

ECOGRAPHY

Software note

wallace 2: a shiny app for modeling species niches and distributions redesigned to facilitate expansion via module contributions

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Released 4 years ago, the *Wallace EcoMod* application (R package *wallace*) provided an open-source and interactive platform for modeling species niches and distributions that served as a reproducible toolbox and educational resource. *wallace* harnesses R package tools documented in the literature and makes them available via a graphical user interface that runs analyses and returns code to document and reproduce them. Since its release, feedback from users and partners helped identify key areas for advancement, leading to the development of *wallace 2*. Following the vision of growth by community expansion, the core development team engaged with collaborators and undertook a major restructuring of the application to enable: simplified addition of custom modules to expand methodological options, analyses for multiple species in the same session, improved metadata features, new database connections, and saving/loading sessions. *wallace 2* features nine new modules and added functionalities that facilitate data acquisition from climate-simulation, botanical and paleontological databases; custom data inputs; model metadata tracking; and citations for R packages used (to promote documentation and give credit to developers). Three of these modules compose a new component for environmental space analyses

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(e.g., niche overlap). This expansion was paired with outreach to the biogeography and biodiversity communities, including international presentations and workshops that take advantage of the software's extensive guidance text. Additionally, the advances extend accessibility with a cloud-computing implementation and include a suite of comprehensive unit tests. The features in *wallace* 2 greatly improve its expandability, breadth of analyses, and reproducibility options, including the use of emerging metadata standards. The new architecture serves as an example for other modular software, especially those developed using the rapidly proliferating R package *shiny*, by showcasing straightforward module ingestion and unit testing. Importantly, *wallace* 2 sets the stage for future expansions, including those enabling biodiversity estimation and threat assessments for conservation.

Keywords: ecological niche model, modular, R, reproducibility, shiny, software, species distribution model

Introduction

As the complexity and breadth of analyses in ecology and evolution continue to expand, it is increasingly difficult for researchers to implement new methodological tools and ensure reproducibility. This is particularly true for models of species niches and distributions (hereafter ENMs: ecological niche models; also termed SDMs: species distribution models). Such models have a multitude of basic and applied uses (Stanton et al. 2012, Uden et al. 2015), and this research area has seen a flurry of new theoretical and methodological developments (Peterson et al. 2011, Guisan et al. 2017). Unfortunately, the pace at which new methods emerge has made entry into the field difficult. Further, programming scripts that accompany published ENM studies can be difficult to repurpose, and tools facilitating reproducibility and providing interactive visualizations to inspect data and models remain scarce. To help lower these barriers, the ecological modeling application *Wallace EcoMod* ver. 1 was produced four years ago (R package *wallace*; Kass et al. 2018; CRAN: https://cran.r-project.org/src/contrib/Archive/wallace/wallace_1.0.tar.gz; Github: <https://github.com/wallaceEcoMod/wallace/releases/tag/v1.0.0>).

Written in R and providing a graphical user interface (GUI), *wallace* was designed to be an accessible tool for researchers, as well as a resource for conservation practitioners and educators. Inspired by the 2015 Nielsen Challenge of the Global Biodiversity Information Facility, the package *wallace* 1 was developed using two packages that enable interactive analyses: *shiny* for development of applications with GUIs (Chang et al. 2021) and *leaflet* for map display and navigation (Cheng et al. 2021). Additionally, it harnesses packages with tools for ENMs documented in the literature and available on CRAN. *wallace* walks users through a modeling analysis, providing visualizations and extensive guidance text and documentation, with clear references to the underlying R packages used. It is hierarchically structured in discrete analysis steps ('components'), each with different methodological options ('modules') organized in a customizable workflow. At any point, users can download R code in an .Rmd file that reproduces the analysis. *wallace* 1 has seen great user interest, with > 51 000 downloads from CRAN (October 2022). The original paper provided a brief overview of recent SDM software applications,

several of them interactive, and how each compared with *wallace* (Kass et al. 2018). Since then, the utility of R-based interactive applications in this research area has increased, evident by the development of other GUI-based software for ENMs that provide different functionalities: *ntbox* (Osorio-Olvera et al. 2020) and *shinyBIOMOD* (<https://gitlab.com/IanOndo/shinybiomod>).

