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Open-source tools in R for landscape ecology

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Abstract **Purpose of review** Landscape ecology, the study of the complex interactions between landscapes and ecological processes, has hugely benefited from the increase in widely available open source software in recent years. In particular, the *R* programming language provides a wealth of community developed tools for landscape ecology. **Recent findings** In this paper, we outline existing packages for downloading, processing and visualisation of spatial data, as well as those specifically developed for ecological analysis. Additionally, we outline the results of a survey of *R* users within the landscape ecology community. **Summary** We found that landscape ecologists are generally satisfied with the functionality available within *R*, and that as a community they are continually further develop the functionality available. Suggested future developments include improvement of computation performance; additional methods for landscape characterisation such as surface metrics; and advanced,

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accessible visualisation tools.

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1 Introduction

Glossary	
API	Application programming interface. A set of protocols for sending and retrieving information from a server
cell	Smallest, rectangular unit of raster data model
CRAN	Comprehensive *R* Archive Network. A repository for *R* package
CRS	Coordinate references systems. A coordinate-based local, regional or global system used to locate geographical entities
EPSG	Public registry of geodetic datums, spatial reference systems, Earth ellipsoids, coordinate transformations and related units of measurement
GDAL	Open source translator library for raster and vector geospatial data formats
GIS	Geographical information system
landscape	Mosaic of land covers, ecosystems, habitat types, land uses
NLM	Neutral landscape model
open-source software	Software released under licenses that allow to use, modify and distribute it
patch	Neighboring cells with same value
PROJ	Open source generic coordinate transformation software
raster	Cell grid based data model
resolution	Size in meter or degree of one cell
R package	User-created software extension to *R* programming language
SDM	Species distribution modelling
Simple Features	A set of standards that specify a common storage and access model of geographic features
vector	Points, lines, and polygons-based data model

1.1 A short introduction to landscape ecology

While human activities have altered the landscapes for millennia [1,2], in the recent centuries, the effects of humans on landscapes have increased to an unknown high, known as the Anthropocene [3]. Today, almost all landscapes are directly or indirectly influenced by human activities [4]. Thus, understanding the complex interactions between landscapes and ecological processes becomes increasingly important for science, conservation, or management [5].

Landscape ecology focuses on how ecological processes are influenced by the heterogeneous landscapes they occur in and how the ecological processes themselves influence the landscapes [6,7,5]. In this context, landscape ecology predominantly focuses on i) spatial and temporal dynamics of heterogeneous landscapes, ii) interactions, fluxes, and exchanges within these landscapes, iii) how the landscapes influence ecological processes (and vice versa), and lastly, iv) and can guide how to manage these heterogeneous landscapes [8,6].

Because landscapes are defined as mosaics of different land covers, ecosystems, habitat types, or land uses [9,10,11], spatial context is important and ecological processes can vary spatially [5]. The importance of scale was already raised decades ago [12,13,14] and is still of relevance today [15,16]. Thus, landscape ecology emphasizes spatial patterns to a high degree [8] and consequently relies on software to preprocess, modify, model, analyze, and visualize spatial data.

1.2 Open-source software and *R*

Software to manage and analyze data becomes increasingly important in modern scientific research [17] and many scientific studies would not have been possible without open-source software [18]. Open-source software includes all software that is released under licenses that allow to use, modify and distribute the software [19]. Open-source software development has many advantages, such as fast innovation, transparency, reliability, and longevity, mainly due to many diverse contributors [20,19]. Additionally, the use of open-source software facilitates (computational) reproducibility and can allow a better understanding of the methodology of a study [18,21]. Furthermore, open-source software allows other scientists to reuse code and not “reinvent the wheel” [18] by customizing existing software to their specific needs [22]. Importantly, though not strictly necessary by definition of open-source [22,23], most open-source software is also free-of-cost, in contrast to often expensive proprietary software [20,22,23]. This democratizes scientific research as free-of-cost software removes one gatekeeper for researchers without access to proprietary software.

One successful example of an open-source project is the *R* programming language, and its extensions called packages [24]. Packages allow to easily share code and make functionality and documentation available to users and by that extent the capability of the *R* programming language [25]. Firstly released in 1995 [26], today this programming language is among the most popular programming languages, especially in ecology [27]. Originally introduced as a statistical programming language, a growing body of packages designed to analyze spatial data subsequently emerged for the *R* programming language [28,29]. The expanding CRAN Task Views (curated lists of packages related to a certain topic) document this: *Analysis of Spatial Data* [30] and *Handling and Analyzing Spatio-Temporal Data* [31] currently list about 300 packages in total. Since the task views are maintained manually by just a few people, the actual amount of *R* packages related to spatial data is most likely higher. The growing popularity of the *R* programming language for spatial data analysis and landscape ecology can also be seen with the increasing number of related textbooks [32,33,29,34]. A recent overview over the progress of *R* to handle spatial data in general can be found in [35].

Even though many other open-source tools [36,37,38] and suitable programming languages (e.g. Python) for landscape ecology exist, in this review we focus on software implemented in the *R* programming language. We acknowledges that there are reasons and circumstances to also use other software tools and progamming languages, however, a comprehensive discussion of pro and cons is outside the scope of this manuscript. For more general overviews of open-source software for landscape ecology studies see [39,22,23,40]. The *R* programming language can be a very powerful tool. In addition to handling spatial data, other analytical tasks such as statistical modeling, creation of publication-ready figures, and even complete reports can be done within the *R* environment (Fig. 1). The growing body of *R* packages related to spatial data processing and analysis results in a high capability of this language for landscape ecology.

Thus, in the first part of this article, we present an overview of existing *R* packages for landscape ecology and closely related fields (Table 1). In the second part, we present a survey in which we asked the community how they currently use the *R* programming language and to identify topics for which *R* packages are presently missing for landscape ecology.

2 Existing packages

Most *R* packages are developed and maintained by the community, which shows how open-source software development can facilitate innovation, reproducibility, and reuse of code. There are three major online platforms to host *R* packages and make them accessible to potential users: CRAN, GitHub, and Bioconductor. The last one focuses on tools for the analysis of genomic data; therefore, in this review we focus on only the former two".

CRAN (the *Comprehensive R Archive Network*) provides large visibility to the community, ease of installation, and a technical quality standard, including checks for common problems on all major operating systems [25]. *GitHub* hosts source code under version control, and allows users to install packages with one line of code using the *remotes* [41] package. Additionally, hosting a package on *GitHub* provides many useful features to collaborate and communicate between developers and users [25], or integrated unit testing (i.e. testing if functions return an expected value).

The guaranteed technical quality standard of *CRAN* requires more initial work for developers compared to *GitHub*, while it ensures for users that the package can be installed on their machine. Additionally, the technical quality standard of *CRAN* also facilitates reproducibility and reuse of code, as shown by many reverse dependencies of *R* packages, i.e., package x requires and uses code from package y. CRAN also provides archived versions of outdated or orphaned packages and thus ensuring long term availability and reproducibility of code. Thus, most packages can be found on both platforms, and many

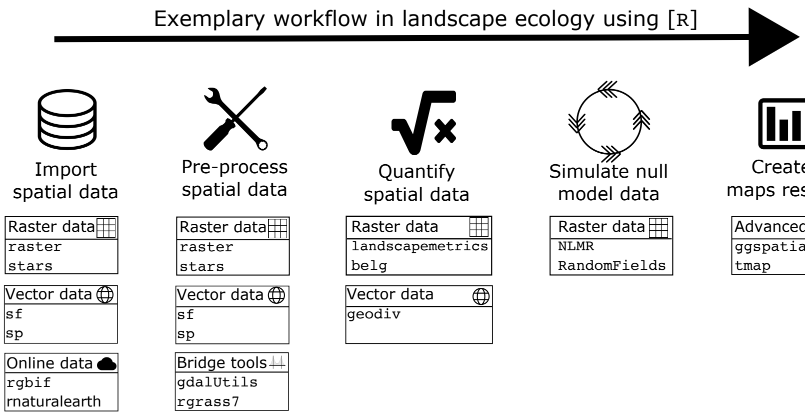

Fig. 1: Exemplary workflow of spatial data analyses for landscape ecology using the *R* programming language. For all major tasks, some example *R* packages are listed.

developers use *GitHub* for regular development and *CRAN* to publish stable releases of the packages. Furthermore, online communities like *rOpenSci* also provide a peer-review process for code quality. However, while the package environment has many advantages, its highly dynamic characteristic with constant updates by the community might also be a threat to reproducibility since backwards compatibility is not always ensured. Packages that deal with such issue include *groundhog* [42], *packrat* [43], or *renv* [44]. These packages facilitate reproduciability to a high degree by preserving the project enviroment, including specific package versions, used for an analysis. For more information about *R* package development in general, see [25].

