Article

Calculating the uncertainty associated to the forecast of species dispersals: Stochastic Flow Connectivity

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Abstract
To date, corridors for species dispersals have been thought as deterministic outputs emerging from some kind of model. Uncertainty about the individuation of biotic corridors has never been considered. Flow connectivity (FC) is a methodology first introduced in 2013 to forecast biotic flows over real landscapes, alternative to both circuit theory and least-cost modelling. Its name is due to the fact that it resembles in some way the motion characteristic of fluids over a surface. FC predicts species dispersal by minimizing at each time step the potential energy due to fictional gravity force over a frictional 3D landscape built upon the real landscape. In this work, FC is further developed to find a solution to the problem of calculating the uncertainty associated to the forecast of species dispersals. The output of this method is an “uncertainty polygon” (e.g., 5% or 10% uncertainty) around the predicted biotic flow. The importance of this new variant of FC is clear: when planning greenways for biodiversity, uncertainty about biotic flows prediction must be taken into account and the planned corridors must encompass the “uncertainty polygon” as well, otherwise they are at serious risk to underestimate the necessary space required by animal species to flow over landscape.

Keywords biotic flows; dynamical GIS; flow connectivity; gene flow; landscape connectivity; species dispersal; sensitivity analysis; uncertainty.

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1 Introduction

Flow connectivity (FC hereafter) is a methodology first introduced in 2013 (Ferrarini, 2013) to forecast biotic flows over real landscapes, alternative to circuit theory (McRae, 2006; McRae and Beier, 2007; McRae et al., 2008) and least-cost modelling (Dijkstra, 1959). Its name is due to the fact that it 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 built upon the real landscape. FC considers connectivity to be a function of a continuous gradient of permeability values rather than attempting to distinguish discrete patches based on subjective thresholds of habitat area, quality, or ownership. A comparison with circuit theory and least-cost modelling are discussed in Ferrarini (2013) and Ferrarini (2014e).

At present FC presents many variants (Table 1), each devoted to a particular topic of species dispersals over landscape. In this paper, I introduce a new variant called Stochastic FC, aimed to calculate uncertainty associated to the individuation of biotic corridors of species dispersals. The output of this method is an “uncertainty polygon” (e.g., 5% or 10% uncertainty) around the predicted biotic flow. The importance of this new variant to FC is clear: when planning greenways for biodiversity, uncertainty about biotic flows prediction must be taken into account and the planned corridors must encompass the “uncertainty polygon” as well, otherwise they are at serious risk to underestimate the necessary space required by animal species to flow over landscape.

Table 1 Flow Connectivity and its developed variants, each with a particular purpose.

Name	Purpose	Year	Reference
Flow Connectivity	Predicting biotic flows over landscape	2013	Ferrarini A. 2013
Reverse Flow Connectivity	Assigning true-to-life friction values to biotic flows	2014	Ferrarini A. 2014
Backward Flow Connectivity	Tracing biotic dispersals back in time	2014	Ferrarini A. 2014b
Sloping Flow Connectivity	Detecting barriers and facilities to species dispersal	2014	Ferrarini A. 2014c
Bottleneck Flow Connectivity	Detecting landscape bottlenecks of species dispersal	2015	Ferrarini A. 2015
Climatic Flow Connectivity	Incorporating climatic change into biotic connectivity	2015	Ferrarini A. 2015b
What-if Flow Connectivity	Integrating landscape changes into biotic connectivity	2015	Ferrarini A. 2015c
Momentum Flow Connectivity	Mapping landscape impulses to species dispersal	2015	Ferrarini A. 2015d
Stochastic Flow Connectivity	Associating uncertainty to biotic flows prediction	2016	this work

2 Stochastic Flow Connectivity: 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 unfavorable) to the species under study.