The characteristics of *wallace* – accessible, open, expandable, flexible, interactive, instructive, and reproducible – do not exist together in any other currently available software. Notably, these characteristics also make it an ideal resource for education. The application offers users the ability to build and explore both models and mapped predictions without having to stitch together programming code, which is time-consuming, tedious, and error-prone. Since its release, the application has been used globally in university coursework and by professionals in governmental and NGO positions. Additionally, *wallace* was featured in a free and comprehensive ENM web course (ENM 2020, Peterson et al. 2022) and educational webinars in multiple languages (Supporting information). Thanks to vibrant worldwide user feedback, mostly via its Google Group (<https://groups.google.com/g/wallaceecomod>), various software bugs were identified and addressed and several requested new features added (ver. 1.1; CRAN archive: https://cran.r-project.org/src/contrib/Archive/wallace/wallace_1.1.0.tar.gz; Github tag: <https://github.com/wallaceEcoMod/wallace/releases/tag/v.1.1>).

Building on the success of *wallace* to date and user feedback, we identified six key areas for advancement, leading us to restructure and expand the software. These key areas were: simplified addition of new modules (and unit tests), ability to make models for multiple species in the same session, production of detailed analysis metadata, increased options for inputting and downloading data, and ability to save and load unfinished analysis sessions. To do so, the core development team made major changes to the underlying structure of *wallace* (concomitant with a major redesign for the R package *ENMeval* (Kass et al. 2021) that builds and evaluates models) and honed the process of module addition with collaborators while developing extensions that reflected their areas of expertise. This expanded the application broadly (Fig. 1), with new functionalities centering on the key areas for advancement and including nine new modules (Fig. 2) documented via an updated vignette (<https://>

(A)

Component: Obtain Occurrence Data

Species menu: Bassaricyon neblina

Log window:

- Bassaricyon neblina | #CiteTheDOI: cbif.org (20 April 2022)
- CBIF Occurrence Download https://doi.org/10.15468/dl.chqarc
- > Bassaricyon neblina | Total gbif records returned [51] out of [51] total. Records without coordinates removed [0]; Duplicated records removed [8]. Remaining records [43].

Module: Query Database (Present)

R packages: BIEN, occCite, spocc

Choose Database: GBIF (selected), VertNet, BISON, BIEN

Keep only occurrences with uncertainty values

Include Data Source Citations

GBIF User ID: *****, GBIF email: *****, GBIF password: *****

Enter species scientific name: Bassaricyon neblina

Query Database

Module Developers: Jamie M. Kass, Bruno Vilela, Gonzalo E. Pinilla-Bultago, Hannah Owens, Cory Merow, Robert P. Anderson

BIEN references

Tools for Accessing the Botanical Information and Ecology Network Database

Package Developers: Brian Maitner

[CRAN documentation](#)

occCite references

Querying and Managing Large Biodiversity Occurrence Datasets

Package Developers: Hannah L. Owens, Cory Merow, Brian Maitner, Jamie M. Kass, Vijay Barve, Robert P. Guralnick, Damilano Oldoni for rOpenSci, see <<https://github.com/rOpenSci/software-review/issues/407>>

About Team How To Use Load Prior Session

Load session

Users now have the option to stop and save their work, so that they can resume at a later time. Each component (Obtain Occurrence Data, Obtain Environmental Data, etc.) has a Save Session feature within the 'Save' tab, allowing users to save their progress up to that point as an RDS file (.rds).

This file can be uploaded here, in the Load Session tab, allowing the user to continue the workflow where they left off.

Browse... No file selected

Load RDS

(B)

Map Occurrences Results Component Guidance Module Guidance Save

Map

Occurrences

Results

Component Guidance

Module Guidance

Save

(C)

Note: To save your session code or metadata, use the Reproduce component

Save Session

By saving your session into an RDS file, you can resume working on it at a later time or you can share the file with a collaborator.

