

APPLICATION

geomorph v4.0 and gmShiny: Enhanced analytics and a new graphical interface for a comprehensive morphometric experience

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Abstract

1. Geometric morphometric (GM) tools are essential for meaningfully quantifying and understanding patterns of variation in complex traits like shape. In this field, the breadth of answerable questions has grown dramatically in recent years through the development of new analyses and increased computational efficiency.
2. In this note, we describe the ways in which *geomorph*, a widely used R package for quantifying and analysing GM data, has grown with the field.
3. We present *geomorph* v4.0 and describe the ways in which this version has dramatically improved upon previous versions. We also present a new graphical user interface for easy implementation, *gmShiny*.
4. These contributions position *geomorph* to be the primary tool for GM analyses, particularly those employing a phylogenetic comparative approach.

KEYWORDS

generalized Procrustes analysis, geometric morphometrics, *geomorph*, *shiny*

1 | INTRODUCTION

Quantifying the incredible diversity of life is a foundational ambition of biological research. Concomitant with this goal, biologists have sought ways of measuring and characterizing complex anatomical structures, for the purposes of deciphering patterns of variation in phenotypic traits, and its covariation with other variables. The field of *geometric morphometrics* (GM) provides a set of tools for accomplishing these tasks (Adams et al., 2013; Bookstein, 1991; Rohlf & Marcus, 1993). Many of these tools utilize sets of landmark coordinates—from anatomical points, curves and surfaces—as the basis of shape quantification, and from which patterns of shape variation are determined. Over the past several decades, the analytical theory of geometric morphometrics has

continued to develop, and so too has the need for improved computational tools to implement these approaches. While stand-alone GM software continues to be utilized (e.g. *TPS-series*: Rohlf, 2015; *MorphoJ*: Klingenberg, 2011), an increasing number of packages are found within the R-computational environment (e.g. *shapes*: Dryden, 2004; *Momocs*: Bonhomme et al., 2014; *Morpho*: Schlager, 2017; *mvMORPH*: Clavel et al., 2015), including *geomorph* (Adams & Otárola-Castillo, 2013).

In the years since its initial release, *geomorph* has become a major tool for geometric morphometrics, permutation-based statistics and macroevolutionary inference. For macroevolutionary studies, several packages are available for select statistical analyses for morphometric data (e.g. *TPS-tree* and *TPS-regr*: Rohlf, 2015; *MorphoJ*: Klingenberg, 2011; *mvMORPH*: Clavel et al., 2015; *geomorph*:

TABLE 1 Summary of all of `geomorph` v4.0 functions and their implementation in `gmShiny`. Some functions have limited flexibility in `gmShiny`, while others have not yet been added to the app. For full utility of `geomorph` v4.0 functions, use `geomorph` directly in R or R Studio. The functions that have been added or improved upon since the initial launch of `geomorph` are bolded. *This function has been moved to `RRPP`, a dependency of `geomorph`

Type	Function	gmShiny location (page; tab)
Analytical functions	bilat.symmetry	Shape Patterns; Symmetry
	compare.evol.rates	Linear Models; Model Design
	compare.multi.evol.rates	Shape Patterns; Modularity
	compare.pls	Not yet implemented
	estimate.missing	Data Prep; Generalized Procrustes Alignment
	fixed.angle	Not yet implemented
	globalIntegration	Shape Patterns; Integration
	gm.prcomp	Morphospace and Warp Grids
	gpagen	Data Prep; Generalized Procrustes Alignment
	integration.test	Shape Patterns; Integration
	modularity.test	Shape Patterns; Modularity
	morphol.disparity	Linear Models; Model Design
	mshape	Data Prep; Visualize Outliers and Individual Specimens
	phylo.integration	Shape Patterns; Integration
	phylo.modularity	Shape Patterns; Modularity
	physignal	Shape Patterns; Phylogenetic Signal
	procD.lm	Linear Models; all tabs
	procD.pgls	Linear Models; all tabs
	shape.predictor	Morphospace and Warp Grids
	trajectory.analysis*	Shape Patterns; Trajectory Analysis
two.b.pls	Not yet implemented	
Utility functions	arrayspecs	
	buildtemplate	
	combine.subsets	
	coords.subset	
	digit.curves	
	digit.fixed	
	digitize2d	
	digitsurface	
	editTemplate	
	findMeanSpec	
	geomorph.data.frame	Linear Models; all tabs
	interlmkdist	
	read.morphologika	
	read.ply	
	readland.nts	Data Input
	readland.shapes	Data Input
	readland.tps	Data Input
	readmulti.nts	
	rotate.coords	
	two.d.array	
writeland.tps	Data Prep; Generalized Procrustes Alignment	

