

## Open-source tools in R for landscape ecology

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## 1 Introduction

### Glossary

CRAN	Comprehensive R Archive Network
CRS	Coordinate references systems
GIS	Geographical information system
NLM	Neutral landscape model
raster	Cell grid based data model
R packages	Software extension to R programming language
SDM	Species distribution modelling
vector	Points and lines based data model

### 1.1 A short introduction to landscape ecology

5 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  
 10 increasingly important [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  
 15 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  
 20 ecological processes 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]. Firstly released in 1995 [25], today the programming language is among the most popular programming languages, especially in ecology [26]. Originally introduced as a statistical programming language, a growing body of packages designed to analyze spatial data subsequently emerged for the *R* programming language [27, 28]. The expanding CRAN Task Views document this: *Analysis of Spatial Data* [29] and *Handling and Analyzing Spatio-Temporal Data* [30] 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 [31, 32, 28, 33]. A recent overview over the progress of *R* to handle spatial data in general can be found in [34].

The growing body of *R* packages related to spatial data processing and analysis results in a high capability of this language for landscape ecology. Even though many other open-source tools [35, 36, 37] and suitable and common programming languages (e.g. Python) for landscape ecology exist, in this review, we focus on software implemented in the *R* programming language. For more general overviews of open-source software for landscape ecology see [38, 22, 23, 39]. Because in addition to handling spatial data, tasks such as statistical modeling, creation of publication-ready figures, and even preparation of complete reports can be done in the same working environment (Fig. 1), the *R* programming language can be a very powerful tool. Thus, in the first part, we present an overview of existing *R* packages for landscape ecology (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, we focus on only the former two in this review. 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 [40]. *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 [40], or integrated unit testing.

The guaranteed technical quality standard on *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 on *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* [20, 19, 22, 18, 21]. CRAN also provides archived versions of outdated or orphaned packages and thus ensuring long term availability of code. Thus, most packages can be found on both platforms, and many developers use *GitHub* for regular development and *CRAN* to publish stable releases of the packages. Furthermore, 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]. For more information about *R* package development in general, see [40].

### 2.1 Spatial data representations

While *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, because there is a substantial interest in spatial data analysis, support for spatial data is now provided by many *R* packages ([28], 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

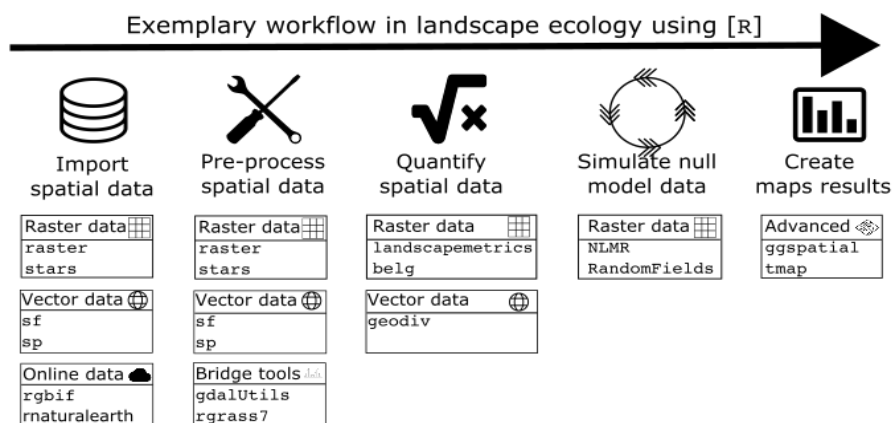


Fig. 1: Exemplary workflow of spatial data analyses for landscape ecology using the R programming language. For all major tasks, a few example R packages are listed. .

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 now 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 . 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].

## 2.2 Spatial data download

Nowadays, spatial data for many scales is available from an abundance of online-accessible sources. A lot of this data is 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* [56] to access the Natural Earth database, the *elevatr* package to access raster elevation data [57], the *rgbif* package to access the Global Biodiversity Information Facility (GBIF) portal [58], the *BIEN* package [59] to access the Botanical Information and Ecology Network Database, the *marmap* to download bathymetry data from the ETOPO1 database [60], or the *FedData* package [61] to access the National Land Cover Database (NLCD) data for the USA. Furthermore, the *getlandsat* package [62] allows users to download data from the Landsat 8, the *MODIS* package [63] to download MODIS products, and *sen2r* [64] 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 (for WorldClim v2, see the in-development package *geodata* ). Additionally, the *rgee* package [65] 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 . 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 . 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 we want to keep intact (e.g., does not distort areas, shapes, distances, or angles) and be appropriate for a given study area. 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 [66]. Furthermore, *landscapetools* is a collection of various utility functions for the raster data model [67].