Download Data

Download data/results from analyses from currently selected module

Download PCA results: ZIP File

Download Occurrence density grid: PNG File

Download Niche Overlap plot: PNG File

Figure 1. Highlights of *wallace* 2 interface. (A) Main panel showing active component 'Obtain Occurrence Data' with new species menu (dashed green line) and database DOI citation in log window (dashed red line). Also note new features (dashed yellow line): tabs for Reproduce component (offering reworked downloads of session code, metadata, and package references), support tab with help links, and 'shutdown' button. (B) New option to load prior sessions located in the 'Intro' component. (C) New 'Save' tab with expanded download options.

wallaceecomod.github.io/wallace/articles/tutorial-v2.html. The new modules include: two for new data acquisition (download paleontological occurrences and climate simulations), two for more flexible user inputs (draw background extent and model transfer to user-specified environmental data), two for metadata (download model metadata and citations for R packages used), and three composing a new environmental space comparison component. Below, we introduce the key advances of *wallace* ver. 2; highlight the new component, modules, and functionalities; explain outreach activities and novel accessibility options; and discuss future directions for growth.

Key advances of *wallace* 2

Simplified module addition

Open software development in ecology, evolution, and biogeography thrives via community partnerships like the flagship R Project for Statistical Computing (<https://www.r-project.org/>). Such partnerships have enabled modular toolsets that cover a wide breadth of analyses (e.g., BEAST ([Bouckaert et al. 2019](#)), Bioconductor ([Huber et al. 2015](#))). Modularity allows for new features to be shared among groups. Collaborative module addition is fundamental to

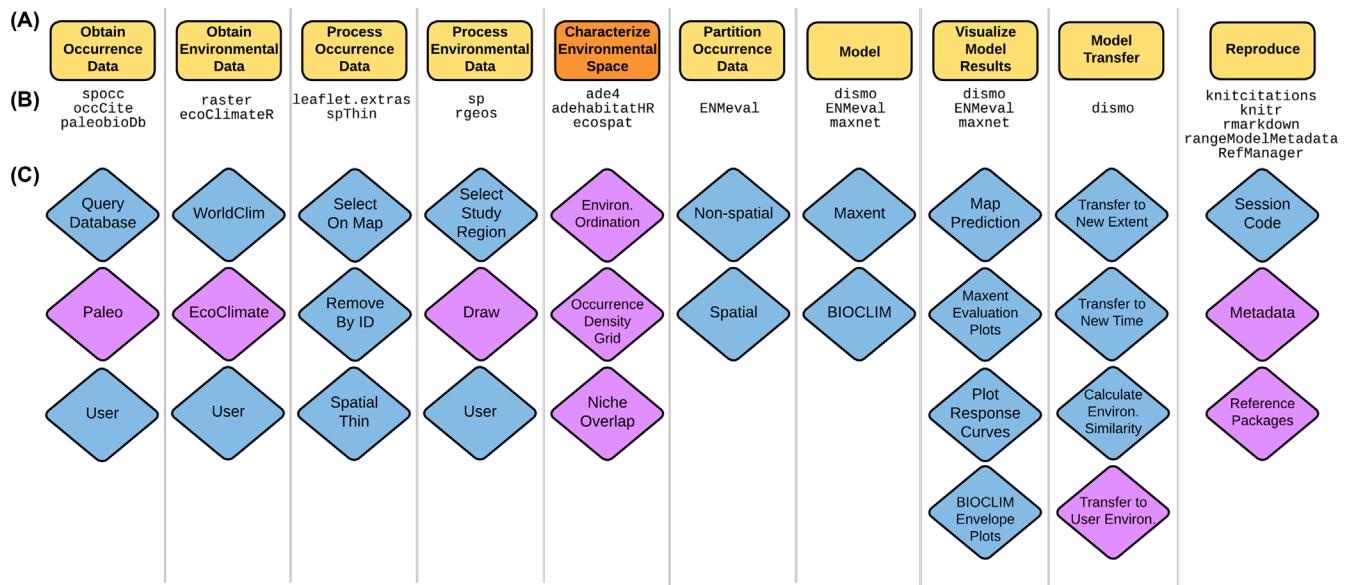


Figure 2. Schematic for updated *wallace* 2 workflow options. (A) All components or main steps of analysis (yellow for existing, orange for new). (B) R packages used for each component. (C) All modules, or major methodological options within components (blue for existing, purple for new). These new features enable environmental space comparisons for two species; data acquisition from climate-simulation, botanical and paleontological databases; custom data inputs; model metadata tracking; and citations for R packages used.

the *Wallace EcoMod* project, which emphasizes community involvement as an engine to make the software pluralistic and track advancements in the field. When *wallace* 1 was developed, *shiny* programming in R was relatively new, with few modular examples available and no illustrations of functionality for straightforward addition of modules by users. For the first release, the application was engineered to allow the insertion of *shiny* modules, which necessitated modifying the main *shiny* application scripts. Although this process allowed for expansion, it nonetheless posed significant barriers because of the specific programming knowledge needed.

