

APPLICATION

voluModel: Modelling species distributions in three-dimensional space

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Abstract

1. Ecological niche modelling (ENM), species distribution modelling and related spatial analytical methods were first developed in two-dimensional (2-D) terrestrial systems; many common ENM workflows organize and analyse geographically structured occurrence and environmental data based on 2-D latitude and longitude coordinates. This may be suitable for most terrestrial organisms, but pelagic marine species are distributed not only horizontally but also vertically. Extracting environmental data for marine species based only on latitude and longitude coordinates may result in poorly trained ENMs and inaccurate prediction of species' geographical distributions, as water conditions may vary strikingly with depth.
2. We developed the voluModel R package to efficiently extract three-dimensional (3-D) environmental data for training ENMs (i.e. presences and absences/pseudoabsences/background). voluModel also provides tools for 3-D ENM projection visualization and estimation of model extrapolation risk.
3. We present the main features of the voluModel R package and provide a simple modelling workflow for Luminous Hake, *Steindachneria argentea*, as an example. We also compare results from 2-D and 3-D spatial models to demonstrate differences in how the modelling methods perform.
4. The use of 3-D environmental data generates more precise estimates of environmental conditions for training ENMs. This method also improves inference of species' suitable abiotic ecological niches and potential geographic ranges. 3-D niche modelling is important step forward for marine macroecology and biogeography, as it will yield more accurate estimates of ocean species richness and potential past and future changes in the horizontal and vertical dimensions of species' geographic ranges. The latter is particularly relevant considering ongoing climate change that may cause redistribution of species in environmental space (both in latitude and depth) over time.

KEYWORDS

3-D, ecological niche model, geographic range, marine, pelagic, R package, species distribution model, visualization

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1 | INTRODUCTION

Ecological niche modelling and species distribution modelling techniques (ENM and SDM respectively) were first developed to infer putative suitable environmental conditions for species in terrestrial systems. While there are distinctions to be made between ENM and SDM, hereafter we primarily use the term 'ENM', as SDMs can be considered ENMs that have subsequently been projected into geographic space (Warren, 2012). ENM workflows and stand-alone programmes generally accept a set of points, expressed as latitudinal and longitudinal coordinates, representing where a species of interest has been observed (i.e. presences or occurrences). Depending on the algorithm, coordinate datasets may also include points representing species' absences, pseudoabsences or background data representing the full range of environments accessible to the species (Barve et al., 2011; Elith et al., 2011). In some workflows, observed environmental conditions accompany these data; in others, data on environmental conditions (e.g. temperature, precipitation, salinity, etc.) are extracted at occurrence points from a set of 2-D data layers representing environmental conditions. Once an ENM is calibrated, it can then be used to model the potential geographical distribution of a species by projecting modelled suitable environmental conditions using raster layers of environmental conditions within the area of interest.

Critically for marine species, two-dimensionally summarized environmental data extracted at occurrence coordinates may provide an inaccurate estimate of abiotic ecological conditions where a species has been observed, as environmental conditions may change strikingly with depth (Figure 1; Duffy & Chown, 2017). One early approach to explicitly incorporating depth-structured data for pelagic marine modelling combined all vertical layers in an environmental dataset side by side into a continuous 2-D grid for model projection (Bentlage et al., 2013); another approach trained the model based on environmental data directly extracted from occurrence and pseudoabsence points and then projected the results onto each vertical layer (Duffy & Chown, 2017). However, neither of these methods have been widely adopted by marine niche modellers. This may be partly due to a lack of accessible tools—both studies supply bespoke scripts to repeat the analyses they present, but do not provide easily generalizable or scalable workflows that would facilitate more widespread methodological adoption. There remains a need for tools to explicitly and efficiently model ecological niches and species distributions in three dimensions (Melo-Merino et al., 2020). Here, we present voluModel, an R (R Core Team, 2021) package to facilitate simple, repeatable 3-D marine ecological niche modelling workflows.

2 | THE R PACKAGE VOLUMODEL

We designed voluModel to aid in processing of ENM modelling inputs and outputs (Table 1), while allowing the user maximum flexibility in study design and algorithm choice. The process starts with down-sampling occurrence point data to the voxel (3-D pixel equivalent) resolution of environmental data represented in a RasterBrick (i.e.