(Continues)

TABLE 1 (Continued)

Type	Function	gmShiny location (page; tab)
Plotting functions	<code>make_ggplot</code>	
	<code>picknplot.shape</code>	Morphospace and Warp Grids
	<code>plotAllometry</code>	Linear Models; Allometry
	<code>plotAllSpecimens</code>	Data Prep; Define Links and Semi-Landmarks
	<code>plotGMPhyloMorphoSpace</code>	Morphospace and Warp Grids
	<code>plotOutliers</code>	Data Prep; Visualize Outliers and Individual Specimens
	<code>plotRefToTarget</code>	Morphospace and Warp Grids
	<code>plotspec</code>	
	<code>shapeHulls</code>	
	<code>warpRefMesh</code>	
	<code>warpRefOutline</code>	

Adams et al., 2021). Nevertheless, as these fields have grown, *geomorph* has continued to expand its repertoire, incorporating innovations in statistical theory, high-dimensional shape analysis, phylogenetic comparative methods, data visualization and computational efficiency. For instance, recent new methods have been proposed for the multivariate quantification of evolutionary rates (K_{mult} ; Adams, 2014), new methods for evaluating modularity (Adams, 2016) and for comparing integration or modular signal in high-dimensional geometric morphometric data (Adams & Collyer, 2016, 2019), among others. *geomorph* has kept pace with the field by providing readily available functions for such analyses based on these new analytical approaches (e.g. `compare.evol.rates`, `compare.multi.evol.rates`, `modularity.test` and `integration.test` respectively).

In this manuscript, we briefly describe the various developments in *geomorph* since 2013, now available as *geomorph* v4.0. Specifically, we highlight the improvements in analytical scope, computational efficiency and data visualization. We also introduce a web-based R/Shiny graphical user interface for *geomorph*, *gmShiny*. This Shiny app is designed to make the computationally rigorous functions of *geomorph* available to a broader audience of users, removing coding-related accessibility barriers. The improvements and expansions described herein position *geomorph* to be the premier resource for fast, statistically robust analysis of morphometric and macroevolutionary inquiry for all users.

2 | ANALYTICAL SCOPE

The field of geometric morphometrics has expanded in recent decades to address a wide variety of novel biological questions. Corresponding with the cutting edge of this methodology, *geomorph* v4.0 enables users to quantify and analyse shape disparity (`morphol.disparity`), symmetry (`bilat.symmetry`), modularity (`modularity.test`, `phylo.modularity`), integration (`integration.test`, `phylo.integration`), allometry (`procD.lm`, `procD.pgls`), phylogenetic signal (`physignal`), evolutionary rates (`compare.evol.rates`, `compare.multi.evol.rates`), attributes of

shape change trajectories (`trajectory.analysis`: RRPP; Collyer & Adams, 2018, 2019) and more (Table 1). Nearly all of these functions are also accompanied by tools to quantify and compare the corresponding effect sizes (Z-scores), and where applicable, do so in a phylogenetic context. The complexity and flexibility of linear model fitting has also grown to accommodate complex model designs, pairwise comparisons (`pairwise`) and model comparison.

The utility of data processing in *geomorph* has also expanded. For instance, users can now import *StereoMorph* (Olsen & Haber, 2017; Olsen & Westneat, 2015) shape files (`readland.shapes`), which allows for post-landmarking evaluation and modification of the number of semi-landmarks sampled from any given curve. Users can also combine landmarks from, or subset landmarks into, various configurations based on degree of phenotypic integration (`combine.subsets`, `coords.subset`: Collyer et al., 2020). Other examples of *geomorph* v4.0's expanded utility include a broader use of summary and plot functions, quantification of inter-landmark distances (`interlmkdist`), landmark rotation (`rotate.coords`) and writing `.tps` files (`writeland.tps`).

