Documentation

# Reconnect approach

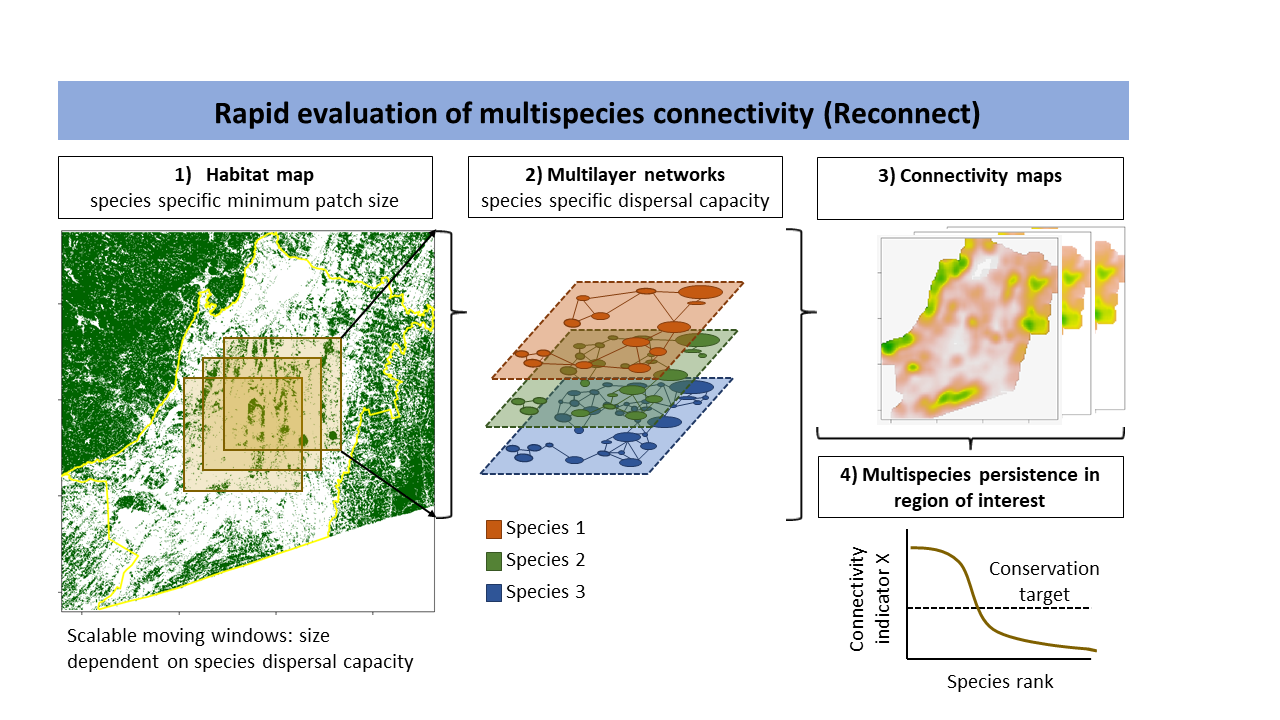
Jacqueline Oehri

22.03.2024

The “Rapid Evaluation of Multispecies Connectivity” (Reconnect) approach, is a scalable and generalizable workflow to rapidly generate and evaluate ensemble connectivity maps for a range of species with different habitat needs, in order to support spatial prioritization for connectivity conservation management.

## Approach Overview

The Reconnect approach (Figure 1) allows for the simultaneous computation of connectivity indicators (Table 1) for multiple species based on simple habitat distribution maps and a parallel implementation of moving windows. Connectivity results in moving windows can be aggregated to generate ensemble connectivity maps at pixel-, patch-, or landscape-level. Finally, connectivity results for multiple species can be evaluated by ranking connectivity values for each species in any region of interest and comparison with a target connectivity value (“Conservation target” in Figure 1).