2.1 Spatial data representations

While base *R* has several built-in data structures, including vectors, matrices, data frames, and lists, it has no internal support for reading, processing, or visualizing spatial data. However, as discussed previously, one strength and core idea of the *R* programming language are its expandability by pacakges. Because there is a substantial interest in spatial data analysis, support for spatial data is now provided by many *R* packages ([29], page 10, Table 1). Most spatial data belong to one of two data models, namely spatial raster and spatial vector model, and both data models have several implementations in the *R* language. Importantly, main *R* packages for spatial data use the external *GDAL* [45] and *PROJ* [46] libraries, which allow for reading and writing of hundreds of spatial data formats, and coordinates transformation. Additionally, *R* allows for conversion between data models and specific implementations, which can be useful if given methods only exist for a particular data model or implementation.

In the raster data model, surfaces are divided into cells, where each cell stores a numeric value. The values could represent discrete phenomena, such as a class number of a land cover category, or continuous phenomena, such as elevation values. Currently, the most prominent package allowing for raster data representation is *raster* [47]. A *raster* successor, *terra*, aimed at the simpler interface and improved performance is being developed [48], however, it could take several years for this package to be adopted by other developers and users. Alternatively, the *stars* package can be used to read and process raster data focusing on spatial-temporal data cubes [49]. Additionally, there are packages that improve some basic raster operations in terms of computational performance or compatibility between raster and vector operations, such as *fasterize* [50], *rasterDT* [51], or *exactextractr* [52].

The vector data model consists of two main elements i) geometries (such as points, lines, polygons) and ii) attributes, where each geometry is connected to a row in the attribute table. In many cases, this data model allows a more realistic representation of landscape features, however, with the cost of higher computational demands [29]. The *sp* package was the standard for vector data representation for more than ten years [53,54]. As of 2020, more than 500 *R* packages directly depend or imports *sp*. However, *sp* is not actively developed anymore, and its recommended successor is the *sf* package [55]. Besides many advantages and strength of the *sf* package in terms of spatial data handling, it also integrates into the widely used *tidyverse* packages [56]. The *tidyverse* is a collection of *R* packages developed for almost all major tasks of any data science project. Because all *tidyverse* packages follow the same data philosophy structures, one strength of the *tidyverse* is its high consistency of usage across its packages [56]. *sf* builds on the idea of "simple features," a standard used to describe spatial geometries using points, lines (two connected points) and polygons (several connected points) and attributes connected to these geometries [34].

2.2 Spatial data download

Nowadays, spatial data at many scales is available from an abundance of online-accessible sources. A lot of this data are publicly available, either as a direct download or through an API connection, and several packages can use this to download the spatial data directly into an *R* session. Since publicly available data is becoming more prominent, so are *R* packages to access them. Packages include *rnaturalearth* [57] to access the Natural Earth database to download region and country data, the *elevatr* package to access raster elevation data [58], the *rgbif* package to access the Global Biodiversity Information Facility (GBIF) portal [59], the *BIEN* package [60] to access the Botanical Information and Ecology Network Database, the *marmap* to download bathymetry data from the ETOPO1 database [61], or the *FedData* package [62] to access the National Land Cover Database (NLCD) data for the USA. Furthermore, the *getlandsat* package [63] allows users to download Landsat 8 satellite data, the *MODIS* package [64] to download MODIS products, and *sen2r* [65] to download Sentinel-2 optical images. Also, the `getData()` function from the *raster* package allows users to download climatic and bioclimatic data from WorldClim v1.4. Additionally, the *rgee* package [66] gives access to an extensive catalog of data from Google Earth Engine, including climate data, land cover maps, and satellite imagery.

2.3 Spatial data processing

Coordinate references systems (CRS) describe how spatial data is projected from the earth's three-dimensional surface to a two-dimensional surface as required for spatial analysis or creating maps [29,34]. This is also referred to as the spatial projection and is often the first barrier in spatial data analysis. It is not only required to have all of the used data in the same projection, but also to select a proper CRS. This is of importance because the projection into a two-dimensional surface unavoidable leads to distortion, and different CRS are optimized for different properties, regions of the world, and scales [54, 29]. Coordinates in spatial data represent one of many coordinate reference systems. Two main groups of CRS, namely geographical and projected, exist, with each having many members. Using geographical CRS, positions are specified by latitude and longitude coordinates in degrees. However, most landscape ecology studies should utilize projected CRSs, which use some measurement units (e.g., meters). The selection of projected CRS should be based on the property of spatial data that needs to be kept intact (e.g., no distortion of areas, shapes, distances, or angles) and be appropriate for a given study area. A common way to refer to different CRS is to used codes developed by the European Petrol Survey Group (EPSG). Tools to find an appropriate CRS for a certain region can be found at `https://spatialreference.org`, `https://epsg.org`, or `http://epsg.io`. All packages from Section 2.1 have interfaces for coordinates transformations, allowing unification of spatial projections when the used data have different CRS.

Another common spatial data processing task is required when the available data extends over a larger area than the study region. In this case, the pre-processing of spatial data should include vector clipping or raster cropping. Related to that, masking certain areas of the study region using spatial filters (e.g. water bodies, urban areas) can be required. Packages from Section 2.1 also allow for these operations. Additionally, they offer many other operations, such as merging or joining spatial data, extracting values from one dataset into another, raster resolution changes, or vector data simplifications. A comprehensive collection of methods to aggregate raster values to a coarser resolution can also be found in the *grainchanger* package [67]. Furthermore, *landscapetools* is a collection of various utility functions for the raster data model [68].

Finally, there are a number of tools for landscape ecology implemented in GIS software, such as `r.li` or `r.pi` for GRASS GIS [69,70,38], terrain analysis methods in SAGA GIS [71], or morphological operations for Google Earth Engine. It is possible to control several GIS software directly from *R* using dedicated packages, such as *rgrass7* [72] for GRASS GIS, *RSAGA* [73] for SAGA GIS, and *rgee* [66] for Google Earth Engine. By being able to access these GIS software directly from within *R*, these packages can allow to create easily reproducibale and sharable *R* scripts, even if functionality is currently only available in the corresponding GIS software.

2.4 Creating maps

Creating maps is essential when working with spatial data. Maps play an important role in checking the spatial and value-related quality of data, data exploration, and finally communicating results. *R* allows two major types of maps. Firstly, static maps in which the developer has full control over the presentation of the map and secondly, interactive maps in which the user has the possibility to modify the map by e.g. changing the displayed values. All packages listed in Section 2.1 have build-in methods for plotting spatial data using the generic `plot()` function (Fig. 2a). However, the generic functions are focused on quick visual inspection of the data (Fig. 2a), rather than the creating complete maps as they do not directly support additional map elements (e.g., scale bar, north arrow) nor multiples maps.

The popular plotting package *ggplot2* (Fig. 2b) can also visualize spatial data and is build on a layered grammar of graphics, which allows to create maps by combining individual graphical elements (e.g., raster and vector elements) [74]. Additionally, there is an extension especially designed to plot spatial data named *ggspatial*, which provides additional map elements [75]. For more information about *ggplot2* in general, see [74]. The *tmap* package provides a provides a coherent plotting system intended for drawing maps (Fig. 2c) [76]. This package operates in two modes, static and interactive, which means that the same code can be used to create static or interactive maps. Quick interactive visualization of spatial data can be done with the *mapview* package[77]. Both, *tmap* and *mapview* build upon the *leaflet* package and leaflet javascript library [78]. Static thematic maps, including proportional symbols, choropleth, or typology maps, can be created with the *cartography* package [79]. Further plotting methods for raster objects can be found in the *rasterVis* package [80]. A slightly different approach to visualizing spatial data is adapted by the *rayshader* package [81] that creates topographic 2D and 3D maps.

