Article

Ecological connectivity: Flow connectivity *vs*. least cost modelling

Alessandro Ferrarini
Department of Evolutionary and Functional Biology, University of Parma, Via G. Saragat 4, I-43100 Parma, Italy
E-mail: sgtpm@libero.it, alessandro.ferrarini@unipr.it

Received 2 June 2014; *Accepted 5 July 2014*; *Published online 1 December 2014*

Abstract

Recently I have introduced a modelling approach (flow connectivity) to ecological connectivity that is alternative to circuit theory, and is able to fix the weak point of the “from-to” connectivity approach. Flow connectivity also holds for mountain and hilly landscapes that are not composed of source and sink habitats.

In this paper I compare the recently-introduced flow connectivity (FC) modelling to the commonly-used least cost (LC) modelling. LC path analysis is an attractive technique for analysing and designing habitat corridors because it: 1) allows quantitative comparisons of potential movement routes over large study areas, 2) can incorporate simple or complex models of habitat effects on movement and 3) offers the potential to escape the limitations of analyses based solely on structural connectivity (i.e. designating areas as patch, matrix or corridor) by modelling connectivity as it might be perceived by a species on a landscape. I evidence here that flow connectivity has the same advantages when compared to LC modelling as with regard to circuit theory. Four main differences emerged. LC modelling a) is a “from-to” approach to ecological connectivity, b) it seeks global path optimization, c) it allows for biotic paths where the biotic effort is ascending, and d) it is undirected (it does not depend on the direction of the path). FC has opposite properties. Moreover, cost-distance models are based on two biologically improbable assumptions: (1) dispersers have complete knowledge of their surroundings, and (2) they do select the least cost route from this information. Instead, the predicted path lengths and the biotic efforts predicted by both FC and LC modelling in a case study about wolf in the Ceno valley (Parma, Italy) resulted not significantly different, but this result is contingent upon the case study.

Keywords biotic flows; flow connectivity; gene flow; landscape connectivity; least cost modeling; species dispersal.

Computational Ecology and Software
ISSN 2220-721X
URL: http://www.iaees.org/publications/journals/ces/online-version.asp
RSS: http://www.iaees.org/publications/journals/ces/rss.xml
E-mail: ces@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

Landscape connectivity was initially introduced as “*the degree to which the landscape facilitates or impedes movements among resource patches*” (Taylor et al., 1993). The way in which animals disperse is pivotal for the management and conservation of fragmented populations. Landscape heterogeneity and fragmentation affect how organisms are distributed in the landscape (Kennedy and Gray, 1997), determine the chance of a patch being colonized (Hanski and Ovaskainen, 2000), reduce inbreeding in small populations and maintains evolutionary potential (Couvet, 2002).

The prediction of animal dispersal is an useful tool for biotic conservation planning (King and With, 2002). Due to the difficulty in gathering experimental results on species dispersal, simulation models have become a cost-effective approach to predict dispersal dynamics (Tischendorf, 1997; Tischendorf and Fahrig, 2000). Simulation models with spatially-explicit landscapes enable the integration of the relationships between species and the landscape, and provide representation of the spatial elements that promote or constrain dispersal.

Several dispersal models with spatially explicit landscapes have been developed (Gustafson and Gardner, 1996; With et al., 1997; Gardner and Gustafson, 2004). Recently, concepts and algorithms from electrical circuit theory have been adjusted for these purposes (McRae, 2006; McRae, 2007; McRae et al., 2008). In circuit theory, landscapes are represented as conductive surfaces, with resistance proportional to the easiness of species dispersal or gene flow. Low resistances are assigned to habitats that are most permeable to movement or best boost gene flow, and high resistances are given to poor dispersal habitat or to barriers. The application of circuit theory to ecological problems is motivated by intuitive connections between ecological and electrical connectivity: rigorous connections between circuit and random walk theories mean that current, voltage, and resistance in electrical circuits have concrete interpretations in terms of species dispersal probabilities (McRae et al., 2008). Circuit theory offers several advantages, including a theoretical basis in random walk theory and the ability to evaluate contributions of multiple dispersal pathways. For example, effective resistances calculated across landscapes have been shown to markedly improve predictions of gene flow for plant and animal species (McRae, 2007).

