Landsc Ecol (2022) 37:2195–2224
https://doi.org/10.1007/s10980-022-01469-x

REVIEW ARTICLE

An overview of computational tools for preparing, constructing and using resistance surfaces in connectivity research

Trishna Dutta · Sandeep Sharma · Ninon F. V. Meyer · Jeremy Larroque · Niko Balkenhol

Received: 14 June 2021 / Accepted: 3 June 2022 / Published online: 1 August 2022

Abstract
Context Connectivity between habitat patches is a recognized conservation action to conserve biodiversity in a rapidly changing world. Resistance surfaces, a spatial representation of cost of movement across the landscape, are often the foundation for connectivity analyses but working with them can be daunting due to the diversity and complexity of software tools.
Objectives We present an overview of the steps involved when working with resistance surfaces, identify tools that perform specific tasks, evaluate user experience with the tools, identify needs of the user community, and present some recommendations for users and developers.
Methods We identified tools applicable at each of the three steps (i) preparing data, (ii) constructing and optimizing surfaces, and (iii) using resistance surfaces. We conducted an online survey of the connectivity user community to assess the popularity and experience with tools on five criteria and identified characteristics important in the selection of connectivity tools.
Results We reviewed a total of 43 tools, of which 10 are useful for data preparation, 27 allow construction, and 30 tools that use resistance surfaces. A total of 148 survey participants working in 40 countries were familiar with 37 tools. Tools are ranked heterogeneously for the five criteria. Crucial avenues for future development of connectivity tools identified by respondents are incorporation of uncertainties, dynamic connectivity modelling, and automated parameter optimization.
Conclusions Since resistance surfaces are used for a variety of applications, it is important that users are aware about the appropriate tools. We anticipate that future tools for connectivity research will incorporate

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-022-01469-x.

T. Dutta (✉) · N. F. V. Meyer · J. Larroque · N. Balkenhol
Wildlife Sciences, Faculty of Forest Sciences and Forest Ecology, University of Goettingen, Göttingen, Germany
e-mail: trishnad@gmail.com

T. Dutta
European Forest Institute, Platz der Vereinten Nationen 7, 53113 Bonn, Germany

S. Sharma
German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

S. Sharma
Institute of Biology, Martin Luther Univ. Halle-Wittenberg, Halle, Germany

N. F. V. Meyer
Conservation Science Research Group, School of Environmental and Life Sciences, The University of Newcastle, Callaghan, NSW, Australia

N. F. V. Meyer
Wildlife Ecology and Management, Faculty of Natural Resource and Environment, Tennenbacherstr. 4, 79106 Freiburg, Germany

more complex and biologically more realistic analytical approaches.

Keywords Circuit theory · Cost surface · GIS · Landscape connectivity · Landscape resistance · Least-cost path · Least-cost corridor · Movement ecology · R packages

Introduction

The pace of human-induced environmental change continues to grow and threaten biodiversity across the globe. Loss and fragmentation of habitats, hastened by climate induced changes, are restricting species to small and isolated patches of habitat, where they may face a higher risk of extinction (Crooks et al. 2017). Complementary to protecting and restoring habitats across large spatial extents, maintaining and restoring connectivity between habitat patches is an effective conservation action to facilitate animal movement, gene flow, and increase the persistence of populations and species in fragmented landscapes (Crooks and Sanjayan 2006). Connectivity also influences ecological and evolutionary processes such as local adaptation (Lopez et al. 2009) and the spread of diseases (Hess 1994; Fountain-Jones et al. 2021).

While *structural* connectivity refers to the physical connectedness of habitat patches, *functional* connectivity is the species-specific degree to which a landscape facilitates or impedes the movement of individuals, their genes or propagules (Taylor et al. 2006). A high degree of functional connectivity increases the effective amount of habitat available to a species (Villard and Metzger 2014), facilitates range shifts in response to climate change (Lenoir et al. 2020), and allows individuals to serve as mobile links within ecosystems (Jeltsch et al. 2013). Hence, maintaining connectivity, for example via corridors, may effectively decrease the rate of biodiversity loss despite habitat fragmentation through the persistence of species in metapopulations (Shtilerman and Stone 2015). Consequently, the last decade has seen a substantial growth in connectivity research (Correa Ayram et al. 2016), leading to the development of a myriad of analytical approaches (Cushman et al. 2013) and an abundance in associated computational tools for connectivity modelling.

One of the main approaches in connectivity science is built upon a set of methods that aim to quantify landscape resistance, which describes the degree of willingness, physical ability, or success of an organism to cross a particular environment (Zeller et al. 2012). The environment is represented by spatial data (usually raster layers) and different elements of the landscape are assigned values indicating movement cost for the species under study, resulting in a resistance surface. Resistance surfaces are often the foundation for connectivity analyses, and once parametrized, can be used for various applications.

Due to the large variety of methods and tools, it can be very challenging to navigate and find the appropriate method and associated tools for resistance-based connectivity research. This is especially true since not all interested scientists (e.g., ecologists, geneticists, biologists) and conservation practitioners have experience with the methods required for the numerous steps needed to estimate resistance surface such as handling and manipulating spatial data, or using the relevant software. While concepts and approaches for parameterizing resistance surfaces have been summarized before (see Spear et al., (2010, 2015); Zeller et al., (2012)), the computational tools available for preparing and working with landscape resistance surfaces have not yet been reviewed.

In order to provide a guide to the available options, we reviewed tools (programs and packages) that are commonly used in connectivity studies based on resistance surfaces. Our objectives are to provide (i) an overview of the tools involving resistance surfaces for connectivity analyses, (ii) an outline of a typical workflow in resistance-based connectivity analyses, (iii) a summary of user experiences with the most frequently used tools, and (iv) key avenues and features for development of future tools that would address the needs of the scientific and conservation community. We anticipate that this overview will help both novice and experienced researchers navigate through the maze of tools, and help developers focus on those aspects or methods that render analytical tools most useful for the research and practitioner community.

Steps involved in resistance-based connectivity analyses

Connectivity analyses based on resistance surfaces typically involve three steps (Fig. 1).

Step 1: Preparing data for resistance surfaces.

First, researchers have to gather and process spatial environmental data that they wish to use in their analyses. This *preparation* step necessitates the identification of relevant environmental variables for the study species/system, and their respective data sources. Accessing such data has been reviewed in Kwok (2018). Since resistance surfaces are usually created from multiple data layers, it is often necessary to manipulate individual layers, so that they all have the same coordinate reference system, spatial extent and spatial resolution. In addition to the spatial resolution (e.g., pixel size), the thematic resolution (e.g., number of habitat classes) can greatly affect connectivity studies (Cushman and Landguth 2010; Zeller et al. 2017). Similarly, when trying to assess impacts of environmental change on connectivity, the temporal resolution of the data should capture the process of interest (e.g., seasonal dynamics or landscape before and after infrastructure development), so that changes across time are adequately represented by the data.

Step 2: Constructing and optimizing resistance surfaces.

Second, researchers have to *construct* the actual resistance surface by translating the information of the environmental data layers into meaningful resistance values that reflect the study species and research question of interest. This parameterization can be done via expert opinion and literature reviews, or based on empirical data collected for the focal species. There are several ways of parameterizing resistance surfaces with different data types, such as occurrence, movement, or genetic data (reviewed in Spear et al. 2010, 2015; Zeller et al. 2012; Wade et al. 2015), or a combination of different data types (e.g., Zeller et al. 2017; Meyer et al. 2020).

Resistance values can be estimated by conducting expert-opinion surveys, reviewing literature, empirical data obtained for the species, or any combination thereof. Whenever possible, it is recommended to not rely entirely on expert-opinion as the only source of information (Clevenger et al. 2002; Shirk et al. 2010; Zeller et al. 2012). When empirical data is available, it can be used to directly estimate resistance values, for example by quantifying the effect of the environment on movement probabilities using point, step- or path-selection functions from telemetry data (Zeller et al. 2012; Osipova et al. 2019; Goicolea et al. 2021). Methods for these selection functions are implemented in various R packages, including *amt* (Signer et al. 2019) and *adehabitatLT* (Calenge 2006). Another popular approach for constructing resistance surfaces from empirical data is to convert habitat suitability values into resistance values. Habitat suitability models constructed from point data (i.e., presence-absence or presence only) via resource selection functions (RSFs e.g., in R package *ResourceSelection,* Lele et al. 2019) or species distribution models (e.g., in R package *maxent,* Phillips 2021) need to be transformed into resistance values, with the general idea that lower suitability will lead to greater resistance to movement and/or gene flow. A simple linear inversion of suitability values into resistance is usually not ideal, as organisms are often able and willing to traverse sub-optimal habitats (e.g., Mateo-Sánchez et al. 2015; Keeley et al. 2017). Negative exponential relationships between habitat suitability and resistance, which can be modelled using different conversions may therefore be more accurate (see e.g., Trainor et al. 2013; Keeley et al. 2016). Thus, while habitat suitability models are an appealing way to obtain resistance values, they may not always be optimal for capturing the processes of interest in connectivity analyses (Scharf et al. 2018). However, even non-linear conversions may not adequately represent resistance to dispersal and gene flow, because organisms dispersing through the landscape can behave very differently compared to their usual within-home range behavior (Elliot et al. 2014). Therefore, data reflecting long-distance movements, exploratory behavior or actual dispersal events are often more suitable for estimating resistance, compared to data reflecting movements within home ranges (e.g., Gastón et al. 2016; Dondina et al. 2022). Genetic data is often used as a measure of functional connectivity as it represents successful reproduction post-dispersal processes. The classical use of genetic data in resistance surface modelling is through a landscape genetics framework (Manel et al. 2003), wherein estimates of gene flow are evaluated against measures of effective geographic distance under alternative resistance surfaces to find the best estimates of resistance.

