## Open-source tools in R for landscape ecology

Maximillian H.K. Hesselbarth  $\cdot$  Jakub Nowosad  $\cdot$  Johannes M. Signer  $\cdot$  Laura J. Graham  $\cdot$ 

Received: date / Accepted: date

Abstract max. (200 words) Abstract Abst

Maximillian H.K. Hesselbarth

Department of Ecosystem Modelling, University of Goettingen, Buesgenweg 4, 37077 Goettingen, Germany Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, 48109, USA

E-mail: mhk.hesselbarth@gmail.com

Jakub Nowosad

Institute of Geoecology and Geoinformation, Adam Mickiewicz University, Krygowskiego 10, 61-680 Poznan, Poland

E-mail: nowosad.jakub@gmail.com

Johannes M. Signer

Department of Wildlife Sciences, University of Göttingen, Büsgenweg 3, 37077 Göttingen, Germany

E-mail: j.m.signer@gmail.com

Laura J. Graham

Geography and Environment, University of Southampton, Highfield Rd, Southampton SO17 1BJ, United Kingdom

E-mail: 1.graham@bham.ac.uk

Abstract Abstract Abstract Abstract Abstract Abstract Abstract

**Keywords** spatial data  $\cdot$  statistical programming language  $\cdot$  R packages  $\cdot$  reproducibility  $\cdot$  . . .  $\cdot$ 

#### 1 Introduction

## 1.1 A short introduction to landscape ecology

Landscape ecology focuses on how ecological processes are influenced and modified by the heterogeneous landscapes they occur in and how the ecological processes themselves influence the landscapes [1,2,3]. In this context, landscape ecology considers, besides others, i) spatial and temporal dynamics of heterogeneous landscapes, ii) interactions, fluxes, and exchange within these landscapes, iii) how the landscapes influence ecological processes (and vice versa), and lastly, iv) how to manage these heterogeneous landscapes [4,1].

While human activities have altered the landscapes for millenniums [5,6], in the past centuries, the effects of humans on landscapes have increased to an unknown high, known as the Anthropocene [7]. Today, almost all landscapes are directly or indirectly influenced by human activities [8]. Thus, understanding the complex interactions between landscapes and ecological processes becomes increasingly important [3].

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 vary spatially [3]. To this, the importance of scale was already raised decades ago [12,13,14] and is still of relevance until today [15, 16]. Thus, in contrast to many other sub-disciplines of ecology, landscape ecology emphasizes spatial patterns to a high degree [4]. Consequently, the field of landscape ecology 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 used 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]. Last but not least, even

though not strictly necessary by definition [22,23], most open-source software is also free-of-cost, which allows using the software without any costs in contrast to often expensive proprietary software [20,22,23]. This democratize scientific research as free-of-cost software removes one gatekeeper for researches 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 even 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 [31,28,32]. A recent overview over the progress of R to handle spatial data in general can be found in [33].

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 for landscape ecology exist [34,35, 36], 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 [37,22,23,38]. Because in addition to handling spatial data, also 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 [39]. GitHub hosts source code under

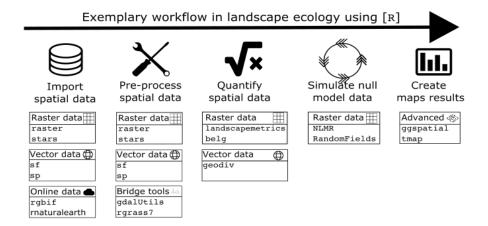


Fig. 1: Exemplary workflow of spatial data analyses for landscape ecology using the R programming language. For all major tasks, a few example R packages are listed. .

version control, and allows users to install packages with one line of code using the *remotes* [40] package. Additionally, hosting a package on *GitHub* provides many useful features to collaborate and communicate between developers and users [39], 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. For more information about R package development, see [39].