Recently I have introduced a modelling approach (flow connectivity; Ferrarini, 2013a) to ecological connectivity that is alternative to circuit theory, and is able to fix the weak point of the “from-to” approach. Landscape connectivity as estimated by circuit theory relies on a strong assumption that is possibly untrue, unproven or very challenging to be demonstrated: species dispersals are “from-to” movements, i.e. from source points (patches) of the landscape to sink ones. Source and sinks are suitable areas present within a matrix that is partially or completely hostile to the species. Two aspects of this approach are questionable. Firstly, a source-sink habitats model can be suitable to describe lowland landscapes where few suitable patches (e.g. protected areas) are surrounded by a dominant, hostile (or semi-hostile) anthropogenic landscape. By the way, mountain and hilly landscapes are not composed of source and sink habitats, instead they’re a continuum with a natural matrix where the source-sink habitats model loses its rationale. Second, assuming that a species aims to go from “patch A” to “patch B” means that such species is supposed to plan such dispersal path (i.e. global optimization). This could be true for short-range dispersals where the final point is visible from the starting one, but for wide-range movements, and for plant species in particular, the dispersal model postulated by circuit theory is unsuitable.

In addition, I’ve introduced “reverse flow connectivity” (Ferrarini, 2014a) that couples evolutionary algorithms to partial differential equations in order to fix the problem of subjectivity in the attribution of friction values to landscape categories. Reverse flow connectivity prevents from the risk of using expert opinions on an arbitrary scale. I’ve also showed that flow connectivity can be used to predict biotic movements happened in the past (backward flow connectivity; Ferrarini, 2014b), and to detect landscape barriers and facilities to species movements (Ferrarini, 2014c).

In this paper, I compare flow connectivity to another commonly-used tool for connectivity modelling: least cost modeling (Dijkstra, 1959). Least-cost path analysis (LaRue and Nielsen, 2008; Phillips et al., 2008) is an attractive technique for analysing and designing habitat corridors because it: 1) allows quantitative comparisons of potential movement routes over large study areas, 2) can incorporate simple or complex models of habitat effects on movement and 3) offers the potential to escape the limitations of analyses based solely on structural connectivity (i.e. designating areas as patch, matrix or corridor) by modelling connectivity as it might be perceived by a species on a landscape.

I show here that flow connectivity has the same advantages when compared to least cost modelling as with regard to circuit theory.

2 Frictional Landscape: Mathematical Formulation

Let $L(x,y,z,t)$ be a real 3D landscape at generic time *t*, where $L \in [1,...,n]$. In other words, *L* is a generic (categorical) landcover (or land-use) map with *n* classes. At time $T_{0,}$

$$L_0 = L(x,y,z,t_0) \tag{1}$$

Let $\varphi(L)$ be the landscape friction (i.e. how much each land parcel is unfavourable) to the species under study. In other words, $\varphi(L)$ is a function that associates a friction value to each pixel of *L*. At time T_0,

$$\varphi_0 = \varphi(L_0) \tag{2}$$

Let $L_s(x,y,\varphi(L))$ be a landscape where, for each pixel, the *z*-value is equal to the friction for the species under study. In other words, L_s is a 3D fictional landscape with the same coordinates and geographic projection as *L*, but with pixel-by-pixel friction values in place of real *z*-values. Higher elevations represents areas with elevated friction to the species due to whatever reason (unsuitable landcover, human disturbance etc), while lower altitudes represent the opposite. At time T_0,

$$L_{s0} = L_s(x,y,\varphi(L_0)) \tag{3}$$

3 Least-cost Modelling: Mathematical Formulation

Least cost (LC) modelling is an algorithm that computes a deterministic trajectory (also termed least cost path; LCP hereafter) between a start and an end point moving along a frictional landscape.

A LCP minimises the sum of frictions of all pixels along the path, being the sum of the overall friction cost (OFC from now on).

Thus LCP is the path having the minimum OFC calculated as:

$$OFC_{\min} = \int_{LCP} L_s(x,y,\varphi(L))dp = \min \iint_{path_i} L_s(x,y,\varphi(L))dxdy \tag{4}$$

where the symbol *dp* may be intuitively interpreted as an elementary path length with *dx* and *dy* components. Each LCP is described by its length (in m), its OFC (unitless) and its per-km OFC (in km^{-1}). Recent applications of least-cost modelling involve measures of landscape connectivity (Drielsma et al., 2007), tracking of animal migration routes (Epps et al., 2007), planning of optimal paths within protected areas (Ferrarini et al., 2008).

4 Flow Connectivity: Mathematical Formulation

Flow connectivity (FC) modelling starts with the assignment of true-to-life coefficients to L_s.