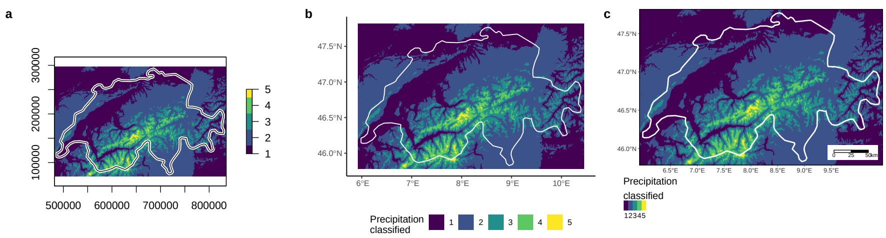

Fig. 2: Comparison of different options to create maps of the total annual precipitation in Switzerland using a) base plot, b) *ggplot2* package, and c) *tmap* package. All three approaches result in similar-looking outputs, but their syntax and capabilities differ. All maps show the total annual precipitation of Switzerland. Data were downloaded with the *raster* package (precipitation data) and *rnaturalearth* package (country borders) package. The code to create the maps can be found in the Appendix.

2.5 Ecological analysis

Quantify landscape characteristics One of the most fundamental steps of landscape ecology analyses is to describe and quantify landscape characteristics [7,82]. For discrete land cover classes, the composition (number and abundance) and configuration (spatial arrangement) of the landscape are often described using landscape metrics [83,84,85,86]. These metrics allow the comparison of different landscapes, quantification of temporal and spatial landscape changes and investigation of interactions between landscape characteristics and ecological processes [84].

The introduction of the *FRAGSTATS* in 1995 heavily facilitated the use of landscape metrics software [87,88,86] and the *landscapemetrics* package [89] allows to calculate the most widely used landscape metrics in within the *R* environment.

More recently, surface metrics were suggested as an alternative to landscape metrics for continuous raster data [90]. The *geodiv* package [91] allows calculation of gradient surface metrics to facilitate continuous analysis of landscape features. Additionally, the *belg* package allows calculation of the Boltzmann entropy of a landscape gradient [92].

Most landscape metrics are represented by a single number depicting specific characteristics of a local landscape. Another possibility is to derive spatial signatures - a multi-value representation of landscape composition and configuration, such as a co-occurrence histogram [93]. Spatial signatures calculated for many landscapes can be compared using one of a set of existing distance measures (e.g. Euclidian, Manhattan, Mahlanobis). This enables several types of spatial analysis on categorical raster data, such as searching for similar landscapes, detecting changes between landscape patterns, and spatial clustering of landscapes based on their composition and configuration. All of the spatial signatures methods mentioned above are implemented in the *motif* package [93].

Spatial statistics Spatial statistics are complimentary to landscape metrics, and can be used to analyze patterns in continuous data (e.g., normalized difference vegetation index, disturbance intensity, topography). In landscape ecology, spatial statistics has three key uses: i) detecting and correcting for spatial autocorrelation; ii) quantifying and comparing landscape patterns; iii) interpolating data.

Point pattern analysis uses event-level data, such as locations of individuals, and links the spatial pattern to the ecological process. The *spatstat* package [94] contains functionality for point pattern analysis, including exploratory analysis; simulation of point process models; and modeling fitting, inference, and diagnostics. A comprehensive textbook covering both theoretical background as well as applied examples can be found here [95].

Distance-based methods allow to detect and correct for spatial autocorrelation in data. It is key to do so as landscape data are highly spatially autocorrelated, and this non-independence can affect inferences from statistical modeling. The *spdep* package [54] has methods for quantifying multiple metrics of spatial autocorrelation and correcting these in a spatial autoregressive model. The *rinla* [96] (`https://www.r-inla.org`) and *inlabru* [97] packages also provide functionality for modeling of spatially structured data.

Finally, the spatial structure of continuous landscapes can be quantified and compared with geostatistical tools, such as variograms and correlograms. *R* packages *geoR* [98] and *gstat* [99] provide functionality for this type of analysis, as well as interpolation methods, known as (co-)kriging. Geostatistics also allows for spatial data simulations.

Species distribution modeling Species distribution modeling (SDM) examines how landscape patterns (e.g., habitat suitability or resources availability) influence and determine the patterns of species' distributions, mainly to infer ecological processes and predict future species' distributions [100]. Originated in the 1970s, SDM has experienced numerous methodological advancement, and a numerous body of literature exists today [101,102]. Additionally, textbooks introducing basic concepts of SDM in *R* exists [103,33].

Because the used modeling approaches are diverse [104,105,33], there is also a large number of *R* packages used for SDMs. Popular approaches and packages include generalized linear models using, e.g., the *stats* [24] package; generalized additive models using, e.g., the *mgcv* [106] or *lme4* [107] package; classification and regression trees (CART) using, e.g., the *rpart* [108], *randomForest* [109] or *ranger* [110] package or multivariate data analysis using , e.g., the *ade4* [111] or *vegan* [112] package. Also, packages specifically designed for SDM exist, including the *dismo* [113], *sdm* [114], *ecospat* [115], *biomod2* [116], *PresenceAbsence* [117], or *zoon* [118] packages. Additionally, packages such as *ENMeval* [119] provide functionality for model tuning and evaluation.

Related to SDMs, there is a growing number of *R* packages to analyze data from tracked animals, to study their movement characteristics, space use, and interaction with other animals and the environment. These analyses often use results of landscape ecological analyses as predictor variables to explain variation in space use [120], behavioral states [121], or habitat selection [122]. Widely used *R* packages include *ctmm* [123] and *adehabitatHR* [124] for home-range estimation, *moveHMM* [125] for the classification of behavioral states, and *amt* [126] for habitat selection. A recent and very comprehensive overview of *R* packages for the analysis of animal movement data is given by [127].

Connectivity Connectivity is one of the core elements of landscape structure [128] and thus one of the core concepts of landscape ecology [5]. Landscape connectivity describes how landscape characteristics facilitate or hinder the movement of species [129] or other aspects of mobility, such as dispersal, gene or nutrient flow [5]. While structural connectivity focuses only on landscape characteristics (e.g., movement corridors, barriers), functional connectivity also includes behavior characteristics of the species such as habitat associations and dispersal distances [129, 5]. Given its broad concept, many different measures of connectivity exist [130]. At the patch level, structural connectivity can be measured using nearest-neighbor distances or characterizations of the patch neighborhood (e.g., amount of suitable habitat) [130, 5]. Such measures are provided within the *landscapemetrics* package (see 2.5). Furthermore, the *lconnect* package [131] and *Makurhini* package [132] provide several landscape connectivity metrics. Another way to describe connectivity is based on graph theory with the advantage that functional connectivity can also be included [130]. In graph theory [133], landscapes are described by nodes (i.e., habitat patches) connected by and functional connections called links (or edges) [133]. The *grainscape* package [134] provides a tool to model connectivity based on spatially explicit networks. More generally, the *igraph* package [135] provides functionality for graph theoretic analyses. Resistance surfaces and least-cost paths are other tools to model functional connectivity which include attributes of the matrix. The resistance surface describes the effects of facilitating or hindering the landscape's characteristics for an organism moving within it [136]. Least-cost paths can be calculated using the *gdistance* package [137]. Absorbing Markov chains quantify landscape connectivity as the combination of movement and mortality based on the landscape characteristics [138], and is provided by the recently published *samc* package [139].

Landscape genetics Landscape genetics investigates how characteristics of landscapes interact with gene flow, genetic drift, and selection [140]. Such insights improve our understanding of metapopulation dynamics, speciation, species' distributions, and conservation [141]. By explicitly including landscape characteristics, landscape genetics provides a more detailed analysis than more abstract concepts (e.g., metapopulation genetics) [142]. As a result of its interdisciplinarity, landscape genetics draws together methods from multiple fields, including landscape ecology, spatial statistics, geography, and population genetics [141].

Since describing connectivity between two locations is one of the fundamental steps of landscape genetics, all packages useful for connectivity (see 2.5) are also important for landscape genetics. Further functionality for landscape genetics such as quantifying and analysing population genetic structure, and hierarchical decomposition analysis can be found in the *graphs4lg* [143], *PopGenReport* [144,145], *HierDpart* packages [146], or *GeNetIt* [147].