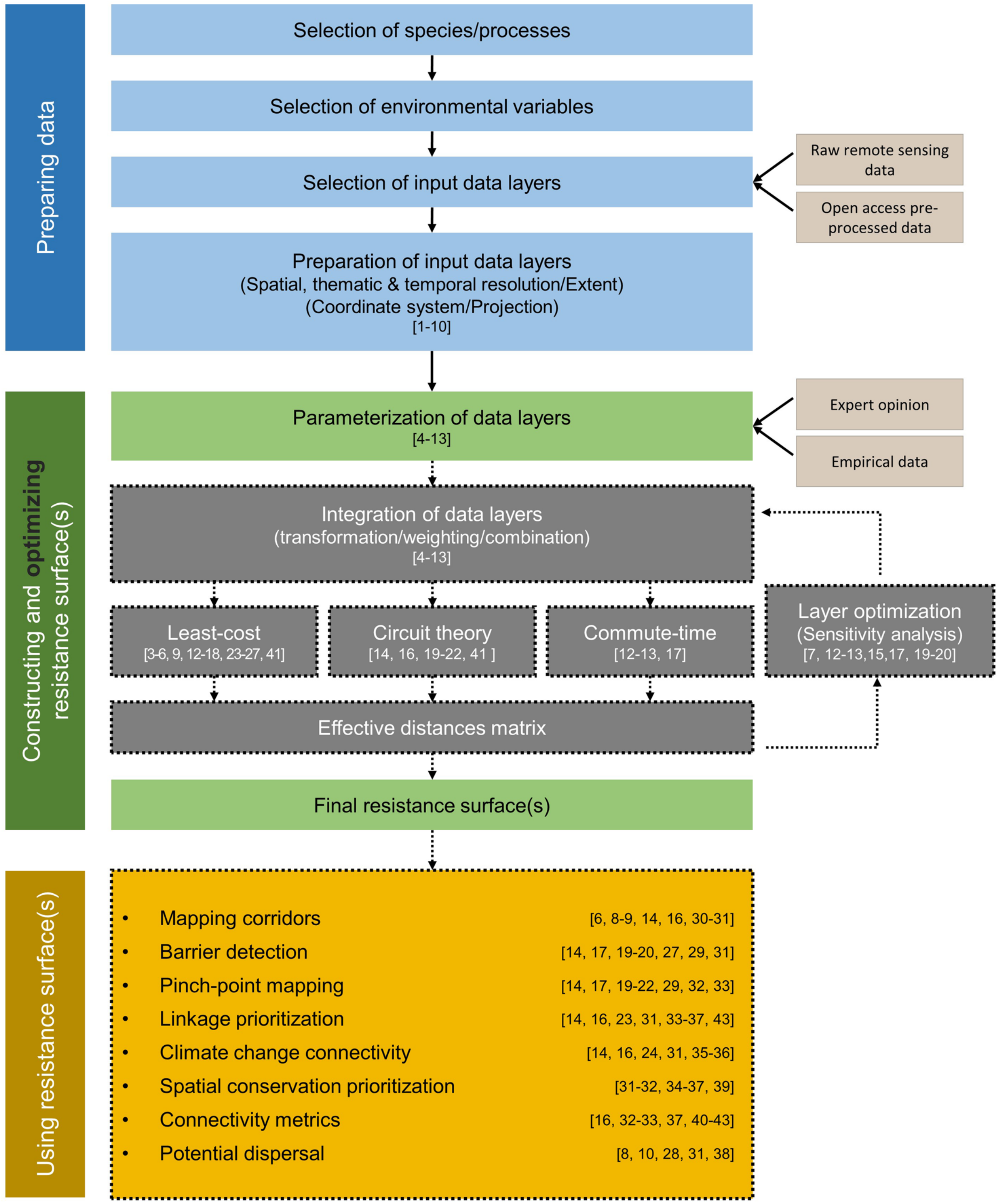


Fig. 1 Outline of workflow in resistance-based connectivity modelling along with available tools for each step in the process. Optional steps are shaded in grey and outlined by the dotted lines. Numbers in square brackets correspond to tools described in Table 1, 2 and 3. Please refer to the tables (descriptions are color-coded to match the corresponding steps in this figure) for more attributes. Supplementary material S1 provides a detailed narrative of these three steps, files in S5 present a tutorial with sample data and a typical workflow for resistance surface modeling in the R statistical computing environment, and S2 provides users with a decision tree to guide users through the entire process of working with resistance surfaces

Once a resistance surface is created, it is recommended to *optimize* the surface so that it truly represents the ecological and biological needs of the species. Empirical data can be used to both *construct and optimize* resistance layers. In optimization, resistance values are parameterized in a way so that they best match connectivity patterns derived from empirical data. For example, a typical approach in landscape genetics is to compare estimates of genetic connectivity (e.g., genetic distances) against estimates of functional connectivity (e.g., least-cost paths or circuit-theoretic resistances) derived from multiple resistance surfaces representing different research hypotheses. The best resistance surface is then identified as the one that leads to the highest statistical fit between the genetic and functional connectivity estimates. Optimization can be *constrained* when researchers explore a relatively limited parameter space, for example by assessing how well a selected set of various resistance surface realizations and their combinations match empirical data, or *unconstrained* where a much wider parameter space and can searched. These steps can be accomplished by different computational algorithms (e.g., Peterman 2018; Peterman and Pope 2021). Even when such optimization processes are not possible, it is highly recommended to conduct sensitivity analyses to account for the myriad sources of uncertainty in the modeling process and the propagation of errors (Zeller et al. 2012).

Regardless of how the construction and optimization are done, the final output of this second step is usually a single resistance surface that is based on all environmental variables that were identified as important in the study system for the species of interest, and parameterized to reflect the impact of the environment on the process of interest (e.g., dispersal, movement, or gene flow).

Step 3: Using resistance surfaces.

Finally, the resistance surface obtained from Step 2 can be *used* for a variety of purposes in landscape connectivity research and planning. For some studies, it is sufficient to optimize resistance surfaces, as this optimization in itself can tell us which environmental variables impact functional connectivity and how strongly they do so. However, resistance surfaces can also be used to delineate corridors, detect barriers, map pinch-points, prioritize linkages, compute connectivity metrics, and identify climate-resilient connectivity networks. Hence, it is this last step that makes connectivity analyses based on resistance surfaces particularly valuable for applied ecology and conservation. Many of these tools require not only a resistance surface or measures derived from it, but also additional user input, such as the spatial location, size and quality of source and target habitat patches.

More details on these three steps are provided in supplementary material S1, accompanied by a decision tree to guide users through the process of resistance surface construction in S2 and on the conservation corridor website https://conservationcorridor.org/corridor-toolbox/programs-and-tools/, and a tutorial in S5 containing sample data and a typical workflow for resistance surface modeling in the R statistical computing environment.

Methods

Identification of the tools

We used our own experience to collate analytical tools that are currently being actively maintained and for which we could find functional links, i.e., that can still be downloaded and used on contemporary versions of platforms (for example, tools that require ESRI's ArcView and have not been updated were not included in our assessment). We supplemented our experience by searching for published papers about landscape connectivity, scanned through the Corridor Conservation website (www.conservationcorridor.org), and included suggestions offered by respondents to our online survey (see Sect. 2.2 below). We only included tools that involve a resistance surface, either as an input or an output. To help users select tools according to the resources available to them and their analytical requirements, we describe each tool based on seven characteristics: (1) the type of tool (i.e., a stand-alone program, an R package, or a GIS extension/plugin), (2) its main purpose, (3) whether it operates in a graphical user interface (GUI) and/or command line (CL), (4) the input data format required, (5) the compatibility with different operating system (OS), (6) the year of last update as of March 30, 2021, and (6) particular functions or abilities that

Table 1 Summary of tools used in data preparation

Tool No.	Tool name	Purpose	IF and OS	Input data format and Last update	Citation /Weblink	Remarks	Applicable functions
1	R ***rgdal, rgeos, sp, sf***	Read and manipulate spatial data.	CL	Raster, Vector 2020	(Bivand et al., 2021) https://cran.r-project.org/web/packages/rgdal/index.html (Bivand et al., 2020) https://cran.r-project.org/web/packages/rgeos/index.html (Pebesma, Bivand, Rowlingson, et al., 2021) https://cran.r-project.org/web/packages/sp/index.html (Pebesma, Bivand, Racine, et al., 2021) https://cloud.r-project.org/web/packages/sf/index.html		Many functions to work with spatial data handling and manipulation, including projections, extents, resolutions, classification, etc.
2	ArcGIS ***Export to Circuitscape***	Export multiple ArcGIS vector and raster data into one or more ASCII rasters, with identical cell sizes, extents, and spatial reference.	GUI	Raster, Vector 2011	http://www.jennessent.com/arcgis/Circuitscape_Exp.htm		Prepares ASCII files for use in downstream processes.
3	**SA** ***GuidosTolbox***	Geospatial analysis, pre and post processing, and visualization of raster data.	GUI/CI (Linux)	Raster 2020	(Vogt & Riitters, 2017) (2017)	Command line version available only for Linux.	Contains a wide variety of generic raster image processing routines. Generates input file for Conefor.
		Morphological Spatial Pattern Analysis to analyze fragmentation, connectivity, and restoration potential. Resistance surfaces can be imported to create least cost paths.			https://forest.jrc.ec.europa.eu/en/activities/lpa/gtb/	Next version will include a dedicated Restoration Planner module providing spatially explicit, quantitative restoration analysis based on user-driven resistance surface analysis.	Maps the least-cost path.

Table 1 (continued)

4	***ArcGIS***	A proprietary GIS program; several generic analysis modules to handle and manipulate spatial data layers, and perform analysis to create resistance, corridors and map the output.	GUI	Raster, Vector, Text 2020	https://www.esri.com/en-us/arcgis/about-arcgis/overview	Several toolboxes/extensions available for connectivity analysis. Example: Linkage Mapper, SDM toolbox The R-ArcGIS Bridge enables users to access ArcGIS data and bring it into R for specialized statistical analysis.	Several tools and modules to handle and manipulate spatial data layers. Parametrize, integrate, transform, combine spatial layers. Cost-distance analysis workflow included in ArcGIS to calculate cost-distances and least cost paths.
5	***QGIS***	An open-source software to create, edit, visualize, analyze and publish geospatial information.	GUI	Raster, Vector, Text	https://qgis.org/en/site/	Free add-ins can be used with QGIS for advanced connectivity analysis. Example: Graphab and Biodispersal.	Several tools and modules to handle and manipulate spatial data layers. Parametrize, integrate, transform, combine spatial layers, and generate least-cost paths and least-cost-corridors.
6	***SDM toolbox***	Create and map least cost paths and least cost corridors among all sites or among shared haplotypes.	GUI	Raster, Vector, Text 2020	(Brown, 2014) http://www.sdmtoolbox.org/	For full functionality of all the tools, requires ArcGIS with the Spatial Analyst Extension.	Includes many spatial-data manipulation tools such as in the *Commonly used ArcMap Tools, Raster Tools (extract by mask, reclassify, project, convert raster to ASCII* and vice versa, etc). Parametrize, integrate, transform, combine spatial layers. *Landscape connectivity* toolbox calculates pairwise distance matrix and least-cost paths. *Create Friction Layer* inverts a species distribution model to create a resistance surface. *Landscape connectivity* toolbox calculates and least-cost path densities and corridors.

Table 1 (continued)

7	***Raster***	Read, write, manipulate, analyze raster data.	CL	Raster 2020	(Hijmans & van Etten, 2016) https://cran.r-project.org/web/packages/raster/index.html	Can be used in the iterative optimization step.	Many functions to work with rasters such as *projectRaster, compareCRS, compareRaster, extent, extend*, etc. Parametrize, integrate, transform, combine spatial layers using raster algebra (e.g., *arith-methods, logic-methods*) and cell based computation (*calc, overlay*), etc.
8	***BioDispersal***	Produce habitat permeability and potential dispersal maps for one or several species using cumulative costs.	GUI	Raster, Vector 2018	(Chailloux, 2018/2021) https://www.theia-land.fr/en/product/biodispersal-en/		Provides many in-built functions in the *Parameters* tab to prepare *the extent, resolution, projection*, etc. Parametrize, integrate, transform, combine spatial layers. *Compute friction layer* assigns cost values, *weighting* of the friction layer to create resistance surface. *Disperal* module models potential dispersal on friction layer according to maximum dispersal cost units.
9	ArcGIS ***Corridor Designer Toolbox***	Create habitat suitability map and help identify habitat patches to map potential habitat linkages for land management planning.	GUI	Raster, Vector, Text 2008	(Majka et al., 2007) http://corridordesign.org/downloads	Requires the Spatial Analyst Extension.	*Layer Preparation* toolbox to *clip layers to analysis area* and *create topographic position raster.* Parametrize, integrate, transform, combine spatial layers. *Habitat modelling* toolbox has many functions to create, combine, modify, and create habiat maps than can then be transformed into a resistance surface. *Corridor Modelling* toolbox contains several tools to create, fill holes, and create a union of corridors.