3 | COMPUTATIONAL EFFICIENCY

Geometric morphometric (GM) datasets can be large, so computational efficiency is paramount. The greatest evolution of *geomorph* goes mostly unnoticed: enabling the same results from larger datasets in less time. With *geomorph* v4.0, improved computational efficiency has been achieved by a suite of algorithms, that we term 'linear model checkers'. This approach seeks to avoid calculations involving the many 0s in a linear model hat matrix (places without checkers) which do not contribute to the algebraic calculations, and instead focuses the calculations on the non-0 locations on the board (where there are checkers). This concept is more than the use of sparse matrix data storage and the algebraic tools associated with sparse matrices. Rather, the algorithms also seek to reduce the computer memory burdens of calculations by finding the computationally most expedient and memory-safe options for calculations specific to the dataset,

FIGURE 1 Screenshots of `gmShiny` using the example *Plethodon* dataset. A. Data Prep page, Visualize Outliers and Individual Specimens tab. This plot reflects the `plotOutliers` function using all specimens. An option exists in the Settings panel to plot outliers in groups, as defined by discrete traits. Below this (and all other) plots are two export buttons: one for directly exporting a .pdf of the plot, and another for downloading the `R` code used to generate said plot. When the second of these options is utilized, the user must also export the data in the current state (Export Current Data button in footer) after all settings have been finalized. (b) Morphospace and Warp Grids page. Many settings have been adjusted from default for both the phylo-morphospace and the warp grid. The red arrow in the top plot explicates the reference and target specimens used to generate the below warp grid

especially during iterative processes; that is, working exclusively with the information-rich parts of hat matrices (where checkers are located). Further details are provided in the Supporting Information.

Linear model checkers algorithms have greatly enhanced the computational efficiency of generalized Procrustes analysis (GPA) with semi-landmarks in `geomorph` v4.0, as well as statistical tests performed on the data from GPA. The `gpagen` function offers a cognizant form of linear model checkers via approximated thin-plate spline (TPS) mappings (Donato & Belongie, 2002) for estimating bending energy, for sliding of semi-landmarks. Compared to TPS, approximated TPS seeks to find a bending energy matrix that is smaller and more easily inverted. Specifically, we use the first option of approximated TPS presented by Donato and Belongie (2002), which reduces the number of (fixed) landmarks used to estimate bending energy. Approximated TPS would be most beneficial for large datasets that have both large numbers of fixed and sliding semi-landmarks. Users can choose the fraction of fixed landmarks to use, which are uniformly sampled from the set of all fixed landmarks for the bending energy matrix (all semi-landmarks are used). Because precisely estimating bending energy from all landmarks is not the objective within GPA (minimizing bending energy near semi-landmarks for iterative projections is), the burden of computer memory can be greatly reduced, meaning many more GPA iterations can be run to obtain better convergence. Importantly, running more GPA iterations with approximated TPS can result in better analytical solutions (decreased landmark variance) than running fewer iterations with TPS. Furthermore, in cases where computer memory precludes using TPS (because the bending energy matrix is too large to invert), approximated TPS could be a solution to such a large-data limitation. We provide illustrative examples of both the computational efficiency and application of approximated TPS in the Supporting Information.

Likewise, statistical tests in `geomorph` that require calculating sums of squares (SS) from the often highly multivariate GM data use linear model checkers algorithms to avoid creating large hat matrices and performing linear algebra with them. In the Supporting

Information, we demonstrate that this is possible with recursive algorithms that make analyses with randomization of residuals in a permutation procedure exceptionally fast, without requiring large memory for matrix storage. Whereas using approximated TPS is a cognizant choice for GPA, linear model checkers algorithms for calculating SS are decision-tree algorithms that detect the best method for estimating SS among different model effects, and are capable of using varied methods within the same analysis. (Currently, the linear model checkers algorithms in `geomorph` apply only to univariate-like ANOVA statistics.) These algorithms are explained in more detail in the Supporting Information. Enhanced parallel processing capabilities in `gpagen`, `procD.lm` and `bilat.symmetry` also improve computational efficiency, especially for threaded processors. Table 2 summarizes the improvement of computational efficiency in `geomorph` v4.0, with further details provided in the Supporting Information. Comprehensively, the analytical power of `geomorph` v4.0 is greatly improved and only in the rarest of circumstances might users find their data are too big for the `R` environment.

