Modelling, visualization and analysis with the grainscape package

Paul Galpern* Alex M. Chubaty

Contents

Visual table of contents	3
Introduction	5
Modelling with grainscape	6
Model 1: The minimum planar graph	(
Step 1: Preparing the resistance surface	-
Step 2: Extracting the MPG	8
Step 3: Quick visualization of the MPG	(
Step 4: Reporting on the MPG	(
Step 5: Thresholding the MPG	1
Step 6: Visualizing a thresholded graph	2
Step 7: Next steps	;
Model 2: Patch grains of connectivity	4
Step 1: Begin with a MPG	4
Step 2: Exploring the Voronoi tessellation	١
Step 3: Building GOC models	(
Step 4: Visualizing a GOC model	Ľ
Landscape networks with 1D and 2D nodes	8
Modelling	[8
Planar network with one-dimensional nodes on a Euclidean surface	8
Planar network with one-dimensional nodes on a non-Euclidean resistance surface . 2	2(
Planar network with two-dimensional nodes on a non-Euclidean resistance surface	
(minimum planar graph)	22
Visualization	24
Centroid representation of nodes	24
Perimeter representation of links)[
Spatially-explicit representation of links	2(
Characteristics of nodes (weights)	2
Characteristics of links (weights)	35
Link thresholding by plotting)(
Link thresholding to show components	3
Analysis	};
Network metrics to assess node importance	35
Shortest-path distance between nodes	}∠

^{*}Department of Biological Sciences, University of Calgary, AB, Canada

Scaling landscape networks	37
Modeling	37
Scaling resistance surfaces (lattice grains of connectivity)	37
Scaling networks with two-dimensional nodes (patch grains of connectivity)	38
Visualization	40
Characteristics of grains of connectivity	40
Analysis	41
Corridor analyses at multiple scales	41
Modeling	43
References	45

Visual table of contents

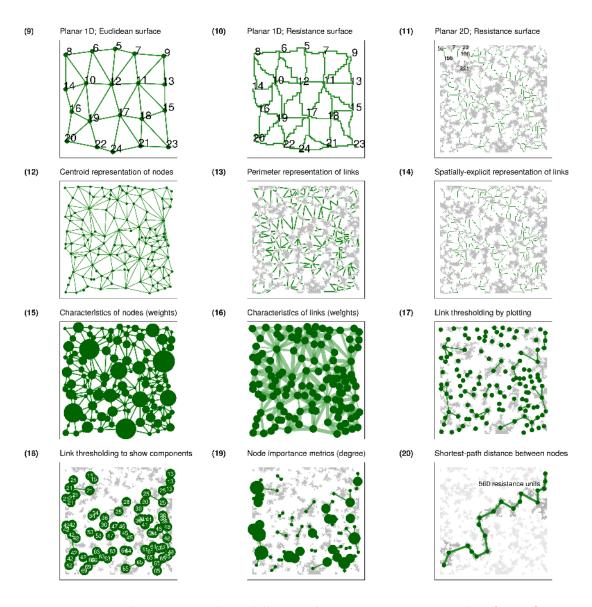


Figure 1: Landscape network modelling with grainscape. Numerals refer to figures.

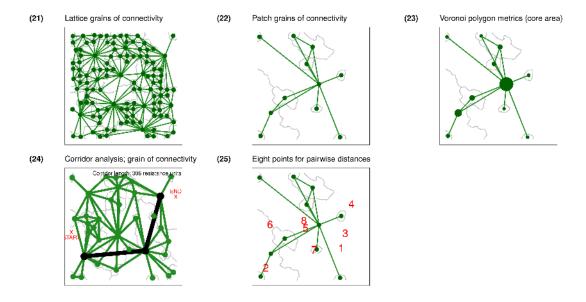


Figure 2: Scaling of landscape networks with grainscape. Numerals refer to figures.

Introduction

The grainscape package enables a range of analyses within R that have applications across the disciplines of ecology, conservation biology and geography. For example, networks extracted by grainscape can be used to model habitat connectivity or evaluate protected area network resilience. These networks can be modelled, visualized and analyzed at multiple spatial scales. A more general contribution is the ability to extract Voronoi tessellations on a continuous resistance surface. This has applications in spatial analysis, for example to model service areas where travel times or the cost of movement vary continuously across space.

The inspiration for the grainscape package is the analysis of landscape connectivity. The approach comes from the patch-based landscape graphs tradition (Urban and Keitt 2001; Fall et al. 2007; Galpern, Manseau, and Fall 2011) where a mathematical graph or network is used to represent the relationships among habitat patches. In grainscape these could equally be protected areas where connectivity for terrestrial ecological processes is of interest, such as ranging behaviour or plant and animal dispersal.

There are two types of models produced by grainscape. The first, a minimum planar graph (Fall et al. 2007) is an efficient approximation of the potential for connectivity among a set of focal two dimensional nodes. In landscape connectivity modelling these nodes might be habitat patches or protected areas.

The second model type is the grain of connectivity, which is based on the minimum planar graph, but extends it in a way that may be useful for scaling (Galpern, Manseau, and Wilson 2012; Galpern and Manseau 2013a, 2013b). Again, using landscape connectivity as an example, these grains can be used for sensitivity analyses of protected area connectivity, or to model highly mobile terrestrial animals, such as ungulates and carnivores, where the habitat patch may be not be a discrete and definable feature but is rather defined probabilistically. The model achieves this by using the complement of the minimum planar graph, a Voronoi tessellation of the map, and modelling the relationships among polygons in a Voronoi tessellation rather than discrete patches. This approach has been shown to improve the ability to model movements of highly-mobile organisms (Galpern, Manseau, and Wilson 2012). For example, grains of connectivity provides continuous coverage of the entire landscape surface in a way that a typical patch-based network does not. It also permits the examination of connectivity at multiple scales, which can accommodate uncertainty in how species may perceive landscape features (Galpern and Manseau 2013a, 2013b).

The grainscape package provides functions to extract the minimum planar graph and create two types of grains of connectivity: patch and lattice forms. This reference begins by introducing these two model types, and concludes by demonstrating a variety of grainscape models, visualizations, and analyses using a consistent visual style. Code and commentary are included throughout. All analyses are reproducible with data distributed with this package.

Modelling with grainscape

In this section we demonstrate how to prepare rasters for modelling with grainscape. Data provided with the package are used as examples. The input to grainscape is a resistance surface, and optionally a second raster describing the focal regions on a raster which will serve as nodes in a network. The resistance surface may represent the resistance to the flow of some ecological process of interest, and the nodes, focal regions where this process has an origin. A typical application is to model connectivity of landscapes for dispersal of terrestrial animals. Here, the resistance surface models the costs to movement, and the nodes habitat from which animals may disperse. Many other applications of nodes and resistance surfaces are equally valid and could represent both ecological and non-ecological processes.

Inputs to grainscape are typically raster images. Rasters may represent a geographical region, and ideally have a projected coordinate system. This raster must contain cells with value >= 1, where values are real or integers. If data are missing, cells must have value == NA (e.g, commonly in the boundary cells of an irregularly shaped region of interest).

The following are key packages required to complete analyses with grainscape. The igraph package provides network analytical functions, while raster provides the the data structure and raster analytical functions upon which grainscape depends to manage data. Finally model and analytical products are compatible with visualizing using the popular ggplot2 idiom.