Therefore, we set out to improve the module-addition process. With dual goals of gaining crucial insight and expanding the functionality of *wallace*, the core development team invited collaborators representing four different research labs (Author contributions) to co-develop new modules. Based on this experience, we engaged with a specialist in *shiny* (DA) to develop a new framework for module addition that significantly reduces the programming burden on contributors (Fig. 3). Unlike the previous implementation, the modifications necessary to contribute new modules to *wallace* 2 are almost exclusively restricted to module-specific ancillary R scripts written without *shiny* functions. This reduces the chances of introducing errors as well as the knowledge required regarding both *shiny* and the structure of *wallace* (module-addition vignette: <https://wallaceecomod.github.io/wallace/articles/module-addition.html>). These architectural changes also facilitate unit testing that automates tests of code functionality, which are crucial to preventing errors during development. Although writing unit tests for R functions is straightforward using available tools, as modules in *wallace* 1 were based on *shiny* modules, standard R unit tests

could not be written for them. In contrast, *wallace* 2 modules are specified as standard R functions, allowing for typical unit tests (R package *testthat*; Wickham 2011). *wallace* 2 now has a comprehensive suite of documented unit tests for all module functions, which serve as templates for future modules (found in the R package in *wallace/tests/testthat*).

Managing multiple species in a single session

We restructured the application to allow users to manage multiple species in the same *wallace* session. While the analysis unit in *wallace* releases prior to ver. 2 was data from a single species, it is now a list of species that allows for batch processing. *wallace* 2 still exclusively makes single-species ENMs (i.e., not joint models). However, users can now download or upload data for multiple species and either make species-specific methodological choices or, using the batch option for given modules, apply the same choices to all species. Additionally, as a product of one of the collaborations, we added a new ‘Characterize Environmental Space’ component with three new modules (‘Environmental Ordination’, ‘Occurrence Density Grid’, ‘Niche Overlap’) that enable comparisons between two species in environmental space using the R package *ecospat* (Di Cola et al. 2017; Fig. 1, 2).

Generation of analysis metadata

The ability for researchers to document key methodological details and reproduce published analyses is crucial for ENMs (Merow et al. 2019, Fitzpatrick et al. 2021). Recently, calls for better reporting and documentation of ENMs have led to reproducibility checklists (Feng et al. 2019), standard