Neutral landscape models Neutral landscape models are used to create structured landscapes in the absence of specific ecological and landscape processes as null models against which hypotheses including specific ecological and landscape processes can be tested statistically [148,149]. Because neutral landscape models are not based on ecological and landscape processes, many different generic algorithms to create landscapes can be found across a couple *R* packages. A comprehensive collection of algorithms to simulate neutral landscape models specifically designed for landscape ecology can be found in the *NLMR* package [68]. Furthermore, the *RandomFields* package [150] allows to simulate Gaussian fields, which could be used as neutral landscape models.

commonly used *R* packages for spatial data and landscape ecology. Packages are sorted by their major application task. The table
s specifically desinged for spatial data or landscape ecology.

Task	*R* package	Describtion	Reference
Spatial data	raster	Raster data handling and analysis	[47]
	terra	Raster (and some vector) data handling and analysis	[48]
	stars	Spatiotemporal raster data handling and analysis	[49]
	fasterize	Polygon to raster conversion	[50]
	rasterDT	Faster alternatives for some raster functions	[51]
	exactextractr	Summarize raster values over polygonal areas	[52]
	sp	Vector data handling and analysis	[53, 54]
	sf	Vector data handling and analysis	[55]
Spatial data download	rnaturalearth	Download region and country data	[57]
	elevatr	Download elevation data	[58]
	rgbif	Download biodiversity data	[59]
	BIEN	Download plant diversity, function and distribution data	[60]
	marmap	Download and manipulate bathymetric data	[61]
	FedData	Download geospatial data from US federal sources	[62]
	getlandsat	Download satellite data from Landsat 8	[63]
	MODIS	Download satellite data from MODIS	[64]
	sen2r	Download satellite data from Sentinel	[65]
Bridge stuff	rgrass7	Interface between GRASS7 and R	[72]
	RSAGA	Interface between SAGA and R	[73]
	rgee	Download data from Google Earth Engine	[66]
Creating maps	rasterVis	Vizualuzation of raster data	[80]
	ggspatial	Spatial extension for ggplot2	[75]
	cartography	Create cartographic maps	[79]
	tmap	Create thematic maps	[76]
	mapview	Interactive viewing of spatial data	[77]
	leaflet	Create interactive web maps	[78]
	rayshader	Create 2D and 3D data visualizations	[81]
Quantifying landscape characteristics	landscapemetrics	Quantify categorical landscape patterns	[89]
	belg	Calculate the Boltzmann entropy	[92]
	motif	Pattern-based spatial analysis	[93]
	geodiv	Quantify continuous landscape patterns	[91]
Spatial statistics	spatstat	Point pattern analysis	[94]
	spdep	Quantify and correct for spatial autocorrelation	[54]
	rinla	Fitting Bayesian spatio-temporal models using INLA	[96]
	inlabru	Fitting Bayesian spatio-temporal models using INLA	[97]
	geoR	Variograms, correlograms and (co-)kriging	[98]
	gstat	Variograms, correlograms and (co-)kriging	[99]
Species distribution modeling	dismo	Methods for species distribution modeling	[113]
	sdm	Species distribution models using individual and community-based approaches	[114]
	ecospat	Species distribution, niche quantification and community assembly	[115]
	biomod2	Species distribution modeling, ensemble of models and ensemble forecasting	[116]
	PresenceAbsence	Evaluating of presence-absence models	[117]
	zoon	Reproducible and remixable species distribution modelling	[118]
	ENMeval	Model tuning and evaluation	[119]
	adehabitatHR, adehabitatHS	Home range and habitat selection modelling	[124]
	amt	Manage and analyze animal movement data	[126]
	ctmm	Fit continuous time movement models	[123]
	moveHMM	Fit hidden Markov models to movement data	[125]
Connectivity	lconnect	Calculate landscape connectivity metrics	[131]
	Makurhini	Calculate fragmentation and landscape connectivity indices	[132]
	grainscape	Calculate minimum planar graph and grains of connectivity models	[134]
	gdistance	Distances and routes on geographical grids	[137]
	samc	Functions for working with absorbing Markov chains	[139]
Landscape genetics	graph4lg	Build graphs for landscape genetics analysis	[143]
	PopGenReport	Framework to analyse population genetic data	[144, 145]
	HierDpart	Calculating and decomposing hierarchical diversity metrics	[146]
	GeNetIt	Spatial graph-theoretic genetic gravity models	[147]
various	NLMR	Simulate neutral landscape models	[68]
	RandomFields	Simulation and analysis of random fields	[150]
	landscapetools	Utility functions for raster data	[68]
	grainchanger	Data aggregation methods for raster data	[67]

3 Survey of *R* usage by landscape ecology community

To better understand how the landscape ecology community uses *R*, we conducted a short survey using mailing lists and social media to reach the community. Thus, the survey was not necessarily representative for all skill levels of *R* users and results are most likely biased towards more advanced users. Also, the survey did not include any personal questions, such as age or country of residence, which might have an effect on the representation of the survey.. All raw data and scripts to analyze the data can be found at `https://github.com/r-spatialecology/Hesselbarth_et_al_CLER`.

In total, the survey was answered by 109 participants, of which the majority were either "PhD students" (33%), followed by "Post-Docs" (26.6%) and "Professors" (14.7%). Other, less frequent answers were "Data scientists", "None of the above", "Government employees", "Master's degree student" and "Bachelor's degree student" (in decreasing order).

Most people use *R* either "daily" (53.2%) or a "few times a week" (36.7%). Almost half of all participants described themselves as "advanced" users (46.8%), while 40.4% described themselves as "intermediate" users. Related to this, about half of the participants either implemented their own package (21.1%) or plan to do so in the future (22%) and most of these packages are hosted on *GitHub* and/or *CRAN*.

We asked the participants to select which terms describe their research topics the best, and options that were selected by more than 10% of participants included "biodiversity," followed by "land use management," "landscape connectivity," and "nature conservation" (Fig. 3a)).

Next, we were interested in the most important tasks to the workflow of the participants. Not surprisingly, "(pre-)processing of data", "spatial statistics", and "creating maps" were the most selected options (Fig. reffig:fig-surveyb). The available options seemed to describe the most important task to the workflow quite well since only very few participants selected the "others" option (all options with less than five total answers were classified as "others").

More people use the raster data model (72.5%) in comparison to the vector data model (27.5%). This was also represented in the most used *R* packages (Fig. 3c). When asked for the three most used packages, participants of the survey listed 93 packages in total. The *raster* package was mentioned the most, followed by the *sf* package. Both packages are designed for basic and advanced data handling and processing of raster and vector data, respectively, representing the results of Fig. 3c. Nevertheless, the large availability and usage of different *R* packages across the community can be seen in the large "others" option (packages mentioned by less than 5 participants; 35.87%).

Lastly, when asked how useful *R* is currently for landscape ecology, the vast majority of participants answered with either "very useful" or "useful" (summarized 90.83%) and only very few participants evaluated *R* as "intermediate," "not useful" or "not useful at all" (summarized 9.17%; Fig. 3d)).

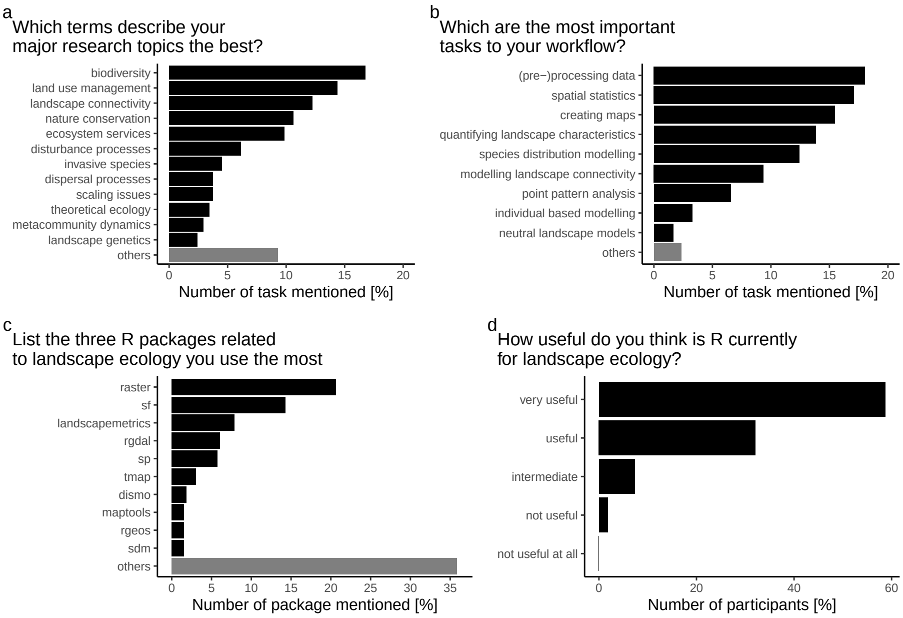

Fig. 3: Results of the online survey about open-source software tools in *R* for landscape ecology. Results include a) which terms describe major research topics the best, b) the most important workflow task, c) the most used *R* packages and d) the overall usefulness or *R* for landscape ecology. The 'others' category includes all answers with less than five total mentions.