Model 1: The minimum planar graph

The minimum planar graph (hereafter MPG) is a spatial representation of a graph or a network that provides an efficient approximation of all possible pairwise connections between graph nodes (Fall et al. 2007). In graph-based landscape connectivity analyses, graph nodes have typically been patches of habitat that are demonstrably important for the species in question (Fall et al. 2007). In the following example we will continue the habitat connectivity modelling objective for clarity, but emphasize that this is not the only task to which these methods can be applied.

An MPG representing habitat connectivity has links that model the possibility for organism movement and dispersal between spatially-adjacent habitat patches. In some cases spatially-adjacent patches may not be linked, if the shortest connection between them can be made through a third patch. In practice, this property means that the MPG can be used to make a simple and easily visualized picture of how a set of habitat patches is connected. The alternative, the complete graph, can quickly become challenging to interpret because these may contain a dense set of graph links making the pattern difficult to discern. A second advantage of the MPG is the much reduced set of graph links; this can be valuable where computational efficiency is important, and essential where the number of habitat patches being modelled numbers in the thousands.

However, there are some types of connectivity analyses where the MPG approximation of the complete graph is not appropriate. For example, assessing community structure within a landscape patch network (*i.e.*, finding sets of patches that are densely connected) is not possible as redundant connections have been removed intentionally. Equally, the MPG is a poor choice for prioritizing the influence of a patch for connectivity, the objective in a number of landscape graph studies (*e.g.*, Pascual-Hortal and Saura 2006). Please see Galpern, Manseau, and Fall (2011) for further discussion of these limitations and of the MPG.

Step 1: Preparing the resistance surface

The MPG has typically been constructed using shortest path links between the perimeters of two dimensional node patches. In habitat connectivity terms, this implies that landscape structure in the "matrix" between patches is influencing movement, and that the organism in question is on average minimizing its costs when moving through this matrix (an assumption possibly appropriate for terrestrial animals, and terrestrial animal-dispersed plants). Equally, MPGs can be constructed using Euclidean links, where the only influence of the matrix on movement is the effect of spatial separation (*i.e.*, distance it presents between neighbouring habitat).

Here, we illustrate just the case where links are shortest paths on a resistance surface. Euclidean links can be produced by passing a uniform cost surface (a constant raster), and a raster describing the patches. An example of this is given later in the document.

We begin by loading a landscape raster distributed with the package. Note that any raster format readable using the raster package can be used here. The .asc format rasters distributed with the package are ESRI ArcASCII format.

```
patchy <- raster(system.file("extdata/patchy.asc", package = "grainscape"))</pre>
```

Then, for convenience, we use R to turn this raster into a resistance surface. In this example we will assume the feature class 1 (*i.e.*, cells with value == 1) are the patches. We will set them to resistance value also equal to 1 (*i.e.*, no additional resistance to movement than distance alone). The river, feature class 2, is assigned the highest resistance of 10. Other features are assigned values in between. The parameterization of resistance surfaces for landscape connectivity modelling is itself a big topic (Zeller, McGarigal, and Whiteley 2012). The matrix isBecomes describes the transformation from feature class to resistance surface. The result is shown in Figure 3.

```
## Create an is-becomes matrix for reclassification
isBecomes <- cbind(c(1, 2, 3, 4, 5), c(1, 10, 8, 3, 6))
patchyCost <- reclassify(patchy, rcl = isBecomes)

## Plot this raster using ggplot2 functionality
## and the default grainscape theme
ggplot() +
   geom_raster(data = ggGS(patchyCost),
    aes(x = x, y = y, fill = value)) +
   scale_fill_distiller(palette = "Paired", guide = "legend") +
   guides(fill = guide_legend(title = "Resistance")) +
   theme(legend.position = "right")</pre>
```

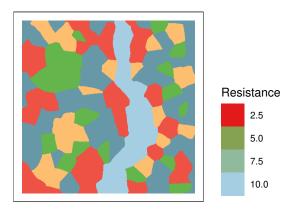


Figure 3: Input raster resistance surface to create the minimum planar graph (MPG). Features with value of 1 (red) will be the patches in the network. A river (light blue) has the highest resistance in this example.

Step 2: Extracting the MPG

With a resistance surface in hand the next step is to create the MPG. Basic use of the function, MPG() to do this is shown here. For simplicity we assume that all areas with the resistance value equal to 1 on the raster are patches. This is a convenient short cut when patches are the only part of the raster where resistance is equal to geographic distance. However, in many applications focal patches will be a subset of these areas, or represent areas with multiple resistance values. These can be accommodated by passing a patch raster to the patch= parameter, created using any method. Equally patches below a certain size could be filtered by passing the patch raster to patchfilter() first.

```
patchyMPG <- MPG(patchyCost, patch = (patchyCost == 1))</pre>
```

Step 3: Quick visualization of the MPG

A quick way to visualize the MPG is provided by the plot method in grainscape. This appears in Figure 4.

plot(patchyMPG, quick = "mpgPlot", theme = FALSE)

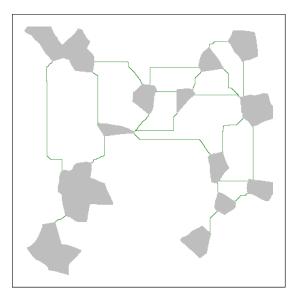


Figure 4: A quick visualization of the minimum planar graph (MPG). Grey areas are patches (nodes) in the graph, and green lines are links showing the shortest paths between the perimeters of the patches on the resistance surface. In depth discussion of how the MPG is generated can be found elsewhere (Fall et al. 2007).

Step 4: Reporting on the MPG

Following extraction, the MPG is available as an igraph object (see patchyMPG@mpg) and can be analyzed using any of the functions in this package. A quick way to report on the structure of the graph in tabular format is provided by the function graphdf():

```
## Extract tabular node information using the graphdf() function
nodeTable <- graphdf(patchyMPG)[[1]]$v

## Render table using the kable function,
## retaining the first three rows
kable(nodeTable[1:3, ], digits = 0, row.names = FALSE)</pre>
```

name	patchId	patchArea	patchEdgeArea	coreArea	$\operatorname{centroid} X$	$\overline{\operatorname{centroidY}}$
5	5	3995	388	3607	81	-33
7	7	1682	189	1493	356	-28
9	9	937	154	783	302	-54

```
## Extract tabular link information using the graphdf() function
linkTable <- graphdf(patchyMPG)[[1]]$e

## Render table using the kable function,
## retaining the first three rows
kable(linkTable[1:3, ], digits = 0, row.names = FALSE)</pre>
```

e1	e2	linkId	lcpPerimWeight	startPerimX	startPerimY	$\operatorname{endPerim} X$	endPerimY
24	37	1	45	315	-259	314	-246
36	37	2	90	342	-273	360	-262
9	12	3	120	289	-70	277	-97

The output in shows the structure of the nodes (vertices) and their attributes under the list element \$v\$ as well as the structure of the graph in the form of an link list (i.e., pairs of nodes e1 and e2 that are connected) and associated link (edge) attributes under the list element \$e. Note that only the first three lines of each has been reproduced here. Please see the manual for the interpretation of the attributes.

Step 5: Thresholding the MPG

A frequent step in the analysis of a network is to threshold it into a series of clusters or components representing connected areas (Urban and Keitt 2001; Galpern, Manseau, and Fall 2011; Galpern, Manseau, and Wilson 2012). This has sometimes been called a scalar analysis (Brooks 2003).

The function threshold() provides a way to conduct a scalar analysis at multiple scales. Here we ask for 5 thresholds, and the function finds five approximately evenly-spaced threshold values in link length.

