Balle B, Valera I (2019) Model-agnostic counterfactual explanations for
388	consequential decisions. arXiv [csLG]
389	Kass JM, Smith AB, Warren DL, et al (2024) Achieving higher standards in species distribution
390	modeling by leveraging the diversity of available software. Ecography. https://doi.org/10.
391	1111/ecog.07346
392	Kellner KF, Doser JW, Belant JL (2025) Functional R code is rare in species distribution and
393	abundance papers. Ecology 106:e4475. https://doi.org/10.1002/ecy.4475
394	Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data: dissim-
395	ilarity coefficients and partitioning. Ecology letters 16:951–963. https://doi.org/10.1111/
396	ele.12141
397	Leroy B, Meynard CN, Bellard C, Courchamp F (2016) virtualspecies, an R package to generate
398	virtual species distributions. Ecography 39:599–607. https://doi.org/10.1111/ecog.01388
399	Marmion M, Parviainen M, Luoto M, et al (2009) Evaluation of consensus methods in predic-
100	tive species distribution modelling. Diversity & distributions 15:59–69. https://doi.org/10.
101	1111/j.1472-4642.2008.00491.x
102	McShea WJ (2014) What are the roles of species distribution models in conservation planning?
103	Environmental conservation 41:93–96. https://doi.org/10.1017/s0376892913000581
104	Merkenschlager C, Bangelesa F, Paeth H, Hertig E (2023) Blessing and curse of bioclimatic
105	variables: A comparison of different calculation schemes and datasets for species distrib-
106	ution modeling within the extended Mediterranean area. Ecology and evolution 13:e10553
107	https://doi.org/10.1002/ece3.10553
108	Mesgaran MB, Cousens RD, Webber BL (2014) Here be dragons: a tool for quantifying novelty
109	due to covariate range and correlation change when projecting species distribution
110	models. Diversity & distributions 20:1147–1159. https://doi.org/10.1111/ddi.12209
111	Mitchell R, Cooper J, Frank E, Holmes G (2021) Sampling Permutations for Shapley Value
112	Estimation. arXiv [statML]
113	Olson DM, Dinerstein E, Wikramanayake ED, et al (2001) Terrestrial ecoregions of the world:
114	A new map of life on earth. Bioscience 51:933. https://doi.org/10.1641/0006-3568(2001)051
1 15	[0933:teotwa]2.0.co;2

- Osborne OG, Fell HG, Atkins H, et al (2022) Fauxcurrence: simulating multi-species occur-
- rences for null models in species distribution modelling and biogeography. Ecography
- 418 2022:e5880. https://doi.org/10.1111/ecog.05880
- Owen RD, Goodin DG, Koch DE, et al (2010) Spatiotemporal variation in Akodon montensis
- 420 (Cricetidae: Sigmodontinae) and hantaviral seroprevalence in a subtropical forest ecosys-
- tem. Journal of Mammalogy 91:467–481. https://doi.org/10.1644/09-MAMM-A-152.1
- Roberts DR, Bahn V, Ciuti S, et al (2017) Cross-validation strategies for data with temporal,
- spatial, hierarchical, or phylogenetic structure. Ecography 40:913–929. https://doi.org/10.
- 424 1111/ecog.02881
- Roesch E, Greener JG, MacLean AL, et al (2023) Julia for biologists. Nature methods 20:655–
- 426 664. https://doi.org/10.1038/s41592-023-01832-z
- 427 Stock A, Gregr EJ, Chan KMA (2023) Data leakage jeopardizes ecological applications
- of machine learning. Nature ecology & evolution 7:1743–1745. https://doi.org/10.1038/s
- 429 41559-023-02162-1
- 430 Strydom T, Poisot T (2023) SpatialBoundaries.jl: edge detection using spatial wombling.
- 431 Ecography 2023:. https://doi.org/10.1111/ecog.06609
- Tuanmu M-N, Jetz W (2014) A global 1-km consensus land-cover product for biodiversity and
- ecosystem modelling: Consensus land cover. Global ecology and biogeography: a journal
- of macroecology 23:1031–1045. https://doi.org/10.1111/geb.12182
- 435 Tuanmu M-N, Jetz W (2015) A global, remote sensing-based characterization of terrestrial
- habitat heterogeneity for biodiversity and ecosystem modelling: Global habitat hetero-
- geneity. Global ecology and biogeography: a journal of macroecology 24:1329–1339.
- 438 https://doi.org/10.1111/geb.12365
- Van Looveren A, Klaise J (2019) Interpretable counterfactual explanations guided by proto-
- 440 types. arXiv [csLG]
- 441 Wadoux AMJ-C, Saby NPA, Martin MP (2023) Shapley values reveal the drivers of soil organic
- carbon stock prediction. SOIL 9:21–38. https://doi.org/10.5194/soil-9-21-2023
- 2443 Zurell D, Elith J, Schröder B (2012) Predicting to new environments: tools for visualizing
- 444 model behaviour and impacts on mapped distributions. Diversity & distributions 18:628–
- 445 634. https://doi.org/10.1111/j.1472-4642.2012.00887.x
- 2446 Zurell D, Franklin J, König C, et al (2020) A standard protocol for reporting species distribution
- 447 models. Ecography 43:1261–1277. https://doi.org/10.1111/ecog.04960