The survey also included a section in which participants could list methods and tools currently missing in *R* and answers to this question were very diverse.

Overall, 23.9% of the participants reported that currently no packages and functionality are missing for them or they lack the overview to answer the question. There were three most common topics across the answers of the participants. Firstly, many participants (12.8%) wished for a better computational performance of *R* in terms of speed and required RAM, especially for larger data. Secondly, participants are missing specific approaches to quantify landscape characteristics (such as surface metrics), or are wishing for an improvement of currently available approaches to quantify landscape characteristics (9.2%). Thirdly, many participants (8.3%) are currently missing advanced and easy-to-apply methods to create high-quality maps or other visualization-related functionality.

4 Conclusions

Since its first introduction in 1995, *R* has come a long way from an exclusively statistical programming language to a powerful landscape ecology tool. Today, many *R* packages, mainly developed by the community itself, provide a vast collection of functions and algorithms aimed at spatial data handling and analysis. The highly dynamic development of *R* packages for landscape ecology also shows the strength of open-source software with its high innovation, transparency, reliability, and longevity. However, since landscape ecology constantly develops and improves, consequently also the *R* programming language and its packages are under constant change to adapt to these new developments.

A comprehensive collection of *R* software packages exists to handle the most common tasks of landscape ecology. Because it is possible to import, modify, analyze, and visualize spatial data all in the same scripted programming environment, *R* allows for transparent and reproducible workflows. This script-based characteristic of the *R* programming language allows to easily share and reproduce analysis, as demonstrated by the R script in the appendix, which is a big advantage over point-and-click software interfaces. This also allows users to easily interchange, modify, or adapt methods from other related and unrelated fields.

The survey revealed that the landscape ecology community is overall satisfied with the capabilities of the *R* programming language for landscape ecology. Furthermore, the survey showed the that many members of the landscape ecology community actively develop *R* packages themselves, demonstrating that tools are constantly added and updated.

Landscape ecology combines many different research topics and methodological approaches and most of them heavily rely on spatial data. While the *R* programming language is generally well suited to handle, analyze and visualize spatial data, the increasing availability of large data sets also leads to the challenges of increased computational demands, in terms of computational time as well as memory requirements, the *R* programming language has to face. Some packages discussed herein, such as *raster* and *terra*, already provide solutions by processing data in chunks small enough to be stored in RAM memory. Furthermore, also parallel processing, and even including the use of high performance clusters, is provided by several *R* packages. While this is outside the scope of this manuscript, further resources about parallel processing in *R* can be found here [151,152,153]. Furthermore, as the individual fields collected under the umbrella of landscape ecology develop, so need the *R* packages related to those fields. But as the development of *R* packages over the past years clearly demonstrated, the landscape ecology community is ready to face these challenges.

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Conflict of interest MHKH and JN are authors of the *landscapemetrics* and *landscapetools* package. JN is author of *belg* and *motif* package. JS is author of the *amt* package. LJG is author of the *grainchanger* package.

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Availability of data and material (data transparency) All raw data and scripts to analyze the data can be found at `https://github.com/r-spatialecology/Hesselbarth_et_al_CLER`.

Author contributions MHKH and JN designed the survey form and analyzed the responses of the participants. MHKH and JN drafted the manuscript with contributions of JS and LJG and all authors contributed critically to the manuscript and gave final approval for publication. We used the 'sequence–determines–credit' approach (SDC) for the sequence of authors.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

4.1.1 Important references

••[35]: Overview of general developments of *R* to analyze spatial data.
••[29]: Textbook about spatial data handling with applied examples in the *R* programming language.
•[27]: Review of the *R* programming language in ecology.
•[86]: Review of quantifying landscape spatial pattern.

References

1. E. Ellis, Anthropogenic transformation of the terrestrial biosphere **369**(1938), 1010. DOI 10.1098/rsta.2010.0331
2. E. Ellis, Ecology in an anthropogenic biosphere **85**(3), 287. DOI 10.1890/14-2274.1
3. P. Crutzen, Geology of mankind **415**(6867), 23. DOI 10.1038/415023a
4. P. Vitousek, Human domination of earth's ecosystems **277**(5325), 494. DOI 10.1126/science.277.5325.494
5. K. With, *Essentials of landscape ecology*, 1st edn. (Oxford University Press)
6. M. Turner, Landscape ecology: The effect of pattern on process **20**(1), 171. DOI 10.1146/annurev.es.20.110189.001131
7. M. Turner, Landscape ecology: What is the state of the science? **36**(1), 319. DOI 10.1146/annurev.ecolsys.36.102003.152614
8. P. Risser, J. Karr, R. Forman, Landscape ecology: Directions and approaches **2**, 7
9. R. Forman, M. Godron, *Landscape ecology* (Wiley)
10. R. Forman, *Land mosaics: The ecology of landscapes and regions* (Cambridge University Press)
11. J. Wiens, in *Mosaic landscapes and ecological processes*, ed. by L. Hansson, L. Fahrig, G. Merriam (Chapman and Hall), pp. 1–26

12. J. Wiens, Spatial scaling in ecology **3**(4), 385. DOI 10.2307/2389612
13. S. Levin, The problem of pattern and scale in ecology **73**(6), 1943. DOI 10.2307/1941447
14. D. Jelinski, J. Wu, The modifiable areal unit problem and implications for landscape ecology **11**(3), 129. DOI 10.1007/BF02447512
15. P. Šímová, K. Gdulová, Landscape indices behavior: A review of scale effects **34**, 385. DOI 10.1016/j.apgeog.2012.01.003
16. L. Estes, P. Elsen, T. Treuer, L. Ahmed, K. Caylor, J. Chang, J. Choi, E. Ellis, The spatial and temporal domains of modern ecology **2**(5), 819. DOI 10.1038/s41559-018-0524-4
17. G. Wilson, D. Aruliah, C. Brown, N. Chue Hong, M. Davis, R. Guy, S. Haddock, K. Huff, I. Mitchell, M. Plumbley, B. Waugh, E. White, P. Wilson, Best practices for scientific computing **12**(1), e1001745. DOI 10.1371/journal.pbio.1001745
18. A. Prlić, J. Procter, Ten simple rules for the open development of scientific software **8**(12), e1002802. DOI 10.1371/journal.pcbi.1002802
19. A. St. Laurent, *Understanding open source and free software licensing* (O'Reilly)
20. G. von Krogh, E. von Hippel, The promise of research on open source software **52**(7), 975. DOI 10.1287/mnsc.1060.0560
21. S. Powers, S. Hampton, Open science, reproducibility, and transparency in ecology **29**(1), e01822. DOI 10.1002/eap.1822
22. S. Steiniger, E. Bocher, An overview on current free and open source desktop gis developments **23**(10), 1345. DOI 10.1080/13658810802634956
23. S. Steiniger, G. Hay, Free and open source geographic information tools for landscape ecology **4**(4), 183. DOI 10.1016/j.ecoinf.2009.07.004
24. R Core Team. R: A language and environment for statistical computing. URL `www.r-project.org`
25. H. Wickham, *R packages: Organize, test, document, and share your code* (O'Reilly)
26. D. Smith. Over 16 years of r project history. URL `https://blog.revolutionanalytics.com/2016/03/16-years-of-r-history.html`
27. J. Lai, C. Lortie, R. Muenchen, J. Yang, K. Ma, Evaluating the popularity of r in ecology **10**(1). DOI 10.1002/ecs2.2567
28. R. Bivand, Implementing spatial data analysis software tools in r **38**(1), 23. DOI 10.1111/j.0016-7363.2005.00672.x
29. R. Lovelace, J. Nowosad, J. Münchow, *Geocomputation with R*, 1st edn. (Chapman and Hall/CRC Press)
30. R. Bivand. Analysis of spatial data. URL `https://CRAN.R-project.org/view=Spatial`
31. E. Pebesma. Handling and analyzing spatio-temporal data. URL `https://CRAN.R-project.org/view=SpatioTemporal`
32. M. Wegmann, B. Leutner, S. Dech (eds.), *Remote sensing and GIS for ecologists: Using open source software*. Data in the wild (Pelagic Publishing)
33. R. Fletcher, M.J. Fortin, *Spatial ecology and conservation modeling. Applications with R* (Springer International Publishing)
34. E. Pebesma, R. Bivand, *Spatial Data Science*. URL `https://www.r-spatial.org/book`
35. R. Bivand, Progress in the r ecosystem for representing and handling spatial data DOI 10.1007/s10109-020-00336-0
36. QGIS Development Team. Qgis. URL `www.qgis.org`
37. GRASS Development Team. Geographic resources analysis support system (grass). URL `http://grass.osgeo.org`
38. C. Porta, L. Spano, F. Pontedera. r.li - toolset for multiscale analysis of landscape structure <https://grass.osgeo.org/grass74/manuals/r.li.html>. URL `https://grass.osgeo.org/grass74/manuals/r.li.html`
39. A. Jolma, D. Ames, N. Horning, H. Mitasova, M. Neteler, A. Racicot, T. Sutton, Chapter ten: Free and open source geospatial tools for environmental modeling and management **3**, 163. DOI 10.1016/S1574-101X(08)00610-8
40. S. István, Comparison of the most popular open-source gis software in the field of landscape ecology **6**(2), 76
41. J. Hester, G. Csárdi, H. Wickham, W. Chang, M. Morgan, D. Tenenbaum. remotes: R package installation from remote repositories, including 'github'. r package version 2.2.0. <https://CRAN.R-project.org/package=remotes>. URL `https://CRAN.R-project.org/package=remotes`