Table 3: The number of components ('nComponents') in the minimum planar graph at five automatically-selected link thresholds ('maxLink).

maxLink	nComponents
0	13
229	6
458	1
687	1
916	1

The \$summary of this analysis can be plotted to explore scales of aggregation in the landscape. Figure 5 shows a scalar analysis of this landscape with 100 thresholds, where the response variables is the number of components or sub-graphs created by the thresholding.

```
scalarAnalysis <- threshold(patchyMPG, nThresh = 100)
ggplot(scalarAnalysis$summary, aes(x = maxLink, y = nComponents)) +
    geom_line(colour = "forestgreen") +
    xlab("Link Threshold (resistance units)") +
    ylab("Number of components") +
    scale_x_continuous(breaks = seq(0, 1000, by = 100)) +
    scale_y_continuous(breaks = 1:20) +
    theme_light() + theme(axis.title = element_text())</pre>
```

Other independent variables describing the components (e.g., area of patches) could, of course, be calculated by processing the thresholded graphs scalarAnalysis\$th and their attributes using the igraph function components().

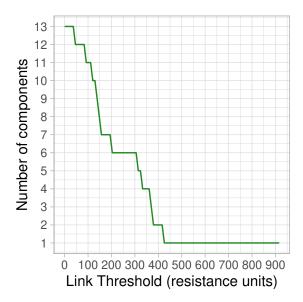


Figure 5: A scalar analysis at 100 thresholds of the MPG in Figure 4. When the landscape is a single component at higher link thresholds all patches are completely connected. As an example, an organism able to disperse 250 resistance units would experience this landscape as six connected regions.

Step 6: Visualizing a thresholded graph

Consider an organism able to disperse a maximum of 250 resistance units. According to Figure 5 this organism would experience this landscape as 6 connected regions. This is visualized in Figure 6.

- ## Warning in f(...): Raster pixels are placed at uneven horizontal intervals ## and will be shifted. Consider using geom_tile() instead.
- ## Warning in f(...): Raster pixels are placed at uneven vertical intervals ## and will be shifted. Consider using geom_tile() instead.

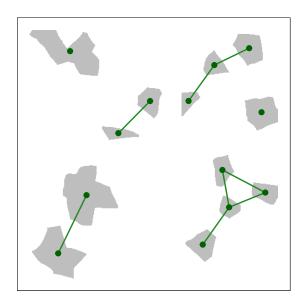


Figure 6: The thresholded MPG depicted with a link length of 250 resistance units. An organism that can disperse a maximum of 250 resistance units would experience this landscape as 6 connected regions in the depicted spatial configuration. Note that the plotting has been customized to emphasize which patches are connected. This was done by plotting links with less than the threshold length from the centroids of patches

Step 7: Next steps

With the MPG in hand, several additional types of analyses are possible. Grains of connectivity (GOC), the subject of the next section, is an example of using the MPG and its complement the Voronoi tessellation.

When programming your own analyses in R based on the MPG it is helpful to observe that the patchyMPG@patchId and patchyMPG@lcpLinkId rasters contain the numerical IDs of the patches (nodes) and links respectively. These are also contained as attributes in the igraph object patchyMPG@mpg. Using these three data objects together gives flexibility to visualize any graph analysis. Additional example visualizations and analyses are contained later in this document.

Model 2: Patch grains of connectivity

Grains of connectivity (hereafter GOC) was initially developed in three papers (Galpern, Manseau, and Wilson 2012; Galpern and Manseau 2013b, 2013a). Please refer to these papers for much more detail on this method. In summary, grains of connectivity describes a tessellation of functionally-connected regions of the map. In this example we present these in the context of modelling landscape connectivity for highly-mobile terrestrial organisms that are not obligate patch occupants.

Step 1: Begin with a MPG

Here, we repeat the steps as before for the same patchy resistance surface explored in the MPG examples. Any of the variations imaginable for the MPG modelling can provide a valid basis to build a GOC.

```
## Load the patchy raster distributed with grainscape
patchy <- raster(system.file("extdata/patchy.asc", package = "grainscape"))

## Create an is-becomes matrix for reclassification
isBecomes <- cbind(c(1, 2, 3, 4, 5), c(1, 10, 8, 3, 6))
patchyCost <- reclassify(patchy, rcl = isBecomes)

## Create the MPG model using cells = 1 as patches
patchyMPG <- MPG(patchyCost, patch = (patchyCost == 1))</pre>
```

Step 2: Exploring the Voronoi tessellation

Before we build the GOC graph, we should explore the essential building block of GOC, which is the Voronoi tessellation. This particular Voronoi tessellation was first described elsewhere (Fall et al. 2007) and is the complement of the MPG. It is identified by finding the region of proximity in resistance units around a resource patch. In contrast to the well-known Voronoi tessellation where the generators are points and distance is Euclidean, this tessellation uses two-dimensional patches as generators and distance is calculated in cost or resistance space. The tessellation is found in grainscape using a marching algorithm implemented in C++.

The Voronoi tessellation is extracted as part of finding the MPG(). A plot with the Voronoi tessellation and the patches superimposed is shown in Figure 7.

```
patchPlusVoronoi <- patchyMPG@voronoi
patchPlusVoronoi[patchyMPG@patchId] <- 0

ggplot() +
  geom_raster(data = ggGS(patchPlusVoronoi), aes(x = x , y = y, fill = value))</pre>
```



Figure 7: A Voronoi tessellation. This is the complement of the MPG. The patches (darkest blue) are used as generators, and regions of proximity (polygons of different colours) are found in cost or resistance units. The method was first described by Fall et al. (2007).

Step 3: Building GOC models

GOC analysis is essentially a scalar or thresholding analysis (see threshold() and above) except the graph being thresholded is one of Voronoi polygons rather than patches. In particular, it is the MPG of Voronoi polygons that is thresholded. As links are added, and Voronoi polygons linked, the relevant polygons are combined describing larger connected regions. An additional step is that the links connecting a pair of polygons are the mean value of all links connecting any patches in each of the two polygons from the MPG (Galpern, Manseau, and Wilson 2012).

The function GOC() builds GOC models at multiple thresholds. As with threshold() we can specify the number of thresholds, or grains of connectivity models, we want to create using the nThresh parameter.

patchyGOC <- GOC(patchyMPG, nThresh = 10)</pre>

Step 4: Visualizing a GOC model

To get a quick sense of the connected regions described by a GOC model at a given threshold (or scale of movement) we can use the function grain(). This example uses the functions plotting mechanism to plot the 6th threshold in the patchyGOC object. Figure 8 shows the resulting plot.

```
plot(grain(patchyGOC, whichThresh = 6), quick = "grainPlot", theme = FALSE)
```

Extracting voronoi boundaries...

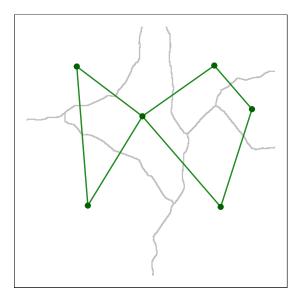


Figure 8: A visualization of a GOC model. In this case it is the 6th scale or threshold extracted. Voronoi polygons imply regions that are functionally-connected at the given movement threshold.

The remainder of this document serves as a reference to modelling, visualization and analysis using the grainscape package. Please refer to the visual table of contents.