Finally, there are a number of tools for landscape ecology implemented in GIS software, such as `r.li` or `r.pi` for GRASS GIS [68,69,37], terrain analysis methods in SAGA GIS [70], or morphological operations for Google Earth Engine. Gladly, it is possible to control several GIS software directly from R using dedicated packages, such as *rgrass7* [71] for GRASS GIS, *RSAGA* [72] for SAGA GIS, and *rgee* [65] for Google Earth Engine.

## 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. However, the generic functions are focused on quick visual inspection of the data, rather than the creating complete maps.

The *tmap* package provides a coherent plotting system for static and interactive maps that is based on the layered grammar of graphics [73] and aims for creating publication-ready maps. Static thematic maps, including proportional symbols, choropleth, or typology maps, can be created with the *cartography* package [74]. Also the popular plotting package *ggplot2* [75] has an extension especially designed for plotting spatial data named *ggspatial* [76].

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].

A slightly different approach to visualizing spatial data is adapted by the *rayshader* package [79] that creates topographic 2D and 3D maps.

## 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, 80]. For discrete land cover classes, the composition (number and abundance) and configuration (spatial arrangement) of the landscape are often described using landscape metrics [81, 82, 83, 84]. 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 [82].

The introduction of the *FRAGSTATS* in 1995 heavily facilitated the use of landscape metrics software [85, 86, 84]. However, while *FRAGSTATS* is free to download at the developers' homepage, it is not open-source software. This restricts its transparency, reproducibility, and extensibility. Recently the *landscapemetrics* package [87] was developed to provide a truly open-source solution to calculate landscape metrics. The package allows calculation of the most widely used landscape metrics in a transparent and reproducible workflow within the *R* environment.

More recently, surface metrics were suggested as an alternative to landscape metrics for continuous raster data [88]. The *geodiv* package [89] 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 [90].

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. Spatial signatures calculated for many landscapes can be compared using one of a set of existing distance measures (e.g. Euclidian, Manhattan, Mahalanobis). 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 methods mentioned above are implemented in the *motif* package [91].

*Geostatistics* Geostatistics, or 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, geostatistics has three key uses: (1) detecting and correcting for spatial autocorrelation; (2) quantifying and comparing landscape pattern; (3) interpolating data.

Point pattern analysis is one such method. This uses event-level data, such as locations of individuals, and links the spatial pattern to the ecological process. The *spatstat* package contains functionality for point pattern analysis, including exploratory analysis; simulation of point process models; and modelling fitting, inference and diagnostics. A comprehensive text book covering



both theoretical background as well as applied examples can be found here [92].

Distance-based methods allow us 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 modelling. The *spdep* package has methods for quantifying multiple metrics of spatial autocorrelation, and to correct for these in a spatial autoregressive model. The *rinla* and *inlabru* packages also provide functionality for modelling of spatially structured data.

Finally, with variograms and correlograms, the spatial structure of continuous landscapes can be quantified and compared. R packages *geoR* and *gstat* provide functionality for this type of analysis, as well as interpolation methods, known as (co-)kriging.

*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 [93]. Originated in the 1970s, SDM has experienced numerous methodological advancement, and a numerous body of literature exists today [94,95]. Additionally, textbooks introducing basic concepts of SDM in R exists [96,32].

Because the used modeling approaches are diverse [97,98,32], 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* [99] or *lme4* [100] package; classification and regression trees (CART) using, e.g., the *rpart* [101], *randomForest* [102] or *ranger* [103] package or multivariate data analysis using, e.g., the *ade4* [104] or *vegan* [105] package. Also, packages specifically designed for SDM exists, including includes the *dismo* [106], *sdm* [107], *ecospat* [108], *biomod2* [109], *PresenceAbsence* [110], or *zoon* [111] packages.

Related to SDMs, there are 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 explanatory variables to explain variation in space use [112], behavioral states [113], or habitat selection [114]. Widely used R packages include *ctmm* [115] and *adehabitatHR* [116] for home-range estimation, *moveHMM* [117] for the classification of behavioral states, and *amt* [118] for habitat selection. A recent and very comprehensive overview of R packages for the analysis of animal movement data is given by [119].

