

Article

## A criticism of connectivity in ecology and an alternative modelling approach: Flow connectivity

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### Abstract

Modelling ecological connectivity across landscape is pivotal for understanding a large number of ecological processes, and for achieving environmental management aims such as preserving plant and animal populations, predicting infective disease spread and conserving biodiversity. Recently, concepts and models from electrical circuit theory have been adjusted for these purposes. In circuit theory, landscapes are represented as conductive surfaces, with resistance proportional to the easiness of species dispersal or gene flow. I observe in this paper that landscape connectivity as estimated by circuit theory relies on a strong assumption that is possibly false, unproven or very challenging to be demonstrated: species dispersals are thought as “from-to” movements, i.e. from source patches to sink ones. To this reason, I offer here a modelling approach to ecological connectivity assessment that is alternative to circuit theory and is able to fix the weak point of the “from-to” connectivity approach. The proposed approach holds also for mountain and hilly landscapes. In addition, it doesn’t assume any intention for a species to go from source points to sink ones, because the expected path for the species is determined locally (pixel by pixel) by landscape features. I’ve called this approach “flow connectivity” since it resembles in some way the motion characteristic of fluids over a surface. Flow connectivity can be applied for conservation planning and for predicting ecological and genetic effects of spatial heterogeneity and landscape change.

**Keywords** circuit theory; flow connectivity; gene flow; landscape connectivity; metapopulation theory; partial differential equations; species dispersal.

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### 1 Introduction

Modelling ecological connectivity across landscape is pivotal for understanding a large number of ecological processes, and for achieving environmental management aims such as preserving plant and animal populations, predicting infectious disease spread, and conserving biodiversity (Crooks et al., 2006; McRae, 2007). Understanding broad-scale ecological processes that depend on connectivity and incorporating such

connectivity into conservation planning needs to assess how connectivity is affected by environmental features (McRae et al., 2008; Shah and McRae, 2008).

Hence, there is a demand for efficient and reliable models that relate landscape composition and pattern to connectivity of ecological processes. Recently, concepts and algorithms from electrical circuit theory have been adjusted for these purposes (McRae, 2006; 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. Effective resistances, current densities, and voltages calculated across the landscapes can then be related to ecological processes (McRae et al., 2008). 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). More details can be found in McRae (2006), McRae (2007) and McRae et al. (2008).

By the way, I observe that 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 thought as “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 partially or completely hostile to the species. There are two aspects of this approach that are questionable. First, a source-sink habitats model can be suitable to describe only a lowland landscape where few suitable patches (e.g. protected areas) are surrounded by a dominant, hostile (or semi-hostile) anthropogenic landscape. But, can we think the same of mountain or hilly landscapes? It’s clear that such 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 shifts, and for plant species in particular, the dispersal model postulated by circuit theory is unsuitable.

To this reason, I offer here a modelling approach to connectivity assessment that is alternative to circuit theory, and that is able to fix weak points of the “from-to” connectivity approach. I’ve called this approach “flow connectivity” since it resembles in some way the motion characteristic of fluids over a surface. Flow connectivity can be used for conservation planning and for predicting ecological and genetic effects of spatial heterogeneity and landscape change.

## 2 Flow Connectivity: Mathematical Formulation

Let  $L(x, y, z, t)$  be a real 3D landscape at generic time  $t$ , where  $L \in [1, \dots, n]$ . In other words,  $L$  is a generic (categorical) landcover or land-use map with  $n$  classes. At time  $T_0$ ,

$$L_0 = L(x, y, z, t_0) \quad (1)$$

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  $T_0$ ,

$$\varphi_0 = \varphi(L_0) \quad (2)$$

Landscape friction has 2 components, i.e. the structural and the functional one, and the overall friction should be equal to their product (not the sum) since they're interactive:

$$\varphi(L) = \varphi_{STR}(L) * \varphi_{FUNC}(L) \quad (3)$$

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. Barriers (structural or functional) can be simulated using very elevated friction values.

At time  $T_0$ ,

$$L_{s0} = L_s(x, y, \varphi(L_0)) \quad (4)$$

Let  $S(x, y, t)$  be a binary landscape (of which  $S_{xyt}$  represents the value of the generic pixel at time  $t$ ) with the same coordinates and geographic projection as  $L_s$  and  $L$ , but with binary values at each pixel representing species presence/absence at generic time  $t$ . At time  $T_0$ ,

$$S_0 = S(x, y, t_0) \quad (5)$$

Now I define the biotic flow over the fictional landscape  $L_s$  as follows

$$\frac{\delta S(x, y, t)}{\delta t} = \text{div } S = \nabla \cdot S = \frac{\delta S}{\delta x} + \frac{\delta S}{\delta y} \quad (6)$$

with initial conditions  $S_0$  at time  $T_0$ .