Landscape networks with 1D and 2D nodes

Modelling

Planar network with one-dimensional nodes on a Euclidean surface

One-dimensional nodes (*i.e.*, points) can represent map locations of an ecological or spatial process of interest. While the Euclidean distance between these points is easily calculated in R using the dist() function, we may be interested in the path distance to just the immediate neighbours of each point. A *planar* network extracted on a Euclidean resistance surface can be used to identify which nodes are neighbours and find their pairwise distances (Fall et al. 2007; Galpern, Manseau, and Fall 2011). In grainscape a Euclidean resistance surface is simply a resistance surface where all values are = 1)

```
## Make a new resistance raster of 400 by 400 cells
## with a coordinate system that corresponds to cells
res <- raster(xmn = 0, xmx = 100, ymn = 0, ymx = 100, resolution = 1)
## Assign all values to 1
res[] <- 1
## Create 20 "random" points representing nodes,
## (i.e. the loci of a process of interest)
pts \leftarrow data.frame(x = rep(seq(10, 90, length.out = 5), 4),
                  y = seq(10, 90, length.out = 4)) +
  cbind(runif(20) * 10, runif(20) * 10)
## Represent these on a patch raster
## by duplicating the resistance raster and
## setting the relevant cells to 1
patchPts <- res
patchPts <- setValues(patchPts, 0)</pre>
patchPts[cellFromXY(patchPts, pts)] <- 1</pre>
## Extract the MPG
mpg <- MPG(res, patchPts)</pre>
## Plot the result using the quick 'network' visualization
## setting and add labels (dodging them by 3 to the upper-right)
figure09 <- plot(mpg, quick = "network", theme = FALSE) +
  geom_text(data = ggGS(mpg, "nodes"),
            aes(x = x + 3, y = y + 3, label = patchId)) +
  ggtitle("Planar 1D; Euclidean surface")
figure09
```

Warning in f(...): Raster pixels are placed at uneven horizontal intervals ## and will be shifted. Consider using geom_tile() instead.

Warning in f(...): Raster pixels are placed at uneven vertical intervals ## and will be shifted. Consider using geom_tile() instead.



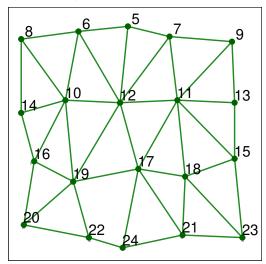


Figure 9: A planar network with one-dimensional point nodes extracted using grainscape. Nodes are represented as points and labelled with their patchId. Links are line segments among nodes.

The distance between nodes can be extracted from the objects. Note how the distances are integers, because they do not represent the Euclidean distance, but rather the accumulated path distance among nodes. On this particular raster one cell equals one unit of distance, therefore distances are the count of cells separating nodes.

```
## Here we show the first five rows of the link attribute table
## extracted from the mpg object. This shows selected columns,
## using the formatting function kable()
neighbours <- graphdf(mpg)[[1]]$e[, c(1, 2, 4)]
neighbours <- neighbours[order(neighbours[,1]), ][1:5, ]
names(neighbours) <- c("Node 1", "Node 2", "Path distance (Euclidean)")
kable(neighbours, row.names = FALSE)</pre>
```

Node 1	Node 2	Path distance (Euclidean)
5	7	19
5	6	20
5	12	32
6	8	24
6	10	31

Planar network with one-dimensional nodes on a non-Euclidean resistance surface

Similarly, when the distance among points, or nodes, is best explained by some cost or resistance, neighbour distance can be modelled in an identical manner, leveraging the planarity of the network. The only difference in the code from the previous 1D Euclidean example is the use of the resistance surface rather than a raster consisting only of the value 1. We will borrow objects made in previous steps to keep the code concise.

```
## Add some cost values to the resistance
## surface we used in the last step
## Here we use random integers >= 2
res2 <- res
res2[] <- floor(runif(ncell(res2))*10 + 1)
## Extract the minimum planar graph using the
## raster made previously which represents the points only
mpg <- MPG(res2, patchPts)</pre>
## Plot the result using the quick 'mgplot' visualization
## setting and add labels (dodging them by 3 to the upper-right)
## This demonstrates the non-linear paths.
figure 10 <- plot(mpg, quick = "mpgPlot", theme = FALSE) +
 geom_text(data = ggGS(mpg, "nodes"),
            aes(x = x + 3, y = y + 3, label = patchId)) +
  ggtitle("Planar 1D; Resistance surface")
figure10
```

Planar 1D; Resistance surface

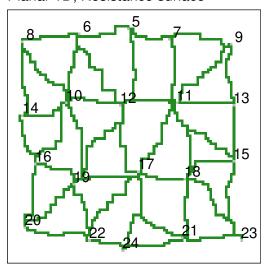


Figure 10: A planar network with one-dimensional nodes extracted on a resistance surface. Nodes are represented by grey-coloured cells and labelled with their patchId. Links are green paths between nodes, shown in a spatially-explicit representation.

The distances between nodes are still integers, and they also represent a path distance. Now, this

is rather the shortest accumulated path distance through the resistance surface between nodes. Once again, their metric is an integer because resistance values were also integers. The table below demonstrates that the non-Euclidean path distance is longer among the same pairs of nodes, and they are not perfectly correlated, as we expect.

```
## Here we show the first five rows of the link attribute table
## extracted from the mpg object. This shows selected columns, using
## the formatting function kable()
resNeighbours <- graphdf(mpg)[[1]]$e[ , c(1, 2, 4)]
resNeighbours <- resNeighbours[order(resNeighbours[,1]), ][1:5, ]
comparison <- cbind(neighbours, resNeighbours)[, -c(4,5)]
names(comparison)[4] <- c("Path distance (Resistance)")
kable(comparison, row.names = FALSE)</pre>
```

Node 1	Node 2	Path distance (Euclidean)	Path distance (Resistance)
5	7	19	74
5	6	20	110
5	12	32	123
6	8	24	106
6	10	31	126

Planar network with two-dimensional nodes on a non-Euclidean resistance surface (minimum planar graph)

This is the minimum planar graph (MPG) (Fall et al. 2007), and the inspiration for the grainscape package. Please see the first part of this document for a more thorough presentation of the MPG. Andrew Fall and colleagues originally articulated this graph theory-based model as a spatial graph. It was an approach that built a graph (or a network) of patches and, critically, it was aware of a spatially-explicit landscape. This incorporated multiple landscape elements that might be visible on a map, such as the shape, size and configuration of two-dimensional node patches as well as continuous geographic variation in the spaces between the nodes (i.e., the matrix). In a minimum planar graph (MPG) the matrix presents resistance to connectivity and influences the paths and therefore the lengths of the links. The shape, size and configuration of patches with respect to their neighbours that influences where on the patch perimeters these links begin and end. The value of using patch perimeters rather than centroids is that it potentially improves the estimation of the shortest paths among patches.

An MPG can be understood as a planar network (*i.e.*, no links "cross" nodes), that provides an efficient representation of connections among neighbouring nodes. Its nodes are two-dimensional patches and its links are the shortest paths through a resistance surface.

The following example uses a more realistic resistance surface based on a simulated land cover raster.

```
## Load a land cover raster distributed with grainscape
frag <- raster(system.file("extdata/fragmented.asc", package = "grainscape"))</pre>
## Convert land cover to resistance units
## Use an "is-becomes" reclassification
isBecomes \leftarrow cbind(c(1, 2, 3, 4), c(1, 5, 10, 12))
fragRes <- reclassify(frag, rcl = isBecomes)</pre>
## Extract a network using cells = 1 on original raster
## as the focal patches or nodes
patches <- (frag == 1)</pre>
fragMPG <- MPG(fragRes, patch = patches)</pre>
## Plot the minimum planar graph with node labels for several
## focal nodes of interest
figure11 <- plot(fragMPG, quick = "mpgPlot", theme = FALSE) +</pre>
  geom_text(data = ggGS(fragMPG, "nodes"),
            aes(x = x, y = y,
                label = ifelse(patchId %in% c(7, 23, 52, 106, 158, 221),
                                patchId, "")),
            size = 2) +
  ggtitle("Planar 2D; Resistance surface")
figure11
```

The distances from the perimeters of the nodes along the paths of the links (green in figure) are available in the output object in the same manner as before.