*Connectivity* Connectivity is one of the core elements of landscape structure [120] and thus one of the core concepts of landscape ecology [5]. Landscape connectivity describes how landscape characteristics facilitate or hinder the movement of species [121] 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 [121,5]. Given its broad concept, many different measures of connectivity exist [122]. 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) [122,5]. Such measures are provided within the *landscapemetrics* package (see 2.5). Furthermore, the *lconnect* package [123] and *Makurhini* package [124] 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 [122]. In graph theory [125], landscapes are described by nodes (i.e., habitat patches) connected by and functional connections called links (or edges) [125]. The *grainscape* package [126] provides a tool to model connectivity based on spatially explicit networks. More generally, the *igraph* package [127] 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 [128]. Least-cost paths can be calculated using the *gdistance* package [129]. Absorbing Markov chains quantify landscape connectivity as the combination of movement and mortality based on the landscape characteristics [130], and is provided by the recently published *samc* package [131].

*Landscape genetics* Landscape genetics investigates how characteristics of landscapes interact with gene flow, genetic drift, and selection [132]. Such insights improve our understanding of metapopulation dynamics, speciation, species' distributions, and conservation [133]. By explicitly including landscape characteristics, landscape genetics provides a more detailed analysis than more abstract concepts (e.g., metapopulation genetics) [134]. As a result of its interdisciplinarity, landscape genetics draws together methods from multiple fields, including landscape ecology, spatial statistics, geography, and population genetics [133].

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 ... can be found in the *graphs4lg* [135], *PopGenReport* [136,137], *HierDpart* packages [138], or *GeNetIt* [139].

*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 [140,141]. Because neutral landscape models are not based on ecological and landscape processes, many different generic algorithms to create landscapes can be found across various *R* packages. A comprehensive collection of algorithms to simulate neutral landscape models specifically designed for landscape ecology can be found in the *NLMR*

package [67]. Furthermore, the *RandomFields* package [142] allows to simulate Gaussian fields, which could be used as neutral landscape models.

### 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. In total, the survey was answered by 103 participants, of which the majority were either “PhD students” (34%), followed by “Post-Docs” (28.2%) and “Professors” (12.6%). 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” (54.4%) or a “few times a week” (36.9%). Almost half of all participants described themselves as “advanced” users (46.6%), while 40.8% described themselves as “intermediate” users. Related to this, about half of the participants either implemented their own package (21.4%) or plan to do so in the future (23.3%) 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. 2 A)).

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. 2 B). Interestingly, 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”).

Interestingly, more people use the raster data model (72.8%) in comparison to the vector data model (27.2%). This was also represented in the most used *R* packages (Fig. 2 C)). When asked for the three most used packages, participants of the survey listed 83 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. 2 C). 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; 33.44%).

Lastly, when asked how useful *R* is currently for landscape ecology, the vast majority of participants answered with either “very useful” or “useful” (summarized 91.26%) and only very few participants evaluated *R* as “intermediate”, “not useful” or “not useful at all” (summarized 8.74%; Fig. 2 D)).

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.

Table 1: Overview of commonly used R packages for landscape ecology. Packages are sorted by their major application task. Only packages focused on spatial data and landscape ecology are included.

Task	R package	Description	Reference
Spatial data	raster	Raster data handling and analysis	[47]
	terra	Basic data handling and analysis	[48]
	stars	Spatiotemporal raster data	[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]
Spatial data download	sf	Vector data handling and analysis	[55]
	rnaturalearth	Download region and country data	[56]
	elevatr	Download elevation data	[57]
	rgbif	Download biodiversity data	[58]
	BIEN	Download plant diversity, function and distribution data	[59]
	marmap	Download and manipulate bathymetric data	[60]
	FedData	Download US federal data	[61]
	getlandsat	Download satellite data from Landsat 8	[62]
	MODIS	Download satellite data from MODIS	[63]
	sen2r	Download satellite data from Sentinel	[64]
Creating maps	mapview	Interactive viewing of spatial data	[77]
	tmap	Create thematic maps	[73]
	leaflet	Create interactive web maps	[78]
	cartography	Create cartographic maps	[74]
	ggspatial	Spatial extension for ggplot2	[143]
	rayshader	Create 2D and 3D data visualizations	[79]
Quantifying landscape characteristics	landscapemetrics	Quantify categorical landscape patterns	[87]
	belg	Calculates the Boltzmann entropy	[90]
	motif	Not on CRAN?	[91]
	geodiv	Quantify continuous landscape patterns	[89]
Species distribution modeling	dismo	Add description	[106]
	sdm	Add description	[107]
	ecospat	Add description	[108]
	biomod2	Add description	[109]
	PresenceAbsence	Add description	[110]
	zoon	Add description	[111]
	adehabitatHR, adehabitatHS	Add description	[116]
Connectivity	amt	Add description	[118]
	lconnect	Add description	[123]
	Makurhini	Add description	[124]
	grainscape	Add description	[126]
	gdistance	Add description	[129]
	samc	Add description	[131]
Landscape genetics	raphs4lg	Add description	[135]
	PopGenReport	Add description	[136, 137]
	HierDpart	Add description	[138]
	GeNetIt	Add description	[139]
various	NLMR	Simulate neutral landscape models	[67]
	RandomFields	Add description	[142]
	landscapetools	Utility functions for raster data	[67]
	grainchanger	Data aggregation methods for raster data	[66]