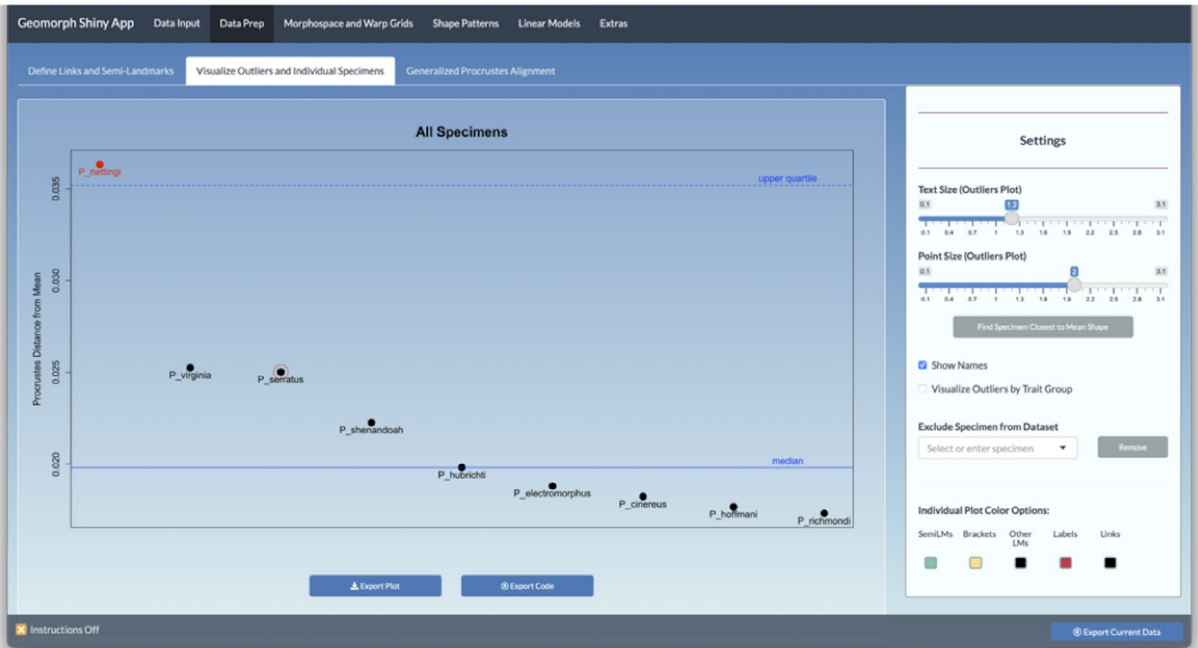
4 | DATA VISUALIZATION

The visualization options in `geomorph` v4.0 have improved in a variety of ways. One major change is that `plotTangentSpace` has been deprecated and separated into different functions for each of its component parts of analysis (`gm.prcomp`), plotting (`plot.gm.prcomp`) and shape deformation (`picknplot.shape`). This satisfied the user demand for greater flexibility in colour, size and shape settings in (phylo)morphospace visualization. This change also allows users to produce shape deformation grids for any point in morphospace, whether occupied by a specimen or not, and the separation of these functions more appropriately represents the distinct analytical steps included in the original function. `gm.prcomp` also now provides a variety of alignment options; users can choose between a standard principal component analysis (PCA), a phylogenetic

Package, version, function, options	Moderate sample size, many landmarks	Large sample size, moderate number of landmarks
<code>geomorph</code> 3.3 <code>gpagen</code>	Over 1 hr	About 20 min
<code>geomorph</code> 4.0 <code>gpagen</code>	2–2.5 min	2–2.5 min
<code>geomorph</code> 4.0 <code>gpagen</code> approximated TPS and parallel processing	~45 s	~30 seconds

TABLE 2 Summary of enhanced computation efficiency for generalized Procrustes analysis (GPA) in `geomorph` v4.0. Analyses were run on the same computer and should be regarded as a relative comparison. Further details are found in the Supporting Information [Correction added on 29 September 2021, after first online publication: In Table 2, the value '30 sections' has been changed to '30 seconds'.]

