Methods in Ecology and Evolution

Methods in Ecology and Evolution 2017, **8,** 1425–1432 doi: 10.1111/2041-210X.12750

APPLICATION

LandScape Corridors (LSCORRIDORS): a new software package for modelling ecological corridors based on landscape patterns and species requirements

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Summary

1. Maintaining connectivity is one of the main challenges for biodiversity conservation world-wide. Ecological corridors are important to maintain landscape connectivity, but their efficiency depends on landscape patterns and species responses at different spatial extents and landscape contexts.

2. We developed a new ecologically oriented free software package, LandScape Corridors (LSCORRIDORS), to improve ecological corridor design by considering biodiversity responses to landscape attributes at a variety of spatial extents. LandScape Corridors considers stochastic variation, species perception and landscape influence on organisms in the design of ecological corridors. In addition to the least cost path algorithm, we propose four different methods for the simulation of multiple-path functional ecological corridors. One method uses the information for each pixel separately, whereas the three other methods permit corridor simulation considering the landscape context at different spatial extents.

3. LandScape Corridors permits to simulate corridors for species with different requirements and considers that different species perceive and respond to the surrounding landscape in different ways, as many species may choose to move through areas that may not be the most permeable ones in the landscape. Two parameters in LSCORRIDORS modulate the stochasticity in corridors simulations. The first parameter is the level of variability added to the input resistance map in each simulation, resulting in more variable and spatially spread-out corridors. The other parameter is the spatial extent that may influence each pixel; larger extents result in larger spatial zones affecting each pixel during corridors simulations. In addition, when considering spatial influence, the simulations may be performed for species highly, medially or less sensitive to habitat quality.

4. Some currently available software are not free or depend on a paid GIS software to work. In addition, some software do not support large matrices in their simulations, limiting their use. LandScape Corridors is designed to deal with large rasters, is based on strictly freeware software, and is freely available online. This allows the users to implement new methods for modelling multi-scale and ecologically based corridors.

5. LandScape Corridors is a potential tool for the identification of protected areas, as corridor simulation considers species movement and landscape connectivity, essential characteristics to aid in large-scale biodiversity conservation, especially in anthropogenic landscapes. LandScape Corridors provides what we may call a zone for conservation, showing a set of connected areas in the landscape which may be ordered according to their potential for ecological corridors or which may be used as an aid for conservation strategies or ecological restoration projects.

Key-words: corridor modelling, landscape connectivity, landscape ecology, matrix permeability, species perception

Introduction

The reduction in landscape connectivity has negative impacts on biodiversity world-wide, as landscape connectivity is essential for population persistence due to dynamic processes such as recolonization, seasonal migration and dispersion (Tischendorf & Fahrig 2000; Rayfield, Fortin & Fall 2010; Beier *et al.* 2011). Thus, maintaining connectivity is one of the main challenges for biodiversity conservation (Castellón & Sieving 2006), particularly where other land uses, such as agricultural areas and transport infrastructure, are expanding and replacing natural habitats in short time spans.

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Ecologically and functionally efficient corridors are seen as conservation strategies to ensure landscape connectivity and have received much attention in the literature (Orrock & Danielson 2005; Damschen *et al*. 2006). Well-planned and well-managed corridors may facilitate species dispersal and the related processes such as gene flow and natural regeneration, and thus bring benefits to the local and regional biodiversity (Rosenberg, Noon & Meslow 1997).

However, the efficiency of this strategy depends not only on the existence of structural connections between habitat patches but also on habitat quality and spatial arrangement, stepping stones, matrix permeability and the target organisms' responses to these elements (Tischendorf & Fahrig 2000; Baum *et al*. 2004). Thus, for corridors to be truly functionally efficient, they must facilitate dispersal, which in turn enables flow of genetic information, and take into account species life-history requirements (Rosenberg, Noon & Meslow 1997).

Corridors delineation frequently considers species' movement capacities through heterogeneous landscapes. Generally, this is done by generating resistance surface maps, where pixels with high resistance values correspond to low likelihood of movement of a given species in the landscape and pixels with low resistance correspond to high likelihood of movement (Adriaensen *et al*. 2003). A set of least-cost path algorithms is then used to identify a swath of pixels corresponding to the lowest-cost path between pairs of points, patches or regions (Zeller, McGarigal & Whiteley 2012; Correa Ayram *et al*. 2015). In general, the higher the pixels' resistance, the lower the chances of a sequence of pixels being selected as good options for ecological corridor placement.