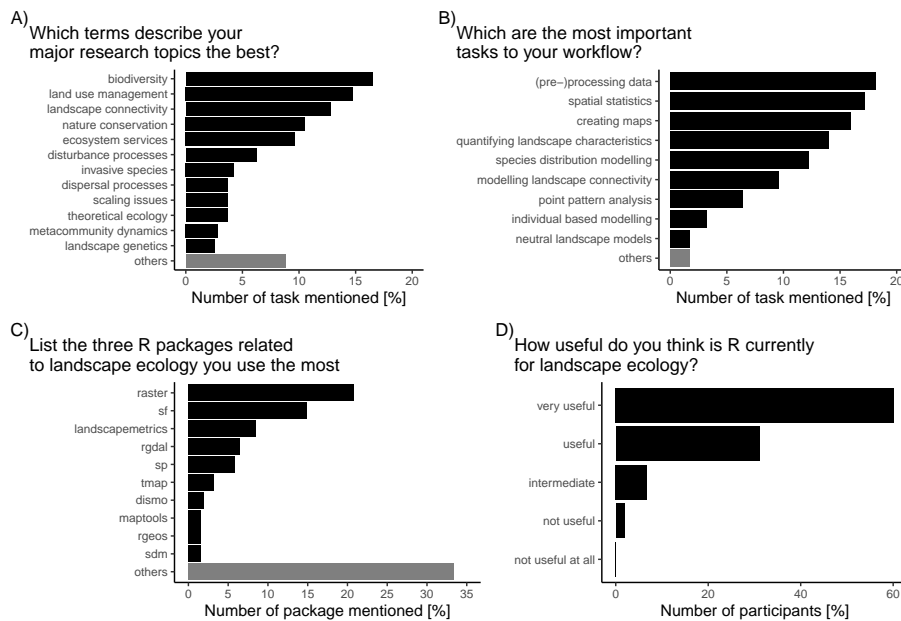


Fig. 2: Results of the online survey about open-source software tools in R for landscape ecology. Results include A) which terms describe major research topics the best, B) the most important workflow task, C) the most used R packages and D) the overall usefulness of R for landscape ecology. The 'others' category includes all answers with less than five total mentions.

Overall, 22.3% 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 (13.6%) 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 (9.7%). Thirdly, many participants (8.7%) 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, the *R* programming language and its packages need to change and adapt to these changes.

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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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#### References

1. E. Ellis, Anthropogenic transformation of the terrestrial biosphere, *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **369**(1938), 1010 (2011)
2. E. Ellis, Ecology in an anthropogenic biosphere, *Ecological Monographs* **85**(3), 287 (2015)
3. P. Crutzen, Geology of mankind, *Nature* **415**(6867), 23 (2002)
4. P. Vitousek, Human Domination of Earth’s ecosystems, *Science* **277**(5325), 494 (1997)
5. K. With, *Essentials of Landscape Ecology*, 1st edn. (Oxford University Press, Oxford, UK, 2019)
6. M. Turner, Landscape ecology: The effect of pattern on process, *Annual Review of Ecology and Systematics* **20**(1), 171 (1989)
7. M. Turner, Landscape ecology: What is the state of the science?, *Annual Review of Ecology, Evolution, and Systematics* **36**(1), 319 (2005)
8. P. Risser, J. Karr, R. Forman, Landscape ecology: Directions and approaches, *Illinois Natural History Survey Special Publication* **2**, 7 (1984)
9. R. Forman, M. Godron, *Landscape Ecology* (Wiley, New York, 1986)