(a)



(b)

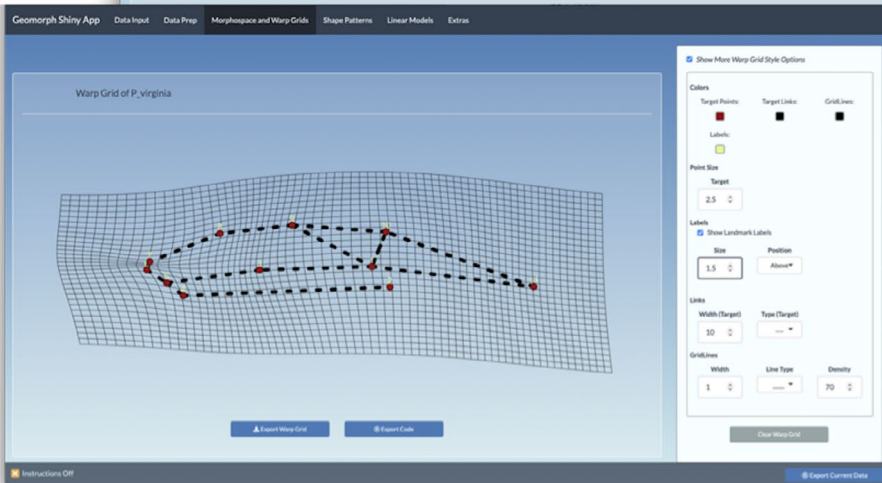
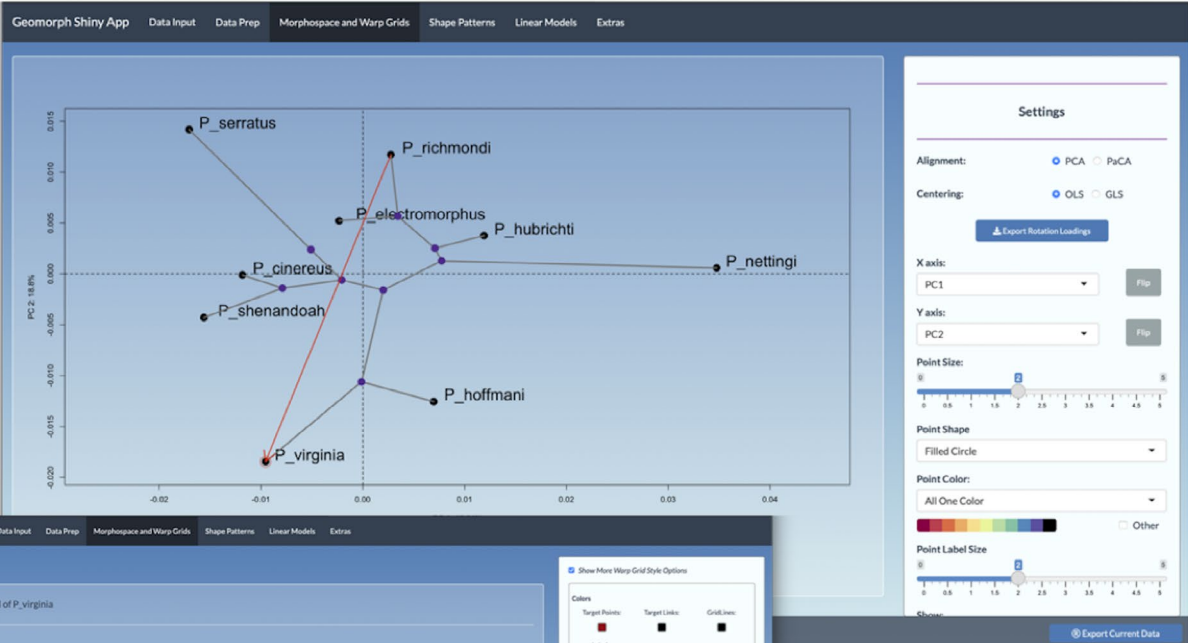


FIGURE 2 Screenshots of *gmShiny* using the example *Plethodon* dataset continued. (a) Shape Patterns page, Modularity tab. The two modules tested here have been modified from the default, and the main visible plot allows the user to see how the modules have been defined. (b) Linear Models page, Model Design tab. Here a linear model using the Discrete Example Data A and Centroid Size has been calculated under PGLS. Similarly, pairwise comparisons, morphological disparity and evolutionary rate analyses have been run across Discrete Example Data A. All individual data tables can be exported as .csv files, along with the code for all included tests. In the same manner as is described in Figure 1a, the data in the current state must be downloaded alongside the code in order for the user to replicate the results

PCA (pPCA: Revell, 2009) and a phylogenetically aligned component analysis (PACA: Collyer & Adams, 2021) to produce particular rotations of data spaces. Another new function, `shape.predictor`, produces shape deformations based on one or more linear predictors. New vignettes help guide users through the function updates, and provide step by step instructions for the creation of quality plots and the visualization of shape change within them. Finally, *geomorph* v4.0 has functions for converting *geomorph* plots into *ggplot* (Wickham, 2011)-compatible formats (`make_ggplot`). These improvements allow for greater flexibility and a broader scope of visualization options for shape data.