Table 1 (continued)

10	R ***SimRiv***	Simulate and analyze spatially-explicit individual-based multistate movement models in linear, dendritic, heterogeneous and homogeneous spaces, based on resistance raster.	CL (Windows, Mac, Linux)	Raster, Vector 2019	(Quaglietta & Porto, 2019) https://cran.r-project.org/web/packages/SiMRiv/index.html	The function *resistanceFromShape* rasterizes a given shapefile and optionally stacks it with other rasters.	Parametrize, integrate, transform, combine spatial layers. *resistanceFromShape* builds resistance raster by combining shapefiles. Computes accumulated resistance for each simulated step (*sampleMovement*).	*simulate* performs spatially-explicit simulations of potential connectivity on the optimized resistance surface.

SA Standalone package, R r package; Python package; ArcGIS extension; QGIS extension; Windows; Mac; Linux

IF Interface: GUI (Graphical User Interface); CL (Command Line); **OS** (Operating System)

Applicable functions in the tool are italicized.

make the tool suitable for either of the three steps (Table1).

Survey on user experience

To assess awareness of the tools, experience, and characteristics of tools important to the connectivity community, we conducted an online survey from June 01- July 19, 2020. The survey was conducted through the Qualtrics platform and consisted of 4 main sections. In Sect. 1, we asked respondents for their background (education and institutional affiliation), their research profile (taxonomic groups, ecosystems and geographic region of research), and self-assessment of their expertise with connectivity analysis. In Sect. 2, we provided a list of 39 tools and asked respondents to select those that they are familiar with. There was also the possibility to add additional tools not already included in the list provided. In Sect. 3, we asked respondents to rate all the tools that they had used according to 5 criteria—(1) ease of data formatting, (2) speed of analysis, (3) stability, (4) ease of customizing the tool, and (5) availability of help. Finally, in Sect. 4, we asked users to rank criteria they considered important when selecting tools to conduct connectivity analyses using resistance surfaces. In January 2021, we followed up the survey and asked participants to (1) identify existing methods or approaches for connectivity research that should be implemented in software tools, and (2) comment on future methodological and conceptual improvements that they envisage for connectivity research based on resistance surfaces.

Data analysis

We used a 3-point scale to rate respondents' experience with the tools (poor, OK, super) or selection criteria (mandatory, important but not mandatory, not a concern). For Sect. 3 (rating user experience for different criteria), we only analyzed tools that received more than five evaluations. We calculated a score for each of the five criteria (data formatting, speed, stability, customization, help) by multiplying the percentage of responses that rated a tool as super with 1, neutral (OK) with 0.5, and poor with -1 and created a cumulative score by adding across all the criteria. We categorized tools according to the step it is useful

Table 2 Summary of tools used in constructing resistance surfaces

Tool No.	Tool name	Purpose	IF and OS	Input data format and Last update	Citation /Weblink	Remarks	Applicable functions
Several tools described in Table 1 (Tool Nos. 3,4,5,6,7,8,9,10) and Table 3 (Tool No. 41) are also useful in constructing resistance surfaces. Please refer to the descriptions in the respective tables.							
11	***Gnarly Landscape Utilities***	Create habitat layers, resistance, and map core areas.	GUI	Raster, Text 2016	(McRae et al., 2013) https://circuitscape.org/gnarly-landscape-utilities/		*Resistance and Habitat Calculator* toolboxes parametrize, integrate, transform, and combine values in excel spreadsheets to create resistance surface. Can be used to create multiple resistance surfaces for sensitivity analyses.
12	***ResistanceGA***	Use a genetic algorithm to optimize resistance surfaces based on pairwise genetic data and effective distances using circuit theory, least cost path and random-walk commute times.	CL	Raster, Text 2018	(Peterman, 2018) https://github.com/wpeterman/ResistanceGA	Depends on Circuitscape and/or gdistance R package. Tends to be slow because it requires high computational resources. No online support. Can be used in the iterative optimization step.	Parametrise using *CS.prep* or *gdist.prep,* combine using *Combine_Surfaces* transform continuous and categorical rasters using *Resistance.tran,* to create and optimize multiple resistance surfaces individually using *SS_optim* or simultaneously using *MS_optim.*
13	***radish***	Use the Newton-Raphson algorithm to optimize resistance surfaces based on pairwise genetic data, and effective distances using circuit theory.	CL	Raster, Text 2020	(Peterman & Pope, 2021) https://github.com/nspope/radish	Can be used in the iterative optimization step.	Parametrize, integrate, transform, combine spatial layers. For example, *radish_distance* calculates resistance across a grid and *conductance_surface* estimates parametrized conductance models.

Table 2 (continued)

14	ArcGIS	***LinkageMapper*** **	Identify and map linkages between core areas using least cost distance, and circuit-theory to delineate least cost corridors, detect pinchpoints and barriers.	GUI	Raster, Vector 2018	(McRae & Kavanagh, 2011) https://circuitscape.org/linkagemapper/	Can be slow and often crashes, depending on the number of linkages and extent/resolution of resistance surface. Very active help forum.	Euclidean distances between core areas are calculated with an ArcInfo-level license through Conefor. Least-cost paths can be estimated, and uses circuit theory in the *PinchPoint Mapper* module. Uses the resistance surface to map corridors (*Linkage mapper*), quantify centrality of patches and linkages (*Centrality Mapper*) identify pinchpoints (*Pinchpoint Mapper*), etc.
15	R	***topoDistance***	Calculate the distance along the shortest topographic path between points, and distance along least cost path.	CL	Raster, Text 2019	(Wang, 2020) https://cran.r-project.org/web/packages/topoDistance/index.html	Considers both the landscape resistance to movement and the topography. Calculate non-isotropic LC distance. Can be used in the iterative optimization step.	Several *topo* functions calculate topographic distances (e.g., *topoDist, topoLCP*), identify (e.g., *topoPaths*) and plot topographic paths (e.g., *topoPathMap, topoProfile*).
16	SA	***Connectivity Analysis Toolkit***	Map linkages using LCP, current flow, and network flow. Calculate centrality metrics.	GUI, CL	Raster, Text 2014	(Carroll et al., 2012) http://www.klamathconservation.org/science_blog/software/	Some functionalities also predict how landscape suitability for a species will change over time.	Provides multiple ways to map linkages from habitat suitability models, least-cost paths, and circuit theory. Provides landscape connectivity metrics, maps corridors, prioritizes linkages using different centrality metrics, and provides time-series of landscape suitability for species.
17	R	***gdistance***	Calculate various distance measures and routes (incl. least cost path, random walk) in heterogeneous geographic spaces.	CL	Raster 2020	(Etten, 2017) https://cran.r-project.org/web/packages/gdistance/index.html	Can be used in the iterative optimization step.	Distance functions calculate the least cost distance (*costDistance*), commute time (*commuteDistance*), and the cost incurred during the random walk (*rSPDistance*). The Randomized Shortest Path algorithm can be used to map functional connectivity and identify high connectivity intensity areas (pinchpoints and corridors) using the function *passage*.

Table 2 (continued)

18	SA	***SAGA-GIS (Least-Cost Path tool)***	Estimate least cost paths with user-defined cost surface and sources.	GUI	Raster, Vector 2010	http://www.saga-gis.org/saga_tool_doc/6.3.0/grid_analysis_5.html		This tool allows to compute least cost paths.
19	SA	***Circuitscape***	Run connectivity analysis using circuit theory.	GUI, CI	Raster, Text (through INI files) 2019	(McRae et al., 2008) https://circuitscape.org/downloads/	Can be run through R in Windows, https://gist.github.com/rmarrotte/28c8bc65fa043ea29828. Can be used in the iterative optimization step.	Uses circuit theory to map random walks, i.e., all possible pathways between the source areas. Functional connectivity can be mapped to identify high connectivity intensity areas (pinchpoints and corridors).
20	SA	***Circuitscape.jl***	Run connectivity analysis using circuit theory on Julia computing platform.	CL	Raster, Text (through INI files) 2020	(Hall et al., 2021) https://github.com/Circuitscape/Circuitscape.jl	A faster version of circuitscape. Can be called from R by using the JuliaCall R package, and from Python using the pyjulia Python package. Can be used in the iterative optimization step.	More efficient implementation of circuit theory on Julia to map random walks, i.e., all possible pathways between the source areas. Functional connectivity can be mapped to identify high connectivity intensity areas (pinchpoints and corridors).
21	SA	***GFlow***	Run connectivity analysis using circuit theory on a high performance computing platform.	CL	Raster, Text 2017	(Leonard et al., 2017) https://github.com/gflow/GFlow	Suitable for very large spatial scale, and is fast due to utilization of high performance computing.	High-performance computing of circuit theory to map random walks, i.e., all possible pathways between the source areas. Functional connectivity can be mapped to identify high connectivity intensity areas (pinchpoints and corridors).

Table 2 (continued)

22	**SA**	***Omniscape***	Analyze and generate maps of omni-directional habitat connectivity using circuit theory.	CL	Raster, Text (through INI files) 2021	(Landau et al., 2021) https://github.com/Circuitscape/Omniscape.jl		Implements circuit theory to estimate connectivity between every possible pair of start and endpoints in the landscape. It also provides estimates of connectivity under a 'null' resistance condition. Functional connectivity can be mapped to identify high connectivity intensity areas (pinchpoints and corridors).
23	ArcGIS	***MatrixGreen***	Generate the node and connection files required as an input for Conefor (see tool #36), including the effective LC distance between pairs of nodes.	GUI	Raster, Vector 2014	(Andersson & Bodin, 2009) https://www.stockholmresilience.org/research/matrixgreen	Consumes high internal memory, thus relatively slow. Different versions depending on the ArcMap version. No example data set. Results can be exported to ConeFor Sensinode.	Following distances can be calculated: Euclidean, between the center points of each patch, between the closest edges of each pair of patches, or least-cost path. Prioritizes linkages based on *betweeness centrality.*
24	ArcGIS	***LandFacet Corridor Designer***	Design corridors based on land facets (topographic and soil-traits based units).	GUI	Raster 2013	(Brost & Beier, 2012) http://corridordesign.org/downloads	Selection of ideal TPI (Topographic Positioning Index) is difficult to calculate. Processing time will vary with study area and TPI neighborhood size. Output data tables can be exported to R for further analysis.	Resistance maps are created using the land facet approach, based on the departure of any cell from the prototypical cell of the focal land facet using Mahalanobis distance as the resistance metric. Designs linkages for the continuity and interspersion of land facets, or recurring landscape units of relatively uniform topography and soils.
25	R	***movecost***	Calculate non-isotropic accumulated cost surface and least-cost paths using a number of human-movement-related cost functions.	CL	Raster, Text 2019	(Alberti, 2019) https://cran.r-project.org/web/packages/movecost/index.html	Multiple functions to calculate cost functions with a combination of terrain features and energy expenditure.	Cost allocation carried out by function *movealloc and movecost* to create least-cost corridors *(movecorr), and* compare least-cost paths generated using different cost functions *(movecomp*).