In other words, $\varphi(L)$ is a function that associates a friction value to each pixel of *L*. Landscape friction has 2 components (structural and functional) and the overall friction should be equal to their product since they’re interactive:

$$\varphi(L) = \varphi_{STR}(L) * \varphi_{FUNC}(L) \tag{2}$$

At time T_0,

$$\varphi_0 = \varphi(L_0) \tag{3}$$

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. At time T_0,

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

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,

$$S_0 = S(x, y, t_0) \tag{5}$$

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

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

with initial conditions S_0 at time T_0. The symbol δ is a notation for a differential (i.e. ∂) or a difference (i.e. Δ) partial equation depending on the kind of landscape under study. For a high-resolution frictional landscape it represents a differential operator that simulates almost continuous movements over such landscape, conversely for a low resolution landscape it describes discrete movements both in space and time.

As showed in Ferrarini (2013), the equation of resulting biotic flow can be solved as follows:

$$\frac{\delta S}{\delta t} = \begin{cases} 0 \quad if \quad \dfrac{\delta S}{\delta x} = \dfrac{\delta S}{\delta y} = 0 \\ 1 \quad if \quad (\dfrac{\delta S}{\delta x} = 1 \; and \; \dfrac{\delta S}{\delta y} = 0) \\ \qquad or \; (\dfrac{\delta S}{\delta x} = 0 \; and \; \dfrac{\delta S}{\delta y} = 1) \\ \qquad or \; \dfrac{\delta S}{\delta x} = \dfrac{\delta S}{\delta y} = 1 \end{cases} \tag{7}$$

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

$$\frac{\delta S(x, y, t)}{\delta t} = \nabla \cdot S = 0 \tag{8}$$

Thus, a stability point exists when one species finds itself in a portion of the frictional landscape where all the surrounding pixels have equal o higher frictional values. When this happens, FC assumes that the study species has no reasons to move further.

True-to-life coefficients for $\varphi(L)$ can be calculated in flow connectivity as depicted in Ferrarini (2014), 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

$$B = \mathrm{mod}(\int P dx - \int P^* dx) \tag{9}$$

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

$$B = \begin{cases} \int P dx - \int P^* dx & \text{where } P > P^* \\ \int P^* dx - \int P dx & \text{where } P^* > P \end{cases} \tag{10}$$

True-to-life coefficients for landscape friction can now be calculated by optimizing *B*, as follows:

set B to 0 (11)

or, at least,

minimize B (12)

In other words, FC assigns realistic resistance values to each land cover type by making null the bias *B* between the predicted dispersal and the detected one. To do this, it builds up the optimized fictional landscape $L_s(x, y, \varphi(L))$ so that the predicted biotic flow *P* corresponds to the one (i.e. *P**) detected *in situ*.

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, 2011; Ferrarini, 2013b; Ferrarini, 2013c; Ferrarini, 2013d; Ferrarini, 2013e; Ferrarini, 2014d).

Alternatively, a simpler solution used by FC to the assessment of realistic friction coefficients is the application of suitability modelling to the detected points of species presence over the landscape. In particular, MAXENT methodology (Phillips et al., 2006) is particularly well suited to determine suitability maps starting from points of species presence. MAXENT computes the suitability scores $\mu(L)$ for each portion of the landscape in the 0-100 range. Thus, friction coefficients can be properly calculated as complementary to 100 of suitability:

$$\varphi(L) = 100 - \mu(L) \tag{13}$$

Although the achieved frictional coefficients should be considered reliable (as they're based on *in situ* experiments), uncertainty about the achieved optimized coefficients can be simulated by FC as follows

$$\frac{\delta \widetilde{S}_i}{\delta t} = \nabla \cdot \widetilde{S}_i \tag{14}$$

where $\widetilde{S}_i$ represents the simulation of the *i-th* biotic flow over $L_s(x, y, \widetilde{\varphi(L)})$ and where

$$0.95 * \varphi(L_k) \leq \widetilde{\varphi(L_k)} \leq 1.05 * \varphi(L_k) \tag{15}$$

or alternatively

$$0.90 * \varphi(L_k) \leq \widetilde{\varphi(L_k)} \leq 1.10 * \varphi(L_k) \tag{16}$$

In other words, $\widetilde{\varphi(L_k)}$ represents a 5% (or 10%) uncertainty about $\varphi(L)$ for each generic *k-th* landscape pixel. If we stochastically vary n times (e.g. 10,000 times) $\varphi(L)$ for each generic *k-th* landscape pixel, we can compute n predicted biotic flows around the predicted (deterministic) one. The minimum circumscribed polygon around such n paths hence represents the 5% (or 10%) uncertainty boundary due to our uncertainty about the landscape friction at each *k-th* landscape pixel.