This resistance surface should reflect the species' movement capacity in the landscape based on behavioural and physiological aspects such as energy expenditure, mortality risk and willingness to cross a particular land use (Zeller, McGarigal & Whiteley 2012; Mateo-Sánchez *et al*. 2015). The generation of an appropriate resistance surface is a key part of ecological corridor design and, given the variety of approaches and the lack of information on how organisms respond to different land uses, is still under debate among corridor designers (Mateo-Sánchez *et al*. 2015).

While the use of expert knowledge remains the most used approach for resistance surface generation, it may not estimate precisely the landscape effects on animal movement, leading researchers to use empirical data to model habitat suitability of different land uses which is afterwards used to generate resistance surface maps (Zeller, McGarigal & Whiteley 2012; Correa Ayram *et al*. 2015). As land use and land cover maps are the most common input maps for landscape analysis worldwide, we need to be able to convert the land use and cover classes into ecologically meaningful resistance maps to generate the resistance maps for ecological modelling.

Seeking to contribute to ecologically based corridor simulation, we developed a free software package, LandScape Corridors (LSCORRIDORS), which aims to model multiple possible ecologically functional corridors between large sets of source and target areas at once, to maximize the possibilities for species movement. LSCORRIDORS introduces a new approach for ecological corridor design by including (i) stochastic variation in the resistance surface and (ii) landscape influence on organisms in the simulations. This stochastic variation is a combination of several parameters that the user can define before starting the simulations (see below; differences between LSCORRIDORS and other software are explored in Appendix S1 and Table S1, Supporting Information).

LandScape Corridors thus permits to identify conservation corridors, which may indicate possible priority areas for biodiversity conservation and regional or large-scale ecological restoration. The selection of these areas is one of the major challenges faced by decision makers confronted with agricultural expansion, deforestation and species extinctions.

We proposed four different methods for the simulation of ecologically functional corridors, all of which permit simulating multiple-path corridors. One method considers only the information for each pixel separately, whereas the three other methods also include the landscape context at larger spatial extents in the corridor simulations. Including landscape influence on resistance is particularly important because it permits to consider species with different levels of sensitivity to landscape modifications and to take their perceptual range into account.

The LSCORRIDORS software package

LandScape Corridors is a free software package developed in Python language. We built a simple-to-use Graphical User Interface (Fig. 1) that allows the user to store or load data (generally maps) using the free Geographic Information System GRASS GIS - Geographic Resources Analysis Support System (Neteler *et al*. 2012). LandScape Corridors software package is fully available online at GitHub (https://github.com/LEEClab/LS_CORRIDORS). Upgrades, demonstration maps, testing scripts and online tutorial are freely available at the GitHub server: https://github.com/LEEClab/LS_CORRIDORS/wiki.

The installation is very simple and having GRASS GIS version 7.0.X is the only requirement for running the software package. The current version of LSCORRIDORS operates in Ubuntu Linux and in Windows Vista, 7, 8 and 10 operational systems, but versions for Mac OS will also be made available in the near future. To ensure free copying, distribution and modifications of the software package and its source code, LSCORRIDORS is distributed under the terms of a GNU General Public License, version 2 (GPLv2; see http://www.gnu.org/licenses/).

Input and output data

The software package uses as input two raster maps loaded from the GRASS GIS interface or imported directly into LSCORRIDORS. The first map refers to a resistance surface representing how much the landscape facilitates or hampers individual movement, with lower resistance values corresponding to areas with a greater probability of a corridor route passing through them and higher values corresponding to a smaller