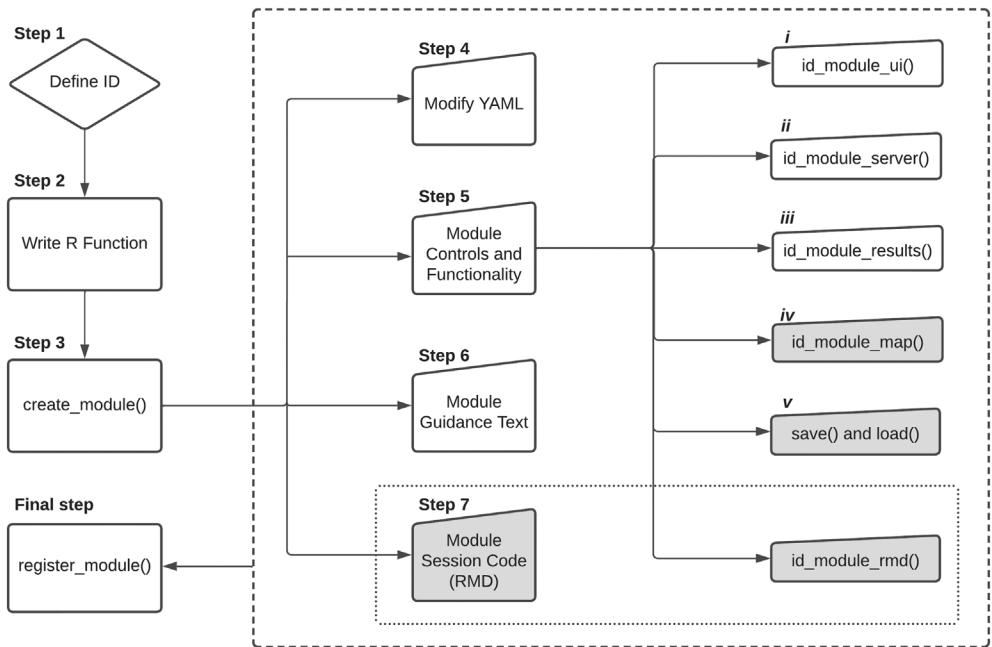


Figure 3. Steps for adding a module in *wallace* 2 using the new simplified process, showing mandatory steps (white shapes) and recommended ones (gray shapes; see module authorship vignette <https://wallaceecomod.github.io/wallace/articles/module-addition.html>). 1) Pick short module name. 2) Write R function with same name as module, including required arguments. 3) Create required module template files using `create_module()`. 4) Modify configuration file (.yml) that specifies module parameters. 5) Create module controls and functionality: i) define user interface; ii) define server functionality; iii) create user-interface output for results (e.g., plot, table); iv) write functionality to plot results on *leaflet* map; v) enable module to record information for saving and reloading. 6) Compose guidance text. 7) Write to downloadable ‘Session Code’ .Rmd file to enable reproducibility (requires modifying two files (dotted line)). Final) Register module to be included in the interface via `register_module()` (dashed line).

metadata protocols such as ODMAP (Zurell et al. 2020) and best practices and guidelines (Araújo et al. 2019, Sofaer et al. 2019). *wallace* 1 generated R Markdown scripts (R package *rmarkdown*; Allaire et al. 2021), which embedded R code within narrative text and could be run to reproduce results. This allowed non-programmers to conduct a reproducible analysis—a first for ENM software. However, there was also a desire for metadata describing analysis decisions, following emerging community platforms.

Therefore, via module partnerships, we made two new additions to generate different kinds of metadata. One partnership dovetailed with the development of the first programming toolset for ENM metadata: the Range Model Metadata Standards (RMMS), implemented with the *rangeModelMetadata* R package (Merow et al. 2019) as an editable R object that *wallace* now uses to record methodological decisions by the user. Notably, RMMS provided the technical foundation upon which the ODMAP reporting framework operates (Zurell et al. 2020). The RMMS object is now available for download at any stage of a *wallace* analysis via a new module ‘Metadata’ under the ‘Reproduce’ component tab (Fig. 1). The standardized metadata that *wallace* now produces can be used to help populate ODMAP (Zurell et al. 2020) and even facilitate scoring of ENM analyses for applied uses (Araújo et al. 2019, Sofaer et al. 2019). Another partnership was with the developers of the R package *occCite* (Owens et al. 2021), which gives users the option

to generate a unique and persistent identifier for occurrence data downloads from the Global Biodiversity Information Facility (GBIF). When users download occurrence data from GBIF and check the ‘Include Data Source Citations’ option (Fig. 1), they now receive a DOI reference for the occurrence dataset. Finally, a new module ‘Reference Packages’ produces citations for the R packages used in the analysis, promoting documentation and giving credit to their original developers (Fig. 2). These new metadata functionalities help users achieve documentation and reproducibility of both methods and results, though final processed data must still be archived separately (Anderson et al. 2020).

New database connections and download options

wallace now offers database connections for downloading cleaned occurrence data for plants via the Botanical Information and Ecology Network (BIEN, R package *BIEN*; Maitner et al. 2018) and a ‘Paleo’ module for paleontological records using the Paleobiology Database (R package *paleobioDB*; Varela et al. 2020). Complementing the latter, the new module ‘EcoClimate’ also downloads environmental data from the ecoClimate database (Lima-Ribeiro et al. 2015; R package *ecoClimateR* (<https://github.com/ecoClimate/ecoClimateR>)), consisting of bioclimatic variables from 0.5 degree resolution climate simulations derived from general circulation models (GCMs) for multiple time steps for

the past, present and future (Fig. 1, 2). Moreover, expanded options now exist in a dynamic ‘Save’ tab to help users download data in each analysis step (details below).

Ability to save and load unfinished analysis sessions

wallace 2 has the option to save a session in progress and then later continue it. Via the new ‘Save’ tab within an analysis component (Fig. 1), users can save current progress by storing all session data (e.g., occurrences, environmental data, predictions, plots) and user decisions (e.g., parameters, options) in a .rds file (format for storing single R objects). Users can later continue an unfinished analysis by loading the .rds file in the new ‘Load Prior Session’ tab under the ‘Intro’ component.