****

**Figure 1. Rapid Evaluation of Multispecies Connectivity (Reconnect) approach. 1)** The basic data input for the Reconnect approach is a species (or ecoprofile) specific, binary habitat map that can be determined *a priori*[*1–4*](https://sciwheel.com/work/citation?ids=4390866,4390644,14422470,11811379&pre=&pre=&pre=&pre=&suf=&suf=&suf=&suf=&sa=0,0,0,0) or *a posteriori* from species distribution models[5–9](https://sciwheel.com/work/citation?ids=11811510,14049286,6916836,14055707,14055710&pre=&pre=&pre=&pre=&pre=&suf=&suf=&suf=&suf=&suf=&sa=0,0,0,0,0). Note that maps of protected areas or other effective area-based conservation measures (OECMs) could be used as well[10,11](https://sciwheel.com/work/citation?ids=12284564,9647917&pre=&pre=&suf=&suf=&sa=0,0). **2)** Multiple habitat maps can be “stacked” and multilayer habitat networks[10,12,13](https://sciwheel.com/work/citation?ids=12284564,3348050,7542224&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0) can be extracted, in which links between habitat patches are determined using estimates of species-specific dispersal capacities[10](https://sciwheel.com/work/citation?ids=12284564&pre=&suf=&sa=0). These multilayer habitat networks can be computed in moving windows of relevant size[14](https://sciwheel.com/work/citation?ids=12682856&pre=&suf=&sa=0) and variable spatial overlap[15](https://sciwheel.com/work/citation?ids=14424486&pre=&suf=&sa=0). **3)** Multiple connectivity functions can be defined in a simple inifile and computed simultaneously for multiple species in the moving windows. Moving window results can then be aggregated into mosaics, i.e. coherent maps of connectivity at pixel-level, patch-level or landscape-level[16](https://sciwheel.com/work/citation?ids=14606681&pre=&suf=&sa=0) for the species of interest. **4)** The resulting maps can be used to evaluate multiple connectivity indicators for the multiple species, for example by ranking species connectivity values and comparing them with *a priori* definitions of a target connectivity value (“Conservation target” in Figure 1). This approach allows to summarize the number or fraction of species deviating from target connectivity values and allows the identification of vulnerable species with critically low connectivity values in any region of interest.

## Reconnect R-tool

The Reconnect approach is implemented in the **Reconnect R-tool**, which works with one inifile and four sets of functions:

1. inifile (Reconnect\_inifile.xlsx): where connectivity functions, dispersal capacities and habitat needs can be specified. Any function that takes either a binary habitat raster and optionally, resistance surface (e.g. “.tif”), shapefile (e.g. “.shp”), vector of patch areas and distance matrices as input (e.g. “.csv”) can be specified.
2. Reconnect\_functions

Reconnect - core, wrapper and summary functions, as well as general functions for processing geographic data.

* wrapper function (Reconnect\_wrap): specifies scale (window size), resolution in and increment of moving windows, which are computed with a parallel implementation[17](https://sciwheel.com/work/citation?ids=14439892&pre=&suf=&sa=0). The defined spatial grain and extent in any connectivity assessment should match the species and conservation needs of interest[14,16](https://sciwheel.com/work/citation?ids=14606681,12682856&pre=&pre=&suf=&suf=&sa=0,0). For example, the side length of square moving windows could be set to 8,700 m (radius = 4,350 m), which results in landscape areas of ~75 km2, similar to what has been used in previous research[14,18,19](https://sciwheel.com/work/citation?ids=10756785,12682856,12682852&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0). A window overlap of 1,500 m allows for landscape-level connectivity maps at an effective resolution of 1.5 km. Dividing the study area into non-overlapping spatial planning units[19](https://sciwheel.com/work/citation?ids=12682852&pre=&suf=&sa=0) is also possible and less computationally demanding.
* core function (Reconnect\_core): applying connectivity functions (inifile) in moving windows. **Within moving windows, multilayer habitat networks**[**10,20**](https://sciwheel.com/work/citation?ids=187121,12284564&pre=&pre=&suf=&suf=&sa=0,0) can be extracted based on species-specific habitat needs and dispersal capacities. Hence, in one run, connectivity values for multiple species can be generated simultaneously.
* summary function (Reconnect\_summary): aggregating moving window results into a coherent raster or shapefile. **Output can be generated at the pixel-level, patch-level or landscape-level,** depending on the connectivity function (see below).