True-to-life coefficients for $\varphi(L)$ can be calculated in flow connectivity as depicted in Ferrarini (2014a), where I defined P as the predicted path for the species over the fictional landscape L_s, and P^* the real path followed by the species (as detected by GPS data-loggers or *in situ* observations). The bias B between P and P^* is hence calculated as

$$B = \mathrm{mod}\left(\int P dx - \int P^* dx\right) \tag{5}$$

where the function *mod* indicates the module of the difference.
Hence:

$$B = \begin{cases} \int P dx - \int P^* dx & \text{where } P > P^* \\ \int P^* dx - \int P dx & \text{where } P^* > P \end{cases} \tag{6}$$

Now, true-to-life coefficients for landscape friction can be calculated by optimizing B, as follows:

set B to 0 (7)

or, at least,

minimize B (8)

The optimization of $\varphi(L)$ can be properly achieved using genetic algorithms (GAs; Holland, 1975). GAs are powerful evolutionary models with wide potential applications in ecology and biology, such as optimization of protected areas (Parolo et al., 2009), optimal sampling (Ferrarini, 2012a; Ferrarini, 2012b), optimal detection of landscape units (Rossi et al., 2014) and networks control (Ferrarini, 2011a; Ferrarini, 2013b; Ferrarini, 2013c; Ferrarini, 2013d; Ferrarini, 2013e; Ferrarini, 2014d).

Now FC simulates the biotic flow over the frictional landscape L_s as follows (Ferrarini 2013)

$$\frac{\delta S(x,y,t)}{\delta t} = \mathrm{div}\, S = \nabla \cdot S = \frac{\delta S}{\delta x} + \frac{\delta S}{\delta y} \tag{9}$$

with initial conditions S_0 at time T_0. The symbol of derivative used in eq. (9) is a notation for a differential or a difference partial equation depending on the kind of landscape under study. For a high-resolution frictional landscape, it represents a differential operator that simulates continuos movements over such landscape. Conversely, for a low resolution landsape it describes discrete movements both in space and time. It results clear that flow connectivity resembles in some way the motion characteristic of fluids over a surface. In fact, FC predicts species dispersal by minimizing at each time step the potential energy due to fictional gravity force over a frictional 3D landscape. At any position in the frictional landscape, a movement is possible only in the direction that mostly lowers the friction to the species.

As showed in Ferrarini (2013a), the resulting biotic flow is as follows:

$$\frac{\delta S}{\delta t}=\begin{cases} 0 \quad if \quad \dfrac{\delta S}{\delta x}=\dfrac{\delta S}{\delta y}=0 \\ \\ 1 \quad if \quad (\dfrac{\delta S}{\delta x}=1\ and\ \dfrac{\delta S}{\delta y}=0) \\ \qquad or\ (\dfrac{\delta S}{\delta x}=0\ and\ \dfrac{\delta S}{\delta y}=1) \\ \qquad or\ \dfrac{\delta S}{\delta x}=\dfrac{\delta S}{\delta y}=1 \end{cases} \tag{10}$$

FC assumes that the species dispersal ends at a stability point, if exists, where:

$$\frac{\delta S(x,y,t)}{\delta t}=\nabla\cdot S=0 \tag{11}$$

Now, if we define *P* as the predicted path for the species over the fictional landscape L_s, and under the hypothesis that L_s remains equal to L_{S0} due to the short time-period considered, the species effort (i.e., work) *E* for going through such path can be computed as:

$$E=\int_P L_s(x,y,\varphi(L))dp=\iint_P L_{s0}dxdy \tag{12}$$

where the symbol *dp* represents an elementary path length with *dx* and *dy* components. *E* is thus the result of a local (pixel-by-pixel) path optimization. In other words, the model assumes a greedy, local effort-minimization for the species dispersal that do not necessarily corresponds to the global minimization. In order to apply flow connectivity modelling to real landscapes, I wrote the *ad hoc* software Connectivity Lab (Ferrarini, 2013f).

5 A Comparative Example

The Ceno valley is a 35,038 ha wide valley situated in the Province of Parma, Northern Italy. It has been mapped at 1:25,000 scale (Ferrarini, 2005; Ferrarini et al., 2010) using the CORINE Biotopes classification system. The landscape structure of the Ceno Valley has been widely analysed (Ferrarini and Tomaselli, 2010; Ferrarini, 2011b; Ferrarini, 2012c; Ferrarini, 2012d). From an ecological viewpoint, the most interesting event registered in the last years is the shift of wolf populations from the montane belt to the lowland. Several populations have been recently observed *in situ* by life-watchers, environmental associations and local administrations.

I have applied both FC and LC modelling to a portion of the Ceno valley above 1000 m a.s.l. close to the municipality of Bardi (Fig. 1). The area is a square of about 20 km * 20 km. Optimized friction values $\varphi(L)$ to wolf presence are borrowed from Ferrarini (2012e).

FC modelling provides the results depicted in Fig. 2. Red lines represent the predicted biotic flows, while blue triangles are the detected stability points. I have then repeated the simulations via LC modelling (Fig. 3) using the starting points of Fig. 1 and the stopping points individuated by FC modelling.