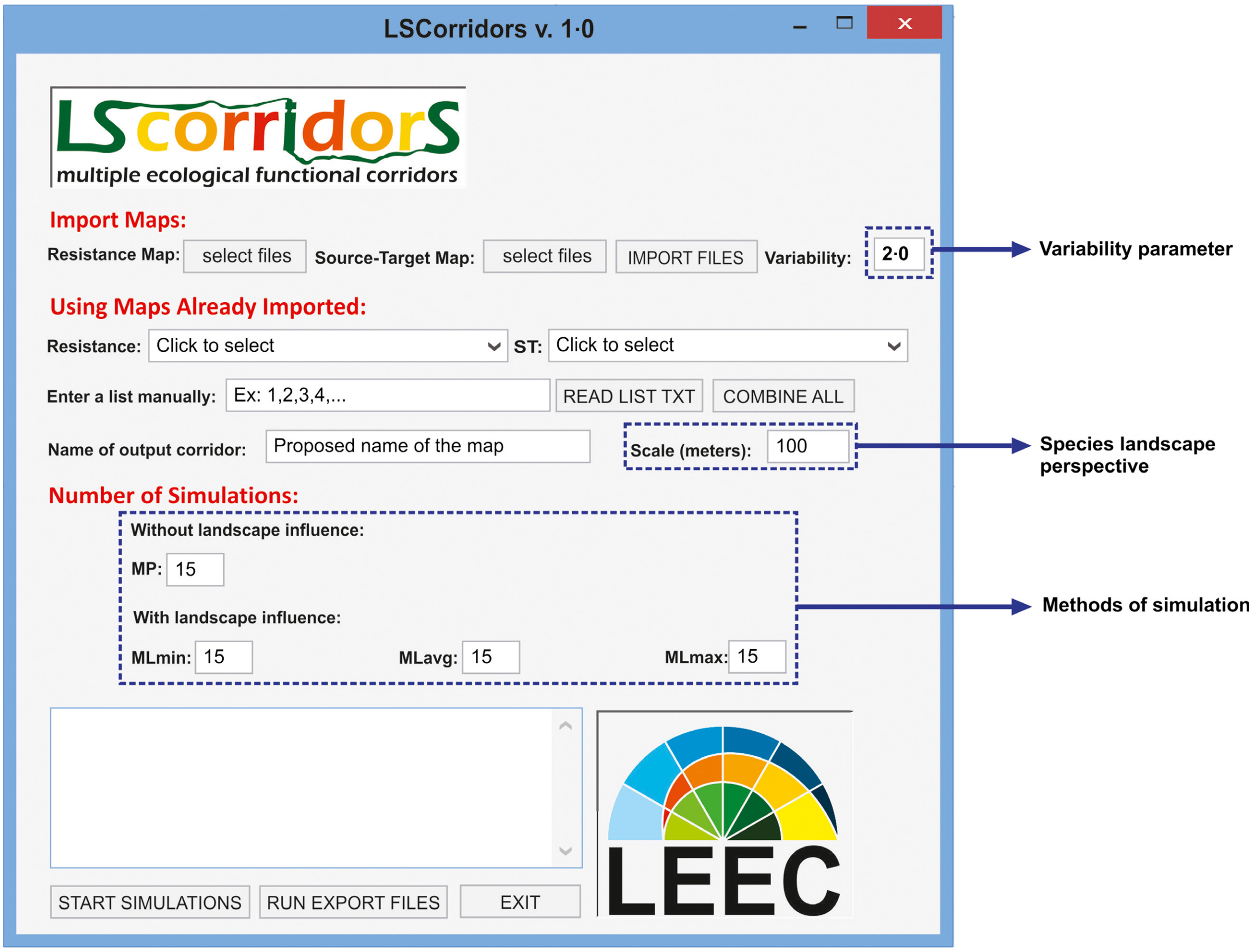

Fig. 1. LSCORRIDORS graphical user interface, with the main biological parameters highlighted. Each biological parameter is shortly explained in the LSCORRIDORS interface. First, it is necessary to run the GRASS interface and set the working directory. Second, it is necessary to run python command and to open the lscorridors.py file available at https://github.com/LEEClab/LS_CORRIDORS.

probability (Rayfield, Fortin & Fall 2010; Pinto, Keitt & Wainright 2012). The second raster map contains the identification of the pixels belonging to the source-target patches, i.e. the areas to be connected in the corridor simulations. The source-target patches may correspond to any land use for which a high connectivity is desirable and may contain different land uses (see the LSCORRIDORS tutorial for more details). LandScape Corridors then generates multiple-path corridor maps which include the perceptual range of species of interest in their modelling.