Table 2 (continued)

26	***leastcostpath***	Model least cost pathways and movement potential using cost surfaces based on slope and other landscape features.	CL	Raster, Text 2021	(Lewis, 2021) https://cran.r-project.org/web/packages/leastcostpath/index.html	Has functionality to calculate Stochastic Least Cost Paths, Probabilistic Least Cost Paths, and Least Cost Paths, and validate the accuracy of calculated Least cost paths.	Multiple ways to create least-cost paths (*create_banded_lcps, create_CCP_lcps, create_wide_lcp, create_lcp_network*), cost corridors (create_cost_corridor), and incorporate barriers in cost surface (*create_barrier_cs*). *create_stochastic_lcp* created random least-cost paths.
27	***Python based GIS tools for landscape genetics***	Convert files, visualize genetic relatedness, and measure landscape connectivity using least-cost path analysis.	GUI	Raster, Text 2011	(Etherington, 2011, 2021) https://doi.org/10.5281/zenodo.4654049		Calculates Euclidean distances, cost-mapping, and produces least-cost paths. Mainly developed to visualize pair-wise genetic relatedness. *Line Barrier Matrix* and *Zone Barrier Matrix* tools provide ways to test the presence of barriers.

for (preparing data, constructing resistance surfaces, and using resistance surfaces as given in Fig. 1), and ranked tools within each step by the cumulative score.

Results

Tools identified for resistance-based analysis

We reviewed 43 tools in total, of which 10 are useful for data preparation (Table 1), 27 allow to construct and/or optimize resistance surfaces (Table 2), and 30 are suitable for connectivity analysis based on resistance surface (Table 3). All the tools we reviewed have a manual with the possibility to get help either through online forums or though the developers directly. These tools are available as R packages (n = 16), as stand-alone software (n = 16), or as GIS extensions (ArcGIS, n = 13, QGIS, n = 5), a few tools being available across more than one platform (n = 4). In addition to the tools listed in Fig. 1, we also found a few tools that were not included, either because they are no longer maintained, unavailable online (e.g., *FunCon,* Peer et al. 2011 and *FunConn* Theobald et al. 2006), no longer operational because of outdated platforms, (e.g., *PATHMATRIX*, Ray 2005), or are not tools per se but customized published scripts (e.g., Graves et al. 2014). The number of tools has increased sharply since 2005, when *PATHMATRIX* was the only tool available, to around 38 tools in early 2021, of which ~ 20 tools were added since 2014 (Fig. S3).

Features of analytical tools

Of the ten tools we identified for the preparation step only three (export to *Circuitscape*, *BioDispersal*, and *Corridor Designer Toolbox*) are specifically designed for connectivity analyses. Since this preparation step involves a lot of basic spatial data manipulation, several R packages (e.g., *rgdal*, *raster*, *SIMRIV*), other tools (*SDM* and *Guidos Toolbox*), and GIS software (e.g., ArcGIS and QGIS) are helpful in this step.

Specialized tools for resistance-surface based connectivity analyses feature prominently in the steps for constructing, optimizing, and using resistance surfaces. Some of the tools listed in Step 2 (constructing and optimizing tools) are perhaps more popular for their application in using resistance surfaces (e.g.,

Table 3 Summary of tools for using resistance surfaces

Tool No.	Tool name	Purpose	IF and OS	Input data format and Last update	Citation /Weblink	Remarks	Applicable functions
Several tools described in Table 1 (Tool Nos. 6, 8, 9, 10) and Table 2 (Tool Nos. 14, 16, 17, 19, 20, 21, 22, 23, 24, 27) also use resistance surfaces. Please refer to the descriptions in the respective tables.							
28 **SA**	***RangeShifter 2.0*** ***RangeShiftR***	Individual-based model integrating population dynamics and dispersal behavior to model functional connectivity.	GUI, CL	Raster (only in text format) 2020	(Bocedi et al., 2020; Malchow et al., 2020) https://rangeshifter.github.io/		Estimates potential connectivity by simulating and comparing occupancy probabilities (e.g., *ColonisationStats*) under various demographic (e.g., *StageStructure, Demography*) and dispersal (e.g., *Dispersal*) parameters. Also provides a dispersal heatmap.
29 **SA**	***HexSim***	Evaluate landscape connectivity, impacts of barriers, designs of restoration, mitigation and reintroduction strategies.	GUI	Raster, Vector, Text 2020	(Schumaker & Brookes, 2018) https://www.hexsim.net/		Simulates the impacts of barriers such as roads. Options to simulate gene flow while accounting for demographic complexity. The *Dispersal flux* module quantifies the number of times an animal passes through each hexagon during dispersal movements.
30 **SA**	***LandScape Corridors***	Simulate multiple functional ecological corridors between multiple source-target patches using species habitat requirement and LCP algorithm.	GUI, CI	Raster, Text 2016	(Ribeiro et al., 2017) https://github.com/LEEClab/LS_CORRIDORS/wiki	Can set the level of uncertainty and stochasticity in simulations. Runs in GRASS. R script provided to summarize simulations. No online support.	Generates multiple corridors between multiple source-target locations by simulating dispersal (e.g., *Biological scale, simulation methods MP, MLmin, MLavg, and MLmax*) and incorporating uncertainty. in resistance surface (e.g., *variability pattern*)

Table 3 (continued)

31	SA	***UNICOR 2.0***	Identify corridors and estimate resistant kernel connectivity using Dijkstra's shortest path algorithm to individual-based simulations using a resistance surface.	GUI, CI	Raster, Text 2019	(Landguth et al., 2012) https://github.com/ComputationalEcologyLab/UNICOR		Provides functionalities to quantitatively compare spatially explicit conservation and restoration scenarios and prioritize actions and areas of greatest concern due to climate change, designate sites as potential source or sink populations, and identify corridors and barriers.
32	ArcGIS	***ArcMap extension for evaluating corridors***	Allow users to evaluate and compare alternative corridor designs through various metrics.	GUI	Outputs from the Corridor Designer toolbox 2014	http://www.corridordesign.org/downloads		Identifies pinchpoints (*bottleneck analysis* toolset), produces frequency distributions of habitat quality for each focal species in each corridor (*histograms and habitat suitability statistics*), statistics for corridors (*general statistics*) and conducts cross-tabulations of any two corridor attributes (*cross-tabulation table)*.
33	R	***Grainscape***	Analyze connectivity using patch networks within a spatially explicit framework.	CL	Raster 2020	(Chubaty et al., 2020) https://cran.r-project.org/web/packages/grainscape/index.html	Provides tools to scale and visualize connectivity.	Given a landscape resistance surface, creates minimum planar graph (*MPG*) and grains of connectivity (*GOC*) models that can be used to calculate effective distances for landscape connectivity at multiple scales (*threshold*).
34	SA	***Zonation***	Decision support tool for ecologically based land use planning, including applications in spatial conservation planning and ecological impact avoidance.	GUI	Raster, Text 2020	(Lehtomäki & Moilanen, 2013) https://www.syke.fi/en-US/Research__Development/Nature/Specialist_work/Zonation_in_Finland/Zonation_software	Can include information on habitat connectivity to compare the ecological impact of different planning scenarios.	Uses corridors generated in different programs and embeds it in spatial prioritization (or ranking) process using a penalty mechanism. Corridors are used as an input feature or mask, and a *corridor loss*. *penalty* is implemented by defining *penalty strength* and *corridor width*

Table 3 (continued)

35	ArcGIS SA	***Environmental Evaluation Modeling System (EEMS)***	Decision support tool to evaluate current and future potential habitat value, ecological/development conflict, and landscape vulnerability to climate change.	GUI	Raster, Text 2019	(Sheehan & Gough, 2016) https://eemsonline.org/?model=4gkfUC0B4ytq3jg8fD6QJcSSdHxKAs0A	EEMS is a tree-based, fuzzy logic modeling system.	Web-tool displays results from Linkage mapper, such as corridors, priority linkages, etc.
36	SA	***MultyLink***	Decision-support tool in spatial conservation planning. Optimizes selection of linkages for multiple species in distinct types of habitat.	GUI	Text 2012	(Brás et al., 2013) https://www.iseg.ulisboa.pt/aquila/homepage/rbras/projectos/multylink	Output can be used in GIS software, spreadsheets or other statistical applications. No online support.	Provides users the flexibility to assign costs, friction values and habitat-specific barriers as input data. Based on these scores MulTyLink retrieves a network of linkages which may be visualized as a whole solution or independently for each habitat type.
37	R	***Makurhini***	Calculate various measures of fragmentation and connectivity. Assess the importance of landscape elements for connectivity.	CL	Raster, Vector	(Godínez-Gómez & Correa Ayram, 2020) https://connectscape.github.io/Makurhini/	Metrics similar to those in Conefor. No online support.	Evaluate priority linkages by estimating centrality measures (e.g.,*MK_RMCentrality.* Provides several connectivity metrics *(e.g., MK_dPCIIC, MK_dECA, MK_ProtConn, etc).*
38	R	***samc***	Quantify landscape connectivity using spatial absorbing Markov chain and distinguishing between movement behavior and mortality in space and time.	CL	Raster 2020	(Fletcher et al., 2019) https://cran.r-project.org/web/packages/samc/index.html	Incorporates both short-term and long-term dynamics, SDM and abundance.	Calculates dispersal metrics (*dispersal*) as the probability of individuals visiting locations.
39	SA	***Marxan Connect***	Assist conservation planners with the appropriate use of data on ecological connectivity in protected area network planning.	GUI/CLI	Raster, Text 2019	(Daigle et al., 2020) https://marxanconnect.ca/	The command line version of Marxan Connect is the python package-Marxanconpy.	Calculates and provides visualization of connectivity metrics (*connectivity input* and *connectivity metrics* tabs), exports the metrics for use in Marxan analyses.

Table 3 (continued)

40		***Conefor Sensinode***	Quantify the importance of habitat patches and links for network connectivity.	GUI, CI (windows only)	Specific Input files generated as mentioned in the Remarks section 2017	(Saura & Torné, 2009) http://www.conefor.org/index.html	Can be called from R via the shell function. Conefor inputs can be generated through a suite of extensions: (1) Conefor Input plugin for (a) QGIS or (b) ArcGIS; (2) Guidos (see Table 1); MatrixGreen (see Table 2). No mapping option.	Calculates several landscape connectivity indices (e.g., integral index of connectivity, probability of connectivity).
41	**SA**	***Graphab***	Construction and visualization of graphs, connectivity analyses and metrics from graphs.	GUI, CI	Raster 2020	(Foltête et al., 2021) https://sourcesup.renater.fr/www/graphab/en/home.html	Functions are also available in graph4lg R package.	Estimates the distance between points by calculating the resistance distance in the *Circuit* option in the Distance matrix menu. Calculates several connectivity metrics at global, component, local, and delta metrics.
42	**SA**	***FRAGSTATS*** ***landscapemetrics***	Quantify the landscape structure (composition and configuration) and calculate connectivity indices (Cohesion, Connect, and Traverse) for the landscape.	GUI, CI	Raster 2015	(McGarigal & Marks, 1995) https://www.umass.edu/landeco/research/fragstats/fragstats.html (Hesselbarth et al., 2021) https://cran.r-project.org/web/packages/landscapemetrics/index.html	For ArcGIS 10.3.4, recently developed as a R package-landscapemetrics.	Several functions to identify landscape patches (e.g., *get_patches*), connectivity (e.g., *lsm_c_cohesion)*, and obtain landscape connectivity metrics (e.g., *lsm_c_contig_cv*).
43		***graph4lg***	Build graphs for landscape genetics analysis.	CL	Raster, Text 2020	(Savary et al., 2021) https://cran.r-project.org/web/packages/graph4lg/index.html	Import landscape graphs created with 'GRAPHAB' software.	Functions to facilitate landscape genetic analyses (e.g., *genepop_to_genind, structure_to_genind*), interface with Graphab (e.g., *graphab_to_igraph*), compute connectivity metrics from a graph (e.g., *graphab_metric*), and compare graphs (*graph_modul, graph_node_compar)*.