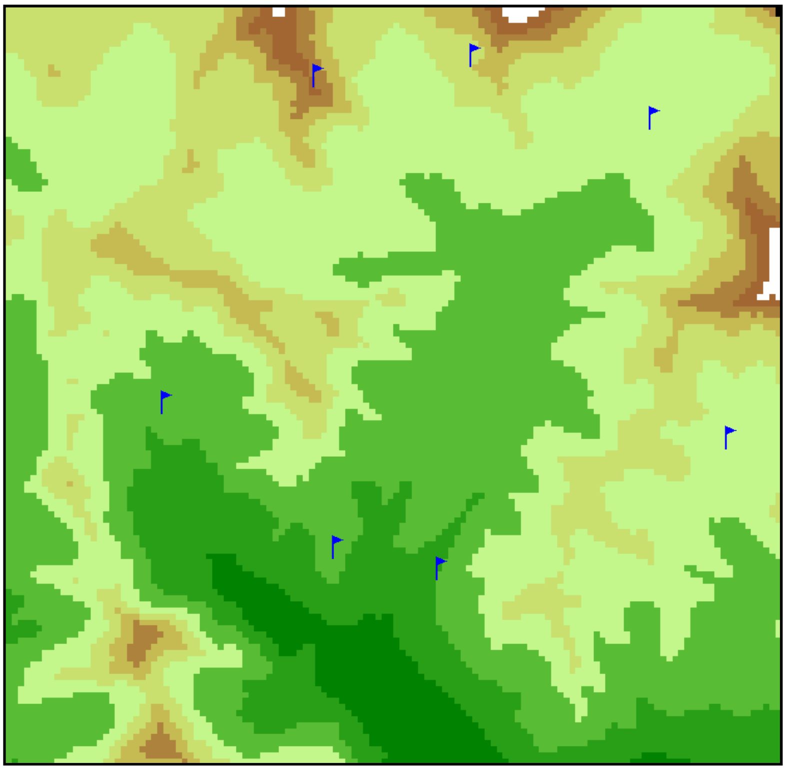

Fig. 1 The frictional landscape *Ls* has been built for wolf upon a portion (20 km * 20 km) of the Ceno valley (province of Parma, Italy) that represents here the real landscape *L(x,y,z,t)*. The elevation represents for each pixel the landscape friction $\varphi(L)$ for the species under study: the higher the elevation, the higher the friction to the species. Blue flags represent sites where the species is simulated to be present (S_0=1).

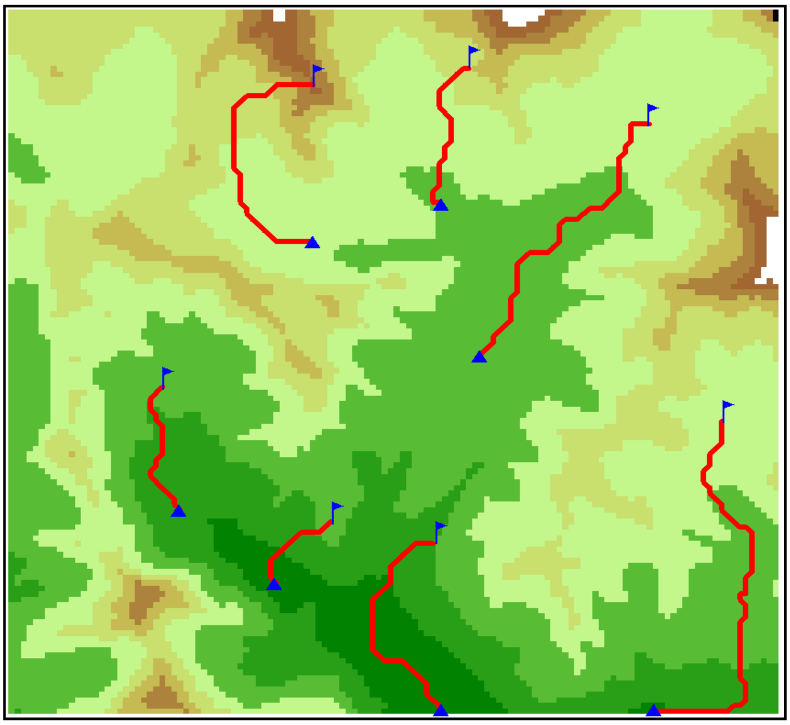

Fig. 2 Starting points (flags), predicted paths (red lines) and predicted stopping points (triangles) of biotic shifts using flow connectivity modelling over the frictional landscape of Fig. 1.