1. CONN\_functions

Functions for calculating a set of connectivity indicators (Table 1). **Distances** can be calculated from edge to edge or centroid to centroid, and can be measured as Euclidean or resistance (if a resistance layer is provided). **Dispersal probabilities** depend on a distance (d) and a dispersal capacity (𝞪) in one of three common dispersal probability functions:

* negative exponential[10,19,21](https://sciwheel.com/work/citation?ids=12682852,12284564,14607060&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0)

(1)

, where describes the probability of dispersing between patch i and j, 𝜶 is usually the species-specific mean gap crossing distance[10,21,22](https://sciwheel.com/work/citation?ids=296054,12284564,14607060&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0) and *dij* is the distance between patch *i* and patch *j* in the habitat network.

* linear decay[19](https://sciwheel.com/work/citation?ids=12682852&pre=&suf=&sa=0)

(2)

, where describes the probability of dispersing between patch i and j, 𝜶 is usually the species-specific maximum gap crossing distance[10,21,22](https://sciwheel.com/work/citation?ids=296054,12284564,14607060&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0) and *dij* is the distance between patch *i* and patch *j* in the habitat network.

* log-sech[18,23](https://sciwheel.com/work/citation?ids=10756785,187166&pre=&pre=&suf=&suf=&sa=0,0)

(3)

where describes the probability of dispersing between patch i and j, 𝜶 is usually the species-specific mean gap crossing distance[10,21,22](https://sciwheel.com/work/citation?ids=296054,12284564,14607060&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0), 𝜷 describes the tail of the dispersal kernel (by default set to 1.77)[23](https://sciwheel.com/work/citation?ids=187166&pre=&suf=&sa=0) and *dij* is the distance between patch *i* and patch *j* in the habitat network.

* quantile[1,24,25](https://sciwheel.com/work/citation?ids=4390866,3741563,2780322&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0)

(4)

, where describes the probability of dispersing between patch i and j, *dij* is the distance between patch *i* and patch *j* in the habitat network and 𝜶 is usually the species-specific median or maximum gap crossing distance, associated with a median or maximum quantile (e.g. 0.5 and 0.1, respectively). The quantile value describes the probability covered by the “tail-distance” on the flat tail of the dispersal-distance function[1,24,25](https://sciwheel.com/work/citation?ids=4390866,3741563,2780322&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0).

1. MPC\_functions

Functions for calculating metapopulation capacity (MPC) and -related indices from binary habitat distribution maps (Table 1). Distances and dispersal probabilities can be calculated as in “CONN\_functions”. A detailed report on the metapopulation capacity indicator and related indices can be accessed here: https://oehrij.shinyapps.io/MPC\_report/

1. NLMC\_functions

Functions for generating simulated and neutral landscapes that are based on the algorithm by Saura and Martinez-Millan 2000[26](https://sciwheel.com/work/citation?ids=14059097&pre=&suf=&sa=0) implemented in the R-package NLMR[27](https://sciwheel.com/work/citation?ids=14657000&pre=&suf=&sa=0).

## Connectivity Indicators

This set of connectivity indicators can be calculated by using the “CONN\_functions” and “MPC\_functions” in the Reconnect R-tool, on the basis of habitat or protected area distribution maps, species-specific habitat needs and dispersal capacities.