Linkage Mapper, *Circuitscape*, *GFlow*). We categorized these tools in Step 2 because they have functions to create outputs that can be used in the iterative optimization step where resistance surfaces are repeatedly processed through the same analytical steps several times before the final resistance surface is generated.

There are a number of tools that can use the final optimized resistance surface in Step 3. These tools cover a wide-range of applications, ranging from individual based modelling of functional connectivity (e.g., *RangeShifter*, *UNICOR*), mapping barriers to movement (e.g., *HexSim*, *Linkage Mapper*), to visualization of graph metrics (e.g., *CONEFOR Sensinode*, *Graphab*).

Several tools can serve more than one Step. Tables 1, 2 and 3 provide a summary of some properties and identify key (non-exhaustive) functions of how tools can be used in the different steps.

Survey profile

We received a total of 148 responses to the online survey, of which 120 people completed the entire survey, 134 people completed up to Sect. 2 on familiarity with tools, and 123 completed up to Sect. 3 on rating tools they have used. A majority of survey respondents were researchers (professors or postdocs; 69%) and students (16%), and affiliated with universities (52%), non-governmental organizations (16%), research or government organizations (13% and 12% respectively) (Fig. S4.1, S4.2). A majority (65%) have PhD, 27% have a Master's degree and 7% have a Bachelor's degree as their highest degree (Fig. S4.3). About 68% of the respondents identified themselves as being experts or having good knowledge of the topic (24 and 44%, respectively) while ~32%, self-identified as beginners in the field of connectivity analysis (Fig. S4.4). Six percent of respondents were conducting connectivity research at global scale, 32% at a continental scale (North America – 36%, Europe – 21%, Africa – 13%, South America and Asia – 12% each, Australia – 7%), and 62% within 40 countries (US, 22%; India, 16%; Canada, 10%). (Fig. S4.5).

We found a strong bias of survey participants who worked on connectivity of vertebrates (69%) in terrestrial ecosystems (73%) (Fig. S4.6). Within the terrestrial ecosystem, 34% worked on mammals, 16% on birds, between 10 and 11% on amphibians, reptiles and insects, and about 15% worked on plants. Within the freshwater ecosystem amphibians (29%) and fish (19%) were the most frequently studied taxa, and within the marine ecosystem, fish (41%) were the most studied taxonomic group. Less than 5% respondents in each ecosystem also worked on abiotic or structural connectivity. Almost half the respondents worked on single taxa (49%), while 20% worked on two or more taxa, and 13% worked across multiple ecosystems, e.g., terrestrial and freshwater. Participants mostly used both ArcGIS and R (~50%) and QGIS (30%) to handle spatial data (Fig. S4.7).

Users experience of tools used in resistance-based connectivity analysis

Of the 43 tools included in our final review, 33 tools were also part of the survey. Respondents who considered themselves to be experts in connectivity analyses were, on average, familiar with significantly more tools than beginners (Student's t-test, $p<0.05$, $df=76$, $t=-3.3$ and -2.8 for experts and beginners, respectively). Experts had heard of a median of eight and used five tools in relation to beginners, who had heard of a median of four and used one tool. Few tools are very popular as a majority of respondents had either used it or at least heard of it (Fig. S4.8). In particular, most users have at least heard of *Circuitscape* (83%), R package *raster* (71%), *ArcMap extension for evaluating corridors* (66%), *Linkage Mapper* (61%), R packages *rgeos/sp/rgdal/sf* (59%), R package *gdistance* (54%), *Conefor* (53%), and *Circuitscape.jl* (51%). In contrast, a majority of people (>90%) were not aware of *MultyLink, Makurhini and MatrixGreen*. There was no correlation between the number of years since a particular tool became available and the percentage of people who had heard of it (Pearson's $r=0.23$, $p>0.5$) or used it (Pearson's $r=0.20$, $p>0.5$). *Circuitscape.jl* was an exception. The tool was released in 2019 and published in 2021 (Hall et al. 2021) but already received 26 evaluations (Fig S4.10), underscoring the popularity of circuit theory based tools in connectivity research.

Based on the sample size of tool ratings, the most widely used connectivity tools are *Circuitscape* ($n=77$), R packages that specifically handle spatial data such as *raster* ($n=76$), *rgeos/sp/rgdal/sf*

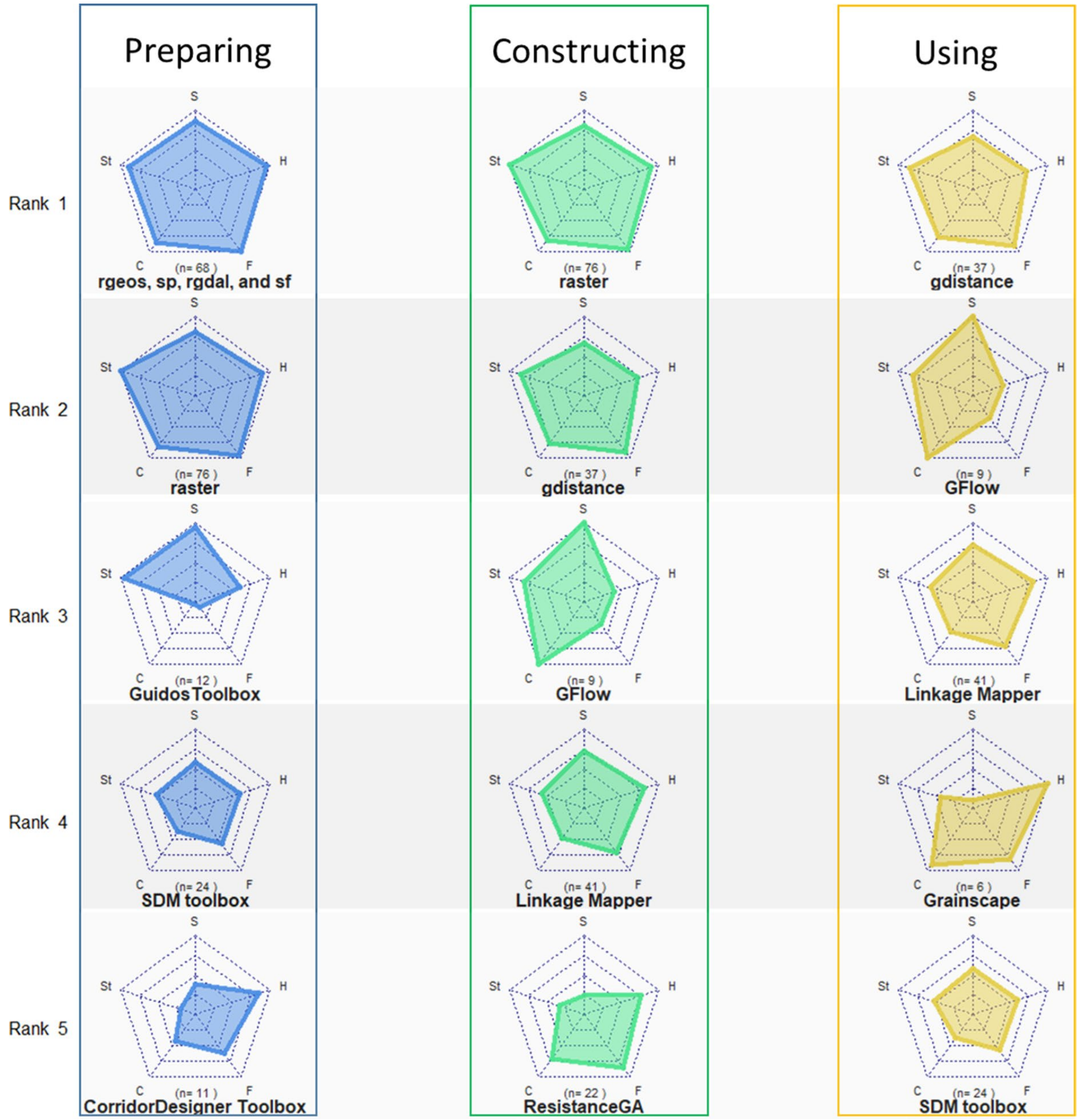


Fig. 2 Spider-plots of the top 5 ranked tools for each step in resistance-based connectivity analyses. The five criteria stability (St), customization (C), data format (F), getting help (H), and speed (S) are arranged in a radial axis with lowest ranks in the center and highest ranks towards the periphery. Tools with a larger and uniform web rank high across all criteria, whereas smaller or non-uniform webs indicate a poor ranking overall, or in the criteria represented by that axis respectively

(n = 68), *Linkage Mapper* (n = 41), and *gdistance* (n = 37). Only 22 tools received evaluations from more than five participants (Fig. 2) and were therefore included in rankings.

Preparing

Out of the 10 tools that allow to prepare the data for further analysis (Table 1), seven were included in the survey and five tools received more than five responses. R packages *rgeos/sp/rgdal/sf* and *raster* were ranked the highest and equally across all the criteria. *Guidos toolbox*, a stand-alone tool, ranked third, but ranked poorly on data formatting and customization. Among ArcGIS toolboxes, *SDM toolbox* ranks evenly across all criteria whereas *Corridor Designer Toolbox* rank high on getting help and data formatting, but rank low on the other criteria.

Constructing

Of the 27 tools that we identified for constructing and optimizing resistance surfaces, 20 were included in the survey and 13 tools had more than five responses. *Raster* package was again ranked high. Of the tools that are specifically developed for this step, *gdistance, GFlow, Linkage Mapper* and *ResistanceGA* ranked in the top five tools. *GFlow,* a tool specifically developed to model circuit theory-based analysis at large extents in a High Performance Computing environment was ranked high in all criteria except getting help and data format requirements. *Linkage Mapper* and *ResistanceGA* have good help and easy formatting requirements, but these tools often crash, leading to poor ranking in stability. Evaluations of the other tools used in constructing and optimizing resistance surfaces are presented in Fig. S4.9.

Using

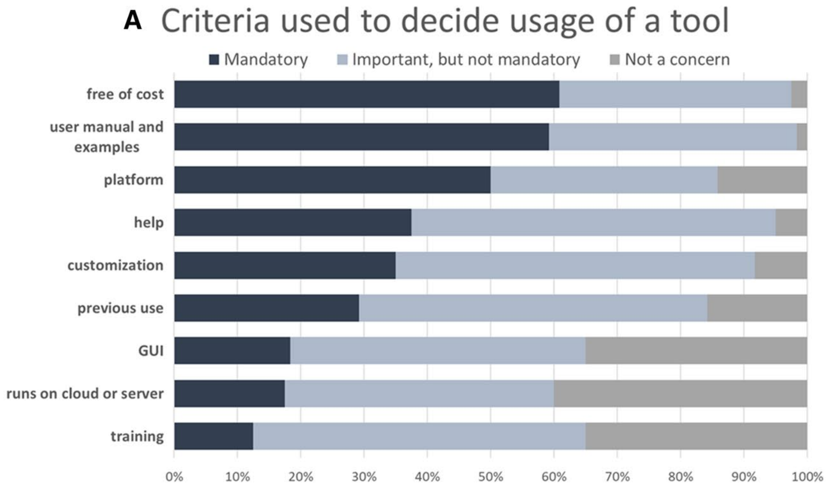
Among the 30 tools that use resistance surfaces, 22 were included in the survey, and 14 tools had more than five responses. *gdistance* ranks high across most criteria. *GFlow* and *Linkage mapper* and *SDM toolbox* also appear in the top five ranked tools in this step. The R package *Grainscape* ranked well in all criteria except for speed and stability whereas *SDM toolbox* Evaluations of the other tools that use resistance surfaces are presented in Fig. S4.10.