I have then calculated the path lengths and the shift efforts predicted by both FC and LC modelling (Fig. 4 and Fig. 5). It resulted that path lengths are always higher (although not in a significant way: t-test, $p>0.05$) for FC than for LC modelling. The reason is clear: as FC is a greedy, local effort minimization of species dispersal, it produces predicted biotic shifts that are much more complex than those produced by LC modelling (that instead seeks global optimization). As a logic consequence, also shift efforts are higher for FC than for LC modelling (although not in a significant way: t-test, $p>0.05$).

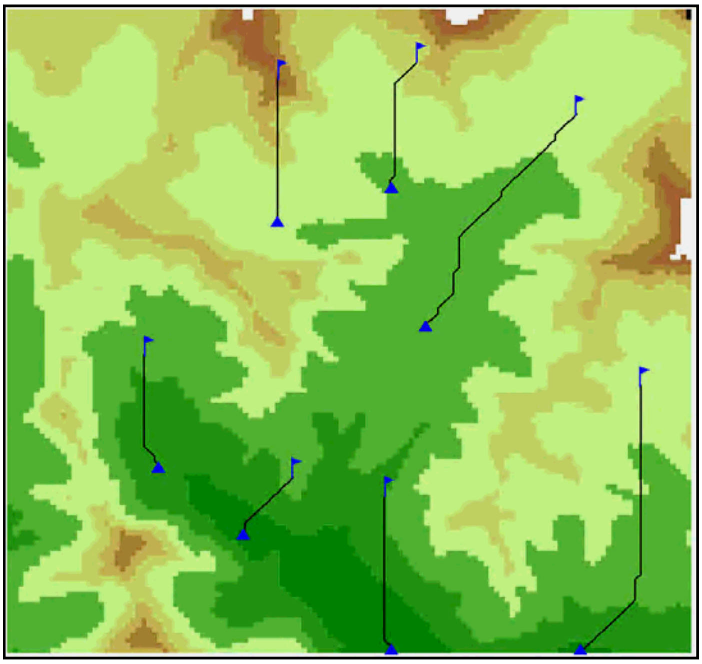

Fig. 3 Starting points (flags), predicted paths (black lines) and stopping points (triangles) of biotic shifts using least cost modelling over the frictional landscape of Fig. 1.

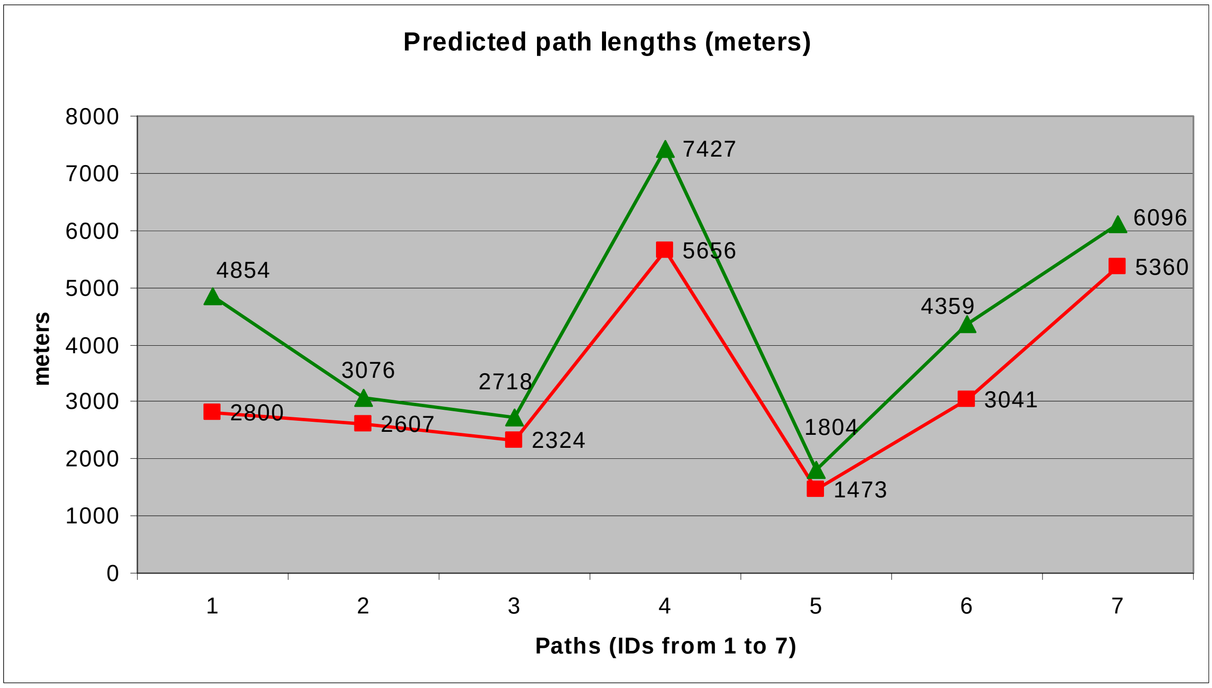

Fig. 4 For each of the 7 predicted paths, the length in meters of each biotic shift is given both for flow connectivity paths (in green) and least cost ones (in red).