42. U. Simonsohn, H. Gruson. groundhog: Reproducible scripts via version-specific package loading. r package version 1.1.0. <https://CRAN.R-project.org/package=groundhog>
43. K. Ushey, J. McPherson, J. Cheng, A. Atkins, J. Allaire. packrat: A dependency management system for projects and their r package dependencies. r package version 0.5.0. <https://CRAN.R-project.org/package=packrat>. URL `https://CRAN.R-project.org/package=packrat`
44. K. Ushey. renv: Project environments. r package version 0.12.3. <https://CRAN.R-project.org/package=renv>. URL `https://CRAN.R-project.org/package=renv`
45. GDAL/OGR contributors, *GDAL/OGR geospatial data abstraction software library*. Open Source Geospatial Foundation. URL `https://gdal.org`
46. PROJ contributors, *PROJ coordinate transformation software library*. Open Source Geospatial Foundation. URL `https://proj.org/`
47. R. Hijmans. raster: Geographic data analysis and modeling. r package version 2.9-5. <https://cran.r-project.org/package=raster>. URL `https://cran.r-project.org/package=raster`
48. R. Hijmans. terra: Spatial data analysis. r package version 1.0-10. <https://CRAN.R-project.org/package=terra>. URL `https://CRAN.R-project.org/package=terra`
49. E.J. Pebesma. stars: Scalable, spatiotemporal tidy arrays for r. r package version 0.3-1. <https://cran.r-project.org/package=stars>. URL `https://cran.r-project.org/package=stars`
50. N. Ross. fasterize: Fast polygon to raster conversion. r package version 1.0.3 <https://CRAN.R-project.org/package=fasterize>. URL `https://CRAN.R-project.org/package=fasterize`
51. J. O'Brien. rasterdt: Fast raster summary and manipulation. r package version 0.3.1 <https://CRAN.R-project.org/package=rasterDT>. URL `https://CRAN.R-project.org/package=rasterDT`
52. D. Baston. exactextractr: Fast extraction from raster datasets using polygons. r package version 0.5.1. <https://CRAN.R-project.org/package=exactextractr>. URL `https://CRAN.R-project.org/package=exactextractr`
53. E.J. Pebesma, R.S. Bivand, Classes and methods for spatial data in r. **5**(2), 9
54. R. Bivand, E. Pebesma, V. Gómez-Rubio, *Applied spatial data analysis with R*, 2nd edn. Use R! (Springer)
55. E.J. Pebesma. sf: Simple features for r. <https://cran.r-project.org/package=sf>. URL `https://cran.r-project.org/package=sf`
56. H. Wickham, M. Averick, J. Bryan, W. Chang, L. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, M. Kuhn, T. Pedersen, E. Miller, S. Bache, K. Müller, J. Ooms, D. Robinson, D. Seidel, V. Spinu, K. Takahashi, D. Vaughan, C. Wilke, K. Woo, H. Yutani, Welcome to the tidyverse **4**(43), 1686. DOI 10.21105/joss.01686
57. A. South. rnaturalearth: World map data from natural earth. r package version 0.1.0 <https://CRAN.R-project.org/package=rnaturalearth>. URL `https://CRAN.R-project.org/package=rnaturalearth`
58. J. Hollister, T. Shah, A. Robitaille, M. Beck, M. Johnson. elevatr: Access elevation data from various apis. r package version 0.3.1. <https://CRAN.R-project.org/package=elevatr/>. URL `https://github.com/usepa/elevatr/`
59. S. Chamberlain, C. Boettiger, R python, and ruby clients for gbif species occurrence data DOI 10.7287/peerj.preprints.3304v1
60. B. Maitner. Bien: Tools for accessing the botanical information and ecology network database. r package version 1.2.4. <https://CRAN.R-project.org/package=BIEN>. URL `https://CRAN.R-project.org/package=BIEN`
61. E. Pante, B. Simon-Bouhet, marmap: A package for importing, plotting and analyzing bathymetric and topographic data in r **8**(9), e73051. DOI 10.1371/journal.pone.0073051
62. R. Bocinsky. Feddata: Functions to automate downloading geospatial data available from several federated data sources. r package version 2.5.7.

<https://CRAN.R-project.org/package=FedData>. URL https://CRAN.R-project.org/package=FedData

63. S. Chamberlain. getlandsat: Get landsat 8 data from amazon public data sets. r package version 0.2.0. <https://CRAN.R-project.org/package=getlandsat>. URL https://CRAN.R-project.org/package=getlandsat
64. M. Mattiuzzi. Modis: Acquisition and processing of modis products. r package version 1.2.3. <https://CRAN.R-project.org/package=MODIS>. URL <https://CRAN.R-project.org/package=MODIS>
65. L. Ranghetti, M. Boschetti, F. Nutini, L. Busetto, “sen2r”: An r toolbox for automatically downloading and preprocessing sentinel-2 satellite data **139**, 104473. DOI 10.1016/j.cageo.2020.104473
66. C. Aybar, Q. Wu, L. Bautista, R. Yali, A. Barja, rgee: An r package for interacting with google earth engine **5**(51), 2272. DOI 10.21105/joss.02272
67. L. Graham, R. Spake, S. Gillings, K. Watts, F. Eigenbrod, Incorporating fine-scale environmental heterogeneity into broad-extent models **10**(6), 767. DOI 10.1111/2041-210X.13177
68. M. Sciaini, M. Fritsch, C. Scherer, C. Simpkins, Nlmr and landscapetools: An integrated environment for simulating and modifying neutral landscape models in r **9**(11), 2240. DOI 10.1111/2041-210X.13076
69. M. Wegmann, B. Leutner, M. Metz, M. Neteler, S. Dech, D. Rocchini, r.pi: A grass gis package for semi-automatic spatial pattern analysis of remotely sensed land cover data **9**(1), 191. DOI 10.1111/2041-210X.12827
70. M. Neteler, M. Bowman, M. Landa, M. Metz, Grass gis: A multi-purpose open source gis **31**, 124. DOI 10.1016/j.envsoft.2011.11.014
71. O. Conrad, B. Bechtel, M. Bock, H. Dietrich, E. Fischer, L. Gerlitz, J. Wehberg, V. Wichmann, J. Böhner, System for automated geoscientific analyses (saga) v2.1.4 **8**(7), 1991. DOI 10.5194/gmd-8-1991-2015
72. R. Bivand. rgrass7: Interface between grass 7 geographical information system and r. r package version 0.2-5. <https://CRAN.R-project.org/package=rgrass7>. URL https://CRAN.R-project.org/package=rgrass7
73. A. Brenning, D. Bangs, M. Becker. Rsaga: Saga geoprocessing and terrain analysis. r package version 1.3.0. <https://CRAN.R-project.org/package=RSAGA>. URL https://CRAN.R-project.org/package=RSAGA
74. H. Wickham, *ggplot2: Elegant graphics for data analysis* (Springer). URL http://ggplot2.org
75. D. Dunnington. ggspatial: Spatial data framework for ggplot2. r package version 1.1.4 <https://CRAN.R-project.org/package=ggspatial>. URL https://CRAN.R-project.org/package=ggspatial
76. M. Tennekes, tmap: Thematic maps in r **84**(6). DOI 10.18637/jss.v084.i06
77. T. Appelhans, F. Detsch, C. Reudenbach, S. Woellauer. mapview: Interactive viewing of spatial data in r. r package version 2.9.0 <https://CRAN.R-project.org/package=mapview>. URL https://CRAN.R-project.org/package=mapview
78. J. Cheng, B. Karambelkar, Y. Xie. leaflet: Create interactive web maps with the javascript 'leaflet' library. r package version 2.0.4.1. <https://CRAN.R-project.org/package=leaflet>. URL https://CRAN.R-project.org/package=leaflet
79. T. Giraud, N. Lambert, cartography: Create and integrate maps in your r workflow **1**(4), 54. DOI 10.21105/joss.00054
80. O. Lamigueiro, R. Hijmans. rastervis: Visualization methods for raster data. r package version 0.49. <https://CRAN.R-project.org/package=rasterVis>. URL https://CRAN.R-project.org/package=rasterVis
81. T. Morgen-Wall. rayshader: Create maps and visualize data in 2d and 3d. r package version 0.19.2. <https://CRAN.R-project.org/package=rayshader>. URL https://CRAN.R-project.org/package=rayshader
82. A. Lausch, T. Blaschke, D. Haase, F. Herzog, R. Syrbe, L. Tischendorf, U. Walz, Understanding and quantifying landscape structure - a review on relevant process characteristics, data models and landscape metrics **295**, 31. DOI 10.1016/j.ecolmodel.2014.08.018