10. R. Forman, *Land Mosaics: The Ecology of Landscapes and Regions* (Cambridge University Press, Cambridge, UK, 1995)
11. J. Wiens, in *Mosaic Landscapes and Ecological Processes*, ed. by L. Hansson, L. Fahrig, G. Merriam (Chapman and Hall, London, UK, 1995), pp. 1–26
12. J. Wiens, Spatial scaling in ecology, *Functional Ecology* **3**(4), 385 (1989)
13. S. Levin, The problem of pattern and scale in ecology, *Ecology* **73**(6), 1943 (1992)
14. D. Jelinski, J. Wu, The modifiable areal unit problem and implications for landscape ecology, *Landscape Ecology* **11**(3), 129 (1996)
15. P. Šímová, K. Gdulová, Landscape indices behavior: A review of scale effects, *Applied Geography* **34**, 385 (2012)
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, *Nature Ecology & Evolution* **2**(5), 819 (2018)
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, *PLoS Biology* **12**(1), e1001745 (2014)
18. A. Prlić, J. Procter, Ten simple rules for the open development of scientific software, *PLoS Computational Biology* **8**(12), e1002802 (2012)
19. A. St. Laurent, *Understanding Open Source and Free Software Licensing* (O'Reilly, Sebastopol, USA, 2008)
20. G. von Krogh, E. von Hippel, The promise of research on open source software, *Management Science* **52**(7), 975 (2006)
21. S. Powers, S. Hampton, Open science, reproducibility, and transparency in ecology, *Ecological Applications* **29**(1) (2019)
22. S. Steiniger, G. Hay, Free and open source geographic information tools for landscape ecology, *Ecological Informatics* **4**(4), 183 (2009)
23. S. Steiniger, E. Bocher, An overview on current free and open source desktop GIS developments, *International Journal of Geographical Information Science* **23**(10), 1345 (2009)
24. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing (2019)
25. D. Smith. Over 16 years of R Project history (2016)
26. J. Lai, C. Lortie, R. Muenchen, J. Yang, K. Ma, Evaluating the popularity of R in ecology, *Ecosphere* **10**(1) (2019)
27. R. Bivand, Implementing spatial data analysis software tools in R, *Geographical Analysis* **38**(1), 23 (2006)
28. R. Lovelace, J. Nowosad, J. Münchow, *Geocomputation with R*, 1st edn. (Chapman and Hall/CRC Press, Boca Raton, USA, 2019)
29. R. Bivand. Analysis of Spatial Data (2019)
30. E. Pebesma. Handling and Analyzing Spatio-Temporal Data (2020)
31. M. Wegmann, B. Leutner, S. Dech (eds.), *Remote Sensing and GIS for Ecologists: Using Open Source Software*. Data in the Wild (Pelagic Publishing, Exeter, 2016)
32. R. Fletcher, M.J. Fortin, *Spatial Ecology and Conservation Modeling: Applications with R*, 1st edn. (Springer, New York, USA, 2019)
33. E. Pebesma, R. Bivand, *Spatial Data Science* (2019)
34. R. Bivand, Progress in the R ecosystem for representing and handling spatial data DOI 10.1007/s10109-020-00336-0
35. QGIS Development Team. QGIS (2016)
36. GRASS Development Team. Geographic Resources Analysis Support System (GRASS). Open Source Geospatial Foundation (2017)
37. C. Porta, L. Spano, F. Pontedera. R.li - Toolset for multiscale analysis of landscape structure <<https://grass.osgeo.org/grass74/manuals/r.li.html>> (2017)
38. 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, *Developments in Integrated Environmental Assessment* **3**, 163 (2008). DOI 10.1016/S1574-101X(08)00610-8
39. S. István, Comparison of the most popular open-source GIS software in the field of landscape ecology, *Landscape & Environment* **6**(2), 76 (2012)

40. H. Wickham, *R Packages: Organize, Test, Document, and Share Your Code* (O'Reilly, Sebastopol, USA, 2015)
- 500 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>
- 505 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>
- 510 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 (2020). URL <https://gdal.org>
- 515 46. PROJ contributors, *PROJ coordinate transformation software library*. Open Source Geospatial Foundation (2020). 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>> (2019)
48. R.J. Hijmans, *terra: Spatial Data Analysis* (2020). URL <https://CRAN.R-project.org/package=terra>. R package version 0.7-11
- 520 49. E.J. Pebesma. Stars: Scalable, spatiotemporal tidy arrays for R. R package version 0.3-1. <<https://cran.r-project.org/package=stars>> (2019)
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>
- 525 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>
- 530 53. E.J. Pebesma, R.S. Bivand, Classes and methods for spatial data in R., *R News* **5**(2), 9 (2005)
54. R. Bivand, E. Pebesma, V. Gómez-Rubio, *Applied Spatial Data Analysis with R*, 2nd edn. Use R! (Springer, New York, 2013)
- 535 55. E.J. Pebesma. Sf: Simple Features for R. <<https://cran.r-project.org/package=sf>> (2018)
56. 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>
- 540 57. J. Hollister, Tarak Shah, *elevatr: Access Elevation Data from Various APIs* (2017). URL <http://github.com/usepa/elevatr>. R package version 0.1.3, doi:10.5281/zenodo.400259
58. S. Chamberlain, C. Boettiger, R python, and ruby clients for gbif species occurrence data, *PeerJ PrePrints* (2017). URL <https://doi.org/10.7287/peerj.preprints.3304v1>
- 545 59. 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>
- 550 60. 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
61. R.K. Bocinsky, *FedData: Functions to Automate Downloading Geospatial Data Available from Several Federated Data Sources* (2019). URL <https://CRAN.R-project.org/package=FedData>. R package version 2.5.7
- 555