LandScape Corridors allows the user to simulate corridors between all possible source-target pairs or to choose which pairs will be connected in each simulation. The use of all possible source-target pairs can be very time-consuming depending on the raster dimension (number of rows and columns) and/or the number of patches, but is very useful when one wishes to simulate all the potential combinations to obtain nearly complete connection maps. This is aided by the large data support offered by LSCORRIDORS within GRASS GIS – for example we were able to simulate ecological corridors for the entire Atlantic Forest (Brazil) using an input raster map of 200 000 rows and 200 000 columns.

LandScape Corridors generates an output text file in '.txt' format containing one row for each simulation per input map and source-target pair. The output files contain: (i) resistance surface map name, (ii) variability parameter set by the user, (iii) scale parameter set by the user, (iv) modelling method (see next section), (v) number of the simulation, (vi) source and target patches linked by the corridor, (vii) length of the simulated path in metres, (viii) total cost of the simulated path, (ix) the minimum (Euclidean) distance between the source and target patches in metres and (x) the starting and ending geographical coordinates of the path (see the LSCORRIDORS tutorial for more details about these measures and their interpretation).

The software package also outputs raster corridor maps in '.tiff' format for each source-target pair for which corridors were simulated. LandScape Corridors sums all these maps to create a final map showing how many of the corridor simulations passed through each pixel of the map. We call these values the Route Selection Frequency Index (RSFI). High RSFI values indicate areas (pixels) that are more likely to be used as corridors according to species requirements included in the resistance surface and should therefore receive special attention of the decisions makers.

LSCORRIDORS methods for corridor simulation

The software package includes four different route simulation methods (MP, MLmin, MLavg and MLmax) to simulate ecological corridors considering different landscape influence and stochasticity parameters. MP considers only the individual pixels (therefore the 'P') of the resistance maps, whereas the ML methods consider the neighbouring pixels influencing a central pixel according to the species' perception of the landscape context ('L' stands for landscape). These latter methods are based on the assumption that different species may have adapted to the new environmental conditions and may move through a lower quality matrix, for example to move a smaller distance, to move faster or to obtain resources.

All four methods use the resistance surface map as basic input but add two sources of stochastic variation in the simulations, the amount of which may be determined by the user. The simulations are performed assuming that the organisms can leave from and move towards any location within the patches and that different species assume different risks of moving through a high-contrast matrix.

One source of variation is the use of different starting points within the source-target patches: each corridor simulation starts and ends in different points of the source-target patches, increasing the variability between the simulations. For this, in each simulation the software package randomly selects a pixel within the source and target patches, representing the potential departure and arrival points of the corridor in the given simulation. Thus, different routes are expected to begin and end at different points; the probability of the points coinciding in different simulations is small and for most cases the simulations are performed between different parts of the source-target patches.

This is similar to what occurs in real landscapes, where individuals do not depart from the same spot within the patch, partly because of variation in landscape perception among individuals and species. Instead, the individuals depart from different points within the patch and arrive at different points of the target patch, using different routes, some of which will not correspond to the least-cost path.

The second source of variation used in all simulation methods is described below (differences between the methods are explained below and further explored in Appendix S2).

The MP Method (Measures by Pixel): without spatial influence

We consider MP to be the simplest method. In this method, to add random variation to the resistance surface map, in each simulation the software package generates a map with uniformly distributed random values between 0 and 1 and multiplies this map by a variability parameter, which is an integer equal to or greater than 0 (when variability = 0, no stochasticity is added to the resistance surface). The software package then adds 1 to each value resulting from the multiplication, and the new random map is multiplied by the resistance surface map that has been defined by the user. In practice, if the variability parameter is represented by x, it means that the resistance value of each pixel is multiplied by a random value in the interval $[1, x + 1]$.

The default value of the variability parameter is 2·0, but this value may be altered by the user; high variability values introduce high spatial stochasticity in the simulated corridors, which would be particularly appropriate for generalist species. As the variability parameter increases, organisms tend to select different routes and the median cost of corridors tends to increase, as this variability increases the values of the resistance surface. More details on the effects of variability on the modelled corridors are shown in Appendix S2.

