R package gdistance: distances and routes on geographical grids (version 1.1-4)

Jacob van Etten
December 22, 2012

1 Introduction

This vignette describes gdistance, an R package which provides functionality to calculate various distance measures and routes in heterogeneous geographic spaces represented as grids. Distances are fundamental to geospatial analysis (Tobler 1970). The most commonly used geographic distance measure is the great-circle distance, which represents the shortest line between two points, taking into account the curvature of the earth. However, the great-circle distance does not correspond very well to expected travel time/effort between two points. Travel time and the real distance travelled depend on the means of transport, the mode of route-finding, and the characteristics of landscapes and infrastructure. The great-circle distance could be considered as referring to a special case: goal-directed movement with no obstacles, 'as the crow flies'. Other distance measures are needed when travel is not (or less) goal-directed and landscape characteristics affect movement in a spatially heterogeneous way. Package gdistance was created to calculate distances and determine routes using geographical grids (rasters) to represent landscape heterogeneity. It provides the following distance and route calculations.

- The least-cost distance mimics route finding 'as the fox runs', taking into account obstacles and the local 'friction' of the landscape.
- A second type of route-finding is the random walk, which has no predetermined destination (a 'drunkard's walk'). Resistance distance reflects the average travel time from origin to goal of the (Brownian) random walk (McRae 2006).

• 'Randomised shortest paths' are an intermediate form between shortest paths and Brownian random walks, introduced by Saerens et al. (2009).

The functionality of gdistance corresponds to other software like ArcGIS Spatial Analyst, GRASS GIS (r.cost, r.walk functions), and CircuitScape (random walk / resistance distance). The gdistance package also contains specific functionality for geographical genetic analyses. The package implements measures to model dispersal histories first presented by Van Etten and Hijmans (2010). Section 10 below introduces with an example how gdistance can be used in geographical genetics.

2 Raster basics

Package gdistance uses functionality from a number of other R packages. The most important among these packages is raster. The raster package is memory-efficient and user-friendly. It provides comprehensive geographical grid functionality.

To use gdistance and to understand the details of this vignette, the reader has to be familiar with the basic functionality of raster. The following code shows how to make a raster.

```
> library(raster)
> r <- raster(ncol=3,nrow=3)</pre>
> r[] <- 1:ncell(r)
> r
class
            : RasterLayer
            : 3, 3, 9 (nrow, ncol, ncell)
dimensions
resolution : 120, 60 (x, y)
            : -180, 180, -90, 90 (xmin, xmax, ymin, ymax)
coord. ref. : +proj=longlat +datum=WGS84
data source : in memory
            : layer
names
values
            : 1, 9 (min, max)
```

In the first line, we create a simple raster with 3 columns and 3 rows. In the second line, we assign the values 1 to 9 as the grid values. We see that the resulting object holds the grid values and geographic data. This is an object of the class RasterLayer, which holds only one layer of grid data. There are other classes which allow more than one layer of data: RasterStack and RasterBrick. Collectively these classes are referred to as Raster*. The use

of classes in R makes it possible to construct objects that hold different types of data together in the different *slots*. The main advantage of using these classes is that data that goes together remains coherent. Because of this, operations that are geographically incorrect (like, for instance, adding the values of two rasters of different projections) can be detected by the software and throw the pertinent error. The package gdistance also uses these classes (S4) to construct objects.

One important thing to know about raster is how grid data are stored internally in Raster* objects. Cell numbers in rasters go from left to right and from top to bottom. The 3 x 3 raster we just created would have the cell numbers in the order shown in Figure 1.

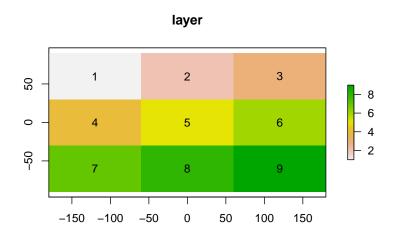


Figure 1: Cell numbers of a 3 x 3 raster

This is the code used to make Figure 1.

- > plot(r)
- > text(r)

3 Transition* classes

Distances and other measures are calculated in various steps. Rather than calculating the distances directly from the Raster* objects, we create an intermediate object that contain a transition matrix, based on the grid values.