**Table 1. Selected key-set of connectivity indicators**. Distance type: can be Euclidean or scaled by a resistance surface[1](https://sciwheel.com/work/citation?ids=4390866&pre=&suf=&sa=0),[28](https://sciwheel.com/work/citation?ids=14049335&pre=&suf=&sa=0),[5](https://sciwheel.com/work/citation?ids=11811510&pre=&suf=&sa=0). Scale: the scale at which indicator is typically calculated (pixel-, patch-, or landscape-level). Landscape-level indicators can also be calculated at patch level using the “general patch importance” computation (**Ipi**), or in the case of metapopulation capacity, the dominant eigenvector value for patch i (**λi**). Note that patch-level indicators can usually be aggregated at the landscape-level, using any aggregation function of interest (e.g. mean, range, variation). Note that the Reconnect approach (Figure 1) is not limited to these indicators but can be implemented with any connectivity indicator that is computable on the basis of habitat, protected area or resistance surface maps.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Nr** | **Abbre-viation** | **Description** | **Formula** | **Unit [value range]** | **Interpretation** | **Scale and distance type** |
| **1** | **MPC** | Metapopulation Capacity[22,29,30](https://sciwheel.com/work/citation?ids=296054,577280,12682833&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0) | , where 𝞴m is the leading eigenvalue of a square ‘landscape matrix’ m, in which elements mij reflect rates of change for the occupancy of patches i (pi) as a function of patch attributes (often patch area in m2, ai and aj), a dispersal probability function of interpatch distance f(dij) and an extinction probability constant x (commonly set to 0.5). | no unit  [0,𝜆max]  , where 𝞴max corresponds to the leading eigenvalue of the maximum landscape matrix, i.e. where the rates of change of patch occupancy is 1 for all patches. | -metapopulation carrying capacity, based on area and connectance of habitat  -focus on potential long-term species persistence[22,29,30](https://sciwheel.com/work/citation?ids=296054,577280,12682833&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0) | - landscape  - Euclidean and resistance |
| **2** | **ECA** | Equivalent Connected Area index[31](https://sciwheel.com/work/citation?ids=3610800&pre=&suf=&sa=0), based on the probability of connectivity index (PC[32](https://sciwheel.com/work/citation?ids=960796&pre=&suf=&sa=0)) | , where n is the total number of habitat patches in the landscape, ai and aj are attributes of habitat patches i and j (commonly area) and pij\* is the maximum product probability of dispersal between patches i and j. | unit of a (e.g. area) [0,Al]  , where Al is the attribute (e.g. area) of the entire landscape. | * the size of a single habitat patch that would provide the same probability of connectivity than the actual habitat pattern in the landscape[31](https://sciwheel.com/work/citation?ids=3610800&pre=&suf=&sa=0) * focus on connectivity of habitat, and potential species dispersal | - landscape  - Euclidean and resistance |
| **3** | **ECAAp** | Fraction of habitat that is connected (ECA divided by the total habitat area) | , where Ap is the total area of habitat in a given landscape. | no unit  [0,1] | * size of equivalent connected area (ECA) relative to maximum possible with a given habitat area * focus on underused connectivity potential | - landscape  - Euclidean and resistance |
| **4** | **ECAAl** | Fraction of habitat that is connected (ECA divided by the total landscape area, cf. ProtConn[33](https://sciwheel.com/work/citation?ids=3610797&pre=&suf=&sa=0) index) | , where Al is the total area of a given landscape. | no unit  [0,1] | -size of equivalent connected area (ECA) relative to maximum possible in a landscape  -focus on underused connectivity potential | - landscape  - Euclidean and resistance |
| **5** | **BC** | Betweenness centrality[1,34](https://sciwheel.com/work/citation?ids=4390866,1908200&pre=&pre=&suf=&suf=&sa=0,0),[35](https://sciwheel.com/work/citation?ids=1907383&pre=&suf=&sa=0) | , where givj is the total number of shortest paths between each pair of habitat patches ij going through a focal patch v in the habitat network. gij, is the total number of all the shortest paths between each pair of habitat patches ij in the habitat network. | no unit  [0,]  , where n corresponds to the number of patches in the landscape. | -number of shortest paths between each pair of habitat patches passing through a focal patch  -focus on the degree to which a habitat patch is a stepping stone at short and long distances in the habitat network[36](https://sciwheel.com/work/citation?ids=10896670&pre=&suf=&sa=0) | - patch  - Euclidean and resistance |
| **6** | **ND** | Node Degree[37](https://sciwheel.com/work/citation?ids=3953810&pre=&suf=&sa=0) | , where evj denotes a habitat patch j connected to the focal patch v. A habitat patch can be considered connected (evj = 1) if pij\*, the maximum product probability of dispersal between patches j and v is greater than a threshold probability c. | no unit  [0,n-1]  , where n corresponds to the number of patches in the landscape. | -number of other habitat patches connected to a focal patch  -focus on the number of patches reachable within a given distance[37](https://sciwheel.com/work/citation?ids=3953810&pre=&suf=&sa=0), the degree to which a patch is a stepping stone at short distances in the habitat network | - patch  - Euclidean and resistance |
| **7** | **invCR** | Omnidirectional inverse cumulative resistance[1](https://sciwheel.com/work/citation?ids=4390866&pre=&suf=&sa=0) | , where n is the number of pairs of locations selected in a given landscape and CRk is the cumulative resistance of the shortest paths between each pair of locations k. | variable unit  (0,+∞) | -ease of traversability of the landscape  -focus on contribution to global, omnidirectional connectivity | - pixel and landscape  - resistance |
| **8** | **Irel** | Indicator value relative to minimum threshold[14,30,38](https://sciwheel.com/work/citation?ids=12682833,12682858,12682856&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0) | , where I is the indicator value of the entire habitat network in a landscape and Imin is the estimated minimum value required for species persistence. | no unit  [0,+∞) | -indicator value, relative to an estimated minimum for species persistence  -focus on potential species persistence[22,29,30](https://sciwheel.com/work/citation?ids=296054,577280,12682833&pre=&pre=&pre=&suf=&suf=&suf=&sa=0,0,0) | - landscape  - Euclidean and resistance |
| **9** | **Iv** | General estimate of patch importance[32](https://sciwheel.com/work/citation?ids=960796&pre=&suf=&sa=0) | , where I is an index value when habitat patch v is present and I′ is the same index value when patch v is not present in the landscape. | no unit  [0,100] | -the degree to which a patch contributes to the connectivity value of the habitat network | - patch  - Euclidean and resistance |
| **10** | **MPCi** | Patch importance: leading eigenvector at position i[22](https://sciwheel.com/work/citation?ids=296054&pre=&suf=&sa=0) | , where 𝞴mi is the leading eigenvector at position i, for patch i of a square ‘landscape matrix’ m, in which elements mij reflect rates of change for the occupancy of patches i (pi). ai and aj are patch attributes (often patch area in m2), f(dij) is a dispersal probability function of interpatch distance x denotes an extinction probability constant (commonly set to 0.5). | no unit  [0,𝜆max]  , where 𝞴max corresponds to the leading eigenvalue of the maximum landscape matrix, i.e. where the rates of change of patch occupancy is 1 for all patches. | -the degree to which a patch contributes to the metapopulation capacity value of the habitat network | - patch  - Euclidean and resistance |