Users expectations in the future

Of the nine criteria we provided, consideration of the cost of tools, availability of user manuals and sample datasets, and the OS platform were critical factors in deciding which tools users would select for their analyses (Fig. 3a). In addition, good availability of help, ability to customize tools, and previous use as evidenced in reports and peer reviewed publications for example, were considered important in making this decision. In contrast, availability of a GUI, ability to run analyses on a cloud or server, and training workshops were not of much concern. We received an abundance of other criteria that are important to users when deciding which tool to use for their analyses (Fig. S4.11, Sect. 4 in S4). Some common themes that emerged are that details about the assumptions and caveats should be clearly stated, and that tools should be grounded in ecology and life-history of species. Users need high computational ability (i.e., the tool should be able to handle large high-resolution datasets at a high speed), compatibility with other processes in the workflow (i.e., not just limited to one step), and would prefer tools that run on commonly used open-source programming languages such as R or python. Participants also prefer tools that use input files in common data formats (e.g., *.tif, *.csv), and produce outputs that can be interpreted by stakeholders and decision-makers (e.g., visualization, maps).

We received a total of 20 responses to our two follow-up questions regarding existing methods that should be implemented in the future. Participants did not identify any existing approach for resistance analysis that is not currently implemented in an analytical tool, but they stressed the need to computationally optimize existing methods so that large data sets can be handled in a time-efficient manner. They also recommended improved visualizations, flexibility to deal with a diversity of datasets, and tools with interactive interfaces to facilitate usage by practitioners. In response to our question about future conceptual improvements, participants called for more explicit consideration of the uncertainties involved in resistance surface parameterization, e.g., Rayfield et al. (2011). Automated parameter optimization methods, e.g., *ResistanceGA* (Peterman 2018) or *radish* (Peterman and Pope 2021) are seen as an important ways to reduce some of these uncertainties while ensuring that such methods have reasonable computational demands. Another suggestion was to include dynamic connectivity to address changing spatio-temporal variability in connectivity. Some of the other recommendations are to increase biological realism by considering individual behavioral variability and demographic effects, and developing methods that can simultaneously estimate and predict different components of connectivity. For example, it would be useful to obtain a more differentiated picture of when and

Fig. 3 Important criteria in the development and usage of connectivity tools. Importance of criteria provided in the online survey (**A**). Our suggestions to users to improve their experience with tools (**B**), and developers to improve the usage and future development of tools (**C**)



B Our suggestions for users

- Pre-select tools. Use the decision tree and workflow to prepare a shortlist of tools that may work for you. Try to run the example data set provided with the user manual and select those that you understand the best.
- Select tools that can run your analysis efficiently. Test-run a subset of your dataset with the tools you shortlisted. Note problems, and criteria important to you - did it crash? How much time did it take? Did your machine become very slow? Will the default settings suffice, or are you able to run it in parallel mode, or on a super computer or server?
- Strive to maintain a streamlined analytical pipeline. Look through your entire workflow. Do you need to switch GIS systems several times in the process (R/ QGIS/ ArcGIS)? Perhaps you would want to choose tools that allow you to run all or majority of your analyses on the same GIS system.
- Make use of resources and the user community. Try to attend a workshop, or suggest one at the next conference you attend. Several online workshops and recorded tutorials are also available.

C Our suggestions for developers

- Strive to create new tools and transfer existing tools to open-access platforms.
- Provide visualization options (if applicable).
- Modelling can be complex, but the output should be simple enough to be understood by practitioners.
- Maintain an online forum where people can help each other, and also trouble-shoot recurring problems.
- Provide a detailed user manual with sample data (details in discussion).
- Develop tools for dynamic connectivity modelling which also accounts for uncertainties.

where connectivity will likely occur, of what quality it will be (e.g., range shift to new habitats vs. dispersal among existing habitats), and whether it will be of sufficient strength to affect patterns and processes of interest (e.g., connectivity effects on survival or population growth). Based on our review, and responses to Sect. 4 of the survey and follow up questions, we summarize key recommendations for users and developers in Fig. 3B and 3C.

Discussion

Connectivity science is a rapidly growing field (Correa Ayram et al. 2016), accompanied by a proliferation of tools to perform such analysis (Fig. S3). Given that landscape connectivity is now part of global (CBD 2020) and regional (European Commission 2020) targets, it can be expected that the number of new tools will continue to rise, making the selection of tools even more challenging, especially for beginners in the field. Through this paper, we summarize available tools, tabulate the key characteristics, and synthesize experiences from the research and conservation community. In order to facilitate an easy entry point for non-experts, we provide a detailed outline of the steps involved (S1), a decision tree that can help users select tools (S2) and a tutorial in R with script and sample data that performs several of the steps (S5). Our snapshot of user experiences with these tools should help non-experts to shortlist tools, and developers to improve the criteria that received low scores in the survey. We emphasize that our goal is not to rank one tool versus the other, but rather to provide an overview of their utilities on the basis of our own experience and of other researchers who have used them.

Limitations

One potential limitation of our study is that the research focus of all authors and a majority of the survey respondents is heavily biased towards academics working in terrestrial ecosystems and vertebrates. Therefore, it is quite possible that we have not covered tools applicable to the aquatic realm of connectivity research as thoroughly. However, we shared the survey on multiple list-serves across all geographic regions, taxonomies and ecosystems, and believe that this bias towards connectivity in terrestrial ecosystems is a true reflection of this field. Correa Ayram et al. (2016) also reported terrestrial landscapes being represented in 88% of published connectivity studies, and a bias towards vertebrates (mammals > birds > reptiles). Despite this extensive effort to receive responses across all sectors, we acknowledge a bias towards academic respondents, who may be more familiar with coding, and therefore could have influenced some of the results, for example the lack of preference for tools with GUI. However, the participants represent a combination of experts and beginners (Fig. S4.4) and were therefore likely to present a balanced perspective of their experiences and what they look for when choosing tools for their projects.

There are several interesting tools available for connectivity research that we did not include in this study, because we focused only on approaches and tools that explicitly involve resistance surfaces. For example, *Condatis* (Wallis and Hodgson 2015) is a decision support tool for habitat creation and restoration which models flows (of individuals or their genes) through a habitat network using habitat area, dispersal kernels (based on Euclidean distances) and emigration rates (Hodgson et al., 2012, 2016). The approach is based on circuit theory, similar to the well-known *Circuitscape* software, but is not based on a resistance surface. Similarly, *LConnect* (Mestre and Silva 2021) uses vector data to derive landscape connectivity metrics and assess connectivity, but not based on resistance surfaces. *ResDisMapper* (Tang et al. 2020) is an interesting R package that uses genotype data and geographic coordinates to generate resistance surfaces, but does not use any environmental data. Additional tools also exist for including wind speed and direction in connectivity analysis e.g., R package *rWind*, (Fernández-López et al. 2020), and for assessing flows and resulting connectivity in stream networks e.g., *FIPEX* (Oldford 2020) with *Dendritic Connectivity Index DCI* (Cote et al. 2009) accessible at https://goldford.github.io/FIPEX_with_DCI_Website/ and R package *smnet* (Rushworth 2020). The fact that we did not include these tools in our overview does not overlook their merit and applicability for connectivity research and conservation.

Assessment of the tools

A major challenge for connectivity research lies in analyzing data across large spatial extents, at fine spatial scales, and with methods that are computationally demanding. It is important to note that in principle, the efficiency of all tools can be improved through additional steps, for example by running ArcGIS tools in batch mode, by stringing steps together in sequential pipelines through ArcGIS model builder and in R, or by running tools in parallel through R. Several tools are much faster and stable if executed through the command line version.

From the survey responses, we can safely conclude that there is no such thing as 'the perfect tool'. Tools that rank the highest in all five criteria e.g., *raster*, and *rgeos, sp, rgdal* and *sf*, are generic tools that mainly help in preparing data for resistance-based analyses. Several tools were rated more heterogeneously across the five criteria, including *ResistanceGA*, which is specifically designed for optimizing resistance surfaces, and different tools that use resistance surfaces (*Linkage Mapper*, *Circuitscape* and *Circuitscape.jl*). They are either too slow, crash frequently, demand a lot of data formatting, are not customizable, or have poor access to help. Although we could not find any clear patterns, we observed trade-offs between speed and stability, and between stability and access to a help forum (Figs. S4.9, S4.10).

While the perfect tool may not exist, users almost always have a choice of several tools that perform similar tasks. This redundancy of tools, dependency on OS platforms and modelling options (e.g., through a GUI or programming languages like R and Python), and heterogeneity of performance across the different criteria provides users the option to decide what trade-offs they are willing and able to make. For example, some users may not have access to a server or high computing facility, so they may choose a tool that is relatively fast but needs some complicated data formatting requirements. Other users working with large landscapes may be willing to sacrifice speed for stability. Much of this decision making depends on the research question, the resources available (some software require paid licenses, or computers with high computational capacity), the extent and resolution of the input data, and the computational skills of the user.

The two most important characteristics that users care about are the associated costs, for example to purchase a license for the software that can implement the tool, and the access to a user manual with detailed instructions and example projects with sample data. While seemingly obvious, this is critical information. It is important to note here that all tools we found are available free of cost, but several toolboxes that run on ESRI ArcGIS or other proprietary software require users to buy a license with advanced extensions. There has been a huge push towards making customizable GIS software available without the need to invest in expensive proprietary software (Steiniger and Hay 2009) that allows collaborators to share data, code, and results seamlessly (Palomino et al. 2017). Although there are other programming languages used by ecologists, R appears to be very popular in the field of ecology because it improves open science, reproducibility of analyses and captures workflows when scripts and codes are included and shared (Lai et al. 2019).

Once the barrier of access (through costs of a GIS software) is removed, it is exceedingly difficult for beginners to start a project if they do not have a well-documented user guide, or no way to resolve questions through a peer group or forum. Here, we would like to emphasize that just providing a manual does not imply that the information is easy to follow. If functions and workflows are not explicitly defined, manuals can lead to large gaps of understanding and thus, limited usefulness of a tool. Most of the information is (usually) available, but often hidden in the manual. This may appear to be trivial and intuitive information for developers. However, during this review, we, experienced researchers in connectivity analyses, spent a significant amount of time sieving through user manuals to extract such basic information.

Recommendations for users

As already mentioned, we recommend users to combine expert-opinion with literature reviews and empirical data wherever possible. When habitat suitability models are used to generate resistance surfaces, we recommend testing a variety of relationships between habitat suitability and resistance (e.g., linear, negative exponential) with different conversions as mentioned earlier. Movement and genetic movement data are 'gold standards' as they capture functional connectivity, but in fact, these two data-types in fact capture different underlying ecological processes and temporal-scales. We reiterate here that the optimization and sensitivity analyses step is essential to overcome several of these issues.

For practical reasons, we recommend the minimum resistance values to be at least 1, as some of the tools that use resistance surfaces cannot handle smaller resistance values. Note that in the case of combining several resistance surfaces (for example when assessing multi-species connectivity), before multiple layers are combined through addition or averaging, their resistance values are often re-scaled to have the same range, and sometimes also standardized (e.g., z-score) to have the same distribution, (e.g., Row et al. 2017). This ensures that no single layer outweighs other layers in their contribution to final resistance values. However, one must be cautious when comparing resistance surfaces among different species, because the resistance values are species-specific meaning that the same landscape can lead to very different minimum and maximum resistance values for, e.g., a bird vs. an amphibian. As a result, the maximum value of a resistance surface will vary between different species.