Now I define  $I_x$  and  $I_y$  as two intervals around the generic pixel  $\langle x, y \rangle$ :

$$I_x = [I_{x-\partial x}, I_{x+\partial x}] \quad (7)$$

and

$$I_y = [I_{y-\partial y}, I_{y+\partial y}] \quad (8)$$

with higher  $\varphi(L)$  with respect to the generic pixel  $\langle x, y \rangle$ .

I further define here flows from neighbours as:

$$\frac{\delta S}{\delta x} = \begin{cases} 0 & \text{if } S_{xyt} = 1 \text{ and } I_{x+} = 0 \\ & \text{or } (S_{xyt} = 0 \text{ and } I_{x+} = 0) \\ & \text{or } (S_{xyt} = 1 \text{ and } I_{x+} = 1) \\ 1 & \text{if } S_{xyt} = 0 \text{ and } I_{x+} = 1 \end{cases} \quad (9)$$

and

$$\frac{\delta S}{\delta y} = \begin{cases} 0 & \text{if } S_{xyt} = 1 \text{ and } I_{y+} = 0 \\ & \text{or } (S_{xyt} = 0 \text{ and } I_{y+} = 0) \\ & \text{or } (S_{xyt} = 1 \text{ and } I_{y+} = 1) \\ 1 & \text{if } S_{xyt} = 0 \text{ and } I_{y+} = 1 \end{cases} \quad (10)$$

where

$$I_{x+} = \begin{cases} 0 & \text{if } \varphi(L)_x > \varphi(L)_{x-\partial x} \text{ and } \varphi(L)_x > \varphi(L)_{x+\partial x} \\ & \text{or } (\varphi(L)_x < \varphi(L)_{x-\partial x} \text{ and } S_{x-\partial x} = 0) \\ & \text{or } (\varphi(L)_x < \varphi(L)_{x+\partial x} \text{ and } S_{x+\partial x} = 0) \\ 1 & \text{if } \varphi(L)_x \leq \varphi(L)_{x-\partial x} \text{ and } S_{x-\partial x} = 1 \\ & \text{or } (\varphi(L)_x \leq \varphi(L)_{x+\partial x} \text{ and } S_{x+\partial x} = 1) \end{cases} \quad (11)$$

and

$$I_{y+} = \begin{cases} 0 & \text{if } \varphi(L)_y > \varphi(L)_{y-\partial y} \text{ and } \varphi(L)_y > \varphi(L)_{y+\partial y} \\ & \text{or } (\varphi(L)_y < \varphi(L)_{y-\partial y} \text{ and } S_{y-\partial y} = 0) \\ & \text{or } (\varphi(L)_y < \varphi(L)_{y+\partial y} \text{ and } S_{y+\partial y} = 0) \\ 1 & \text{if } \varphi(L)_y \leq \varphi(L)_{y-\partial y} \text{ and } S_{y-\partial y} = 1 \\ & \text{or } (\varphi(L)_y \leq \varphi(L)_{y+\partial y} \text{ and } S_{y+\partial y} = 1) \end{cases} \quad (12)$$

Hence, I obtain that

$$\frac{\delta S}{\delta t} = \begin{cases} 0 & \text{if } \frac{\delta S}{\delta x} = \frac{\delta S}{\delta y} = 0 \\ 1 & \text{if } \left( \frac{\delta S}{\delta x} = 1 \text{ and } \frac{\delta S}{\delta y} = 0 \right) \\ & \text{or } \left( \frac{\delta S}{\delta x} = 0 \text{ and } \frac{\delta S}{\delta y} = 1 \right) \\ & \text{or } \frac{\delta S}{\delta x} = \frac{\delta S}{\delta y} = 1 \end{cases} \quad (13)$$