# 2.1 Spatial data representations

While R has several build-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). 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 and PROJ 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 [41]. A raster successor, terra, aimed at the simpler interface and improved performance is now being developed [42]; 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 [43]. Additionally, there are packages that improve some basics raster operations in terms of computational performance or compatibility between raster and vector operations, such as fasterize [44], rasterDT [45], or exactextractr [46].

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 [47,48]. 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 [49].

## 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 [50] to access the Natural Earth database, the elevatr package to access raster elevation data [51], the rgbif to access the Global Biodiversity Information Facility (GBIF) portal [52], the BIEN package [53] to access the Botanical Information and Ecology Network Database, the marmap to download bathymetry data from the ETOPO1 database [54], or the Fed-Data package [55] to access the National Land Cover Database (NLCD) data for the USA. Furthermore, the getlandsat package [56] allows to download data from the Landsat 8, the MODIS package [57] to download MODIS products, and sen2r [58] to download Sentinel-2 optical images. Also, the getData() function from the raster package allows to download climatic and bioclimatic data from WorldClim v1.4 (for WorldClim v2, see the in-development package geodata). Additionally, the rgee package [59] 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. In the first one, geographical, 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 to unify spatial projections when the used data have different CRS.

A second 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 can be required by using, e.g., certain spatial filters such as water bodies. 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 [60]. Furthermore, landscapetools is a collection of various utility functions for the raster data model [61].

Finally, there is a number of tools for landscape ecology implemented in GIS software, such as r.li or r.pi for GRASS GIS [62,63,36], terrain analysis methods in SAGA GIS [64], 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 [65] for GRASS GIS, RSAGA [66] for SAGA GIS, and rgee [59] for Google Earth Engine.

### 2.4 Creating maps

Creating maps is essential when working with spatial data. It has a role in checking the spatial and value-related quality of data, data exploration, and finally communicating results. R allows to create 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 [67] and aims for creating publication-ready maps. Static thematic maps, including proportional symbols, choropleth, or typology maps, can be created with the *cartography* package [68]. Also the popular plotting package *ggplot2* [69] has an extension especially designed for plotting spatial data named *ggspatial* [70]. Quick interactive visualization of spatial data can be done with the *mapview* package [71]. Both, *tmap* and *mapview* build upon the *leaflet* package and leaflet javascript library [72].

A slightly different approach to visualizing spatial data is adapted by the rayshader package [73] 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 [2, 74]. For discrete land cover classes, the composition (number and abundance) and configuration (spatial arrangement) of the landscape are often described using landscape metrics [75,76,77,78]. These metrics allow to compare different landscapes, quantify temporal and spatial landscape changes and investigate interactions between landscape characteristics and ecological processes [76].

The introduction of the FRAGSTATS in 1995 heavily facilitated the use of landscape metrics software [79,80,78]. 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 landscape metrics package [81] was developed to provide a truly open-source solution to calculate landscape metrics. The package allows calculating 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 [82]. The *geodiv* package [83] allows to calculate gradient surface metrics to characterize continuous analysis of landscape

features. Additionally, the *belg* package allows calculating the Boltzmann entropy of a landscape gradient [84].

Most landscape metrics are 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 the existing distance measures. 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 [85].

Species distribution modeling Species distribution modeling (SDM) examine how landscape patterns (e.g., habitat suitability or resources availability) influence and determine the patterns of species distribution, mainly to infer ecological processes and predict future species distributions [86]. Originated in the 1970s, SDM has experienced numerous methodological advancement, and a numerous body of literature exists today [87]. Additionally, textbooks introducing basic concepts of SDM in R exists [88,31].