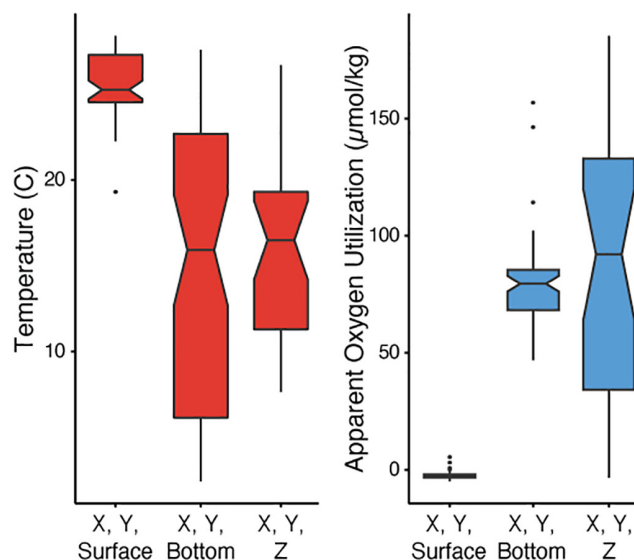


FIGURE 1 Environmental conditions at Luminous Hake observation localities. Environmental conditions extracted to observation coordinates ($n = 113$) from sea surface (X, Y, Surface), deepest available measurement (X, Y, Bottom) and at depth of occurrence (X, Y, Z). Dots indicate statistical outliers (1.5 times interquartile range outside upper and lower quartiles). Further details in 'Introduction to voluModel' vignette (https://cran.r-project.org/web/packages/voluModel/vignettes/a_Introduction.html) and Supporting Information.

a multilayer) object. voluModel also provides tools to interpolate and smooth unevenly sampled environmental raster data in cases where these data are expected to be spatially autocorrelated. If appropriate to the user's algorithm of choice, the user next delimits a training region and draws 3-D background, absence or pseudoabsence points from that training region. Next, voluModel facilitates environmental data extraction using 2-D (e.g. latitude and longitude) and vertical (e.g. depth) coordinates for occurrence, and optionally, background, pseudoabsence or true absence points. The user can then generate niche models using established algorithms that accept points-with-data workflows and perform 3-D geographic projections programmatically using simple scripted loops. Finally, voluModel allows the user to visualize projection results and assess model extrapolation risk in 3-D. In section 4, we provide a simple example of a generalized linear model ENM workflow; an example of a niche envelope model workflow can be found in the 'Introduction to voluModel' vignette (https://cran.r-project.org/web/packages/voluModel/vignettes/a_Introduction.html).

3 | PACKAGE FEATURES

3.1 | Environmental data sampling (vignette: https://cran.r-project.org/web/packages/voluModel/vignettes/c_DataSampling.html)

A key area where voluModel tools facilitate 3-D ENM is the interface between horizontal and vertical coordinates and 3-D environmental data. xyzSample() extracts environmental data from

TABLE 1 Summary of voluModel functions.

Process environmental data	
bottomRaster()	Estimate bottom conditions from SpatialPointsDataFrame
interpolateRaster()	Fill empty cells based on nearby values
smoothRaster()	Smooth values based on nearby values
Sample data for training model	
downsample()	Thin coordinates to template raster resolution
marineBackground()	Create training region from occurrence coordinates
mSampling2D()	Generate 2-D coordinates from training region
mSampling3D()	Generate 3-D coordinates from training region
xyzSample()	Extract data from RasterBrick at 3-D coordinates
Assess model uncertainty	
MESS3D()	Estimates model projection extrapolation
Visualize	
pointMap()	Map single set of points
pointCompMap()	Compare two sets of points
oneRasterPlot()	Map single continuous raster
rasterComp()	Map binary 3-D RasterBrick using transparency

a RasterBrick at a set of 3-D coordinates (e.g. species presences, species absences or background or pseudoabsence points). To reduce the risk of biasing ENM inference due to pseudoreplicated presence data (Aiello-Lammens et al., 2015), downsample() reduces coordinate sampling to the resolution of the environmental dataset; in a 3-D context, the user loops downsample() across layers of a template RasterBrick to reduce a dataset to the template's voxel resolution. That is, if more than one occurrence falls within a given voxel, the coordinates are aggregated and replaced with a single coordinate at the centre of that voxel. The results of downsample() can be compared to the original dataset using pointCompMap(), a plotting function wrapper around ggplot() (ggplot2; Wickham, 2016) comparing 2-D positions of two coordinate datasets. For a single coordinate dataset, pointMap(), also a ggplot() wrapper, generates a formatted map of 2-D positions.