5 | gmShiny

5.1 | Implementation and usage

gmShiny is implemented with a variety of *R* packages (Supporting Information) for data handling and statistical operations, namely the most recent version of *geomorph* (Adams et al., 2021) and *shiny* (Chang et al., 2021). Users can access the *gmShiny* at <https://www.gmshiny.com>, as well as the source code and other relevant files at <https://github.com/geomorphR/gmShiny>. The app is accessible through most major web browsers with current versions installed in Windows, MacOS, Android or Linux. Users are encouraged to follow the instructions or the video tutorials, both of which are available in the app, until comfortable with all the options and workflow. This app is best suited for users with small to moderate dataset sizes, even when run locally. Current information on the app's capacity can be found on the app's News tab on the Extras page. We recommend that users with extremely large datasets (e.g. shape files >10 mb, phylogenies with >1,000 tips) take advantage of the computational efficiency of *geomorph* directly in *R* or *RStudio*.

5.2 | Design

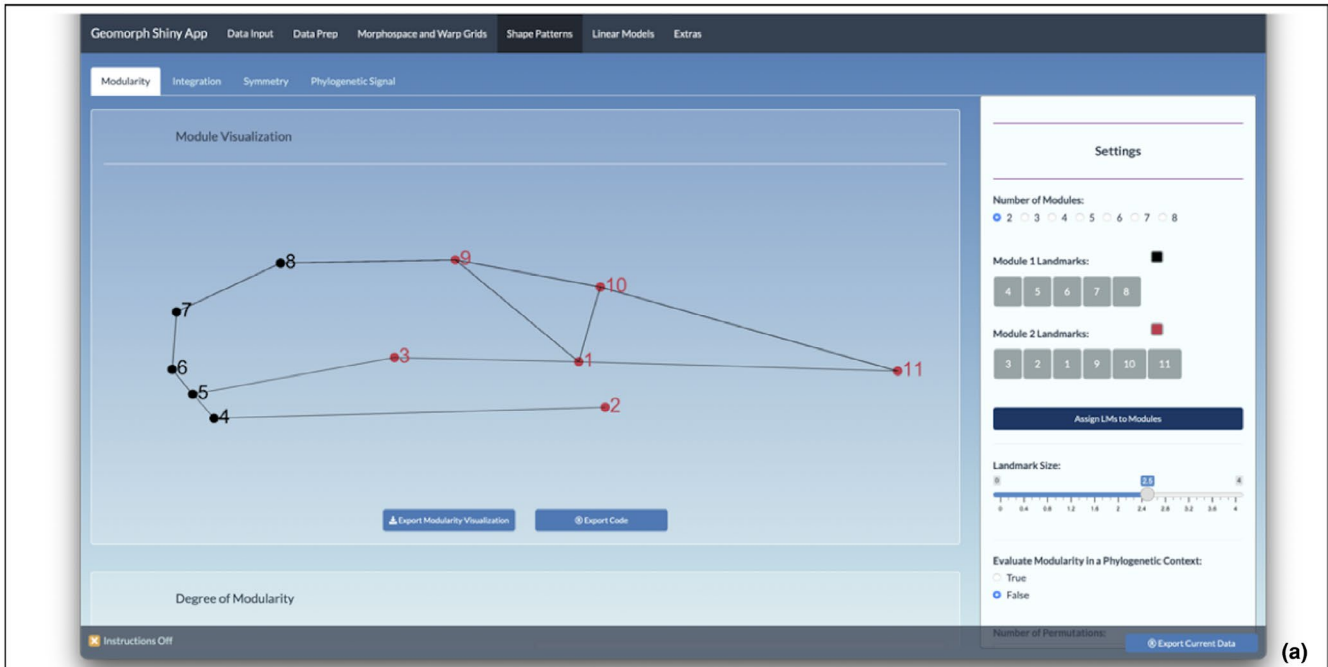
The *gmShiny* app has six main pages (Data Input, Data Prep, Morphospace and Warp Grids, Shape Patterns, Linear Models and Extras; Figures 1 and 2). Most pages have several tabs for the relevant methods, and each tab has a Settings panel with control options for the graphical and analytical outputs displayed in the Main panels. All plots and most analytical results can be exported into .pdf (e.g. Figure 1a) or .csv (e.g. Figure 2b) files respectively. An *R* script and an *R* object containing the current state of the data can also be exported for each plot or analysis (Figures 1 and 2), allowing users

to replicate the results in *R*, further manipulate figures for publication, expand the complexity of the analyses, or share analysis code between researchers.