#### 

## References

[Bibliography](https://sciwheel.com/work/bibliography)

[1. Albert, C. H., Rayfield, B., Dumitru, M. & Gonzalez, A. Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change. *Conserv. Biol.* **31**, 1383–1396 (2017).](https://sciwheel.com/work/bibliography/4390866)

[2. Rayfield, B., Pelletier, D., Dumitru, M., Cardille, J. A. & Gonzalez, A. Multipurpose habitat networks for short-range and long-range connectivity: a new method combining graph and circuit connectivity. *Methods Ecol. Evol.* **7**, 222–231 (2016).](https://sciwheel.com/work/bibliography/4390644)

[3. Rayfield, B., Larocque, G., Daniel, C. & Gonzalez, A. Une priorisation pour la conservation des milieux naturels des Basses-Terres du Saint-Laurent en fonction de leur importance pour la connectivité.](https://sciwheel.com/work/bibliography/14422470)

[4. Meurant, M., Gonzalez, A., Doxa, A. & Albert, C. H. Selecting surrogate species for connectivity conservation. *Biol. Conserv* **227**, 326–334 (2018).](https://sciwheel.com/work/bibliography/11811379)

[5. Shahnaseri, G. *et al.* Contrasting use of habitat, landscape elements, and corridors by grey wolf and golden jackal in central Iran. *Landscape Ecol.* **34**, 1263–1277 (2019).](https://sciwheel.com/work/bibliography/11811510)