My model assumes that species dispersal ends at a stability point, if exists, where:

$$\frac{\delta S(x, y, t)}{\delta t} = \nabla \cdot S = 0 \quad (14)$$

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  $L_0$  due to the short time-period considered, the species effort  $E$  for going through such path can be computed as:

$$E = \iint_P L_s(x, y, \varphi(L)) dx dy = \iint_P L_{s0} dx dy \quad (15)$$

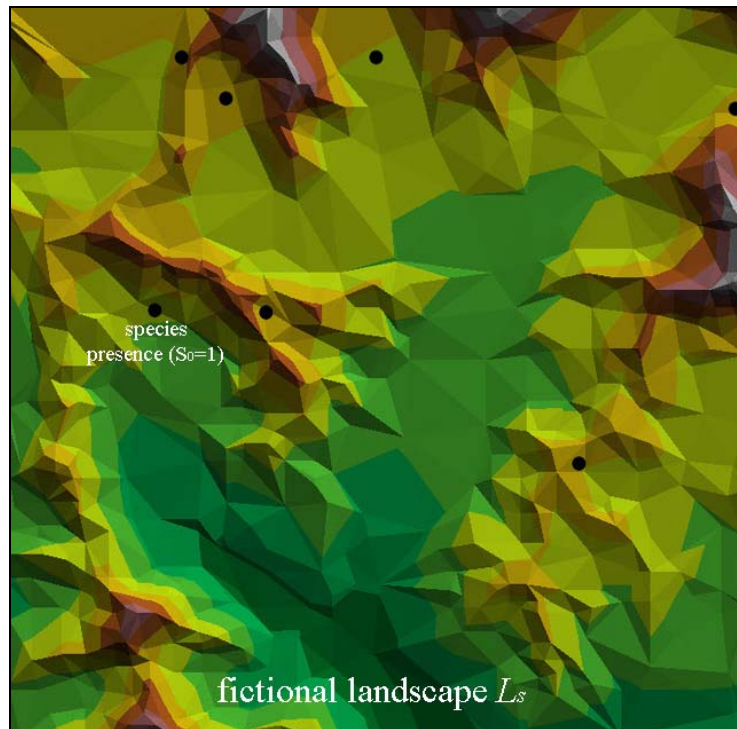
$E$  is thus the result of a pixel-by-pixel path optimization. In other words, the model assumes a greedy, local effort-minimization for the species dispersal that do not necessarily corresponds to the global minimization. Hence, I further introduce a coefficient  $C_{opt}$  of dispersal optimization as follows:

$$C_{opt} = E / E_{\min} = \iint_P L_{s0} dx dy / \iint_{P_{\min}} L_{s0} dx dy \quad (16)$$

$C_{opt}$  ranges from 1 (if species dispersal follows a global optimization) potentially to infinite.

### 3 An Applicative Example

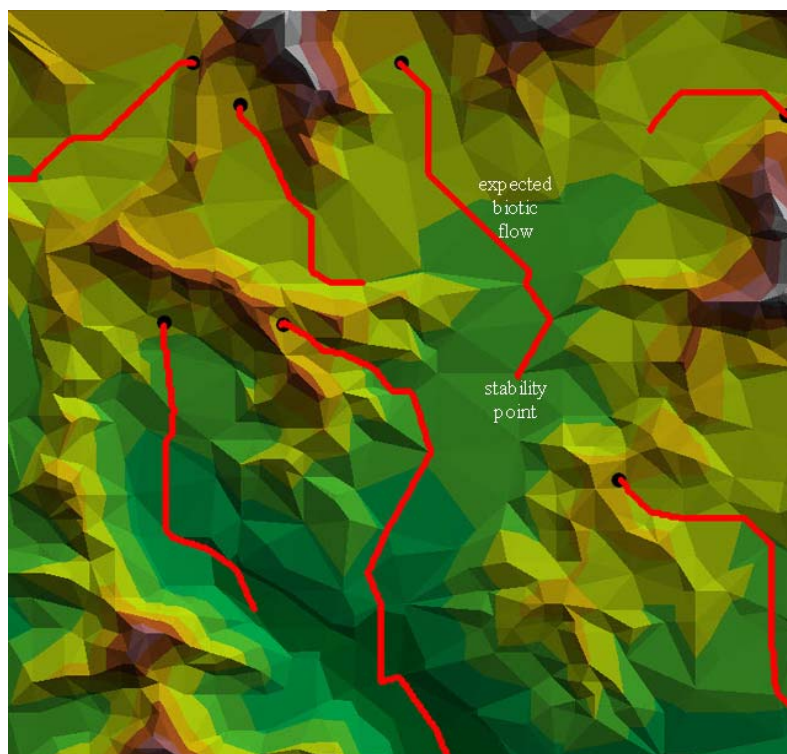
The Ceno valley is a 35,038 ha wide valley situated in the Province of Parma, Northern Italy. It has been mapped at 1:25,000 scale (Ferrarini 2005; Ferrarini et al. 2010) using the CORINE Biotopes classification system. The landscape structure of Ceno Valley has been widely analysed (Ferrarini and Tomaselli 2010; Ferrarini 2011; Ferrarini 2012a; Ferrarini 2012b). It is characterized by a substantial human use in the form of crops (9779 ha, 27.98% of the study area), and wooded landcover given by *Ostrya carpinifolia* (8212 ha, 23.45%) and *Quercus cerris* (4562 ha, 13.02%) woods. Wetlands account for about 1.8% of the study area. 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. For the sake of simplicity, I applied my model to a portion of the Ceno valley (Fig. 1) above 1000 m a.s.l. close to the municipality of Bardi where several small populations of wolves have been recently observed.