Planar 2D; Resistance surface

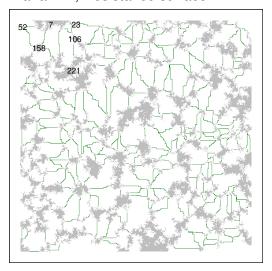


Figure 11: A minimum planar graph (MPG) of a simulated resistance surface. Focal patches are grey regions and green lines indicate spatially-explicit links among patches. Several patches are labelled with their numerical patchId.

```
## Here we show only patch 7 and its neighbours that are labelled on
## the network using the formatting function kable().
fragNeighbours <- graphdf(fragMPG)[[1]]$e[ , c(1, 2, 4)]
fragNeighbours <- fragNeighbours[order(fragNeighbours[,1]), ][1:5, ]
names(fragNeighbours) <- c("Node 1", "Node 2", "Path distance (Resistance)")
kable(fragNeighbours, row.names = FALSE)</pre>
```

Node 1	Node 2	Path distance (Resistance)
7	23	27
7	52	90
7	106	135
7	158	137
7	221	235

Visualization

Centroid representation of nodes

Where nodes represent two-dimensional regions (e.g, patches, protected areas) it can be convenient to visualize nodes as points plotted at the centroid location of the region (Urban and Keitt 2001; Galpern, Manseau, and Fall 2011). While the links themselves may be measured from patch perimeters, or quantities related to the nodes summarized across patch areas, visualization can be improved by omitting complexities such as these. Cases where centroid node representation may be justified include: (1) mapping of the topology of a complex network; (2) mapping the number and distribution of links; (3) mapping the properties of the nodes (see example below); or, (4) where a large plotting extent makes regions hard to see.

This example uses the resistance surface and minimum planar graph from a previous example (fragMPG).

Centroid representation of nodes

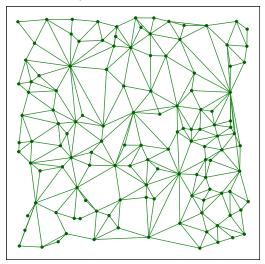


Figure 12: A minimum planar graph (MPG) shown with centroid node representation and linear link representation among these nodes.

Perimeter representation of links

Where the spatially-explicit nature of the connections among these nodes is important, perimeter representation of links and two-dimensional visualization of the nodes may be a useful technique.

Plotting the region covered by a node, and links as lines drawn between the perimeters of these regions is an efficient way to convey the topology of the network and which parts of a node are closest to its neighbours. It also signals that the linking of nodes was done from the perimeter rather than the centroid.

This example extends the previous one, where centroid representation of links was used.

```
## Plot the minimum planar graph using perimeter links
## and two dimensional nodes
figure13 <- plot(fragMPG, quick = "mpgPerimPlot", theme = FALSE) +
    ggtitle("Perimeter representation of links")
figure13</pre>
```

Perimeter representation of links

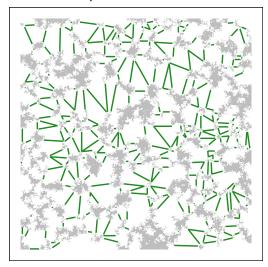


Figure 13: A minimum planar graph (MPG) with links represented from the perimeter of the patches (*i.e.*, at the start and end points of spatially-explicit links). This rendering can simplify visualization.

Spatially-explicit representation of links

Spatially-explicit representation of the links implies both that the end points of links are on the perimeter of the region represented by the node, and that the predicted shortest paths among those node perimeters have coordinates. This approach conveys all available spatial information in the minimum planar graph. It also has the potential to mislead. Shortest paths between nodes are estimates of the shortest distance on the resistance surface and not necessarily of the route by which the process of interest actually flows. This kind of representation should therefore be used with appropriate caution.

However, using this visualization does efficiently communicate how the minimum planar graph model was constructed, and suggests which parts of the resistance surface may influence the pattern of the connections among nodes, both of which may aid in interpretation.

This example uses this same data as the previous one to permit comparison among visualizations.

```
## Plot the minimum planar graph using spatially-explicit links
## and two dimensional nodes.
figure14 <- plot(fragMPG, quick = "mpgPlot", theme = FALSE) +
    ggtitle("Spatially-explicit representation of links")
figure14</pre>
```

Spatially-explicit representation of links

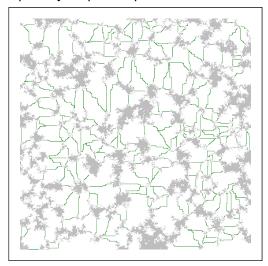


Figure 14: A minimum planar graph (MPG) with the shortest links among patch perimeters rendered as spatially-explicit paths. This rendering can help demonstrate the modelling procedure, but risks overinterpretation of the actual paths involved (see text).

Characteristics of nodes (weights)

Variables that are associated with a focal ecological process at a node can be represented on a network visualization. These variables are sometimes known as node "weights". For example, where nodes represent regions such as patches of habitat or protected areas, a useful node weight may be the area of the region represented by the node. Equally, measures of node quality such as the area of core or edge habitat could be represented. Any metric that is associated with the node can be plotted at that node by varying the shape, size or colour of plotting symbol.

In this example, the area of the patch represented by the node is used to scale the size of the symbol plotted at the centroid of the node.

Characteristics of nodes (weights)

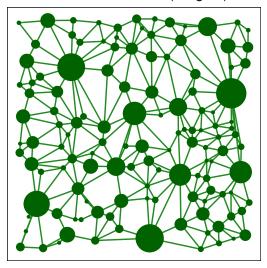


Figure 15: A minimum planar graph (MPG) with centroid node representation and links between centroids, where the plotted size of the node symbol has been scaled with the area of the patch it represents.

Characteristics of links (weights)

Variables associated with links, called link weights, often contain information on the modelled connectivity among nodes. Measures of interest in ecology can include the expected flow of organisms, or a variable correlated with this flow such as geographic distance or the distance of the shortest path across a resistance surface.

In this example, the length of the shortest path between patch perimeters is plotted by varying the width of the link connecting nodes. The link weight is found as a proportion of the Euclidean distance between those nodes. So, proportions higher than 1 imply a resistance to movement greater than expected by distance alone. On the scale used thinner lines describe a greater expectation of connectivity for an ecological process that is influenced by resistance (proportion closer to 1).

Characteristics of links (weights)

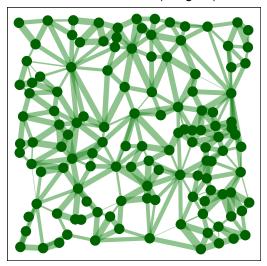


Figure 16: A minimum planar graph with centroid node and link representation where the width of the links has been scaled in proportion to the reduction in connectivity due to resistance. Wider links correspond to reduced connectivity.

Link thresholding by plotting

Removing links with weights that are greater than a threshold value is referred to as *link thresholding* and can be used to identify components, or connected sets of nodes (Urban and Keitt 2001; Galpern, Manseau, and Fall 2011). It is the most basic approach to scaling a network, and the technique upon which *grains of connectivity* is based (see later examples).