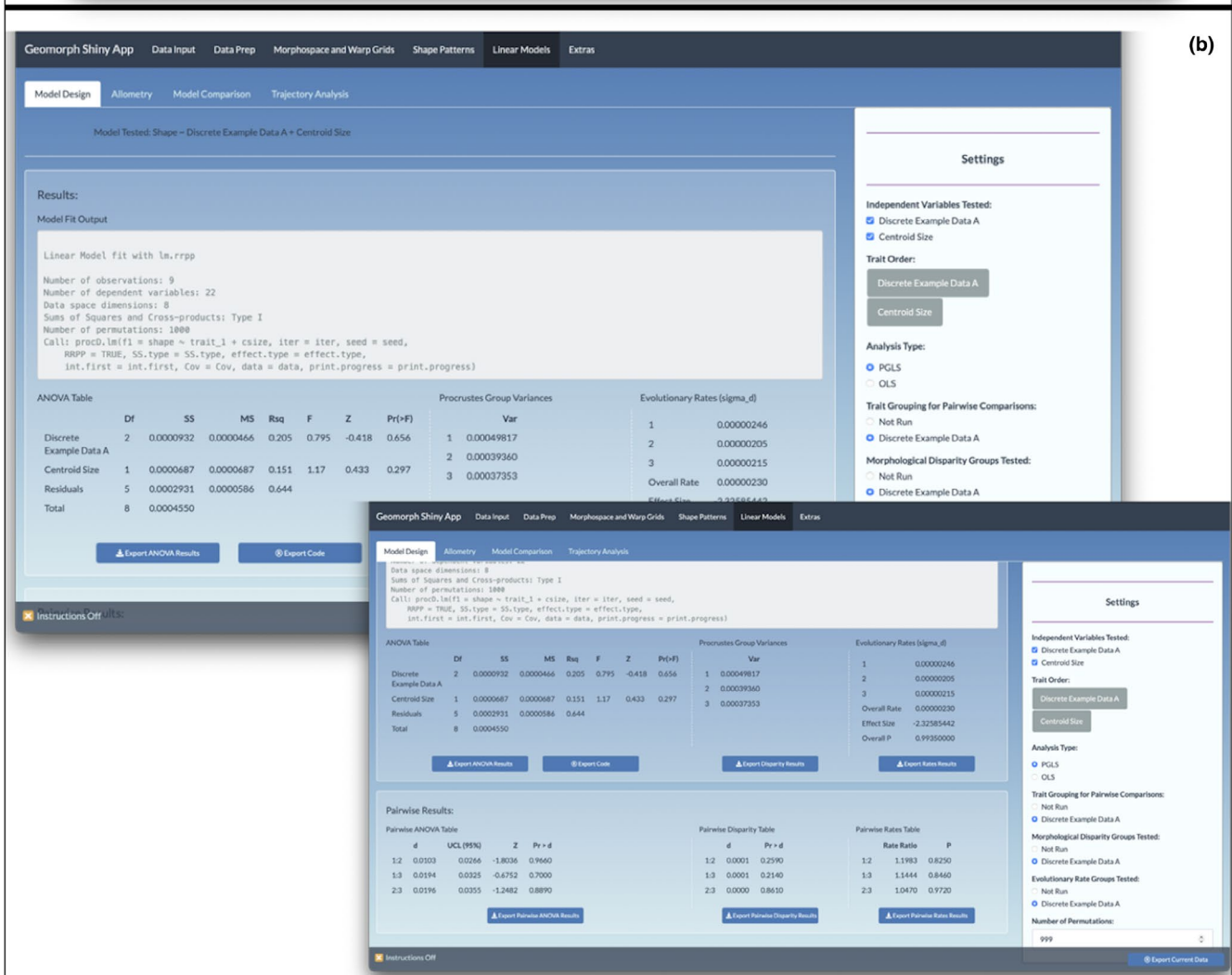
5.3 | Workflow

With the exception of accessing the Tutorials, News and Citation Information tabs on the Extras page, progress through the app must begin with the Data Input and Data Prep pages (in sequence) before moving on to the other pages. An example dataset is made available on the Data Input page to facilitate learning of the app functions. To upload these data, press the 'Use Example *Plethodon* Data' button in the upper-right-hand corner. Alternatively, users can upload their own shape files (.tps, .nts, *StereoMorph*), phylogeny files (.tre) and trait files (.xls, .xlsx or .csv) in a specific organizational format: column 1 is specimen names, corresponding to the naming schemes across datasets, with subsequent columns containing any other individual-based data). After files have been uploaded, various options for data configuration appear. For .tps and .nts shape files, users can specify how to treat landmarks with negative values, whether the uploaded data have been aligned previously, and how to name the individual specimens. For *StereoMorph* files with curves, users can specify the number of landmarks to sample along each curve. For trait files, users can specify which columns to utilize downstream and how to treat said data (i.e. discrete or continuous, log transformation, square root transformation). The final step on the Data Input page is to prune the datasets to match before proceeding. This button ('Prune Datasets to Match') only appears if there is a mismatch between any of the uploaded datasets. Thus, datasets need not be pruned to match prior to upload; the app will reorder the data to match and will identify non-matching specimens, to which this pruning step will apply. Attempting to move forward in the app before pressing said button (if it appears) will result in an error, and users will be returned to the Data Input page.

The Data Prep page contains three tabs: Define Links and Semi-Landmarks, Visualize Outliers and Individual Specimens (Figure 1a), and Generalized Procrustes Alignment, the last of which is only available if the input shape data have not yet been aligned (specified on Data Input page). Using these tabs, users can define links between landmarks that will apply throughout the app, semi-landmarks with corresponding brackets, and outliers that should be removed before alignment. For shape data that have not yet been aligned, the final tab must be visited, and the generalized Procrustes alignment must be run ('Run GPA' button) before proceeding through the app. Failing to do so will result in an error, and users will be returned to this tab.