The variability parameter may represent uncertainty in the values used to produce the resistance surface. However, variability may also be used to represent the proneness of different species in using alternative routes while moving through the landscapes. In principle, modifying the resistance surface is the first (and most laborious) option to modelling connectivity for species that perceive the landscape differently.

A second option is to use the variability parameter, we suggest to use a larger variability parameter for species known to be less sensitive to anthropogenic modifications or that have been recorded to move through or be tolerant to the matrix. This is the case of individuals of species which tend to take greater risks and use alternative and more variable routes not necessarily corresponding to the least-cost path in the landscape.

Including spatial context in corridor modelling: ML (Measures by Landscape) Methods MLmin, MLavg and MLmax

The other methods proposed are based on the same changes to the surface resistance map, but consider biological information by including landscape metrics. In the MLmin, MLavg and MLmax methods the pixels of the input resistance surface are replaced by the minimum (min), average (avg) or maximum (max) value of the surrounding pixels within a certain window radius. Window size, in metres, is defined by the user and can be thought of as the spatial perceptual range of the species being modelled. We recommend to base the window size on the species' landscape perception (see more details in Appendix S2), estimated, for example from their movement capacity or home range size (Mcgarigal, Zeller & Cushman 2016).

Comparison between the four simulation methods

We compared the results between the four methods implemented in LSCORRIDORS by simulating ecological corridors between 22 source-target pairs corresponding to protected areas distributed throughout the Brazilian Atlantic Forest biome (Fig. 2). The entire biome covers an area of 150 million hectares (Ribeiro *et al.* 2009), and we used as input a large raster map with a resolution of 30 m, 200 000 rows and 200 000 columns (see Appendix S3 for details about the simulation).

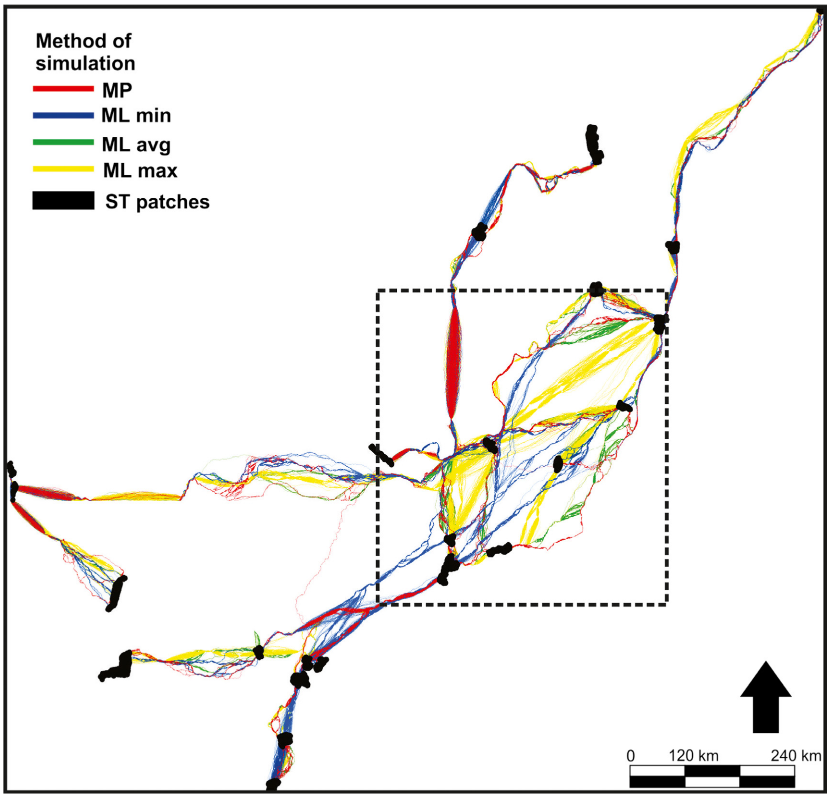

Fig. 2. Corridors simulated with LSCORRIDORS showing the corridors simulated with different methods, where each line colour corresponds to one different method. The dashed line corresponds to the area shown in Fig. 3.