To generate a sample of pseudoabsences and/or background points, it is important to consider the geographic region accessible to the species of interest (Barve et al., 2011) which is referred to ENM literature as the sampling background or **M**, among others. Generally, users should carefully curate sampling backgrounds to reflect the biological and geographical realities of the species they are modelling and the regions being sampled. However, absent specific information on species' dispersal capabilities, algorithmically generating a repeatable sampling background from a clear set of rules may be suitable. We designed

marineBackground() as a wrapper around getDynamicAlphaHull() from rangeBuilder (Rabosky et al., 2016); getDynamicAlphaHull() generates background sampling regions by fitting an alpha hull polygon around an occurrence point dataset. marineBackground() extends getDynamicAlphaHull() functionality to address issues of generating background polygons for marine modelling in two ways: by allowing a user to clip the polygon to only include oceans, deleting unoccupied polygons after clipping (Figure 2a), and by wrapping polygons around the antemeridian (i.e. 180°E or W) instead of truncating them. Once generated, background polygons can be saved as shapefiles and edited by hand in a GIS program of choice, if desired.

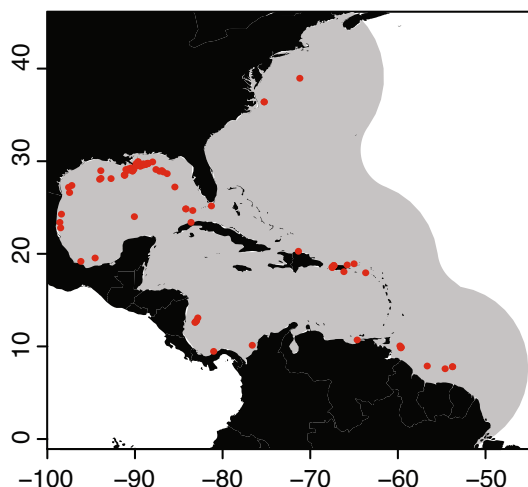
Once the user has downsampled coordinates and defined a sampling background, voluModel provides tools to extract environmental data to input into the user's ENM algorithm of choice. mSampling3D() generates a data.frame of all 3-D coordinates using an input template RasterBrick overlapping with an input polygon (i.e. a background region generated using marineBackground()). Either all RasterBrick depths can be sampled or the user can limit sampling to maximum and minimum depths of an input coordinate dataset, or manually specify maximum and minimum depths for sampling. mSampling2D() performs analogous actions but is limited to sampling from a single raster layer.

3.2 | Raster processing (vignette: https://cran.r-project.org/web/packages/voluModel/vignettes/b_RasterProcessing.html)

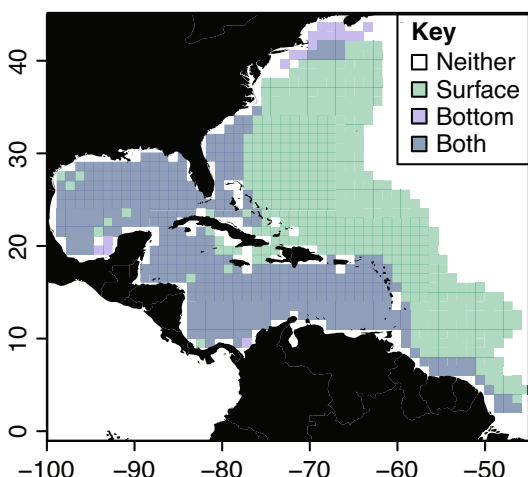
We have designed several tools for issues encountered by commonly used environmental variables (e.g. temperature, salinity, dissolved oxygen) represented by point shapefiles, such as World Ocean Atlas data (Garcia et al., 2018). First, a variable shapefile is read into R as a SpatialPointsDataFrame object; each data.frame row is a set of 2-D coordinates, and each column is a vertical position in the water column. In some cases (e.g. WOA dissolved oxygen, Garcia et al., 2019), measurements are not uniformly distributed across geographic space; missing measurements can be inferred using a thin plate spline model (Boer et al., 2001) with the interpolateRaster() function. smoothRaster() also uses a thin plate spline, but adjusts noisy measurements based on an assumption of spatial correlation (Hutchinson, 1995). Both interpolateRaster() and smoothRaster() use the TPS() function from fields (Nychka et al., 2015) and can accommodate large datasets using the fastTPS() thin plate spline approximation, also from fields.

To assist in comparing 3-D models to previously implemented modelling techniques, bottomRaster() generates a 2-D raster of the deepest measurement in each cell from a SpatialPointsDataFrame. For benthic species, ENMs based on bottom rasters may be more appropriate than those based on 3-D environmental data, but the user should treat these data with care. The deepest measurement in the water column at a particular coordinate is not always a measurement at the true ocean bottom (Sayre et al., 2017).