New component, modules and functionalities

This release premieres a ‘Characterize Environmental Space’ component with three modules, and six other new modules spread across existing components. Most analyses in *wallace* are spatial in nature and thus operate in ‘geographic space’, but the new component features analyses for pairs of species in the space defined by the environmental predictor variables, termed ‘environmental space’ (Peterson et al. 2011). The module ‘Environmental Ordination’ defines the environmental space as the first two axes of a principal component analysis (PCA) on the predictor variables. Within this space, the module ‘Occurrence Density Grid’ generates a kernel density grid for the occurrence localities, where the densest regions have the most occurrences relative to that region’s environment. The third module ‘Niche Overlap’ can calculate the overlap between the occurrence densities of two species in environmental space and then run permutation tests to determine the significance of the empirical overlap value. The analyses featured in these modules are based on methods described in Warren et al. (2008) and Broennimann et al. (2012) implemented in the package *ecospat*.

In addition, six new modules expand data acquisition, data inputs, and metadata, and other new features make improvements to existing modules. First, two new modules enable modeling with paleontological data. Paleontological occurrences and environmental data can now be downloaded using the module ‘Paleo’ (component ‘Obtain Occurrence Data’) and the module ‘EcoClimate’ (component ‘Obtain Environmental Data’). Two other modules enable new customized inputs. In addition to the existing methods that draw shapes around the occurrence localities, background extents defined in the component ‘Process Environmental Data’ can now be drawn on the map with mouse clicks using the module ‘Draw’. Moreover, in the component ‘Model Transfer,’ predictions can now be made to user-specified environmental layers representing new areas or time periods with the module ‘Transfer to User Environments’. Lastly, two modules increase the capacity of *wallace* to provide metadata

on modeling analyses. The module ‘Metadata’ under the ‘Reproduce’ component provides a fully documented RMMS metadata object containing all the details of the analysis; the object can be shared with collaborators or used as supporting information for publications. Lastly, the module ‘Reference Packages’ provides a list of citations for the R packages (and their version numbers) used in the analysis, which promotes documentation and gives credit to the developers of packages that *wallace* uses. Being cited in papers and reports should increase the incentive for researchers to formalize their code into R packages on CRAN and join the *wallace* community to integrate them into future releases. New features for existing modules include the ability to: remove occurrence data that lack quantification of georeferencing uncertainty (helping users focus on the high-quality information; Anderson et al. 2020), map model predictions with a specified quantile of omission, specify categorical variables for modeling, use the new *ENMeval* 2 to tune models via parallel processing and report expanded performance metrics (Kass et al. 2021), visualize aggregate map tiles for downloading 30 arcsecond bioclimatic predictor rasters, and define custom extents for model transfer by drawing or uploading shapefiles.

Example

As an example analysis to highlight some of the advances of *wallace* 2, we focused on two closely related carnivoran mammal species of the genus *Bassaricyon* (Family Procyonidae). To do so, we employed bioclimatic variables from the eco-Climate database to compare the species’ climatic niches and model their ranges, then transferred one of the models into the deep past and near future. *Bassaricyon neblina*, or the olinguito, is found in tropical montane areas of western Colombia and Ecuador. *Bassaricyon alleni*, or the eastern lowland olingo, has a broader range throughout northern South America. The workflow, methodological choices and images of the results are shown in Fig. S1. A more detailed worked analysis of key prior and new functionalities can be found in the current vignette (<https://wallaceecomod.github.io/wallace/articles/tutorial-v2.html>).

Outreach and accessibility

Promoting and increasing access to software meant for open collaboration is essential for its use and expansion. We conducted outreach in two major ways: first by creating and maintaining platforms to gather feedback (necessary for making fixes and guiding the longer-term vision regarding software changes), and second by giving talks and workshops. In addition to maintaining an informational project website (<https://wallaceecomod.github.io/>), we gathered feedback using a number of different platforms, including pre- and post-workshop online surveys, a Google Group (<https://groups.google.com/g/wallaceecomod>), GitHub Issues (<https://github.com/wallaceEcoMod/wallace/issues>), social