This gives us a lot of flexibility to represent the local distances between cells in the grid. The central classes in gdistance are TransitionLayer and TransitionStack. Most operations have an object of one of these classes either as input and sometime also as their output.

Transition* objects can be constructed from an object of class Raster*. The class Transition* takes the necessary geographic references (projection, resolution, extent) from the original Raster* object. It also contains a matrix which represents a transition from one cell to another in the grid. Each row and column in the matrix represents a cell in the original Raster* object. Row/column 1 in the transition matrix corresponds to cell 1 in the original raster, and so on. For instance, the raster we just created would produce a 9 x 9 transition matrix with rows/columns numbered from 1 to 9 (see Figure 2 below).

Normally, we work with transition matrices that represent the conductance between cells¹. Using conductance values may be a bit confusing at first, as other software generally uses friction surfaces to calculate distances. Also, the resulting distances represent accumulated friction or cost, making the use of conductance somewhat counterintuitive.

In fact, the relation between conductance and friction is straightforward: conductance is the *reciprocal* of friction (1/friction). It is not strange to use the word conductance in this context or to use resistance as a synonym for friction. There is an analogy between random walks on geographical grids and electrical current in a mesh of resistors (Chandra et al. 1996, McRae et al. 2008). Some algorithms in gdistance are based on this analogy.

The main advantage of using conductance is that it makes it possible to use computer memory very efficiently, using so-called *sparse* matrices. Sparse matrices only record the non-zero values and information about their location in the matrix. In most cases, cells are connected only with adjacent cells. Consequently, a conductance matrix contains only a small fraction of non-zero values, which occupy much less memory in a sparse matrix than in a dense matrix. The package <code>gdistance</code> makes use of sparse matrix classes and methods from the package <code>Matrix</code>, which gives access to fast procedures implemented in the C language.

The construction of a Transition* object from a Raster* object is straightforward. We can define an arbitrary function to calculate the conductance values from the values of each pair of cells to be connected. Here, we use the raster created earlier and set all values to unit. We then create a TransitionLayer object. The transition value between each pair of cells is

¹'Permeability' is a synonym of conductance. Impedance, resistance, cost and friction are used interchangeably to denote the contrary.

the mean of the two cell values.

```
> library(gdistance)
> r[] <- 1
> tr1 <- transition(r, transitionFunction=mean, directions=8)</pre>
```

We set the directions argument to value 8. This connects all adjacent cells in 8 directions. Cells can also be connected in 4 or 16 connections. In chess terms, setting directions to 4 connects all cells with all possible one-cell rook movements (producing 'Manhattan' distances), while setting directions to 8 connects with one-cell queen movements. With 16 directions, all cells are connected with both one-cell queen movements and knight movements. This can make distance calculations more accurate².

If we inspect the object we created, we see that the resulting TransitionLayer object keeps much information from the original RasterLayer object.

> tr1

```
class : TransitionLayer
```

dimensions: 3, 3, 9 (nrow, ncol, ncell)

resolution : 120, 60 (x, y)

extent : -180, 180, -90, 90 (xmin, xmax, ymin, ymax)

coord. ref. : +proj=longlat +datum=WGS84

values : conductance
matrix class: dsCMatrix

It is also possible to create asymmetric matrices, in which the conductance from i to j is not always the same as the conductance from j back to i. This is relevant, among other things, for modelling travel in hilly terrain, as shown in Example 1 below. On the same slope, a downslope traveler experiences less resistance than an upslope traveler. In this case, the function to calculate conductance values is non-commutative: $f(i,j) \neq f(j,i)$. To make an asymmetric transition matrix, the symm argument in transition needs to be set to FALSE.

```
> r[] <- runif(9)
> ncf <- function(x) max(x) - x[1] + x[2]
> tr2 <- transition(r, ncf, 4, symm=FALSE)
> tr2
```

²Connecting in 16 directions was inspired by the function r.cost in GRASS 6, and the documentation of this function illustrates nicely why connecting in 16 directions can increase the accuracy of the calculations http://grass.itc.it/grass64/manuals/html64_user/r.cost.html. Also, see the section on distance transforms in de Smith et al. (2009).

```
class : TransitionLayer
```

dimensions: 3, 3, 9 (nrow, ncol, ncell)

resolution : 120, 60 (x, y)

extent : -180, 180, -90, 90 (xmin, xmax, ymin, ymax)

coord. ref. : +proj=longlat +datum=WGS84

values : conductance
matrix class: dgCMatrix

The sparse matrix class dsCMatrix is symmetric and holds only half of the non-zero matrix values in memory. The class dgCMatrix holds an asymmetric matrix.