Here, we remove links greater than a threshold of 20. This is measured in the units of the resistance surface. Thresholding at this level implies we wish to remove all links that represent a cumulative path distance on the resistance surface of 20 times the dimension of a raster cell. The resulting components (also called clusters) in the network identify groups of nodes that have a minimum level of connectivity among them.

In the simplest approach to link thresholding, rather than *remove* links from the network that are greater than this threshold, we elect not to plot them. We do this by rendering longer links as transparent (NA is the ggplot2 colour specification for transparency).

This visualization may be useful to demonstrate which nodes are most strongly connected to one another. It does an adequate job of highlighting which groups of nodes are connected as a single component or cluster. However, we can do better. See the next example.

Link thresholding by plotting

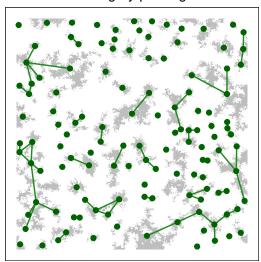


Figure 17: A link threshold representation of a minimum planar graph (MPG), where links connect the centroids of adjacent patches in the same component (cluster). Nodes that form their own component are shown as circles without links.

Link thresholding to show components

As noted in the last example, highlighting which nodes are connected into components (or clusters) after the network has been subjected to link thresholding can improve the visualization of connected regions of the map.

Here, grainscape::threshold() is used to remove links longer than a certain length from the igraph model of the landscape network. The igraph::components() function is then called to label nodes by their membership in a particular component (or cluster). We can then use this information to label the nodes by their component membership. To improve the visualization, the nodes are also plotted as large circles and the labels in a reverse colour. This could also be done (perhaps more effectively) using a colour or shape scale for node symbols that have been carefully selected to accentuate patterns of interest in the figure.

```
## Use the grainscape::threshold() function to create a new network
## by thresholding links
fragTh <- threshold(fragMPG, doThresh = 20)</pre>
## Find the components in that thresholded network using
## an igraph package function
fragThC <- components(fragTh$th[[1]])</pre>
## Extract the node table and append the
## component membership information
fragThNodes <- data.frame(vertex_attr(fragTh$th[[1]]),</pre>
                           component = fragThC$membership)
## We don't want to show nodes that are in components with
## only one node, so remove them
singleNodes <- fragThNodes$component %in% which(fragThC$csize == 1)</pre>
fragThNodes <- fragThNodes[!(singleNodes), ]</pre>
## Rename some columns to improve readability
fragThNodes$x <- fragThNodes$centroidX</pre>
fragThNodes$y <- fragThNodes$centroidY</pre>
figure18 <- ggplot() +
  geom_raster(data = ggGS(fragMPG, "patchId"),
              aes(x = x, y = y, fill = value > 0)) +
  scale_fill_manual(values = "grey") +
  geom_segment(data = ggGS(fragMPG, "links"),
               aes(x = x1, y = y1, xend = x2, yend = y2,
                   colour = lcpPerimWeight > 20)) +
  scale_colour_manual(values = c("forestgreen", NA)) +
  geom_point(data = fragThNodes,
             aes(x = x, y = y), shape = 19, size = 4, colour = "darkgreen") +
  geom_text(data = fragThNodes, aes(x = x, y = y, label = component),
            colour = "white", size = 2) +
```

Link thresholding to show components

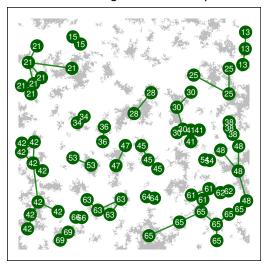


Figure 18: A link threshold representation of a minimum planar graph (MPG), where links connect the centroids of adjacent patches in the same component (cluster). Nodes that are part of a component are labelled with their component membership.

Analysis

Network metrics to assess node importance

There are numerous network metrics available that describe properties of nodes and network topology. The igraph package used by grainscape implements a selection of these metrics. A simple and intuitive node-based network metric is degree. This is a count of the number of links adjacent to a node. A node with a higher degree, then, might be deemed as contributing more to connectivity. The usefulness of this metric depends on the application, and more sophisticated measures of node importance such as centrality may be more appropriate. These are also available in igraph. However caution is appropriate, as the MPG is itself an approximation of all possible links among nodes. Please see Galpern, Manseau, and Fall (2011) for more information on this limitation.

Here we demonstrate how to calculate degree using the igraph package and visualize the result of this simple network analysis. We calculate degree on a link thresholded network, implying that there is a maximum level of link resistance above which we do not consider that link as making a contribution to a node's connectivity.

```
## Assess degree on the nodes of a thresholded network
## made in the previous example (threshold = 20)
fragThDegree <- degree(fragTh$th[[1]])</pre>
## Add degree to the node table
fragThNodes <- data.frame(vertex_attr(fragTh$th[[1]]), degree = fragThDegree)</pre>
## Remove nodes with a degree of O
fragThNodes <- fragThNodes[fragThNodes$degree > 0, ]
## Rename some columns to improve readability
fragThNodes$x <- fragThNodes$centroidX</pre>
fragThNodes$y <- fragThNodes$centroidY</pre>
figure19 <- ggplot() +
 geom_raster(data = ggGS(fragMPG, "patchId"),
              aes(x = x, y = y, fill = value > 0)) +
  scale_fill_manual(values = "grey") +
  geom_segment(data = ggGS(fragMPG, "links"),
               aes(x = x1, y = y1, xend = x2, yend = y2,
                   colour = lcpPerimWeight > 20)) +
  scale_colour_manual(values = c("forestgreen", NA)) +
  geom_point(data = fragThNodes,
             aes(x = x, y = y, size = degree), colour = "darkgreen" ) +
  ggtitle("Node importance metrics (degree)")
figure19
```

Node importance metrics (degree)

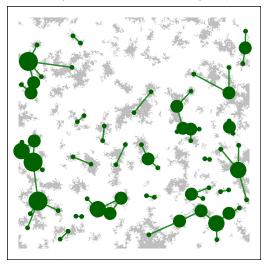


Figure 19: A link threshold representation of a minimum planar graph (MPG), where nodes, plotted at patch centroids, are scaled in proportion to the degree of the node (*i.e.*, the number of links adjacent on the node). Larger circles indicate nodes with a higher degree in the MPG.

Shortest-path distance between nodes

Finding the shortest path through the network from a source to a destination node and the length of that path is a useful prediction of the network model and has many applications (Zeller, McGarigal, and Whiteley 2012; Galpern, Manseau, and Wilson 2012; Adriaensen et al. 2003). It gives an expected distance through the network, taking into account the modelled connectivity among nodes.

This example illustrates how to use **igraph** functions to find the shortest path through the network, calculate its length in the metric of the resistance surface, and visualize the path.