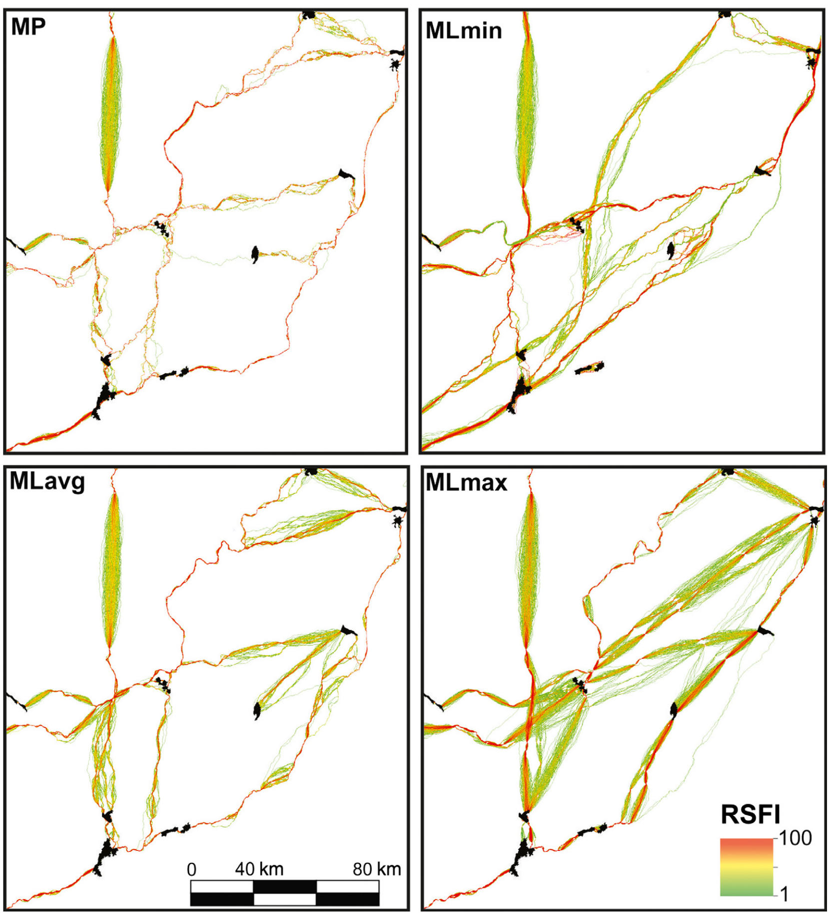

Fig. 3. Corridors simulated with LSCORRIDORS using 22 source-target patches, with 100 simulations per pair. The black areas correspond to the source-target patches. The coloured areas illustrate the difference between the MP, MLmin, MLavg and MLmax methods, where the areas represented by warm colours correspond to higher Route Selection Frequency Index (RSFI) values.

We processed 100 simulations per source-target pair for each simulation method, resulting in a total of 8800 simulated corridors.

Considering that the users can set the number of simulations per method, this number can increase substantially the representativeness of our findings to emphasize LSCORRIDORS' potential for robust processing. Our resistance surface was a map of matrix permeability relative to a hypothetical species with high sensibility to anthropogenic alterations and a landscape perception of 1000 m (see Appendix S3 for details about the resistance surface). Further comparisons between the models are presented in Figs. 2–4.

The different methods generated different routes for the same source-target simulation pairs (Figs. 2 and 3), including more variability in the multiple path algorithm and increasing its potential for ecological analyses. The overlap of the most selected routes among the methods was low, as shown by the low correlation values between RSFI values (Fig. 4c). As expected, corridor cost and length were maximized for the MLmax and minimized for MLmin, which consider, respectively, the maximum and minimum values around each pixel is considered (Fig. 3a,b).