Because the used modeling approaches are diverse [89,90,31], 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 [91] or lme4 [92] package; classification and regression trees (CART) using, e.g., the rpart [93], randomForest [94] or ranger [95] package or multivariate data analysis using , e.g., the ade4 [96] or vegan [97] package. Also, packages specifically designed for SDM exists, including includes the dismo [98], sdm [99], ecospat [100], biomod2 [101], PresenceAbsence [102], or zoon [103] packages. Related to SDM, there are several packages to estimate home ranges and habitat selection, including adehabitatHR and adehabitatHS [104] or amt [105]

Connectivity Connectivity is one of the core elements of landscape structure [106] and thus one of the core concepts of landscape ecology [3]. Landscape connectivity describes how landscape characteristics facilitate or hinder the movement of species [107] or other aspects of mobility, such as dispersal, gene or nutrient flow [3]. While structural connectivity focuses only on landscape characteristics (e.g., movement corridors, barriers), functional connectivity also includes behavior characteristics of the species [107,3]. Given its broad concept, many different measures of connectivity exist [108]. On patch level, structural connectivity can be measured using nearest-neighbor distances or characterizations of the patch neighborhood (e.g., amount of suitable habitat) [108,3]. Such measures are provided within the landscapemetrics package (see 2.5). Furthermore, the lconnect package [109] and Makurhini package [110] 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 [108]. In graph theory [111], landscapes are described by nodes

(i.e., habitat patches) connected by and functional connections called links (or edges) [111]. The grainscape package [112] provides a tool to model connectivity based on spatially explicit networks. More general, the igraph package [113] provides functionality related to graph theory. Resistance surfaces and least-cost paths are other tools to model functional connectivity. The resistance surface describes the effects of facilitating or hindering the landscape's characteristics for an organism moving within it [114]. Least-cost paths can be calculated using the gdistance package [115]. Absorbing Markov chains that combine random walk theory and mortality based on the landscape characteristics [116] and is provided by the recently published same package [117].

Landscape genetics Landscape genetics investigates how characteristics of landscapes interact with gene flow, genetic drift, and selection [118]. Such insights improve our understanding of metapopulation dynamics, speciation, species' distributions, and conservation [119]. By explicitly including landscape characteristics, landscape genetics is a way more realistic way of analysis than, e.g., metapopulation genetics [120]. As a result of its interdisciplinary, landscape genetics combines methods from different disciplines, including landscape ecology, spatial statistics, geography, and population genetics [119].

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 can be found in the graphs4lg [121], PopGenReport [122,123], HierDpart packages [124], or GeNetIt [125].

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 [126,127]. 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 [61]. Furthermore, the RandomFields package [128] allows to simulate Gaussian fields, which could be used as neutral landscape models.

Various

## 3 Survey of R usage by landscape ecology community

To better understand how the landscape ecology community uses\* R\*, we conducted a short survey and used 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

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	Reference
Spatial data	raster	[41]
	terra	[42]
	stars	[43]
	fasterize	[44]
	rasterDT	[45]
	exactextractr	[46]
	$_{ m sp}$	[47, 48]
	sf	[49]
Spatial data download	rnaturalearth	[50]
	elevatr	[51]
	rgbif	[52]
	BIEN	[53]
	marmap	[54]
	FedData	[55]
	getlandsat	[56]
	MODIS	[57]
	sen2r	[58]
Creating maps	mapview	[71]
	tmap	[67]
	leaflet	[72]
	cartography	[68]
	ggspatial	[129]
	rayshader	[73]
Quantifying landscape characteristics	landscapemetrics	[81]
	belg	[84]
	motif	[85]
	geodiv	[83]
Species distribution modeling	dismo	[98]
	sdm	[99]
	ecospat	[100]
	biomod2	[101]
	PresenceAbsence	[102]
	zoon	[103]
	adehabitatHR, adehabitatHS	[104]
	amt	[105]
Connectivity	lconnect	[109]
	Makurhini	[110]
	grainscape	[112]
	gdistance	[115]
	samc	[117]
Landscape genetics	raphs4lg	[121]
	PopGenReport	[122, 123]
	HierDpart	[124]
	GeNetIt	[125]
various	NLMR	[61]
	RandomFields	[128]
	landscapetools	[61]
	grainchanger	[60]

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 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.