83. E. Gustafson, Quantifying landscape spatial pattern: What is the state of the art? **1**, 143. DOI 10.1007/s100219900011
84. E. Uuemaa, M. Antrop, R. Marja, J. Roosaare, U. Mander, Landscape metrics and indices: An overview of their use in landscape research **3**, 1. DOI 10.12942/lrlr-2009-1
85. E. Uuemaa, U. Mander, R. Marja, Trends in the use of landscape spatial metrics as landscape indicators: A review **28**, 100. DOI 10.1016/j.ecolind.2012.07.018
86. E. Gustafson, How has the state-of-the-art for quantification of landscape pattern advanced in the twenty-first century? **34**, 1. DOI 10.1007/s10980-018-0709-x
87. K. McGarigal, S. Cushman, E. Ene. Fragstats v4: Spatial pattern analysis program for categorical and continuous maps. computer software program produced by the authors at the university of massachusetts, amherst. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>. URL `http://www.umass.edu/landeco/research/fragstats/fragstats.html`
88. J. Kupfer, Landscape ecology and biogeography: Rethinking landscape metrics in a post-fragstats landscape **36**(3), 400. DOI 10.1177/0309133312439594
89. M. Hesselbarth, M. Sciaini, K. With, K. Wiegand, J. Nowosad, landscapemetrics: An open-source r tool to calculate landscape metrics **42**(10), 1648. DOI 10.1111/ecog.04617
90. K. McGarigal, S. Tagil, S. Cushman, Surface metrics: An alternative to patch metrics for the quantification of landscape structure **24**(3), 433. DOI 10.1007/s10980-009-9327-y
91. A. Smith, P. Zarnetske, K. Dahlin, A. Wilson, A. Latimer. geodiv: Methods for calculating gradient surface metrics. r package version 0.2.0. <https://CRAN.R-project.org/package=geodiv>. URL `https://CRAN.R-project.org/package=geodiv`
92. J. Nowosad, P. Gao, belg: A tool for calculating boltzmann entropy of landscape gradients **22**(9), 937. DOI 10.3390/e22090937
93. J. Nowosad, motif: An open-source r tool for pattern-based spatial analysis **36**(1), 29. DOI 10.1007/s10980-020-01135-0
94. A. Baddeley, R. Turner, spatstat: An r package for analyzing spatial point patterns **12**(6), 1. DOI 10.18637/jss.v012.i06
95. A. Baddeley, E. Rubak, R. Turner, *Spatial point patterns: Methodology and applications with R* (Chapman and Hall/CRC Press)
96. H. Rue, S. Martino, N. Chopin, Approximate bayesian inference for latent gaussian models by using integrated nested laplace approximations **71**(2), 319. DOI 10.1111/j.1467-9868.2008.00700.x
97. F. Bachl, F. Lindgren, D. Borchers, J. Illian, inlabru: an r package for bayesian spatial modelling from ecological survey data **10**(6), 760. DOI 10.1111/2041-210X.13168
98. P. Diggle, P. Ribeiro, *Model-based geostatistics*. Springer Series in Statistics (Springer New York). DOI 10.1007/978-0-387-48536-2
99. E. Pebesma, Multivariable geostatistics in s: the gstat package **30**(7), 683. DOI 10.1016/j.cageo.2004.03.012
100. Y. Wiersma, F. Huettmann, C. Drew, in *Predictive Species and Habitat Modeling in Landscape Ecology*, ed. by C. Drew, Y. Wiersma, F. Huettmann (Springer New York), pp. 1–6. DOI 10.1007/978-1-4419-7390-0_1
101. N. Zimmermann, T. Edwards, C. Graham, P. Pearman, J.C. Svenning, New trends in species distribution modelling **33**(6), 985. DOI 10.1111/j.1600-0587.2010.06953.x
102. A. Norberg, N. Abrego, F. Blanchet, F. Adler, B. Anderson, J. Anttila, M. Araújo, T. Dallas, D. Dunson, J. Elith, S. Foster, R. Fox, J. Franklin, W. Godsoe, A. Guisan, B. O'Hara, N. Hill, R. Holt, F. Hui, M. Husby, J. Kå lås, A. Lehikoinen, M. Luoto, H. Mod, G. Newell, I. Renner, T. Roslin, J. Soininen, W. Thuiller, J. Vanhatalo, D. Warton, M. White, N. Zimmermann, D. Gravel, O. Ovaskainen, A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels **89**(3). DOI 10.1002/ecm.1370
103. A. Guisan, W. Thuiller, N. Zimmermann, *Habitat Suitability and Distribution Models: With Applications in R*, 1st edn. (Cambridge University Press). DOI 10.1017/9781139028271