62. 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>
63. 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>>
64. L. Ranghetti, M. Boschetti, F. Nutini, L. Busetto, sen2r: An r toolbox for automatically downloading and preprocessing sentinel-2 satellite data, *Computers & Geosciences* **139**, 104473 (2020). DOI 10.1016/j.cageo.2020.104473. URL <http://sen2r.ranghetti.info>
65. C. Aybar, Q. Wu, L. Bautista, R. Yali, A. Barja, rgee: An r package for interacting with google earth engine, *Journal of Open Source Software* (2020)
66. 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
67. M. Sciaini, M. Fritsch, C. Scherer, C. Simpkins, NLMR and landscapetools: An integrated environment for simulating and modifying neutral landscape models in R, *Methods in Ecology and Evolution* **9**(11), 2240 (2018)
68. M. Wegmann, B.F. 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, *Methods in Ecology and Evolution* **9**(1), 191 (2018)
69. M. Neteler, M. Bowman, M. Landa, M. Metz, GRASS GIS: a multi-purpose Open Source GIS, *Environmental Modelling & Software* **31**, 124 (2012). DOI 10.1016/j.envsoft.2011.11.014
70. O. Conrad, B. Bechtel, M. Bock, H. Dietrich, E. Fischer, L. Gerlitz, J. Wehberg, V. Wichmann, J. Böhner, System for automated geoscientific analyses (saga) v. 2.1.4, *Geoscientific Model Development* **8**(7), 1991 (2015). DOI 10.5194/gmd-8-1991-2015. URL <https://gmd.copernicus.org/articles/8/1991/2015/>
71. R. Bivand, *rgrass7: Interface Between GRASS 7 Geographical Information System and R* (2019). URL <https://CRAN.R-project.org/package=rgrass7>. R package version 0.2-1
72. A. Brenning, D. Bangs, M. Becker, *RSAGA: SAGA Geoprocessing and Terrain Analysis* (2018). URL <https://CRAN.R-project.org/package=RSAGA>. R package version 1.3.0
73. M. Tennekes, tmap: Thematic maps in R, *Journal of Statistical Software* **84**(6), 1 (2018). DOI 10.18637/jss.v084.i06
74. T. Giraud, N. Lambert, Cartography: Create and Integrate Maps in your R Workflow **1**(4), 54. DOI 10.21105/joss.00054
75. H. Wickham, *Ggplot2: Elegant Graphics for Data Analysis* (Springer, New York, 2016)
76. D. Dunnington, *ggspatial: Spatial Data Framework for ggplot2* (2020). URL <https://CRAN.R-project.org/package=ggspatial>. R package version 1.1.4
77. T. Appelhans, F. Detsch, C. Reudenbach, S. Woellauer, *mapview: Interactive Viewing of Spatial Data in R* (2020). URL <https://CRAN.R-project.org/package=mapview>. R package version 2.7.8
78. J. Cheng, B. Karambelkar, Y. Xie, *leaflet: Create Interactive Web Maps with the JavaScript 'Leaflet' Library* (2019). URL <https://CRAN.R-project.org/package=leaflet>. R package version 2.0.3
79. 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>
80. 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, *Ecological Modelling* **295**, 31 (2015)
81. E. Gustafson, Quantifying landscape spatial pattern: What is the state of the art?, *Ecosystems* **1**, 143 (1998)
82. E. Uuemaa, M. Antrop, R. Marja, J. Roosaare, Ü. Mander, Landscape metrics and indices: An overview of their use in landscape research, *Living Reviews in Landscape Research* **3**, 1 (2009)