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.

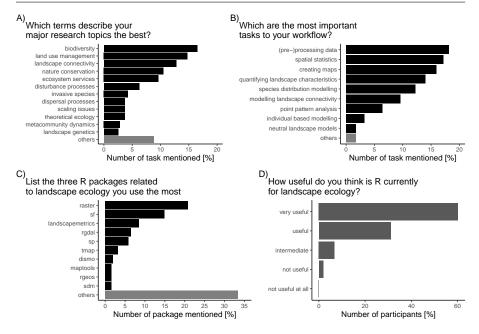


Fig. 2: Results of the online survey about open-source software tools in R for landscape ecology. Results include A) which terms describe major reserach topics the best, B) the most important workflow task, C) the most used R packages and D) the overall usefulnes or R for landscape ecology. The 'others'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

## 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. To-day, 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.

## 4.1 Acknowledgments

Conflict of interest MHKH and JN are authors of the landscapemetrics and landscapetools package. JN is author of belg and motif package.

Funding MHKH was supported by the German Research Association (DFG) Research Training Group 1644 'Scaling Problems in Statistics', grant number 152112243.

- Author contributions MHKH and JN designed the survey form and analyzed the responses of the participants. MHKH and JN drafted the manuscript 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.

#### References

385

390

395

405

410

- M. Turner, Landscape ecology: The effect of pattern on process, Annual Review of Ecology and Systematics 20(1), 171 (1989)
- 2. M. Turner, Landscape ecology: What is the state of the science?, Annual Review of Ecology, Evolution, and Systematics **36**(1), 319 (2005)
- K. With, Essentials of Landscape Ecology, 1st edn. (Oxford University Press, Oxford, UK, 2019)
- P. Risser, J. Karr, R. Forman, Landscape ecology: Directions and approaches, Illinois Natural History Survery Special Publication 2, 7 (1984)
- 5. E. Ellis, Anthropogenic transformation of the terrestrial biosphere, Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences **369**(1938), 1010 (2011)
- 6. E. Ellis, Ecology in an anthropogenic biosphere, Ecological Monographs **85**(3), 287 (2015)
  - 7. P. Crutzen, Geology of mankind, Nature  $\mathbf{415} (6867),\,23 \,\,(2002)$
  - 8. P. Vitousek, Human Domination of Earth's ecosystems, Science  $\bf 277 (5325), 494 (1997)$
- 9. R. Forman, M. Godron, Landscape Ecology (Wiley, New York, 1986)
- R. Forman, Land Mosaics: The Ecology of Landscapes and Regions (Cambridge University Press, Cambridge, UK, 1995)
  - 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)
  - D. Jelinski, J. Wu, The modifiable areal unit problem and implications for landscape ecology, Landscape Ecology 11(3), 129 (1996)
  - P. Šímová, K. Gdulová, Landscape indices behavior: A review of scale effects, Applied Geography 34, 385 (2012)
  - 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)
    - 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)
    - A. Prlić, J. Procter, Ten simple rules for the open development of scientific software, PLoS Computational Biology 8(12), e1002802 (2012)
    - A. St. Laurent, Understanding Open Source and Free Software Licensing (O'Reilly, Sebastopol, USA, 2008)