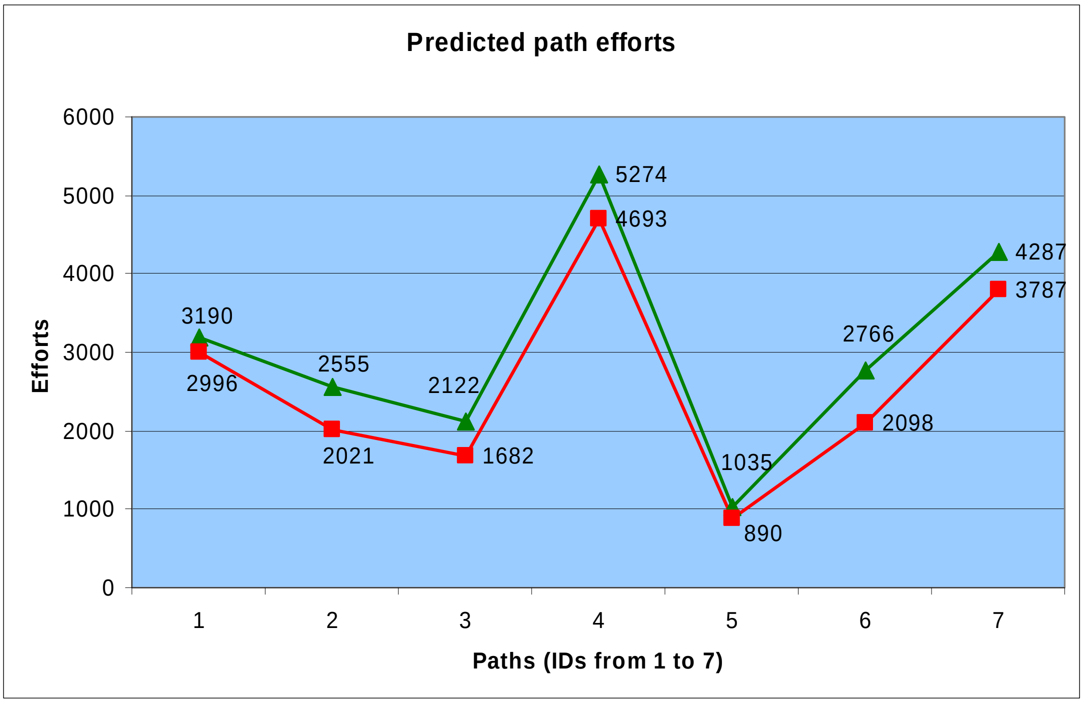

Fig. 5 For each of the 7 predicted paths, the effort of each biotic shifts is given both for flow connectivity paths (in green) and least cost ones (in red).