[6. Salgueiro, P. A. *et al.* Multispecies landscape functional connectivity enhances local bird species’ diversity in a highly fragmented landscape. *J. Environ. Manage.* **284**, 112066 (2021).](https://sciwheel.com/work/bibliography/14049286)

[7. Tarabon, S., Bergès, L., Dutoit, T. & Isselin-Nondedeu, F. Environmental impact assessment of development projects improved by merging species distribution and habitat connectivity modelling. *J. Environ. Manage.* **241**, 439–449 (2019).](https://sciwheel.com/work/bibliography/6916836)

[8. Liu, C., Newell, G., White, M. & Bennett, A. F. Identifying wildlife corridors for the restoration of regional habitat connectivity: A multispecies approach and comparison of resistance surfaces. *PLoS ONE* **13**, e0206071 (2018).](https://sciwheel.com/work/bibliography/14055707)

[9. Rezaei, S., Mohammadi, A., Malakoutikhah, S. & Khosravi, R. Combining multiscale niche modeling, landscape connectivity, and gap analysis to prioritize habitats for conservation of striped hyaena (Hyaena hyaena). *PLoS ONE* **17**, e0260807 (2022).](https://sciwheel.com/work/bibliography/14055710)

[10. Hartfelder, J. *et al.* The allometry of movement predicts the connectivity of communities. *Proc Natl Acad Sci USA* **117**, 22274–22280 (2020).](https://sciwheel.com/work/bibliography/12284564)

[11. Ward, M. *et al.* Just ten percent of the global terrestrial protected area network is structurally connected via intact land. *Nat. Commun.* **11**, 4563 (2020).](https://sciwheel.com/work/bibliography/9647917)

[12. Pilosof, S., Porter, M. A., Pascual, M. & Kéfi, S. The multilayer nature of ecological networks. *Nat. Ecol. Evol.* **1**, 101 (2017).](https://sciwheel.com/work/bibliography/3348050)

[13. Hutchinson, M. C. *et al.* Seeing the forest for the trees: putting multilayer networks to work for community ecology. *Funct. Ecol.* (2018) doi:10.1111/1365-2435.13237.](https://sciwheel.com/work/bibliography/7542224)

[14. Drielsma, M. & Ferrier, S. Rapid evaluation of metapopulation persistence in highly variegated landscapes. *Biol. Conserv* **142**, 529–540 (2009).](https://sciwheel.com/work/bibliography/12682856)

[15. Koen, E. L., Ellington, E. H. & Bowman, J. Mapping landscape connectivity for large spatial extents. *Landscape Ecol.* **34**, 2421–2433 (2019).](https://sciwheel.com/work/bibliography/14424486)

[16. Fletcher, R. J. *et al.* Addressing the problem of scale that emerges with habitat fragmentation. *Global Ecol. Biogeogr.* (2023) doi:10.1111/geb.13658.](https://sciwheel.com/work/bibliography/14606681)

[17. Hughes, J. *et al.* Comparison and Parallel Implementation of Alternative Moving-Window Metrics of the Connectivity of Protected Areas Across Large Landscapes. *Res. Sq.* (2022) doi:10.21203/rs.3.rs-2097460/v1.](https://sciwheel.com/work/bibliography/14439892)

[18. Huang, R., Pimm, S. L. & Giri, C. Using metapopulation theory for practical conservation of mangrove endemic birds. *Conserv. Biol.* **34**, 266–275 (2020).](https://sciwheel.com/work/bibliography/10756785)

[19. Strimas-Mackey, M. & Brodie, J. F. Reserve design to optimize the long-term persistence of multiple species. *Ecol. Appl.* **28**, 1354–1361 (2018).](https://sciwheel.com/work/bibliography/12682852)

[20. Gonzalez, A., Rayfield, B. & Lindo, Z. The disentangled bank: how loss of habitat fragments and disassembles ecological networks. *Am. J. Bot.* **98**, 503–516 (2011).](https://sciwheel.com/work/bibliography/187121)

[21. Moilanen, A. & Nieminen, M. SIMPLE CONNECTIVITY MEASURES IN SPATIAL ECOLOGY. *Ecology* (2002).](https://sciwheel.com/work/bibliography/14607060)