435

455

460

470

- G. von Krogh, E. von Hippel, The promise of research on open source software, Management Science 52(7), 975 (2006)
  - 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)
  - 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)
  - J. Lai, C. Lortie, R. Muenchen, J. Yang, K. Ma, Évaluating 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. R. Fletcher, M.J. Fortin, Spatial Ecology and Conservation Modeling: Applications with R, 1st edn. (Springer, New York, USA, 2019)
  - 32. E. Pebesma, R. Bivand, Spatial Data Science (2019)
  - 33. R. Bivand, Progress in the R ecosystem for representing and handling spatial data DOI 10.1007/s10109-020-00336-0
- 445 34. QGIS Development Team. QGIS (2016)
  - 35. GRASS Development Team. Geographic Resources Analysis Support System (GRASS). Open Source Geospatial Foundation (2017)
  - 36. C. Porta, L. Spano, F. Pontedera. R.li Toolset for multiscale analysis of landscape structure <a href="https://grass.osgeo.org/grass74/manuals/r.li.html">https://grass.osgeo.org/grass74/manuals/r.li.html</a> (2017)
  - 37. 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
    - 38. S. István, Comparison of the most popular open-source GIS software in the field of landscape ecology, Landscape & Environment **6**(2), 76 (2012)
    - H. Wickham, R Packages: Organize, Test, Document, and Share Your Code (O'Reilly, Sebastopol, USA, 2015)
    - 40. 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. <a href="https://CRAN.R-project.org/package=remotes">https://CRAN.R-project.org/package=remotes</a>>. URL https://CRAN.R-project.org/package=remotes
    - 41. R. Hijmans. Raster: Geographic data analysis and modeling. R package version 2.9-5. <a href="https://cran.r-project.org/package=raster">https://cran.r-project.org/package=raster</a>> (2019)
    - 42. R.J. Hijmans, terra: Spatial Data Analysis (2020). URL https://CRAN.R-project.org/package=terra. R package version 0.7-11
    - 43. E.J. Pebesma. Stars: Scalable, spatiotemporal tidy arrays for R. R package version 0.3-1. <a href="https://cran.r-project.org/package=stars">https://cran.r-project.org/package=stars</a> (2019)
    - 44. N. Ross. Fasterize: Fast Polygon to Raster Conversion. R package version 1.0.3 <a href="https://CRAN.R-project.org/package=fasterize">https://CRAN.R-project.org/package=fasterize</a> URL https://CRAN.R-project.org/package=fasterize
    - 45. J. O'Brien. rasterDT: Fast Raster Summary and Manipulation. R package version 0.3.1 <a href="https://CRAN.R-project.org/package=rasterDT">https://CRAN.R-project.org/package=rasterDT</a>. URL https://CRAN.R-project.org/package=rasterDT
    - 46. D. Baston. Exactextractr: Fast Extraction from Raster Datasets using Polygons. R package version 0.5.1. <a href="https://CRAN.R-project.org/package=exactextractr">https://CRAN.R-project.org/package=exactextractr</a>. URL https://CRAN.R-project.org/package=exactextractr
    - E.J. Pebesma, R.S. Bivand, Classes and methods for spatial data in R., R News 5(2), 9 (2005)

505

510

515

520

- 48. R. Bivand, E. Pebesma, V. Gómez-Rubio, Applied Spatial Data Analysis with R, 2nd edn. Use R! (Springer, New York, 2013)
- 49. E.J. Pebesma. Sf: Simple Features for R. <a href="https://cran.r-project.org/package=sf">https://cran.r-project.org/package=sf</a> (2018)
- 50. A. South. Rnaturalearth: World Map Data from Natural Earth. R package version 0.1.0 <a href="https://CRAN.R-project.org/package=rnaturalearth">https://CRAN.R-project.org/package=rnaturalearth</a>
- 51. 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
- 52. 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
- 53. B. Maitner. BIEN: Tools for Accessing the Botanical Information and Ecology Network Database. R package version 1.2.4. <a href="https://CRAN.R-project.org/package=BIEN">https://CRAN.R-project.org/package=BIEN</a>. URL https://CRAN.R-project.org/package=BIEN
- 54. 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
- 55. 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
- 56. S. Chamberlain. Getlandsat: Get Landsat 8 Data from Amazon Public Data Sets. R package version 0.2.0. <a href="https://CRAN.R-project.org/package=getlandsat">https://CRAN.R-project.org/package=getlandsat</a>. URL https://CRAN.R-project.org/package=getlandsat
- 57. M. Mattiuzzi. MODIS: Acquisition and Processing of MODIS Products. R package version 1.2.3. <a href="https://CRAN.R-project.org/package=MODIS">https://CRAN.R-project.org/package=MODIS</a>. URL <a href="https://CRAN.R-project.org/package=MODIS">https://CRAN.R-project.org/package=MODIS</a>
- 58. 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
- 59. 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)
- 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
- 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)
- 62. 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)
- 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
- 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/
- 65. 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
  - 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
- M. Tennekes, tmap: Thematic maps in R, Journal of Statistical Software 84(6), 1 (2018). DOI 10.18637/jss.v084.i06