(a)



Once the Data Input and Data Prep pages have been visited, the user is free to explore a wide variety of analytical and plotting `geomorph` tools. The pages Morphospace and Warp Grids (Figure 1b), Shape Patterns (Figure 2a) and Linear Models (Figure 2b) provide a broad overview of the functionalities available in `geomorph`. See Table 1 for a summary of the available functions and where they are implemented in `gmShiny`.

As `gmShiny` expands, so too will its utility. Currently, we view this app as a tool for new and experienced morphometricians for whom coding in R is a barrier to `geomorph`. Thus, this app could be used as a way to learn about the breadth of analyses available via `geomorph`, as well as for data exploration, plot generation or as an instructive tool in both undergraduate and graduate level courses. Our hope is that by removing this accessibility barrier, we will provide all those with GM data the high-quality analytical and plotting functions available in `geomorph` as it continues to push the field forward for years to come.

6 | CONCLUSIONS

The fields of geometric morphometrics, nonparametric statistics and macroevolutionary comparative methods have grown dramatically since the introduction of the R package, `geomorph`. Accordingly, `geomorph`'s utility and breadth of tools have grown to match, and in some cases have even driven, the forefront of innovation in these fields. This note provides an overview of enhancements made to the package and presents a new user-friendly interface for this toolkit. With these improvements, `geomorph` is positioned to be an important and influential part of quantitative morphometric research for years to come.

7 | SOFTWARE AVAILABILITY

`geomorph` v4.0 is available on CRAN. The `gmShiny` app is available at <https://www.gmshiny.com>. Related source code for this app, allowing users to run the app locally, can be found at <https://github.com/geomorphR/gmShiny>.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

E.K.B. designed `gmShiny`; M.L.C. scripted functions for enhanced computation. All authors contributed to R packages development, editing and testing. All authors helped to write the article.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13723>.

DATA AVAILABILITY STATEMENT

There were no data acquired in this research. All examples use already archived data, as part of the R packages used. R code associated with `gmShiny` v0.0 is available on Zenodo <https://doi.org/10.5281/zenodo.5501387> (Baken et al., 2021).

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