media (Twitter [#WallaceEcoMod] and Facebook), and an email account (wallaceEcoMod (at) gmail.com). We received substantial feedback (> 260 items; January 2018 through October 2022), leading to bug fixes (n=89 reported from January 2018 through October 2022). In-person or virtually, we gave 20 workshops, 24 presentations, and 8 webinars to researchers in East Asia, North America, South America, Southeast Asia and West Africa narrated in English, French, Japanese, Spanish and Vietnamese (see Supporting information for a reference list). *wallace* workshops also have been given by others around the world (not part of the development team), and we have interfaced with organizers to suggest presentation materials. Lastly, we also improved accessibility by including a ‘Support’ tab with links for users to report issues and email questions (Fig. 1), as well as a Docker implementation of *wallace* that facilitates its use in workshops and enables cloud computing (Supporting information).

Future directions

These investments in *wallace* 2 can promote several areas of future development. One key opportunity is to build upon the new metadata feature to embrace emerging community-driven frameworks for methods reporting (Zurell et al. 2020) and quality standards for applied uses (Araújo et al. 2019). Key areas for reaching those goals include the addition of other algorithms, characterizations of uncertainty, and approaches for determining statistical significance of model predictions (Bohl et al. 2019)—all features which would be enabled by recent changes to the underlying *ENMeval* package (Kass et al. 2021). Additionally, the ability of *wallace* 2 to handle data and predictions for multiple species allows future integration of methods to study community-level questions (Schmitt et al. 2017), including uses in conservation biology.

We aim to accelerate growth of the user and contributor communities worldwide to expand the analyses possible in *wallace*. Successful models for sustaining open-source software and training tools through community contributions and other mechanisms include the QGIS Project (<https://www.qgis.org/>), Software Carpentry, rOpenSci (<https://ropensci.org/>), and the R Project for Statistical Computing (<https://www.r-project.org>) itself. Based on the enormous potential for use of ENMs in applied studies in areas as diverse as agriculture, public health, and biodiversity conservation, investments in *wallace* and an eventual self-sustaining model should prove worthwhile and cost-effective.

To cite *wallace* 2 or acknowledge its use, cite this Software note as follows, substituting the version of the application that you used for ‘version 2.0’:

Kass, J. M. et al. 2022. *wallace* 2: a shiny app for modeling species niches and distributions redesigned to facilitate expansion via module contributions. – Ecography 2023: e06547 (ver. 2.0).

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Jamie M. Kass: Conceptualization (equal); Methodology (equal); Software (equal); Validation (supporting); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Gonzalo E. Pinilla-Buitrago:** Conceptualization (supporting); Methodology (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Andrea Paz:** Methodology (supporting); Software (equal); Validation (equal); Writing – review and editing (supporting). **Bethany A. Johnson:** Software (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Valentina Grisales-Betancur:** Methodology (supporting); Software (equal); Validation (supporting); Writing – review and editing (supporting). **Sarah I. Meenan:** Software (supporting); Validation (supporting); Writing – review and editing (supporting). **Dean Attali:** Conceptualization (equal); Software (supporting); Writing – review and editing (supporting). **Olivier Broennimann:** Conceptualization (supporting); Methodology (supporting); Software (supporting); Writing – review and editing (supporting). **Peter J. Galante:** Methodology (supporting); Software (supporting); Writing – review and editing (supporting). **Brian S. Maitner:** Methodology (supporting); Software (supporting); Writing – review and editing (supporting). **Hannah L. Owens:** Methodology (supporting); Software (supporting); Writing – review and editing (supporting). **Sara Varela:** Conceptualization (equal); Methodology (supporting); Software (supporting); Writing – review and editing (supporting). **Matthew E. Aiello-Lammens:** Conceptualization (supporting); Funding acquisition (supporting); Project administration (supporting); Resources (supporting); Software (supporting); Supervision (supporting);

Writing – review and editing (supporting). **Cory Merow:** Conceptualization (supporting); Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Software (supporting); Supervision (supporting); Writing – review and editing (supporting). **Mary E. Blair:** Conceptualization (supporting); Funding acquisition (supporting); Project administration (supporting); Resources (supporting); Supervision (supporting); Writing – review and editing (supporting). **Robert P. Anderson:** Conceptualization (equal); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Resources (lead); Software (supporting); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Occurrence locality data used in the example are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1c59zw402> (Kass et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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