The MLavg and MP methods, which consider the average and the original values of the resistance map, presented

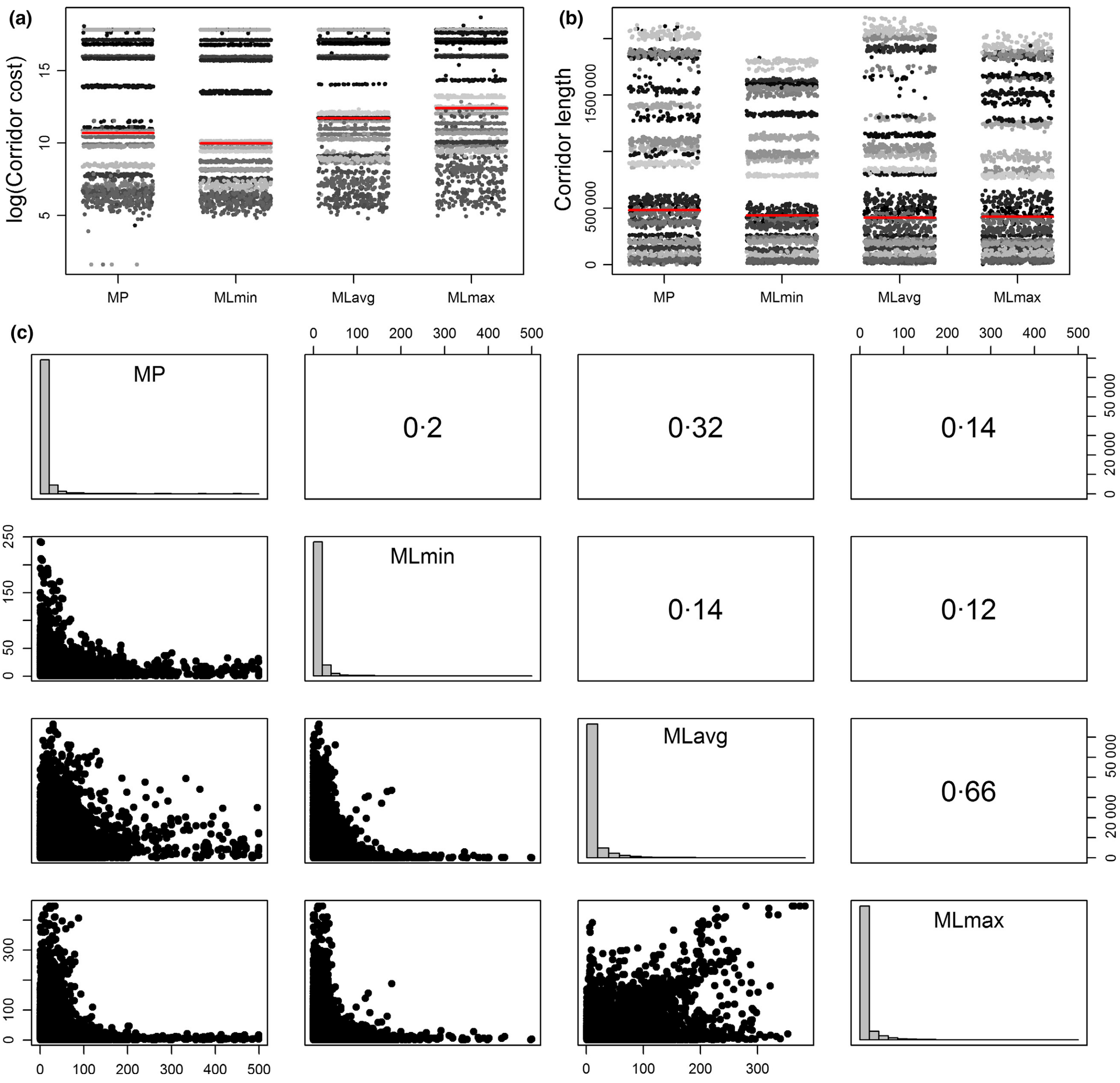

Fig. 4. Jitter plots of the cost (a) and length (b) of the corridors routes provided by LSCORRIDORS using the four different methods and (c) pair plots, histograms and Pearson correlation coefficients of the RSFI values obtained with the different methods. In the jitter plots, each point corresponds to one corridor and the shades of grey represent the different source-target patches. In the pair plots each point corresponds to different pixels in the landscape. Cost refers to the cost value of the pixels through which the least cost routes pass and corridor length refers to the length of corridor routes simulated by the algorithm.

intermediate values for the median corridor cost and length. Interestingly, although MLavg and MLmax corridor costs were very different, some of the areas selected as potential ecological corridors coincide more than for the other methods, as reflected by the higher correlation between these two methods (Fig. 4c, Figs. S2-8 and S2-9). For all ML methods corridor cost and length tend to decrease as the scale of influence increases (Figs. S2-6 to S2-9), which reflects the optimization organisms may perform when they have a broader perception of the landscape context and may choose the most effective among a wide set of distinct routes.