The plot uses links between patch centroids and recolouring of the patch raster to add emphasis. If we were to use a link thresholded network, here, (which we will not for simplicity), the entire network would not be completely connected, so certain patches may not have a shortest path between them. Finding shortest paths on thresholded networks may still be a useful technique, and the absence of a shortest path an important finding.

```
## Extract the nodes and links of this shortest path
shPathN <- as.integer(names(shPath$vpath[[1]]))</pre>
shPathL <- E(fragMPG$mpg)[shPath$epath[[1]]]$linkId</pre>
## Produce shortest path tables for plotting
shPathNodes <- subset(ggGS(fragMPG, "nodes"), patchId %in% shPathN)
shPathLinks <- subset(ggGS(fragMPG, "links"), linkId %in% shPathL)
## Find the distance of the shortest path
shPathD <- distances(fragMPG$mpg,
                     v = which(V(fragMPG$mpg)$patchId == startEnd[1]),
                     to = which(V(fragMPG$mpg)$patchId == startEnd[2]),
                     weights = E(fragMPG$mpg)$lcpPerimWeight)[1]
## Plot shortest path
figure20 <- ggplot() +
  geom_raster(data = ggGS(fragMPG, "patchId"),
              aes(x = x, y = y,
                  fill = ifelse(value %in% shPathN, "grey70", "grey90"))) +
  scale fill identity() +
  geom_segment(data = shPathLinks, aes(x = x1, y = y1, xend = x2, yend = y2),
               colour = "forestgreen", size = 1) +
  geom_point(data = shPathNodes, aes(x = x, y = y), colour = "darkgreen") +
  ggtitle("Shortest-path distance between nodes") +
  annotate("text", 260, 340,
           label = pasteO(shPathD, " resistance units"), size = 2.5)
figure20
```

Shortest-path distance between nodes

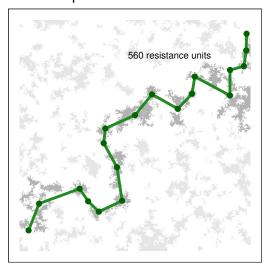


Figure 20: The shortest path through a minimum planar graph (MPG) given a start and end patchId. Links and nodes that form part of this "corridor" are highlighted.

Pairwise distances between a set of nodes can be found using the igraph::distances() function as follows.

```
## Create a pairwise table of shortest path distances among nodes using
## the resistance surface based links
allShPathD <- distances(fragMPG$mpg, weights = E(fragMPG$mpg)$lcpPerimWeight)

## Create a table for the first 8 nodes
tableD <- allShPathD[1:8, 1:8]
tableD[upper.tri(tableD)] <- NA
dimnames(tableD)[[1]] <- paste("patchId", dimnames(tableD)[[1]], sep = " ")
kable(tableD)</pre>
```

	7	10	12	13	19	23	27	52
patchId 7	0							
patchId 10	398	0						
patchId 12	405	65	0					
patchId 13	419	95	30	0				
patchId 19	454	130	65	35	0			
patchId 23	27	371	378	392	427	0		
patchId 27	534	210	145	115	80	507	0	
patchId 52	90	488	495	509	544	117	624	0

Scaling landscape networks

Modeling

Scaling resistance surfaces (lattice grains of connectivity)

Resistance surfaces produced from remotely-sensed land cover or elevation data may be too fine-scaled for the process being modelled. By having a scale that is mismatched with the one of interest, the signal or pattern may be obscured (Cushman and Landguth 2010). A common strategy is to upscale these rasters and remove potentially unimportant variation by coalescing adjacent raster cells and representing these by their mode or mean. Another approach uses moving windows to smooth out variation (Galpern and Manseau 2013a).

grainscape enables a different approach to upscaling a resistance surface based on remotely-sensed data. Lattice grains of connectivity drops a lattice of focal points (or nodes), finds the minimum planar graph and its complementary Voronoi polygons on the resistance surface among these points, and then coalesces adjacent Voronoi polygons using the graph as guidance. It can be classified as a model-based approach to upscaling (where the model is the resistance surface, and its representation of some ecological or geographical process). Unlike arbitrarily upscaling a raster based on cell-proximity, this approach uses spatial information in the surface itself. The grid spacing of the lattice as well as the amount of link thresholding together influence the amount of upscaling that occurs.

This example uses the familiar resistance surface of previous examples. It specifies a lattice grid spacing of 25 cells. We use grainscape grains of connectivity analysis functions to coalesce Voronoi polygons at 5 thresholds or scales. We could examine the resulting lattice grains of connectivity at any of these five scales. We choose the third to illustrate an intermediate level of scaling.

Extracting voronoi boundaries...

figure21

Lattice grains of connectivity

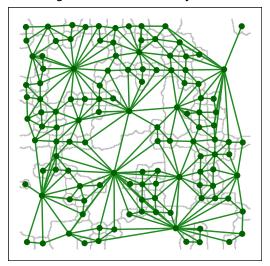


Figure 21: A scaled lattice grains of connectivity (GOC) model showing the outline of Voronoi polygons in grey, and the network connections among polygons as links plotted from adjacent polygon centroids.

Scaling networks with two-dimensional nodes (patch grains of connectivity)

Patch grains of connectivity extends the idea of the point nodes in the lattice model to two-dimensional node regions (Galpern, Manseau, and Wilson 2012). It leverages the minimum planar graph demonstrated in previous examples and its complement the Voronoi tessellation of the resistance surface. Voronoi polygons are identified and coalesced at different thresholds or "grains" in these models.

A key contribution is the capacity to model landscape connectivity at multiple spatial scales, and to account for uncertainty in the nature of the patch and the surrounding matrix (Galpern, Manseau, and Wilson 2012; Galpern and Manseau 2013a). The use of polygons rather than discrete two dimensional nodes (*i.e.*, surrounded by a matrix that presents resistance) allows for uncertainty in patch definition. Such an approach may be particularly valuable in ecology for modelling landscape connectivity in highly-mobile terrestrial animals, for which both patch definition and resistance surface parameterization have large amounts of uncertainty.

The product is a continuously distributed set of two-dimensional nodes, such that every point on the surface is associated with a node. Critically these polygons can be scaled. Relationships among these polygons are based on the relationships among two-dimensional nodes contained within. In a later example we show how grains of connectivity can be used to identify potential spatial corridors between points.

This patch grains of connectivity model uses the familiar resistance surface and the same patches (=1) used in many earlier examples.

```
## Use the MPG extracted in previous examples to find a
## patch grains of connectivity model, where patches
## are cells on the resistance surface equal to 1
## Do this at five thresholds
```

Extracting voronoi boundaries...

figure22

Patch grains of connectivity

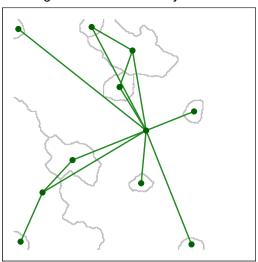


Figure 22: A scaled patch grains of connectivity (GOC) model showing the outline of Voronoi polygons in grey, and the network connections among polygons as links plotted from adjacent polygon centroids.

Visualization

Characteristics of grains of connectivity

The Voronoi polygons that are complementary to a given scale or threshold of a landscape network describe a geographic area. As polygons are coalesced and the network is scaled, grainscape collects summary statistics on several variables in the newly aggregated areal units. These include the total area and core area of two-dimensional nodes that fall within the boundary of the polygon, the median link weight within the cluster, and several others.

Visualizing these quantities at multiple spatial scales (i.e., grains) can support a sensitivity analysis for the area or connectivity of sub-regions in the model. For example, to assess the availability of connected habitat or protected areas, or the risks to the functioning of these elements.