Different mathematical operations can be done with Transition* objects. This makes it possible to flexibly model different components of land-scape friction.

```
> tr3 <- tr1*tr2
> tr3 <- tr1+tr2
> tr3 <- tr1*3
> tr3 <- sqrt(tr1)</pre>
```

Operations with more than one object require that the different objects have the same resolution and extent.

Also, it is possible to extract and replace values in the matrix using indices.

```
> tr3[cbind(1:9,1:9)] <- tr2[cbind(1:9,1:9)]
> tr3[1:9,1:9] <- tr2[1:9,1:9]
> tr3[1:5,1:5]
```

5 x 5 sparse Matrix of class "dgCMatrix"

```
      [1,]
      0.007881319
      0.1166173
      1.592726
      .

      [2,]
      0.5071487
      0.2253533
      0.7927607

      [3,]
      0.3984127
      0.007881319
      .
      .
      .
      .
      0.4003210

      [5,]
      .
      0.007881319
      .
      1.449920
      .
```

The functions adjacency and adjacencyFromTransition can be used to create indices. Example 1 in section 7 below gives an example.

Some functions require that Transition* objects do not contain any isolated 'clumps', islands that are not connected to the rest of the raster cells. This can be avoided when creating Transition* objects, for instance

by giving conductance values between all adjacent cells a small minimum value. It can be checked visually if there are any clumps. There are several ways to visualize a Transition* object. For the first method, you can extract the transition matrix with function transitionMatrix. This gives a sparse matrix which can be vizualized with function image. This shows the rows and columns of the transition matrix and indicates which has a non-zero value, which represents a connection between cells (Figure 1).

> image(transitionMatrix(tr1))

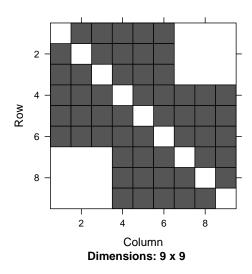


Figure 2: Visualizing a TransitionLayer with function image()

Figure 2 shows which cells are connected to each other. You may wonder why even cell 1 is connected to 5 different cells, as this cell is located in the upper left corner of the original grid. This is explained by the extent of the grid. Since it covers the whole world, the outer meridians (180 and -180 degrees) touch each other. The software takes this into account and as a result the cells in the extreme left column are connected to the extreme right column.

Figure 2 shows which cells contain non-zero values, but gives no further information about levels of conductance. This can be visualized by transforming the transition matrix back into a raster. To summarize the information in transition matrix, we can take means or sums across rows or columns, for instance. You can do this with function raster. Applied to a

TransitionLayer, this function converts it to a RasterLayer. For the different options see method?raster("TransitionLayer"). The default, shown in Figure 3, takes the column-wise means of the non-zero values. All these forms of transformation unavoidably cause information loss, of course.

> plot(raster(tr3))

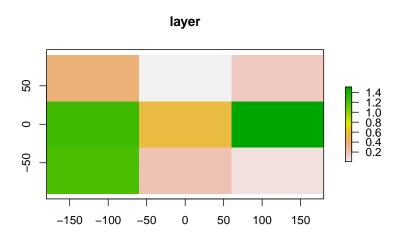


Figure 3: Visualizing a TransitionLayer using the function raster()