We propose that the MP, MLmin and MLavg methods can be used for generalist species that tend to move or disperse more easily through the landscape to obtain resources (Ye, Skidmore & Wang 2014). These methods provide a zone, with the inclusion of a larger number of alternative routes, attributing much importance to the surrounding land uses. These methods also can consider the use or adaptation of such species to the matrix (Umetsu & Pardini 2007; Umetsu, Metzger & Pardini 2008; Gheler-Costa *et al*. 2012; Kay *et al*. 2016). In turn, the MLmax method seems to be more suitable for specialist species. This method generates restrictive corridor routes, most of which pass through areas around which the least suitable land uses have smaller resistance values than in other areas (i.e. lower resistance values within the specified window size).

However, the successful application of these methods depends on the definition of the resistance surface maps, which in turn relies on expert knowledge of species characteristics such as movement capacity and matrix tolerance or, in the best case, on habitat preference and/or movement information obtained from empirical studies. Even though we suggest the use of specific methods for different species and landscape contexts, we do believe that the use of more than one method in the same simulations can improve the outcome by adding more corridor variability and thus reflecting differences between individuals and the effects of stochastic factors.

We conclude that LSCORRIDORS may be a powerful alternative to improve the simulation of multiple corridors using least-cost path algorithm (see Pinto, Keitt & Wainright 2012) and to indicate ways of increasing landscape functional connectivity, as it includes landscape influence on different species and stochasticity in the models. Our software package is not limited to small datasets and presents a great opportunity for understanding ecological processes related to movement and dispersal at large scales, with potential for different applications for conservation purposes.

The fact that LSCORRIDORS uses only open-source software and languages (GRASS GIS and Python) will surely increases the use of this tool for both users and programmers worldwide, enabling it to be adapted for a large range of situations and purposes.

Authors' contributions

J.W.R., J.S.d.S. and M.C.R. dedicated equally efforts to all steps of the manuscript preparation, including software conception, programming, code tests, writing the paper, preparing the figures and manuscript revision; P.D. assisted with writing the paper, preparing the figures and supplementary material, organizing the LSCORRIDORS tutorial and manuscript revision; F.M. assisted with the LSCORRIDORS tutorial, supplementary material and manuscript revision; B.B.N. contributed with the upgraded of LSCORRIDORS code, organized the online tutorial (wiki), prepared the supplementary material, made the unit test, ran the LSCORRIDORS simulations and contributed with manuscript revision.

Acknowledgements

This work was supported by FAPESP (2013/50421-2) and Microsoft Azure Cloud Computing for Research. We thank the members of the Spatial Ecology and Conservation Laboratory (LEEC) for testing previous versions of LSCORRIDORS and suggestions on new landscape metrics calculations and the editor and reviewers for helpful suggestions to the manuscript and software package. M.C.R. and J.S.d.S. received research and postdoctoral grants from the National Council for Scientific and Technological Development (CNPq, process 312045/2013-1). P.D., B.B.N. and F.M. were funded by the Coordination for the Improvement of Higher Education Personnel (CAPES).

Data accessibility

No empirical data were used for this manuscript. The maps used for the simulations are available at https://doi.org/10.5061/dryad.r7kj2 (Ribeiro *et al*. 2017).

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Received 12 November 2016; accepted 5 January 2017
Handling Editor: Timothée Poisot

Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. The material shows a brief comparison between LSCORRIDORS and other softwares also simulate ecological corridors, highlighting the positives and negatives characteristics of the softwares. The LSCORRIDOR's methods are compared with the other softwares.

Appendix S2. The material describe with details as the parameters and LSCORRIDOR's methods works, and as the different methods can be applied to simulate ecological corridors. We made a comparison between LSCORRIDORS methods proposed, based in a case study.

Appendix S3. Details about the data source and parameters used to simulate the ecological corridors showed in the manuscript.