555

560

565

570

575

- T. Giraud, N. Lambert, Cartography: Create and Integrate Maps in your R Workflow 1(4), 54. DOI 10.21105/joss.00054
- 69. H. Wickham, Ggplot2: Elegant Graphics for Data Analysis (Springer, New York, 2016)
- 70. D. Dunnington, ggspatial: Spatial Data Framework for ggplot2 (2020). URL https://CRAN.R-project.org/package=ggspatial. R package version 1.1.4
- 71. 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
- 72. 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
- 73. T. Morgen-Wall. Rayshader: Create Maps and Visualize Data in 2D and 3D. R package version 0.19.2. <a href="https://CRAN.R-project.org/package=rayshader">https://CRAN.R-project.org/package=rayshader</a>>. URL https://CRAN.R-project.org/package=rayshader
- 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)
- 75. E. Gustafson, Quantifying landscape spatial pattern: What is the state of the art?, Ecosystems 1, 143 (1998)
- 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)
- 77. E. Uuemaa, Ü. Mander, R. Marja, Trends in the use of landscape spatial metrics as landscape indicators: A review, Ecological Indicators 28, 100 (2013)
- 78. 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)
- 79. 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. <a href="http://www.umass.edu/landeco/research/fragstats/fragstats.html">http://www.umass.edu/landeco/research/fragstats/fragstats.html</a>. University of Massachusetts (2012)
- 80. J.A. Kupfer, Landscape ecology and biogeography: Rethinking landscape metrics in a post-FRAGSTATS landscape, Progress in Physical Geography 36(3), 400 (2012)
- 81. 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)
- 82. 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-v
- 83. A. Smith, P. Zarnetske, K. Dahlin, A. Wilson, A. Latimer. Geodiv: Methods for Calculating Gradient Surface Metrics. R package version 0.2.0. <a href="https://CRAN.R-project.org/package=geodiv">https://CRAN.R-project.org/package=geodiv</a>. URL https://CRAN.R-project.org/package=geodiv
- 84. J. Nowosad, P. Gao, belg: A tool for calculating boltzmann entropy of landscape gradients, Entropy 22(9), 937 (2020). DOI 10.3390/e22090937. URL https://github.com/r-spatialecology/belg
- 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
- 86. 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
- 87. N. Zimmermann, T. Edwards, C. Graham, P. Pearman, J.C. Svenning, New trends in species distribution modelling, Ecography **33**(6), 985 (2010)
- 88. A. Guisan, W. Thuiller, N. Zimmermann, *Habitat Suitability and Distribution Models:* With Applications in R, 1st edn. (Cambridge University Press, Cambridge, UK, 2017). DOI 10.1017/9781139028271
- 89. 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