4 Correcting inter-cell conductance values

The function transition calculates transition values based on the values of adjacent cells in the input raster. However, the centres of diagonally connected cells are more remote from each other than in the case of orthogonally connected cells. Secondly, on equirectangular (lonlat) projection grids, W-E connections are longer at the equator and become shorter towards the poles. Therefore, the values in the matrix need to be corrected for these two types of distortion. Both types of distortion can be corrected by dividing each conductance matrix value between the inter-cell distance. This is what function geoCorrection does for us.

```
> tr1C <- geoCorrection(tr1, type="c", multpl=FALSE)
> tr2C <- geoCorrection(tr2, type="c", multpl=FALSE)</pre>
```

For random walks on longlat grids, there is an additional consideration to be made. The number of connections in N-S direction remains equal when moving from the equator to the poles. This is problematic, because random walks can be seen as analogous to electrical current through a networks of resistors. The inter-cell connections should be thought of as parallel resistors. Moving away from the equator, the inter-meridian space each individual resistor bridges becomes narrower, tending to zero at the poles. Therefore, the N-S resistance between parallels should decrease when moving away from the equator. The function geoCorrection corrects this distortion by multiplying the N-S transition values with the cosine of the average latitude of the cell centres. This is done with function geoCorrection, by setting the argument type to "r".

```
> r3 <- raster(ncol=36, nrow=18)
> r3 <- setValues(r3, runif(36*18))
> tr3 <- transition(r3, mean, 4)
> tr3C <- geoCorrection(tr3, type="c", multpl=FALSE, scl=TRUE)
> tr3R <- geoCorrection(tr3, type="r", multpl=FALSE, scl=TRUE)</pre>
```

The argument scl is set to TRUE to get reasonable values. If the values are too large, the distance calculation algorithms will not work well.

When similar Transition* objects with equal resolution and extent need to be corrected repetitively, computational effort may be reduced by preparing an object that only needs to be multiplied with the Transition* object to produce a corrected version of it. The following is equivalent to the previous procedure.

```
> CorrMatrix <- geoCorrection(tr3, type="r", multpl=TRUE, scl=TRUE)
> tr3R <- tr3 * CorrMatrix</pre>
```

Object trCorr1Matrix is only calculated once. It can be multiplied with Transition* objects, as long as they have the same extent, resolution, and directions of cell connections. We need to take special care that the geocorrection multiplication matrix (tr1CorrMatrix) contains all non-zero values that are present in the Transition* object with which it will be multiplied (tr1)³.

³A good alternative is to use geoCorrection(mulpl=FALSE) with a Transition* object with cells connected with value 1.

5 Calculating distances

Only now that we have the corrected Transition* object we can calculate distances between points. It is important to note that all distance functions require a Transition* object with *conductance* values, even though distances will be expressed in 1/conductance (friction or resistance) units (see section 3).

To calculate distances, we need to have the coordinates of point locations. This is done by creating a two-column matrix of coordinates. Functions will also accept a SpatialPoints object or, if there is only one point, a vector of length two.

```
> sP \leftarrow cbind(c(-100, 100, -100), c(-50, 50, 50))
```

Calculating a distance matrix is straightforward now.

```
> #costDistance(tr3C, sP)
> commuteDistance(tr3R, sP)
                   2
         1
2 6387.591
3 6125.812 5901.169
> rSPDistance(tr3R, sP, sP, theta=1e-12, totalNet="total")
         [,1]
                   [,2]
                            [,3]
[1,]
        0.000 3664.634 3599.624
[2,] 3780.258
                 0.000 3526.523
[3,] 3540.158 3351.432
                           0.000
```

The costDistance function gives a symmetric or asymmetric distance matrix, depending on the TransitionLayer that is used as input.

Commute distance represents the random walk commute time, e.g. the number of cells traversed on the trip (Chandra et al. 1996).

rSPDistance gives the cost incurred during the same walk (theta approaches zero, so the walk is nearly random). By summing the off-diagonal elements (Dij + Dji), we obtain the commute costs ⁴.

⁴In this case, the commute costs are only slightly higher than (and proportional to) the commute distances. This is because the TransitionLayer tr3R has been scaled, making most of the transition costs unit, except for diagonal connections and W-E connections away from the equator.

6 Dispersal paths

To determine dispersal paths with a random element, we use the function passage. This function can be used for both random walks and randomised shortest paths. The function calculates the number of passages through cells before arriving in the destination cell. Either the total or net number of passages can be calculated. The net number of passages is the number of passages that are not reciprocated by a passage in the opposite direction (see also the previous section).