[22. Hanski, I. & Ovaskainen, O. The metapopulation capacity of a fragmented landscape. *Nature* **404**, 755–758 (2000).](https://sciwheel.com/work/bibliography/296054)

[23. Van Houtan, K. S., Pimm, S. L., Halley, J. M., Bierregaard, R. O. & Lovejoy, T. E. Dispersal of Amazonian birds in continuous and fragmented forest. *Ecol. Lett.* **10**, 219–229 (2007).](https://sciwheel.com/work/bibliography/187166)

[24. Urban, D. & Keitt, T. LANDSCAPE CONNECTIVITY: A GRAPH-THEORETIC PERSPECTIVE. *Ecology* **82**, 1205–1218 (2001).](https://sciwheel.com/work/bibliography/3741563)

[25. Moilanen, A. *et al.* Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proc. Biol. Sci.* **272**, 1885–1891 (2005).](https://sciwheel.com/work/bibliography/2780322)

[26. Saura, S. & Martínez-Millán, J. Landscape patterns simulation with a modified random clusters method. *Springer Science and Business Media LLC* **15**, 661–678 (2000).](https://sciwheel.com/work/bibliography/14059097)

[27. Sciaini, M., Fritsch, M., Scherer, C. & Simpkins, C. E. *NLMR* and*landscapetools* : An integrated environment for simulating and modifying neutral landscape models in R. *Methods Ecol. Evol.* **9**, 2240–2248 (2018).](https://sciwheel.com/work/bibliography/14657000)

[28. Chubaty, A. M., Galpern, P. & Doctolero, S. C. Ther toolboxgrainscape for modelling and visualizing landscape connectivity using spatially explicit networks. *Methods Ecol. Evol.* (2020) doi:10.1111/2041-210X.13350.](https://sciwheel.com/work/bibliography/14049335)

[29. Hanski, I. A Practical Model of Metapopulation Dynamics. *The Journal of animal ecology* **63**, 151 (1994).](https://sciwheel.com/work/bibliography/577280)

[30. Schnell, J. K., Harris, G. M., Pimm, S. L. & Russell, G. J. Estimating extinction risk with metapopulation models of large-scale fragmentation. *Conserv. Biol.* **27**, 520–530 (2013).](https://sciwheel.com/work/bibliography/12682833)

[31. Saura, S., Estreguil, C., Mouton, C. & Rodríguez-Freire, M. Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). *Ecological Indicators* **11**, 407–416 (2011).](https://sciwheel.com/work/bibliography/3610800)

[32. Saura, S. & Pascual-Hortal, L. A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landscape and Urban Planning* **83**, 91–103 (2007).](https://sciwheel.com/work/bibliography/960796)

[33. Saura, S., Bastin, L., Battistella, L., Mandrici, A. & Dubois, G. Protected areas in the world’s ecoregions: How well connected are they? *Ecol. Indic.* **76**, 144–158 (2017).](https://sciwheel.com/work/bibliography/3610797)

[34. Freeman, L. C. Centrality in social networks conceptual clarification. *Soc. Networks* **1**, 215–239 (1978).](https://sciwheel.com/work/bibliography/1908200)

[35. Brandes, U. A faster algorithm for betweenness centrality\*. *J. Math. Sociol.* **25**, 163–177 (2001).](https://sciwheel.com/work/bibliography/1907383)

[36. Keeley, A. T. H., Beier, P. & Jenness, J. S. Connectivity metrics for conservation planning and monitoring. *Biol. Conserv* **255**, 109008 (2021).](https://sciwheel.com/work/bibliography/10896670)

[37. Minor, E. S. & Urban, D. L. A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conserv. Biol.* **22**, 297–307 (2008).](https://sciwheel.com/work/bibliography/3953810)

[38. Hanski, I. *et al.* Ecological and genetic basis of metapopulation persistence of the Glanville fritillary butterfly in fragmented landscapes. *Nat. Commun.* **8**, 14504 (2017).](https://sciwheel.com/work/bibliography/12682858)