(a) **Luminous Hake Occurrence Points and Background Sampling Region, Caribbean Sea and Western Atlantic Ocean**



(b) **Comparison Between Luminous Hake Surface and Bottom GLMs**



(c) **Luminous Hake 3-D Potential Distribution from 5 to 800 m**

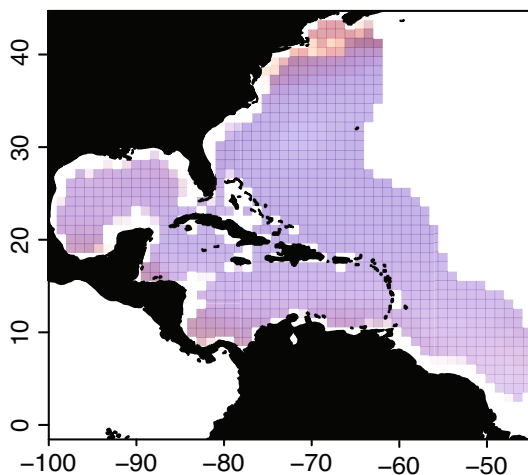


FIGURE 2 Mapping outputs from voluModel GLM workflow. (a) Background sampling region (grey) algorithmically generated from occurrence points (red) using `marineBackground()` function. Note the absence of training region spillover into Pacific. (b) Comparison of 2-D GLM models of suitable habitat for Luminous Hake, *Steindachneria argentea*, mapped using `rasterComp()`. (c) 3-D GLM model plotted using `plotLayers()`. Hues closer to pink indicate suitability at shallower depth layers, hues closer to blue indicate suitability at deeper depth layers. More saturated colours indicate a broader range of suitable depths. Analysis and plotting code used to generate figures supplied in Supporting Information.

3.3 | Raster visualization (vignette: https://cran.r-project.org/web/packages/voluModel/vignettes/d_Visualization.html)

`voluModel` provides several tools that use `spplot()` from `sp` (Pebesma & Bivand, 2005) to generate formatted maps with optional plotting of land shapefiles for geographic context. `rasterComp()` plots two semitransparent binary (i.e. presence/absence) layers to show overlaps, as one may wish to do to compare results of two niche model projections (Figure 2b). `plotLayers()` takes a `RasterBrick` of depth-structured presence/absence projections and plots each brick layer as a semitransparent overlay, colour-coded relatively by depth (Figure 2c). In the resulting plot, pinker hues show shallower potential presences, bluer hues show deeper potential presences and more saturated colours indicate potential presences at a wider range of depths. The `oneRasterPlot()` function generates a map of a single, continuous raster in high-contrast, colour-blind-friendly palettes using `viridis` (Garnier et al., 2021).

3.4 | 3-D analysis of model extrapolation

When projecting an ENM into geographic space, extrapolation into novel environmental conditions may be necessary (Elith et al., 2010). While extrapolation is not necessarily unwarranted and a model may make realistic predictions, this is not always the case (Owens et al., 2013). Several metrics have been proposed to estimate model extrapolation, but by far the most common is the Multivariate Environmental Similarity Surface (MESS; Elith et al., 2010). MESS compares environmental values at given point to a reference set of points (typically those used to train a model), returning negative values if a point is dissimilar to the reference set. `voluModel` provides a 3-D implementation of `mess()` from `dismo` (Hijmans et al., 2021), called `MESS3D()`. `MESS3D()` takes point-associated environmental data used to train an ENM and a named list of `RasterBrick` objects containing 3-D environmental data and produces a single `RasterBrick` of MESS scores. Areas at highest risk for model extrapolation can be visualized by reclassifying negative 3-D MESS values to 1, and positive values to 0, then mapping using `plotlayers()`. Areas of high estimated extrapolation potential can be removed from a species' 3-D distribution using

raster math (see example in '3-D Niche Modelling with the GLM Algorithm' vignette: https://cran.r-project.org/web/packages/voluModel/vignettes/e_GLMWorkflow.html).