Due to the high redundancy of the tools, we recommend that users try out a few of the tools before deciding on any one. Because there are several tools with user-friendly GUIs for all three steps, we believe that users should be able to find tools that cater to their needs and training. We also recommend readers to check the Conservation Corridor website https://conservationcorridor.org/corridor-toolbox/programs-and-tools/ for updates on new tools linked to the decision tree.

Recommendations for developers

We suggest developers to explicitly identify the methods implemented (e.g., is the functional connectivity estimated using least-cost paths or circuit-theory), and refer to our three-step structure (Fig. 1) to systematically indicate for which steps their tool can be used, in the same way researchers refer to the "Overview, Design concepts and Details (ODD)" (Grimm et al. 2010, 2020) or the "Overview, Data, Model, Assessment and Prediction" (ODMAP) (Zurell et al. 2020) protocol to report findings on agent-based simulation and species distribution models respectively. A similar classification and description system in user manuals that state the data and computational requirements, implemented methods, and outputs on the first page of all tools would be very helpful for users to spot suitable tools.

A detailed manual with clear examples can enable researchers to navigate through the tools and learn their functions more easily, minimizing the need for additional support. This information can also be used by other developers to easily identify already existing functions, thus avoiding duplication of tools.

We believe that connectivity analyses will most likely become analytically more complex in the future, especially with the increasing availability of high-resolution remote sensing data (Kwok 2018). Parallel to this computational enhancement, we underscore the need to put greater emphasis on increasing biological realism and producing outputs that are easy to understand by conservation practitioners and policy makers. Connectivity research that is analytically complex can be presented in relatively simple, yet ecologically meaningful indices that can be used in connectivity conservation and landscape planning. For example, several of the connectivity metrics recently reviewed by Keeley et al. (2021) can incorporate effective distances (e.g., least-cost paths or circuit-theoretic resistances) estimated from resistance surfaces, yet these metrics provide numbers that are relatively easy to explain and understand for practical planning and conservation purposes. These kinds of metrics also illustrate that all connectivity analyses need not be resistance-based as the typical input for calculating the metrics are Euclidean (straight-line) distances, or binary assessments on whether patches are connected or not. Overall, we recommend that developers strive to produce tools that are not dependent on proprietary GIS platforms, and encourage them to maintain an active, searchable help forum in addition to a detailed user manual and example data.

Future areas of development identified through the survey to move from static environmental data layers to incorporate dynamic, e.g., seasonal or annual changes which can strongly impact the resistance of a landscape (Osipova et al. 2019; Fenderson et al. 2020; Zeller et al. 2020). There has been a call to incorporate *anthropogenic resistance* in connectivity mapping, that accounts for human behaviors that may impact the way animals use the landscape (Ghoddousi et al. 2021). Recent studies present ways to synthesize resistance surfaces derived from different underlying data-types and modelling approaches to quantify consensus on landscape permeability and therefore be useful for conservation efforts (Schoen et al. 2022). Based on our extensive overview of analytical tool that is further corroborated by the suggestions provided by survey respondents, we identified at-least three key avenues for future development of connectivity tools: (i) better incorporation and presentation of uncertainties in analyses (ii) the importance of including dynamism in connectivity models and (iii) refining and testing methods to automatically optimize resistance surfaces.

Conclusions

Over the past 20 years, the use of resistance surfaces has been pivotal in advancing our understanding of how landscape features affect species movement and gene flow. Such knowledge is vital for effective management of populations in space and time, but the selection of the right tool is critical to many studies and subsequent management decisions. We do not aspire to advise users exactly which tools to use when, but rather to provide a road map (Fig. 1) with a compass (Supplementary S2) to navigate through the plethora of tools that are available. Selecting a particular tool requires a trade-off between some characteristics and is highly dependent upon the research question, the resolution and size of the landscape, and the number of data points used to optimize layers.

We hope this review will help beginners get a smooth entry at resistance-based connectivity research, highlight other available options to experienced researchers, and provide developers with ideas to improve the performance and usefulness of their tools. Ultimately, the diversity of methods, algorithms, and tools should help facilitate a better understanding of drivers of connectivity in fragmented landscapes and aid in conservation of biodiversity on Earth.

Acknowledgements We thank all the respondents of the survey and those who took the time to answer our additional questions. We are grateful to Conservation Corridor for advertising the survey in their newsletter and for providing a platform for our workflow and decision tree. We are thankful to Matt Hayward, Christopher Jordan, Rafael Reyna and Elodie Portanier for testing out initial versions of the survey, and Katharina Westekemper for her valuable contributions in the early phases of this project.

Funding Open Access funding enabled and organized by Projekt DEAL. NB and TD conducted this research as part of project BearConnect, funded through the 2015- 2016 BiodivERsA COFUND call, with national funders Agence Nationale de la Recherche (ANR), France (Grant number: ANR-16-EBI3-0003), National Science Center (NCN), Poland (Grant number: 2016/22/Z/NZ8/00121), Federal Ministry of Education and Research (BMBF) and DLR Project Management Agency (DLR-PT), Germany (Grant number: 01LC1614A), Romanian National Authority for Scientific Research and Innovation, CCCDI – UEFISCDI, Romania (Grant number: BiodivERsA3-2015-147-BearConnect (96/2016) within PNCDI III, and Norwegian 293 Research Council (RCN), Norway (Grant number: 269863). NM was a fellow of the PRIME programme of the German Academic Exchange Service (DAAD) with funds from the German Federal Ministry of Education and Research (BMBF), and received funding from the EU's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No 894290.

Data availability R tutorial and associated data can be accessed at Figshare Link https://doi.org/10.6084/m9.figshare.14371613.v1

Data availability Not applicable.

Code availability An updated version of the decision tree will soon be available at the Programs and Tools page on the Conservation Corridor website https://conservationcorridor.org/corridor-toolbox/programs-and-tools/

Declarations

Conflicts of interest Not applicable.

Consent to participate Not applicable.

Consent for publication All authors consent to the publication.

Ethical approval Not applicable.

References

Alberti G (2019) movecost: an R package for calculating accumulated slope-dependent anisotropic cost-surfaces and least-cost paths. SoftwareX 10:100331

Andersson E, Bodin Ö (2009) Practical tool for landscape planning? An empirical investigation of network based models of habitat fragmentation. Ecography 32:123–132

Bivand R, Rundel C, Pebesma E, et al (2020) rgeos: Interface to Geometry Engine - Open Source ('GEOS'). Version 0.5–5 https://CRAN.R-project.org/package=rgeos

Bivand R, Keitt T, Rowlingson B, et al (2021) rgdal: Bindings for the "Geospatial" Data Abstraction Library. Version 1.5–23 https://CRAN.R-project.org/package=rgdal

Bocedi G, Palmer SCF, Malchow A-K, et al (2020) RangeShifter 2.0: An extended and enhanced platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. bioRxiv 2020.11.26.400119. https://doi.org/10.1101/2020.11.26.400119

Brás R, Cerdeira JO, Alagador D, Araújo MB (2013) Linking habitats for multiple species. Environ Model Softw 40:336–339

Brost BM, Beier P (2012) Use of land facets to design linkages for climate change. Ecol Appl 22:87–103

Brown JL (2014) SDM toolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol Evol 5:694–700

Calenge C (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Carroll C, McRae B, Brookes A (2012) Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. Conserv Biol 26:78–87

CBD (2020) Update of the zero draft of the post-2020 global biodiversity framework (Convention on Biological Diversity, 2020). http://go.nature.com/3jWOnsr

Chailloux M (2021) BioDispersal [Python]. https://github.com/MathieuChailloux/BioDispersal (Original work published 2018)

Chubaty AM, Galpern P, Doctolero SC (2020) The r toolbox grainscape for modelling and visualizing landscape connectivity using spatially explicit networks. Methods Ecol Evol 11:591–595

Clevenger AP, Wierzchowski J, Chruszcz B, Gunson K (2002) GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. Conserv Biol 16:503–514

Correa Ayram CA, Mendoza ME, Etter A, Salicrup DRP (2016) Habitat connectivity in biodiversity conservation: a review of recent studies and applications. Progress Phys Geogr 40:7–37

Cote D, Kehler DG, Bourne C, Wiersma YF (2009) A new measure of longitudinal connectivity for stream networks. Landsc Ecol 24:101–113

Crooks KR, Sanjayan M (2006) Connectivity conservation. Cambridge University Press, Cambridge

Crooks KR, Burdett CL, Theobald DM et al (2017) Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. Proc Natl Acad Sci USA 114:7635–7640

Cushman SA, Landguth EL (2010) Scale dependent inference in landscape genetics. Landsc Ecol 25:967–979

Cushman SA, McRae B, Adriaensen F et al (2013) Biological corridors and connectivity. In: Macdonald DW, Willis KJ (eds) Key topics in conservation biology 2. Wiley, Oxford, pp 384–404

Daigle RM, Metaxas A, Balbar AC et al (2020) Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect. Methods Ecol Evol 11:570–579

Dondina O, Meriggi A, Bani L, Orioli V (2022) Decoupling residents and dispersers from detection data improve habitat selection modelling: the case study of the wolf in a natural corridor. Ethol Ecol Evol https://doi.org/10.1080/03949370.2021.1988724

Elliot NB, Cushman SA, Macdonald DW, Loveridge AJ (2014) The devil is in the dispersers: predictions of landscape connectivity change with demography. J Appl Ecol 51:1169–1178

Etherington TR (2011) Python based GIS tools for landscape genetics: visualising genetic relatedness and measuring landscape connectivity. Methods Ecol Evol 2:52–55

Etherington TR (2021) Python based GIS tools for landscape genetics: visualising genetic relatedness and measuring landscape connectivity. Zenodo. https://doi.org/10.5281/zenodo.4654049

European Commission (2020) EU Biodiversity Strategy for 2030. Bringing nature back into our lives. Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions.