Figure 4 shows the probability of passage through each cell, assuming randomised shortest paths with the parameter theta set to 3.

```
> origin <- SpatialPoints(cbind(0, 0))
> rSPraster <- passage(tr3C, origin, sP[3,], theta=3)</pre>
```

> plot(rSPraster)

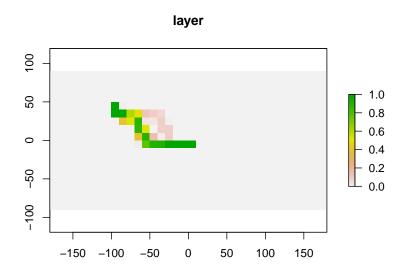


Figure 4: Probability of passage

7 Path overlap and non-overlap

One of the specific uses, for which package gdistance was created, is to look at trajectories coming from the same source (van Etten and Hijmans 2010).

The degree of coincidence of two trajectories can be visualized by multiplying the probabilities of passage (Figure 5). With a more complex formula, we can approximate the non-overlapping part of the trajectory (Figure 6).

```
> r1 <- passage(tr3C, origin, sP[1,], theta=1)
> r2 <- passage(tr3C, origin, sP[3,], theta=1)
> rJoint <- r1 * r2
> plot(rJoint)
```

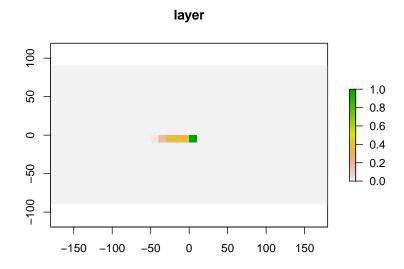


Figure 5: Overlapping part of the two routes

```
> rDiv \leftarrow max(max(r1, r2) * (1 - min(r1, r2)) - min(r1, r2), 0)
```

With the function pathInc we can calculate measures of path overlap and non-overlap for a large number of points. These measures can be used to predict patterns of diversity if these are due to dispersal from a single common source (van Etten and Hijmans 2010). If the argument type contains two elements (divergent and joint), the result is a list of distances matrices.

> plot(rDiv)

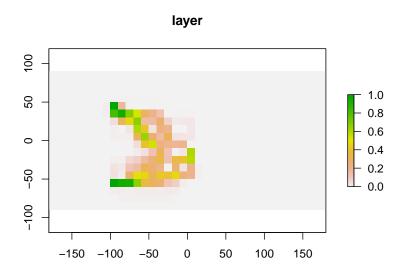


Figure 6: Non-overlapping part of the two routes

8 Example 1: Hiking around Maunga Whau

The previous examples were somewhat theoretical, based on randomly generated values. More realistic examples serve to illustrate the various uses that can be given to this package.

Determining the fastest route between two points in complex terrain is useful for hikers. Tobler's Hiking Function provides a rough estimate for the the maximum hiking speed given the slope of the terrain (Tobler 1993). The maximum speed of off-path hiking (in m/s) is:

```
speed = exp(-3.5 * abs(slope + 0.05))
```

Note that the function is not symmetric around 0 (see Figure 7).

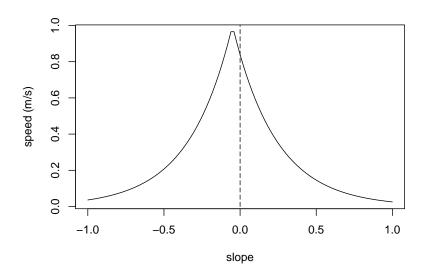


Figure 7: Tobler's Hiking Function

We use the Hiking Function to determine the shortest path to hike around the volcano Maunga Whau (Auckland, New Zealand). First, we read in the altitude data for the volcano. This is a geo-referenced version of the "volcano" data available in Base R datasets (see ?volcano for more information).

```
> r <- raster(system.file("external/maungawhau.grd",
+ package="gdistance"))</pre>
```

The Hiking Function requires the slope as input.

```
slope = difference in height / distance travelled
```