4 | EXAMPLE: POTENTIAL DISTRIBUTION OF LUMINOUS HAKE

To illustrate a potential workflow using voluModel tools, we present an example modelling the distribution of potentially suitable habitat for the Luminous Hake, *Steindachneria argentea*. Luminous Hake is a gadiform codfish found in the Gulf of Mexico and Caribbean Sea (Cohen et al., 1990) and is a diurnal vertical migrant. Daytime surveys have recorded Luminous Hakes at depths from ~200 to ~1300m (Benavides-Morera & Campos-Calderón, 2018); nighttime surveys have recorded Luminous Hakes at depths from ~30 to ~190m (Love et al., 2004). We downloaded occurrence data via R OBIS (obis.org, 24 September 2020 via robis, Provoost & Bosch, 2019) and GBIF (gbif.org, 24 September 2020 via rGBIF, Chamberlain et al., 2021) via occ-Cite (Owens et al., 2021). Full citations for all the natural history collections contributing occurrence data for this example can be found in the '3-D Niche Modelling with the GLM Algorithm' vignette (https://cran.r-project.org/web/packages/voluModel/vignettes/e_GLMWorkflow.html). We use two environmental variables from the World Ocean Atlas (Garcia et al., 2018): mean annual temperature (Locarnini et al., 2018) and mean annual apparent oxygen utilization (AOU; Garcia et al., 2019). We chose these variables for their biological relevance but limited the selection to two variables for simplicity in this example. For real-world analyses, we recommend exploring additional explanatory variables available from the World Ocean Atlas and other similar sources. The occurrence and environmental data used in this example are packaged with voluModel.

The '3-D Niche Modelling with the GLM Algorithm' vignette demonstrates a voluModel workflow with sample code to generate 2-D and 3-D estimates of suitable habitat for the Luminous Hake. The workflow also includes removal of 3-D areas of extrapolation and mapping results; 2-D model results based on surface conditions and bottom conditions (Figure 2b) are compared to 3-D results (Figure 2c). Overall, the surface-based model identified a far more extensive distribution of suitable Luminous Hake habitat than the bottom-based model. The 3-D GLM identified suitable habitat that is shallower at latitudinal extremes and deeper in the open ocean compared to the Gulf of Mexico and Caribbean Sea.

5 | CONCLUSIONS

ENM methods have been applied to investigate questions regarding marine species' abiotic ecological niches and distributions in over 300 studies (Melo-Merino et al., 2020). However, only a handful have attempted to model distributions of pelagic organisms in three

dimensions. Tools in voluModel provide an enhanced workflow for three-dimensional marine correlative modelling by:

1. Efficiently extracting environmental data from 3-D occurrences and pseudoabsence/background points
2. Automatically and repeatably producing more oceanographically appropriate model training regions from which pseudoabsence or background points can be extracted.
3. Generating 3-D estimates of potential model extrapolation
4. Visualizing 3-D geographical ENM projections

voluModel development is ongoing; dependent functions, object classes and methods from raster (Hijmans, 2022a) and rgeos (Bivand & Rundel, 2021), which will soon be retired or replaced with more performance-optimized packages, are being updated with equivalent elements from sf (Pebesma, 2018), terra (Hijmans, 2022b) and stars (Pebesma, 2022). Future versions may also include functions for modelling using additional algorithms (e.g. Maxent; Phillips et al., 2017), tools for estimating additional extrapolation measures (e.g. Most Dissimilar Variable, Elith et al., 2010; Extrapolation Detection, Mesgaran et al., 2014; Movement-Oriented Parity, Owens et al., 2013) and other features requested by users.

The innovations voluModel provides allow marine researchers to generate fine-grained, 3-D ENMs to infer potential distributions of species more efficiently and accurately, addressing a long-standing need of pelagic marine studies. Our method may also allow for 3-D terrestrial modelling for forest canopy- or soil-dwelling organisms, if appropriate environmental data are obtainable. From a modern biodiversity perspective, stacking 3-D distributions inferred with our methods will yield more precise estimates of open-ocean species richness and provide insights into how biodiversity varies with depth. Projecting 3-D distributions through time will provide more accurate estimates of how suitable conditions for how marine species shifted both with latitude and depth in the past, as well as predicting how suitable habitat may shift in the future. Both improved biodiversity estimates and habitat suitability predictions have the potential to contribute substantially towards data-driven conservation efforts, including sustainable biodiversity management plans and robust marine protected area design.

AUTHOR CONTRIBUTIONS

Hannah L. Owens and Carsten Rahbek conceived the idea and designed the methodology; Hannah L. Owens analysed the data and led the writing of the manuscript. Both authors contributed critically to the study and to the final version of the manuscript, and both gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Hannah L. Owens and Carsten Rahbek do not have any conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14064>.

DATA AVAILABILITY STATEMENT

The R package voluModel is available from CRAN: <https://CRAN.R-project.org/package=voluModel>; a development version can be accessed at <https://github.com/hannahlowens/voluModel>. The version of the package used for this manuscript (v1.8; Owens & Rahbek, 2022) can be cited using the DOI: <http://doi.org/10.5281/zenodo.7372599>.

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SUPPORTING INFORMATION

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

Data S1: Supporting information.

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