The following example maps the amount of core area of patches at an intermediate scale by varying the size of symbols plotted at the centroids of the Voronoi polygons. Core area is defined as the area of all patches in the polygon excluding the edges of those patches, which consists of a one-cell wide margin. In this resistance surface node core area appears to be correlated generally with the size of the Voronoi polygon (*i.e.*, larger node circles appear in larger polygons)

Extracting voronoi boundaries...

figure23

Voronoi polygon metrics (core area)

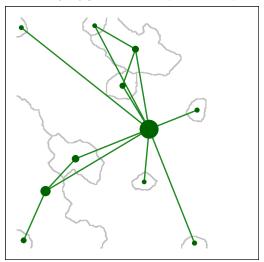


Figure 23: A scaled patch grains of connectivity (GOC) model showing the outline of Voronoi polygons in grey, and the network connections among polygons. Node symbols have been scaled in proportion to the core area of patches (i.e., area excluding edge) contained within the Voronoi polygon.

Analysis

Corridor analyses at multiple scales

Finding the shortest path through a grain of connectivity is conceptually identical to finding the shortest path between nodes in the minimum planar graph. The key difference is that use of a grain permits the scaling of the network. Links between Voronoi polygons in a grain are selected links between components or clusters on the minimum planar graph. In a minimum planar graph we cannot find a shortest path between nodes that are disconnected, but with a grains of connectivity model the goal is rather to find the shortest path between these disconnected components (represented by Voronoi polygons). The links connecting polygons are the shortest of all those that span patches in two components.

An application of grains of connectivity is to scale a corridor analysis, effectively to find a shortest path between two locations on the map and understand how sensitive this path may be to the scale. In this example, we use the grainscape function corridor() to identify and plot this corridor. Because grains of connectivity are continuously distributed across the map we do not need to provide a focal node or patch identifier. Rather, we pass coordinates to the function.

```
## Set coordinates for the start and end of the corridor
startEnd <- rbind(c(5, 180), c(395, 312))

fragCorridor3 <- corridor(fragPatchGOC, whichThresh = 3, coords = startEnd)

## Use the default plotting functionality for corridor objects
figure24 <- plot(fragCorridor3, theme = FALSE) +
   annotate("text", x = startEnd[1, 1], y = startEnd[1, 2] - 20,</pre>
```

Extracting Voronoi boundaries...

figure24

Corridor analysis; grain of connectivity

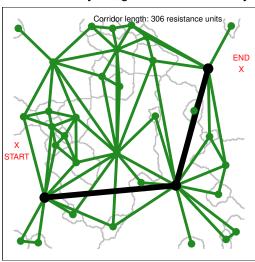


Figure 24: A corridor through a scaled patch grains of connectivity (GOC) model. The black nodes and links demonstrate the corridor between the polygons containing the start and end points (plotted in red as X). Green nodes and links show the remainder of the grains of connectivity network.

Modeling

Distances between polygons at multiple scales

grainscape provides functions to automate corridor analyses at multiple scales (grains), and for multiple points on the map. The products are distance matrices.

In this example, the grain depicted in the previous corridor analysis is used to find the pairwise shortest path distances between eight randomly positioned points. Distances at all of the grains that are available in the GOC object are produced. However, the table that appears below shows distances for only this grain.

```
## Create eight random points on the map
pts <- cbind(sample(1:ncol(fragRes))[1:8], sample(1:nrow(fragRes))[1:8])

## Plot these points and the grains of connectivity network
figure25 <- plot(grain(fragPatchGOC, 4), quick = "grainPlot", theme = FALSE) +
   annotate("text", x = pts[, 1], y = pts[, 2], label = 1:8, colour = "red") +
   ggtitle("Eight points for pairwise distances")</pre>
```

Extracting voronoi boundaries...

figure25

Eight points for pairwise distances

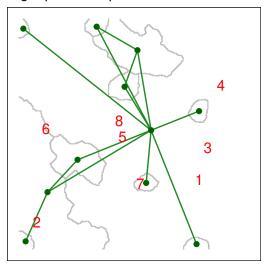


Figure 25: A scaled patch grains of connectivity (GOC) model showing the outline of Voronoi polygons in grey, and the network connections among polygons as links plotted from adjacent polygon centroids. The locations of eight focal points used to calculate a pairwise distance matrix are plotted in red.

```
## Find the pairwise distances between them at all grains
## available in the GOC object created earlier
ptsD <- grainscape::distance(fragPatchGOC, pts)

## Extract distances for the grain of interest (4)</pre>
```

	1	2	3	4	5	6	7	8
Point 1 (Polygon 1)	0.0							
Point 2 (Polygon 6)	150.8	0.0						
Point 3 (Polygon 1)	0.0	150.8	0.0					
Point 4 (Polygon 1)	0.0	150.8	0.0	0.0				
Point 5 (Polygon 1)	0.0	150.8	0.0	0.0	0.0			
Point 6 (Polygon 1)	0.0	150.8	0.0	0.0	0.0	0.0		
Point 7 (Polygon 9)	181.4	332.2	181.4	181.4	181.4	181.4	0.0	
Point 8 (Polygon 1)	0.0	150.8	0.0	0.0	0.0	0.0	181.4	0

References

Adriaensen, F, J P Chardon, G De Blust, E Swinnen, S Villalba, H Gulinck, and E Matthysen. 2003. "The application of 'least-cost' modelling as a functional landscape model." *Landscape and Urban Planning* 64 (4): 233–47. https://doi.org/10.1016/s0169-2046(02)00242-6.

Brooks, C P. 2003. "A scalar analysis of landscape connectivity." *Oikos* 102 (2): 433–39. http://www.jstor.org/stable/3548048.

Cushman, Samuel A, and Erin L Landguth. 2010. "Scale dependent inference in landscape genetics." Landscape Ecology 25 (6): 967–79. https://doi.org/10.1007/s10980-010-9467-0.

Fall, Andrew, Marie-Josée Fortin, Micheline Manseau, and Dan O'Brien. 2007. "Spatial Graphs: Principles and Applications for Habitat Connectivity." Ecosystems~10~(3): 448–61. https://doi.org/10.1007/s10021-007-9038-7.

Galpern, Paul, and Micheline Manseau. 2013a. "Finding the functional grain: Comparing methods for scaling resistance surfaces." *Landscape Ecology* 28 (7): 1269–81. https://doi.org/10.1007/s10980-013-9873-1.

2013b. "Modelling the influence of landscape connectivity on animal distribution: A functional grain approach." *Ecography* 36 (9): 1004–16. https://doi.org/10.1111/j.1600-0587.2012.00081.x.

Galpern, Paul, Micheline Manseau, and Andrew Fall. 2011. "Patch-based graphs of landscape connectivity: A guide to construction, analysis and application for conservation." *Biological Conservation* 144 (1). Elsevier Ltd: 44–55. https://doi.org/10.1016/j.biocon.2010.09.002.

Galpern, Paul, Micheline Manseau, and Paul J Wilson. 2012. "Grains of connectivity: analysis at multiple spatial scales in landscape genetics." *Molecular Ecology* 21 (16): 3996–4009. https://doi.org/10.1111/j.1365-294X.2012.05677.x.

Pascual-Hortal, Lucía, and Santiago Saura. 2006. "Comparison and development of new graph-based landscape connectivity indices: Towards the priorization of habitat patches and corridors for conservation." Landscape Ecology 21 (7): 959–67. https://doi.org/10.1007/s10980-006-0013-z.

Urban, Dean, and Timothy Keitt. 2001. "Landscape Connectivity: A Graph-Theoretic Perspective." Ecology~82~(5):~1205-18.~https://doi.org/10.1890/0012-9658(2001)082[1205:LCAGTP]2.0.CO;2.

Zeller, Katherine A, Kevin McGarigal, and Andrew R Whiteley. 2012. "Estimating landscape resistance to movement: a review." *Landscape Ecology* 27 (6): 777–97. https://doi.org/10.1007/s10980-012-9737-0.