The units of height and distance should be identical. Here, we use meters for both. We calculate the height differences between cells first. Then we use the function geoCorrection() to divide by the distance between cells.

```
> heightDiff <- function(x){x[2] - x[1]}
> hd <- transition(r,heightDiff,8,symm=FALSE)
> slope <- geoCorrection(hd, scl=FALSE)</pre>
```

Subsequently, we calculate the speed. We need to exercise special care, because the matrix values between non-adjacent cells is 0, but the slope between these cells is not 0! Therefore, we need to restrict the calculation to adjacent cells. We do this by creating an index for adjacent cells (adj) with the function adjacent(). Using this index, we extract and replace adjacent cells, without touching the other values.

```
> adj <- adjacent(r, cells=1:ncell(r), pairs=TRUE, directions=8)
> speed <- slope
> speed[adj] <- exp(-3.5 * abs(slope[adj] + 0.05))</pre>
```

Now we have calculated the speed of movement between adjacent cells. We are close to having the final conductance values. Attainable speed is a measure of the ease of crossing from one cell to another on the grid. However, we also need to take into account the distance between cell centres. Travelling with the same speed, a diagonal connection between cells takes longer to cross than a straight connection. Therefore, we use the function <code>geoCorrection()</code> again!

```
> x <- geoCorrection(speed, scl=FALSE)
```

This gives our final "conductance" values.

What do these "conductance" values mean? The function geoCorrection divides the values in the matrix with the distance between cell centres. So, with our last command we calculated this:

```
conductance = speed / distance
```

This looks a lot like a measure that we are more familiar with:

```
travel time = distance / speed
```

In fact, the conductance values we have calculated are the *reciprocal* of travel time.

```
1 / travel time = speed / distance = conductance
```

Maximizing the reciprocal of travel time is exactly equivalent to minimizing travel time!

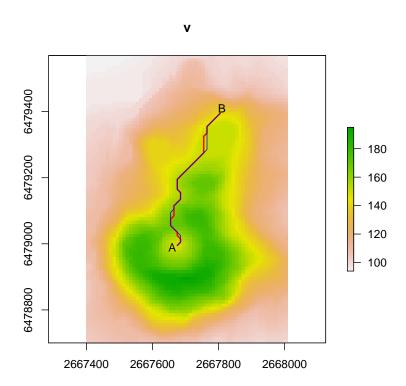


Figure 8: Quickest hiking routes around Maunga Whau

Now we define two coordinates, A and B, and determine the paths between them. We test if the quickest path from A to B is the same as the quickest path from B back to A.

```
> A <- c(2667670,6479000)
> B <- c(2667800,6479400)
> AtoB <- shortestPath(x, A, B, output="SpatialLines")
> BtoA <- shortestPath(x, B, A, output="SpatialLines")
> plot(r)
> lines(AtoB, col="red", lwd=2)
> lines(BtoA, col="blue")
> text(A[1]-10,A[2]-10,"A")
> text(B[1]+10,B[2]+10,"B")
```

A small part of the A-B (red) and B-A (blue) lines in the figure do not overlap. This is a consequence of the asymmetry of the Hiking Function.

9 Example 2: Geographical genetics

The direct relation between genetic and geographic distances is known as isolation by distance (Wright 1943). Recent work has expanded this relationship to random movement in heterogeneous landscapes (McRae 2006). Also, the geography of dispersal routes can explain observed geospatial patterns of genetic diversity. For instance, diffusion from a single origin (Africa) explains much of the current geographical patterns of human genetic diversity (Ramachandran 2005). As a result, the mutual genetic distance between a pair of humans from different parts from the globe depends on the extent they share their prehistoric migration history.

Within a single continent, however, human genetic diversity may have to do with more recent events. Let's look at diversity in Europe, using the data presented by Balaresque et al. (2010). Within Europe, genetic diversity is often thought to be a result of the migration of early Neolithic farmers from Anatolia (Turkey) to the west.