83. E. Uuemaa, Ü. Mander, R. Marja, Trends in the use of landscape spatial metrics as  
615 landscape indicators: A review, *Ecological Indicators* **28**, 100 (2013)
84. E. Gustafson, How has the state-of-the-art for quantification of landscape pattern  
advanced in the twenty-first century?, *Landscape Ecology* **34**, 1 (2019)
85. K. McGarigal, S. Cushman, E. Ene. FRAGSTATS v4: Spatial pattern anal-  
620 ysis program for categorical and continuous maps. Computer software pro-  
gram produced by the authors at the University of Massachusetts, Amherst.  
<<http://www.umass.edu/landeco/research/fragstats/fragstats.html>>. University of  
Massachusetts (2012)
86. J.A. Kupfer, Landscape ecology and biogeography: Rethinking landscape metrics in a  
post-FRAGSTATS landscape, *Progress in Physical Geography* **36**(3), 400 (2012)
- 625 87. M. Hesselbarth, M. Sciaini, K. With, K. Wiegand, J. Nowosad, Landscapemetrics: An  
open-source R tool to calculate landscape metrics, *Ecography* **42**(10), 1648 (2019)
88. 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
- 630 89. 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>
90. J. Nowosad, P. Gao, belg: A tool for calculating boltzmann entropy of landscape gra-  
dients, *Entropy* **22**(9), 937 (2020). DOI 10.3390/e22090937. URL <https://github.com/r-spatialecology/belg>
- 635 91. J. Nowosad, Motif: an open-source r tool for pattern-based spatial analysis, *Landscape  
Ecology* (2020). DOI 10.1007/s10980-020-01135-0. URL <https://doi.org/10.1007/s10980-020-01135-0>
92. A. Baddeley, E. Rubak, R. Turner, *Spatial Point Patterns: Methodology and Applica-  
640 tions with R* (Chapman and Hall/CRC Press)
93. 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,  
New York, USA, 2011), pp. 1–6. DOI 10.1007/978-1-4419-7390-0\_1
94. N. Zimmermann, T. Edwards, C. Graham, P. Pearman, J.C. Svenning, New trends in  
645 species distribution modelling, *Ecography* **33**(6), 985 (2010)
95. A. Norberg, N. Abrego, F. Blanchet, F. Adler, B.J. 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. Kålås, A. Lehtikoinen, M. Luoto,  
H. Mod, G. Newell, I. Renner, T. Roslin, J. Soininen, W. Thuiller, J. Vanhatalo,  
650 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
96. A. Guisan, W. Thuiller, N. Zimmermann, *Habitat Suitability and Distribution Models:  
655 With Applications in R*, 1st edn. (Cambridge University Press, Cambridge, UK, 2017).  
DOI 10.1017/9781139028271
97. M. Hooten, in *Predictive Species and Habitat Modeling in Landscape Ecology*, ed. by  
C. Drew, Y. Wiersma, F. Huettmann (Springer New York, New York, USA, 2011), pp.  
29–41. DOI 10.1007/978-1-4419-7390-0\_3
98. J. Kerr, M. Kulkarni, A. Algar, in *Predictive Species and Habitat Modeling in Land-  
660 scape Ecology*, ed. by C. Drew, Y. Wiersma, F. Huettmann (Springer New York, New  
York, USA, 2011), pp. 9–28. DOI 10.1007/978-1-4419-7390-0\_2
99. S. Wood, *Generalized Additive Models: An Introduction with R*, 2nd edn. (Chapman  
& Hall/CRC, Boca Raton, USA, 2017)
100. D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using  
665 lme4, *Journal of Statistical Software* **67**(1) (2015)
101. T. Therneau, B. Atkinson. Rpart: Recursive partitioning and regression trees. R pack-  
age version 4.1-15. <https://CRAN.R-project.org/package=rpart> (2019)
102. A. Liaw, M. Wiener, Classification and regression by randomForest, *R News* **2**(3), 18  
(2002)
- 670 103. M. Wright, A. Ziegler, Ranger : A fast implementation of random forests for high  
dimensional data in C++ and R, *Journal of Statistical Software* **77**(1) (2017)