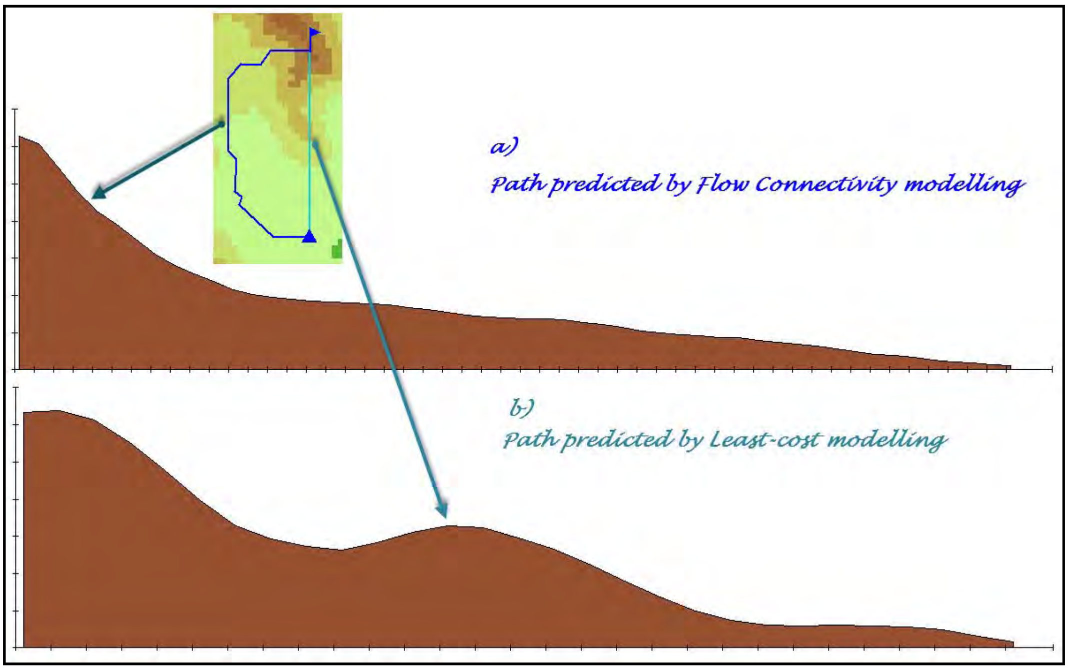

Fig. 6 For one of the 7 predicted paths, the 3D profile of the biotic shift over the frictional landscape predicted by flow connectivity (top) and least cost modelling (bottom) is given.

Last, for one of the predicted paths I have extracted the 3D profile over the frictional landscape (that represents the effort that the species sustains at each single point along the predicted shift; Fig. 6). It is clear a further fundamental difference between FC and LC modelling: in FC the predicted path always presents descending efforts (Fig. 6a), as the species locally optimizes its movements towards fitter areas. Instead, in LC modelling (and in circuit theory) the species can choose a path where effort is also ascending (Fig. 6b) because the species only seeks global optimization.

There’s a further difference between FC and LC: FC has a precise direction (directed movement), i.e. it depends on the direction of the path. Instead LC modelling has not a direction, in fact if one inverts the starting with the stopping point he achieves the same LCP (undirected movement). It should be clear that undirected movements are not very realistic, in fact it’s not plausible that the biotic shift of Fig. 6b has the same probability to happen both in a direction (from left to right) and in the other (from right to left). In fact in the latter case, the shift would be from low-friction areas to high-friction ones, i.e. an ecological nonsense.

6 Conclusions

In this paper I have compared the recent flow connectivity modelling to the commonly-used least cost one.

I have showed here that flow connectivity has the same advantages when compared to least-cost modelling as with regard to circuit theory. Least cost modelling a) is a “from-to” approach to ecological connectivity, b) it seeks global path optimization, c) it allows for biotic paths where the effort is also ascending, and d) it is undirected. Flow connectivity has opposite properties. Moreover, cost-distance models are based on two biologically improbable assumptions: (1) dispersers have complete knowledge of their surroundings, and (2) they select the least cost route from this information.

Instead, the path lengths and the biotic efforts predicted by both FC and LC modelling in this comparative case study about wolf in the Ceno valley (Parma, Italy) resulted not significantly different, by the way this result is contingent upon the case study.

References

Couvet D. 2002. Deleterious effects of restricted gene flow in fragmented populations. Conservation Biology, 16: 369-376

Dijkstra EW. 1959. A note on two problems in connexion with graphs. Numerische Mathematik, 1: 269-271

Drielsma M, Manion G, Ferrier S. 2007. The spatial links tool: automated mapping of habitat linkages in variegated landscapes. Ecological Modelling, 200: 403-411

Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares J.S. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology, 44: 714-724

Ferrarini A. 2005. Analisi e valutazioni spazio-temporale mediante GIS e Telerilevamento del grado di Pressione Antropica attuale e potenziale gravante sul mosaico degli habitat di alcune aree italiane. Ipotesi di pianificazione. Ph.D. Thesis, Università degli Studi di Parma, Parma, Italy

Ferrarini A, Rossi G, Parolo G, Ferloni M. 2008. Planning low-impact tourist paths within a Site of Community Importance through the optimisation of biological and logistic criteria. Biological Conservation, 141: 1067-1077

Ferrarini A, Bollini A, Sammut E. 2010. Digital Strategies and Solutions for the Remote Rural Areas Development. Acts of Annual MeCCSA Conference, London School of Economics, London, UK

Ferrarini A, Tomaselli M. 2010. A new approach to the analysis of adjacencies. Potentials for landscape insights. Ecological Modelling, 221: 1889-1896

Ferrarini A. 2011a. Some thoughts on the controllability of network systems. Network Biology, 1(3-4): 186-188

Ferrarini A. 2011b. Network graphs unveil landscape structure and change. Network Biology, 1(2): 121-126

Ferrarini A. 2012a. Biodiversity optimal sampling: an algorithmic solution. Proceedings of the International Academy of Ecology and Environmental Sciences, 2(1): 50-52

Ferrarini A. 2012b. Betterments to biodiversity optimal sampling. Proceedings of the International Academy of Ecology and Environmental Sciences, 2(4): 246-250