104. M. Hooten, in *Predictive Species and Habitat Modeling in Landscape Ecology*, ed. by C. Drew, Y. Wiersma, F. Huettmann (Springer New York), pp. 29–41. DOI 10.1007/978-1-4419-7390-0_3
105. J. Kerr, M. Kulkarni, A. Algar, in *Predictive Species and Habitat Modeling in Landscape Ecology*, ed. by C. Drew, Y. Wiersma, F. Huettmann (Springer New York), pp. 9–28. DOI 10.1007/978-1-4419-7390-0_2
106. S. Wood, *Generalized additive models: An introduction with R*, 2nd edn. (Chapman & Hall/CRC)
107. D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4 **67**(1). DOI 10.18637/jss.v067.i01
108. T. Therneau, B. Atkinson. rpart: Recursive partitioning and regression trees. r package version 4.1-15. <https://CRAN.R-project.org/package=rpart>. URL `https://CRAN.R-project.org/package=rpart`
109. A. Liaw, M. Wiener, Classification and regression by randomforest **2**(3), 18. URL `https://CRAN.R-project.org/doc/Rnews/`
110. M. Wright, A. Ziegler, ranger: A fast implementation of random forests for high dimensional data in c++ and r **77**(1). DOI 10.18637/jss.v077.i01
111. S. Dray, A.B. Dufour, The ade4 package: Implementing the duality diagram for ecologists **22**(4). DOI 10.18637/jss.v022.i04
112. J. Oksanen, F. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. Minchin, R. O'Hara, G. Simpson, P. Solymos, M. Stevens, E. Szoecs, H. Wagner. vegan: Community ecology package. r package version 2.5-6. <https://CRAN.R-project.org/package=vegan>. URL `https://CRAN.R-project.org/package=vegan`
113. R. Hijmans, S. Phillips, J. Leathwick, J. Elith. dismo: Species distribution modeling. r package version 1.1-4. <https://CRAN.R-project.org/package=dismo>. URL `https://CRAN.R-project.org/package=dismo`
114. B. Naimi, M. Araújo, sdm: A reproducible and extensible r platform for species distribution modelling **39**(4), 368. DOI 10.1111/ecog.01881
115. O. Broennimann, V. Di Cola, A. Guisan. ecospat: Spatial ecology miscellaneous methods. r package version 3.1. <https://CRAN.R-project.org/package=ecospat>. URL `https://CRAN.R-project.org/package=ecospat`
116. W. Thuiller, D. Georges, R. Engler, F. Breiner. biomod2: Ensemble platform for species distribution modeling. r package version 3.4.6. <https://CRAN.R-project.org/package=biomod2>. URL `https://CRAN.R-project.org/package=biomod2`
117. E. Freeman, G. Moisen, Presenceabsence: An r package for presence absence analysis **23**(11). DOI 10.18637/jss.v023.i11
118. N. Golding, T. August, T. Lucas, D. Gavaghan, E. Loon, G. McInerny, The zoon package for reproducible and shareable species distribution modelling **9**(2), 260. DOI 10.1111/2041-210X.12858
119. R. Muscarella, P. Galante, M. Soley-Guardia, R. Boria, J. Kass, M. Uriarte, R. Anderson, Enmeval: An r package for conducting spatially independent evaluations and estimating optimal model complexity for MAXENT ecological niche models **5**(11), 1198. DOI 10.1111/2041-210X.12261
120. J. Signer, N. Balkenhol, M. Ditmer, J. Fieberg, Does estimator choice influence our ability to detect changes in home-range size? **3**(1), 16. DOI 10.1186/s40317-015-0051-x
121. R. Langrock, R. King, J. Matthiopoulos, L. Thomas, D. Fortin, J. Morales, Flexible and practical modeling of animal telemetry data: Hidden markov models and extensions **93**(11), 2336. DOI 10.1890/11-2241.1
122. J. Fieberg, J. Signer, B. Smith, T. Avgar. A 'how-to' guide for interpreting parameters in habitat-delection analyses. DOI 10.1101/2020.11.12.379834
123. J. Calabrese, C. Fleming, E. Gurarie, ctmm: An r package for analyzing animal relocation data as a continuous-time stochastic process **7**(9), 1124. DOI 10.1111/2041-210X.12559
124. C. Calenge, The package "adehabitat" for the r software: A tool for the analysis of space and habitat use by animals **197**(3-4), 516. DOI 10.1016/j.ecolmodel.2006.03.017

125. T. Michelot, R. Langrock, T. Patterson, movehmm: An r package for the statistical modelling of animal movement data using hidden markov models **7**(11), 1308. DOI 10.1111/2041-210X.12578
126. J. Signer, J. Fieberg, T. Avgar, Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses **9**(2), 880. DOI 10.1002/ece3.4823
127. R. Joo, M. Boone, T. Clay, S. Patrick, S. Clusella-Trullas, M. Basille, Navigating through the r packages for movement **89**(1), 248. DOI 10.1111/1365-2656.13116
128. P. Taylor, L. Fahrig, K. Henein, G. Merriam, Connectivity is a vital element of landscape structure **68**(3), 571. DOI 10.2307/3544927
129. L. Tischendorf, L. Fahrig, On the usage and measurement of landscape connectivity **90**(1), 7. DOI 10.1034/j.1600-0706.2000.900102.x
130. P. Kindlmann, F. Burel, Connectivity measures: A review pp. s10,980–008–9245–4. DOI 10.1007/s10980-008-9245-4
131. F. Mestre, B. Silva. lconnect: Simple tools to compute landscape connectivity metrics. r package version 0.1.0. <https://CRAN.R-project.org/package=lconnect>. URL `https://CRAN.R-project.org/package=lconnect`
132. O. Godínez-Gómez, C. Correa Ayram. Makurhini: Analyzing landscape connectivity. r package version 2.0.0 <https://github.com/connectscape/Makurhini>. URL `https://github.com/connectscape/Makurhini`
133. A. Laita, J. Kotiaho, M. Mönkkönen, Graph-theoretic connectivity measures: What do they tell us about connectivity? **26**(7), 951. DOI 10.1007/s10980-011-9620-4
134. A. Chubaty, P. Galpern, S. Doctolero, The r toolbox grainscape for modelling and visualizing landscape connectivity using spatially explicit networks **11**(4), 591. DOI 10.1111/2041-210X.13350
135. G. Csardi, T. Nepusz, The igraph software package for complex network research **Complex Systems**, 1695
136. F. Adriaensen, J. Chardon, G. De Blust, E. Swinnen, S. Villalba, H. Gulinck, E. Matthysen, The application of 'least-cost' modelling as a functional landscape model **64**(4), 233. DOI 10.1016/S0169-2046(02)00242-6
137. J. van Etten, R package gdistance: Distances and routes on geographical grids **76**(13). DOI 10.18637/jss.v076.i13
138. R. Fletcher, J. Sefair, C. Wang, C. Poli, T. Smith, E. Bruna, R. Holt, M. Barfield, A. Marx, M. Acevedo, Towards a unified framework for connectivity that disentangles movement and mortality in space and time **22**(10), 1680. DOI 10.1111/ele.13333
139. A. Marx, C. Wang, J. Sefair, M. Acevedo, R. Fletcher, samc: An r package for connectivity modeling with spatial absorbing markov chains **43**(4), 518. DOI 10.1111/ecog.04891
140. S. Manel, M. Schwartz, G. Luikart, P. Taberlet, Landscape genetics: Combining landscape ecology and population genetics **18**(4), 189. DOI 10.1016/S0169-5347(03)00008-9
141. A. Storfer, M. Murphy, J. Evans, C. Goldberg, S. Robinson, S. Spear, R. Dezzani, E. Delmelle, L. Vierling, L. Waits, Putting the 'landscape' in landscape genetics **98**(3), 128. DOI 10.1038/sj.hdy.6800917
142. R. Holderegger, H. Wagner, A brief guide to landscape genetics **21**(6), 793. DOI 10.1007/s10980-005-6058-6
143. P. Savary. graph4lg: Build graphs for landscape genetics analysis. r package version 0.5.0 <https://CRAN.R-project.org/package=graph4lg>. URL `https://CRAN.R-project.org/package=graph4lg`
144. A. Adamack, B. Gruber, Popgenreport: Simplifying basic population genetic analyses in r **5**(4), 384. DOI 10.1111/2041-210X.12158
145. B. Gruber, A. Adamack, landgenreport: A new r function to simplify landscape genetic analysis using resistance surface layers **15**(5), 1172. DOI 10.1111/1755-0998.12381
146. X. Qin. Hierdpart: Partitioning hierarchical diversity and differentiation across metrics and scales, from genes to ecosystems. r package version 0.5.0. <https://CRAN.R-project.org/package=HierDpart>. URL `https://CRAN.R-project.org/package=HierDpart`
147. M. Murphy, R. Dezzani, D.S. Pilliod, A. Storfer, Landscape genetics of high mountain frog metapopulations **19**(17), 3634. DOI 10.1111/j.1365-294X.2010.04723.x

148. R. Gardner, B. Milne, M. Turnei, R. O'Neill, Neutral models for the analysis of broad-scale landscape pattern **1**(1), 19. DOI 10.1007/BF02275262
149. K. With, A. King, The use and misuse of neutral landscape models in ecology **79**(2), 219. DOI 10.2307/3546007
150. M. Schlather, A. Malinowski, P. Menck, M. Oesting, K. Strokorb, Analysis, simulation and prediction of multivariate random fields with package randomfields **63**(8). DOI 10.18637/jss.v063.i08
151. H. Bengtsson, A unifying framework for parallel and distributed processing in r using futures, arXiv:2008.00553 [cs, stat] (2020)
152. M. Schubert, clustermq enables efficient parallelization of genomic analyses, Bioinformatics **35**(21), 4493 (2019). DOI 10.1093/bioinformatics/btz284
153. Q. McCallum, S. Weston, *Parallel R. Data analysis in the distributed world* (O'Reilly, Beijing, 2012)