104. S. Dray, A.B. Dufour, The *ade4* package: Implementing the duality diagram for ecologists, *Journal of Statistical Software* **22**(4) (2007)
105. J. Oksanen, F. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn,  
675 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> (2019)
106. 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> (2017)
- 680 107. B. Naimi, M. Araújo, *Sdm*: A reproducible and extensible R platform for species distribution modelling, *Ecography* **39**(4), 368 (2016)
108. O. Broennimann, V. Di Cola, A. Guisan. *Ecospat*: Spatial ecology miscellaneous methods. R package version 3.1. <https://CRAN.R-project.org/package=ecospat> (2020)
109. 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> (2020)
- 685 110. E. Freeman, G. Moisen, *PresenceAbsence*: An R package for presence absence analysis, *Journal of Statistical Software* **23**(11) (2008)
111. N. Golding, T. August, T. Lucas, D. Gavaghan, E. Loon, G. McNerny, The *zoon* package for reproducible and shareable species distribution modelling **9**(2), 260. DOI 10.1111/2041-210X.12858
- 690 112. J. Signer, N. Balkenhol, M. Ditmer, J. Fieberg, Does estimator choice influence our ability to detect changes in home-range size?, *Animal Biotelemetry* **3**(1), 16 (2015)
113. R. Langrock, R. King, J. Matthiopoulos, L. Thomas, D. Fortin, J.M. Morales, Flexible and practical modeling of animal telemetry data: hidden markov models and extensions, *Ecology* **93**(11), 2336 (2012)
- 695 114. J. Fieberg, J. Signer, B.J. Smith, T. Avgar, A "how-to" guide for interpreting parameters in resource-and step-selection analyses, *bioRxiv* (2020)
115. J.M. Calabrese, C.H. Fleming, E. Gurarie, *ctmm*: An r package for analyzing animal relocation data as a continuous-time stochastic process, *Methods in Ecology and Evolution* **7**(9), 1124 (2016)
- 700 116. 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
117. T. Michelot, R. Langrock, T.A. Patterson, *movehmm*: an r package for the statistical modelling of animal movement data using hidden markov models, *Methods in Ecology and Evolution* **7**(11), 1308 (2016)
- 705 118. 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
- 710 119. R. Joo, M.E. Boone, T.A. Clay, S.C. Patrick, S. Clusella-Trullas, M. Basille, Navigating through the r packages for movement, *Journal of Animal Ecology* **89**(1), 248 (2020)
120. P. Taylor, L. Fahrig, K. Henein, G. Merriam, Connectivity is a vital element of landscape structure, *Oikos* **68**(3), 571 (1993)
121. L. Tischendorf, L. Fahrig, On the usage and measurement of landscape connectivity, *Oikos* **90**(1), 7 (2000)
- 715 122. P. Kindlmann, F. Burel, Connectivity measures: A review, *Landscape Ecology* pp. s10,980–008–9245–4 (2008)
123. 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>
- 720 124. 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>
125. A. Laita, J. Kotiaho, M. Mönkkönen, Graph-theoretic connectivity measures: What do they tell us about connectivity?, *Landscape Ecology* **26**(7), 951 (2011)
- 725 126. A. Chubaty, P. Galpern, S. Doctolero, The R toolbox grainscape for modelling and visualizing landscape connectivity using spatially explicit networks, *Methods in Ecology and Evolution* **11**(4), 591 (2020)
127. G. Csardi, T. Nepusz, The *igraph* software package for complex network research, *InterJournal Complex Systems*, 1695 (2006)
- 730

128. 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, *Landscape and Urban Planning* **64**(4), 233 (2003)
129. J. van Etten, R Package gdistance : Distances and Routes on Geographical Grids, *Journal Of Statistical Software* **76**(13) (2017)
130. R. Fletcher, J. Sefair, C. Wang, C. Poli, T.A.H. 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, *Ecology Letters* **22**(10), 1680 (2019)
131. A. Marx, C. Wang, J. Sefair, M. Acevedo, R. Fletcher, Samc: An R package for connectivity modeling with spatial absorbing Markov chains, *Ecography* **43**(4), 518 (2020)
132. S. Manel, M. Schwartz, G. Luikart, P. Taberlet, Landscape genetics: Combining landscape ecology and population genetics, *Trends in Ecology & Evolution* **18**(4), 189 (2003)
133. 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, *Heredity* **98**(3), 128 (2007)
134. R. Holderegger, H. Wagner, A brief guide to landscape genetics, *Landscape Ecology* **21**(6), 793 (2006)
135. P. Savary. Graph4lg: Build graphs for landscape genetics analysis. R package version 0.5.0. <https://CRAN.R-project.org/package=graph4lg> (2020)
136. A. Adamack, B. Gruber, PopGenReport: Simplifying basic population genetic analyses in R, *Methods in Ecology and Evolution* **5**(4), 384 (2014)
137. B. Gruber, A. Adamack, Landgenreport: A new R function to simplify landscape genetic analysis using resistance surface layers, *Molecular Ecology Resources* **15**(5), 1172 (2015)
138. 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> (2019)
139. 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
140. R. Gardner, B. Milne, M. Turnei, R. O'Neill, Neutral models for the analysis of broad-scale landscape pattern, *Landscape Ecology* **1**(1), 19 (1987)
141. K. With, A. King, The use and misuse of neutral landscape models in ecology, *Oikos* **79**(2), 219 (1997)
142. 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
143. 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>