- 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, New York, USA, 2011), pp. 9–28. DOI 10.1007/978-1-4419-7390-0\_2
  - 91. S. Wood, Generalized Additive Models: An Introduction with R, 2nd edn. (Chapman & Hall/CRC, Boca Raton, USA, 2017)
- 92. D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4, Journal of Statistical Software 67(1) (2015)
  - 93. T. Therneau, B. Atkinson. Rpart: Recursive partitioning and regression trees. R package version 4.1-15. https://CRAN.R-project.org/package=rpart (2019)
  - 94. A. Liaw, M. Wiener, Classification and regression by randomForest, R News 2(3), 18 (2002)
  - 95. 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)
  - 96. S. Dray, A.B. Dufour, The ade4 package: Implementing the duality diagram for ecologists, Journal of Statistical Software **22**(4) (2007)
- 97. 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 (2019)
  - 98. 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)
  - 99. B. Naimi, M. Araújo, Sdm: A reproducible and extensible R platform for species distribution modelling, Ecography **39**(4), 368 (2016)
  - 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)
- 101. W. Thuiller, D. Georges, R. Engler, F. Breiner. Biomod2: Ensemble platform for species distribution modeling. R package version 3.4.6. https://CRAN.Rproject.org/package=biomod2 (2020)
  - E. Freeman, G. Moisen, PresenceAbsence: An R package for presence absence analysis, Journal of Statistical Software 23(11) (2008)
- 103. 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
  - 104. 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
- 105. 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
  - P. Taylor, L. Fahrig, K. Henein, G. Merriam, Connectivity is a vital element of landscape structure, Oikos 68(3), 571 (1993)
- 635 107. L. Tischendorf, L. Fahrig, On the usage and measurement of landscape connectivity, Oikos 90(1), 7 (2000)
  - P. Kindlmann, F. Burel, Connectivity measures: A review, Landscape Ecology pp. s10,980–008–9245–4 (2008)
- 109. F. Mestre, B. Silva. Lconnect: Simple Tools to Compute Landscape Connectivity
  Metrics. R package version 0.1.0. <a href="https://CRAN.R-project.org/package=lconnect">https://CRAN.R-project.org/package=lconnect</a>
  URL https://CRAN.R-project.org/package=lconnect
  - 110. O. Godínez-Gómez, C. Correa Ayram. Makurhini: Analyzing landscape connectivity. R package version 2.0.0 <a href="https://github.com/connectscape/Makurhini">https://github.com/connectscape/Makurhini</a> URL https://github.com/connectscape/Makurhini
- 111. A. Laita, J. Kotiaho, M. Mönkkönen, Graph-theoretic connectivity measures: What do they tell us about connectivity?, Landscape Ecology 26(7), 951 (2011)
  - 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)
- 113. G. Csardi, T. Nepusz, The igraph software package for complex network research, InterJournal Complex Systems, 1695 (2006)

- 114. 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)
- 115. J. van Etten, R Package gdistance: Distances and Routes on Geographical Grids, Journal Of Statistical Software 76(13) (2017)
  - 116. 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)
- 117. 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)
  - S. Manel, M. Schwartz, G. Luikart, P. Taberlet, Landscape genetics: Combining landscape ecology and population genetics, Trends in Ecology & Evolution 18(4), 189 (2003)
- 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)
  - R. Holderegger, H. Wagner, A brief guide to landscape genetics, Landscape Ecology 21(6), 793 (2006)
  - 121. P. Savary. Graph4lg: Build graphs for landscape genetics analysis. R package version 0.5.0. https://CRAN.R-project.org/package=graph4lg (2020)
    - 122. A. Adamack, B. Gruber, PopGenReport: Simplifying basic population genetic analyses in R, Methods in Ecology and Evolution 5(4), 384 (2014)
- 123. 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)
  - 124. 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)
- 125. 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
  - R. Gardner, B. Milne, M. Turnei, R. O'Neill, Neutral models for the analysis of broadscale landscape pattern, Landscape Ecology 1(1), 19 (1987)
  - 127. K. With, A. King, The use and misuse of neutral landscape models in ecology, Oikos **79**(2), 219 (1997)
  - 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
- 129. D. Dunnington. Ggspatial: Spatial Data Framework for ggplot2. R package version 1.1.4 <a href="https://CRAN.R-project.org/package=ggspatial">https://CRAN.R-project.org/package=ggspatial</a>. URL https://CRAN.R-project.org/package=ggspatial