First we read in the data, including the coordinates of the populations (Figure 9) and mutual genetic distances.

```
> Europe <- raster(system.file("external/Europe.grd",
+ package="gdistance"))
> Europe[is.na(Europe)] <- 0
> data(genDist)
> data(popCoord)
> pC <- as.matrix(popCoord[c("x","y")])</pre>
```

Then we create three geographical distance matrices. The first corresponds to the great-circle distance between populations. The second is the least-cost distance between locations. Travel is restricted to the land mass. The third is the resistance distance (using the same conductance matrix), which is related to the random-walk commute time between points (Chandra et al. 1996, McRae 2006).

```
> geoDist <- pointDistance(pC, longlat=TRUE)
> geoDist <- as.dist(geoDist)
> Europe <- aggregate(Europe,3)
> tr <- transition(Europe, mean, directions=8)
> trC <- geoCorrection(tr, "c", scl=TRUE)
> trR <- geoCorrection(tr, "r", scl=TRUE)
> cosDist <- costDistance(trC,pC)
> resDist <- commuteDistance(trR, pC)
> cor(genDist,geoDist)
```

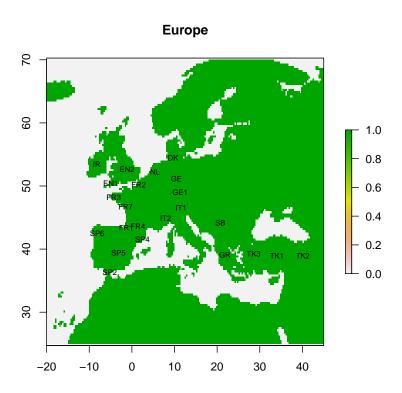


Figure 9: Map of genotyped populations

```
[1] 0.5962655
> cor(genDist,cosDist)
[1] 0.5889319
> cor(genDist,resDist)
[1] 0.192114
```

Interestingly, the great-circle distance between points turns out to be the best predictor of genetic distance. The other distance measures incorporate more information about the geographic space in which geneflow takes place, but do not improve the prediction. But how well does a wave of expansion from Anatolia explain the spatial pattern?

```
> origin <- unlist(popCoord[22,c("x","y")])
> pI <- pathInc(trC, origin=origin, from=pC,
+ functions=list(overlap))
> cor(genDist,pI[[1]])

[1] -0.6560192
```

At least at first sight, the overlap of dispersal routes explain the spatial pattern better than any of the previous measures. The negative sign of the last correlation coefficient was expected, as more overlap in routes is associated with lower genetic distance. While additional work would be needed to improve predictions and compare the different models more rigorously, the promise of dispersal modelling with gdistance is clear.

10 Final remarks

Questions about the use of gdistance can be posted on the r-sig-geo email list. Bug reports and requests for additional functionality can be mailed to jacobvanetten@yahoo.com.

11 References

Balaresque P., et al. 2010. A predominantly Neolithic origin for European paternal lineages. *PLoS Biology* 8(1): e1000285.

- Chandra, et al. 1996. The electrical resistance of a graph captures its commute and cover times *Computational Complexity* 6(4), 312-340.
- de Smith, M.J., M.F. Goodchild, and P.A. Longley. 2009. *Geospatial Analysis*. Matador. 3rd edition.
- McRae B.H. 2006. Isolation by resistance. Evolution 60: 1551–1561.
- McRae B.H., B.G. Dickson, and T. Keitt. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89:2712-2724.
- Ramachandran S., et al. 2005. Support from the relationship of genetic and geographic distance in human populations for a serial founder effect originating in Africa. *PNAS* 102: 15942–15947.
- Saerens M., L. Yen, F. Fouss, and Y. Achbany. 2009. Randomized shortest-path problems: two related models. *Neural Computation*, 21(8):2363-2404.
- Tobler W. 1970. A computer movie simulating urban growth in the Detroit region. *Economic Geography*, 46(2): 234-240.
- Tobler W. 1993. Three Presentations on Geographical Analysis and Modeling. http://www.ncgia.ucsb.edu/Publications/Tech_Reports/93/93-1.PDF
- van Etten, J., and R.J. Hijmans. 2010. A geospatial modelling approach integrating archaeobotany and genetics to trace the origin and dispersal of domesticated plants. *PLoS ONE* 5(8): e12060.
- Wright, S. 1943. Isolation by distance. Genetics 28: 114–138.