**Fig. 1** The fictional landscape  $L_s$  has been built for wolf upon a portion 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. Black points represent sites where the species is simulated to be present ( $S_0=1$ ).

The area is a square of about 20 km \* 20 km. Friction values  $\varphi(L)$  to wolf presence are borrowed from Ferrarini (2012c) in the form of friction coefficients assigned to every land cover classes. A discussion of wolf's frictional coefficients is outside the goals of this paper, so I avoid presenting them. The application of the above depicted flow-connectivity model provides the results of Fig. 2. Red lines represent the expected dispersal paths  $P_i$  of *Canis lupus* populations from simulated presences (black points). Almost all the expected paths are directed toward South, i.e. toward the lower part of the valley. This is in agreement with recent observations of shifts toward the lowland.

In addition, the fictional landscape  $L_s$  suggests that there are routes of dispersal almost obligated for *Canis lupus* in the study area. At the same time, landscape structure determines high barriers to species dispersal that correspond to very low or null dispersal probability. This clear pattern, that emerges from the use of fictional landscape  $L_s$ , also reveals that there are several potential areas of stability, i.e. where the friction of each pixel is almost equal to its surround. I suggest that, where structural aspects of landscape can't determine a differential in friction values, the importance of functional aspects (e.g. a temporary human disturbance) could arise and determine temporary dispersal paths. *In situ* GPS efforts to detect paths followed by wolf populations and to compare them with results of flow-connectivity modelling have been already planned.



**Fig. 2** Expected biotic dispersal paths of *Canis lupus* from simulated presence (black points) are depicted in red. Each path ends when the model detects a stability point. The flow-connectivity model has been applied using the software Connectivity-Lab (Ferrarini 2013).

#### 4 Conclusions

Modelling ecological connectivity across landscapes is necessary for understanding a large number of ecological processes, and for preserving plant and animal populations, predicting infective disease spread and conserving biodiversity.

The approach to ecological connectivity called “circuit theory” is a “from-to” approach. I’ve offered here an alternative approach called “flow connectivity” that holds also for mountain and hill landscapes. In addition, from a theoretical viewpoint, it doesn’t assume any intention of the species to go from source points to sink ones, because the expected path followed by the species is locally (pixel by pixel) determined by landscape features.

Flow connectivity can be useful for conservation planning and for predicting ecological and genetic effects of spatial heterogeneity and landscape change. The *ad hoc* software Connectivity-Lab (Ferrarini 2013) has been realized in order to apply flow-connectivity modelling. A comparative study of “flow connectivity” and “circuit theory” for several species could enhance further theoretical and methodological divergences and help to choose the fittest approach.

#### References

- Crooks KR, Sanjayan M. 2006. Connectivity Conservation. Cambridge University Press, UK
- 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, 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. 2011. Network graphs unveil landscape structure and change. *Network Biology*, 1(2): 121-126
- Ferrarini A. 2012a. Founding RGB Ecology: the Ecology of Synthesis. *Proceedings of the International Academy of Ecology and Environmental Sciences*, 2(2): 84-89
- Ferrarini A. 2012b. Landscape structural modeling. A multivariate cartographic exegesis. In: *Ecological Modeling* (Zhang WJ, ed). 325-334, Nova Science Publishers Inc., New York, USA
- Ferrarini A. 2012c. The Ecological Network of the Province of Parma. Province of Parma, Parma, Italy (in Italian)
- Ferrarini A. 2013. Connectivity-Lab: A Software for Applying Flow Connectivity Modelling. Manual. Italy (in Italian)
- 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
- Shah VB, McRae BH. 2008. Circuitscape: a tool for landscape ecology. In: *Proceedings of the 7th Python in Science Conference (SciPy 2008)* (Varoquaux G, Vaught T, Millman J, eds). 62-66, USA