Ferrarini A. 2012c. Founding RGB Ecology: the Ecology of Synthesis. Proceedings of the International Academy of Ecology and Environmental Sciences, 2(2):84-89

Ferrarini A. 2012d. Landscape structural modeling. A multivariate cartographic exegesis. In: Ecological Modeling (Zhang WJ, ed). 325-334, Nova Science Publishers Inc., New York, USA

Ferrarini A. 2012e. The Ecological Network of The Province of Parma. Province of Parma, Parma, Italy, 124 pages (in Italian)

Ferrarini A. 2013a. A criticism of connectivity in ecology and an alternative modelling approach: Flow connectivity. Environmental Skeptics and Critics, 2(4): 118-125

Ferrarini A. 2013b. Controlling ecological and biological networks via evolutionary modelling. Network Biology, 3(3): 97-105

Ferrarini A. 2013c. Computing the uncertainty associated with the control of ecological and biological systems. Computational Ecology and Software, 3(3): 74-80

Ferrarini A. 2013d. Exogenous control of biological and ecological systems through evolutionary modelling. Proceedings of the International Academy of Ecology and Environmental Sciences, 3(3): 257-265

Ferrarini A. 2013e. Networks control: Introducing the degree of success and feasibility. Network Biology, 3(4): 127-132

Ferrarini A. 2013f. Connectivity-Lab 2.1: A Software for Applying Connectivity-Flow Modelling. Manual, 104 pages (in Italian)

Ferrarini A. 2014a. True-to-life friction values in connectivity ecology: Introducing reverse flow connectivity. Environmental Skeptics and Critics, 3(1): 17-23

Ferrarini A. 2014b. Can we trace biotic dispersals back in time? Introducing backward flow connectivity. Environmental Skeptics and Critics, 3(2): 39-46

Ferrarini A. 2014c. Detecting barriers and facilities to species dispersal: introducing sloping flow connectivity. Proceedings of the International Academy of Ecology and Environmental Sciences, 4(3): 123-133

Ferrarini A. 2014d. Local and global control of ecological and biological networks. Network Biology, 4(1): 21-30

Gardner RH, Gustafson EJ. 2004. Simulating dispersal of reintroduced species within heterogeneous landscapes. Ecological Modelling 171: 339-358

Gustafson EJ, Gardner RH. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77, 94–107

Hanski I, Ovaskainen O. 2000. The metapopulation capacity of a fragmented landscape. Nature, 404: 755-758

Holland JH. 1975. Adaptation in Natural And Artificial Systems: An Introductory Analysis with Applications to Biology, Control and Artificial Intelligence. University of Michigan Press, Ann Arbor, USA

Kennedy M, Gray RD. 1997. Habitat choice, habitat matching and the effect of travel distance. Behaviour, 134: 905-920

King AW, With KA. 2002. Dispersal success on spatially structured landscapes: when do dispersal pattern and dispersal behaviour really matter? Ecological Modelling, 147: 23-39

LaRue MA, Nielsen CK. 2008. Modeling potential dispersal corridors for cougars in Midwestern North America using least-cost path methods.Ecological Modeling, 212: 372-381

McRae BH. 2006. Isolation by resistance. Evolution, 60: 1551-1561

McRae BH, Beier P. 2007. Circuit theory predicts gene flow in plant and animal populations. Proceedings of the National Academy of Sciences of the USA, 104: 19885-19890

McRae BH, Dickson BG, Keitt TH, Shah VB. 2008. Using circuit theory to model connectivity in ecology and conservation. Ecology, 10: 2712-2724

Parolo G, Ferrarini A, Rossi G. 2009. Optimization of tourism impacts within protected areas by means of genetic algorithms. Ecological Modelling, 220: 1138-1147

Phillips SJ, Williams P, Midgley G. 2008. Optimizing dispersal corridors for the Cape Proteaceae using network flow. Ecological Applications, 18: 1200-1211

Rossi G, Ferrarini A, Dowgiallo G, Carton A, et al. 2014. Detecting complex relations among vegetation, soil and geomorphology. An in-depth method applied to a case study in the Apennines (Italy). Ecological Complexity, 17(1): 87-98

Taylor PD, Fahrig L, Henein K. et al. 1993. Connectivity is a vital element of landscape structure. Oikos 68: 571-573

Tischendorf L. 1997. Modelling individual movements in heterogeneous landscapes: potentials of a new approach. Ecological Modelling, 103: 33-42

Tischendorf L, Fahrig L. 2000. How should we measure landscape connectivity? Landscape Ecology, 15: 633-641

With KA, Gardner RH, Turner MG. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos, 78: 151-169