Fenderson LE, Kovach AI, Llamas B (2020) Spatiotemporal landscape genetics: investigating ecology and evolution through space and time. Mol Ecol 29:218–246

Fernández-López J, Schliep K, Arjona Y (2020) rWind: Download, edit and include wind and sea currents data in ecological and evolutionary analysis. Version 1.1.5 https://CRAN.R-project.org/package=rWind

Fletcher RJ, Sefair JA, Wang C et al (2019) Towards a unified framework for connectivity that disentangles movement and mortality in space and time. Ecol Lett 22:1680–1689

Foltête J-C, Clauzel C, Vuidel G (2012) A software tool dedicated to the modelling of landscape networks. Environ Model Softw 38:316–327

Foltête J-C, Vuidel G, Savary P et al (2021) Graphab: an application for modeling and managing ecological habitat networks. Software Impacts 8:100065

Fountain-Jones NM, Kraberger S, Gagne RB, et al (2021) Host relatedness and landscape connectivity shape pathogen spread in the puma, a large secretive carnivore. Commun Biol 4:1–9

Gastón A, Blázquez-Cabrera S, Garrote G et al (2016) Response to agriculture by a woodland species depends on cover type and behavioural state: insights from resident and dispersing Iberian lynx. J Appl Ecol 53:814–824

Ghoddousi A, Buchholtz EK, Dietsch AM et al (2021) Anthropogenic resistance: accounting for human behavior in wildlife connectivity planning. One Earth 4:39–48

Godínez-Gómez O, Correa Ayram CA (2020) connectscape/Makurhini: Analyzing landscape connectivity (v1.0.0). Zenodo

Goicolea T, Gastón A, Cisneros-Araujo P, et al (2021) Deterministic, random, or in between? Inferring the randomness level of wildlife movements. Mov Ecol 9:1–14

Graves T, Chandler RB, Royle JA et al (2014) Estimating landscape resistance to dispersal. Landsc Ecol 29:1201–1211

Grimm V, Berger U, DeAngelis DL et al (2010) The ODD protocol: a review and first update. Ecol Model 221:2760–2768

Grimm V, Railsback SF, Vincenot CE et al (2020) The ODD protocol for describing agent-based and other simulation models: a second update to improve clarity, replication, and structural realism. J Artif Soc Soc Simul 23:185

Hall KR, Anantharaman R, Landau VA et al (2021) Circuitscape in Julia: empowering dynamic approaches to connectivity assessment. Land 10:301

Hess GR (1994) Conservation corridors and contagious disease: a cautionary note. Conserv Biol 8:256–262

Hesselbarth MHK, Sciaini M, Nowosad J, et al (2021) landscapemetrics: Landscape Metrics for Categorical Map Patterns. Version 1.5.2 https://CRAN.R-project.org/package=landscapemetrics

Hijmans RJ, van Etten J (2016) raster: Geographic data analysis and modeling. R package version 2.

Hodgson JA, Thomas CD, Dytham C, et al (2012) The speed of range shifts in fragmented landscapes. PLOS ONE 7:e47141

Hodgson JA, Wallis DW, Krishna R, Cornell SJ (2016) How to manipulate landscapes to improve the potential for range expansion. Methods Ecol Evol 7:1558–1566

Jeltsch F, Bonte D, Peer G et al (2013) Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. Mov Ecol 1:6

Keeley ATH, Beier P, Gagnon JW (2016) Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc Ecol. https://doi.org/10.1007/s10980-016-0387-5

Keeley ATH, Beier P, Keeley BW, Fagan ME (2017) Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. Landsc Urban Plan 161:90–102

Kwok R (2018) Ecology's remote-sensing revolution. Nature 556:137–138

Lai J, Lortie CJ, Muenchen RA, et al (2019) Evaluating the popularity of R in ecology. Ecosphere https://doi.org/10.1002/ecs2.2567

Landau VA, Shah VB, Anantharaman R, Hall KR (2021) Omniscape.jl: software to compute omnidirectional landscape connectivity. J Open Source Softw 6:2829

Landguth EL, Hand BK, Glassy J et al (2012) UNICOR: a species connectivity and corridor network simulator. Ecography 35:9–14

Lehtomäki J, Moilanen A (2013) Methods and workflow for spatial conservation prioritization using Zonation. Environ Model Softw 47:128–137

Lele SR, Keim JL, Solymos P (2019) Package 'ResourceSelection'. Available at https://cran.r-project.org/web/packages/ResourceSelection/index.html

Lewis J (2021) leastcostpath: modelling pathways and movement potential within a landscape (Version 1.8.0). Version 1.8.0 https://CRAN.R-project.org/package=leastcostpath

Lenoir J, Bertrand R, Comte L et al (2020) Species better track climate warming in the oceans than on land. Nat Ecol Evol 4:1044–1059

Leonard PB, Duffy EB, Baldwin RF et al (2017) gflow: software for modelling circuit theory-based connectivity at any scale. Methods Ecol Evol 8:519–526

Lopez S, Rousset F, Shaw FH et al (2009) Joint effects of inbreeding and local adaptation on the evolution of genetic load after fragmentation. Conserv Biol 23:1618–1627

Majka D, Jenness J, Beier P (2007) CorridorDesigner: ArcGIS tools for designing and evaluating corridors

Mestre F, Silva B (2021) lconnect: simple tools to compute landscape connectivity metrics. Version 0.1.1 https://CRAN.R-project.org/package=lconnect

Malchow A-K, Bocedi G, Palmer SCF, et al (2020) RangeShiftR: an R package for individual-based simulation of spatial eco-evolutionary dynamics and species' responses to environmental change. bioRxiv 2020.11(17): 384545.

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol 18:189–197

Mateo-Sánchez MC, Balkenhol N, Cushman S et al (2015) Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data. Ecosphere 6:1–16

McGarigal K, Marks BJ (1995) Spatial pattern analysis program for quantifying landscape structure. USDA Forest Service Pacific Northwest Research Station, Portland

McRae B, Kavanagh DM (2011) Linkage mapper connectivity analysis software. The Nature Conservancy, Seattle

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724

McRae BH, Shirk AJ, Platt JT (2013) Gnarly landscape utilities: resistance and habitat calculator uer guide. The Nature Conservancy, Fort Collins

Meyer NFV, Moreno R, Reyna-Hurtado R, et al (2020) Towards the restoration of the Mesoamerican Biological Corridor for large mammals in Panama: comparing multi-species occupancy to movement models. Mov Ecol 8:3

Oldford G (2021) FIPEX-with-the-DCI-10.4. Available at https://github.com/goldford/FIPEX-with-the-DCI-10.4

Osipova L, Okello MM, Njumbi SJ et al (2019) Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons. Anim Conserv 22:35–48
Palomino J, Muellerklein OC, Kelly M (2017) A review of the emergent ecosystem of collaborative geospatial tools for addressing environmental challenges. Comput Environ Urban Syst 65:79–92
Pebesma E (2018) Simple Features for R: standardized support for spatial vector data. R J 10:439
Pebesma E, Bivand R, Racine E, et al (2021a) sf: Simple Features for R. Version 0.9-8 https://CRAN.R-project.org/package=sf
Pebesma E, Bivand R, Rowlingson B, et al (2021b) sp: classes and methods for spatial data. Version 1.4–5 https://CRAN.R-project.org/package=sp
Pe'er G, Henle K, Dislich C, Frank K (2011) Breaking functional connectivity into components: a novel approach using an individual-based model, and first outcomes. PLoS ONE 6:e22355
Phillips S (2021) maxnet: Fitting "Maxent" species distribution models with "glmnet." Version 0.1.4 https://CRAN.R-project.org/package=maxnet
Peterman WE (2018) ResistanceGA: an R package for the optimization of resistance surfaces using genetic algorithms. Methods Ecol Evol 9:1638–1647
Peterman WE, Pope NS (2021) The use and misuse of regression models in landscape genetic analyses. Mol Ecol 30:37–47
Quaglietta L, Porto M (2019) SiMRiv: an R package for mechanistic simulation of individual, spatially-explicit multistate movements in rivers, heterogeneous and homogeneous spaces incorporating landscape bias. Mov Ecol 7:11
Ray N (2005) pathmatrix: a geographical information system tool to compute effective distances among samples. Mol Ecol Notes 5:177–180
Rayfield B, Fortin M-J, Fall A (2011) Connectivity for conservation: a framework to classify network measures. Ecology 92:847–858
Ribeiro JW, Silveira dos Santos J, Dodonov P et al (2017) LandScape Corridors (lscorridors): a new software package for modelling ecological corridors based on landscape patterns and species requirements. Methods Ecol Evol. https://doi.org/10.1111/2041-210X.12750
Row JR, Knick ST, Oyler-McCance SJ et al (2017) Developing approaches for linear mixed modeling in landscape genetics through landscape-directed dispersal simulations. Ecol Evol 7:3751–3761
Rushworth A (2020) smnet: smoothing for stream network data. Version 2.1.2 https://CRAN.R-project.org/package=smnet
Saura S, Torné J (2009) Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environ Model Softw 24:135–139
Savary P, Foltête J-C, Moal H et al (2021) graph4lg: A package for constructing and analysing graphs for landscape genetics in R. Methods Ecol Evol 12:539–547
Scharf AK, Belant JL, Beyer DE et al (2018) Habitat suitability does not capture the essence of animal-defined corridors. Mov Ecol 6:18
Schoen JM, Neelakantan A, Cushman SA et al (2022) Synthesizing habitat connectivity analyses of a globally important human-dominated tiger-conservation landscape. Conserv Biol. https://doi.org/10.1111/cobi.13909
Schumaker NH, Brookes A (2018) HexSim: a modeling environment for ecology and conservation. Landsc Ecol 33:197–211
Sheehan T, Gough M (2016) A platform-independent fuzzy logic modeling framework for environmental decision support. Eco Inform 34:92–101
Shirk AJ, Wallin DO, Cushman SA et al (2010) Inferring landscape effects on gene flow: a new model selection framework. Mol Ecol 19:3603–3619
Shtilerman E, Stone L (2015) The effects of connectivity on metapopulation persistence: network symmetry and degree correlations. Proc R Soc B 282:20150203
Signer J, Fieberg J, Avgar T (2019) Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecol Evol 9:880–890
Spear SF, Balkenhol N, Fortin M-J et al (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Mol Ecol 19:3576–3591
Spear SF, Cushman SA, McRae BH (2015) Resistance surface modeling in landscape genetics. In: Landscape genetics. Wiley, pp 129–148
Steiniger S, Hay GJ (2009) Free and open source geographic information tools for landscape ecology. Ecol Inform 4:183–195
Tang Q, Fung T, Rheindt FE (2020) ResDisMapper: an R package for fine-scale mapping of resistance to dispersal. Mol Ecol Resour 20:819–831
Taylor PD, Fahrig L, With KA (2006) Landscape connectivity: a return to the basics. In: Crooks KR, Sanjayan M (eds) Connectivity conservation. Cambridge University Press, Cambridge, pp 29–43
Theobald DM, Norman JB, Sherburne MR (2006) FunConn v1 user's manual: ArcGIS tools for functional connectivity modeling. Natural Resource Ecology Lab, Colorado State University, Fort Collins
Trainor AM, Walters JR, Morris WF et al (2013) Empirical estimation of dispersal resistance surfaces: a case study with red-cockaded woodpeckers. Landsc Ecol 28:755–767
van Etten J (2017) R package gdistance: distances and routes on geographical grids. J Stat Softw 76:1–21
Villard M-A, Metzger JP (2014) REVIEW: Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. J Appl Ecol 51:309–318
Vogt P, Riitters K (2017) GuidosToolbox: universal digital image object analysis. Eur J Remote Sens 50:352–361
Wade AA, McKelvey KS, Schwartz MK (2015) Resistance-surface-based wildlife conservation connectivity modeling: Summary of efforts in the United States and guide for practitioners. Gen Tech Rep RMRS-GTR-333 Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station 93 p 333: https://doi.org/10.2737/RMRS-GTR-333

Wallis DW, Hodgson JA (2015) Condatis: software to assist with the planning of habitat restoration v0.6.0. Zenodo
Wang IJ (2020) Topographic path analysis for modelling dispersal and functional connectivity: calculating topographic distances using the topoDistance r package. Methods Ecol Evol 11:265–272
Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landsc Ecol 27:777–797
Zeller KA, Vickers TW, Ernest HB, Boyce WM (2017) Multilevel, multi-scale resource selection functions and resistance surfaces for conservation planning: pumas as a case study. PLoS ONE 12:e0179570
Zeller KA, Lewsion R, Fletcher RJ et al (2020) Understanding the importance of dynamic landscape connectivity. Land 9:303
Zurell D, Franklin J, König C et al (2020) A standard protocol for reporting species distribution models. Ecography 43:1261–1277