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 the Ceno Valley has been widely analyzed (Ferrarini and Tomaselli, 2010; Ferrarini, 2011b; Ferrarini, 2012c; Ferrarini, 2012d). Several wolf populations have been recently observed *in situ* by life-watchers, environmental associations and local administrations. I have applied stochastic FC to a portion of the Ceno valley above 1000 m a.s.l. close to the municipality of Bardi (Fig. 1).

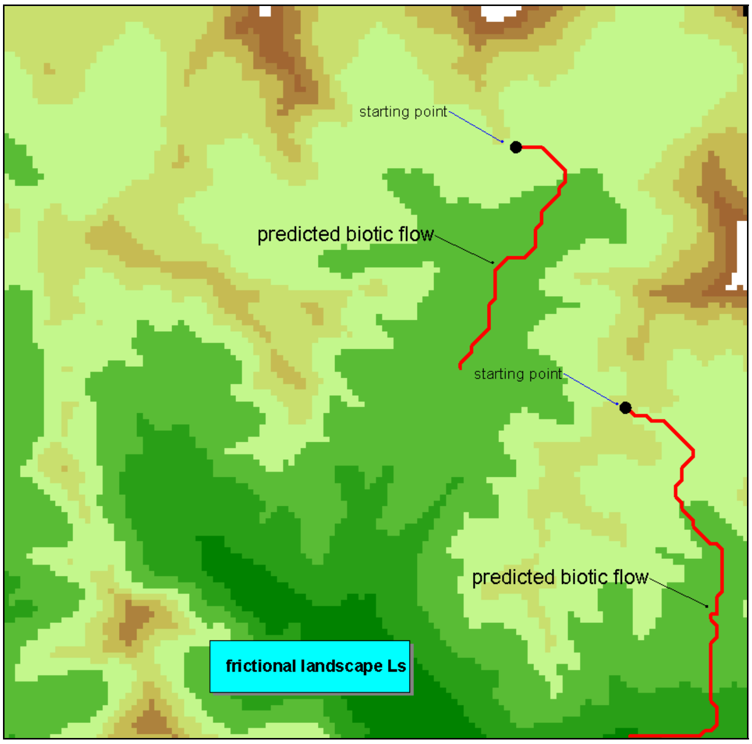

Fig. 1 The frictional landscape L_s has been built for wolf upon a portion (20 km * 20 km) of the Ceno valley (province of Parma, Italy) that represents here the real landscape $L(x,y,z,t)$. The elevation represents for each pixel the landscape friction to the species under study: the higher the elevation, the higher the friction to the species. Black points represent the simulated presence of wolf specimens. Red lines represent the predicted biotic flows from such points. Flows end where FC detects a stability point, i.e. a portion of the frictional landscape where all the surrounding pixels have equal or higher frictional values.

The area is a square of about 20 km * 20 km. Optimized friction values to wolf presence are borrowed from Ferrarini (2012e). Stochastic FC applied to the predicted dispersal routes of Fig 1 provides the results depicted in Fig. 2 and Fig 3. Red lines represent the predicted biotic flows, while blue polygons depict the 10% uncertainty polygons about the predicted dispersal routes. For each pixel of the frictional landscape, a 10% uncertainty has been simulated and 1000 random values in the 10% uncertainty interval have been simulated. This mean, for instance, that during simulations a pixel with a friction value equal to 5 can get any values in the range [4.5, 5.5]. This has been realized 1000 times for each pixel, and each time the resulting biotic flow has been recalculated. The resulting uncertainty polygons (in blue in Figs. 2 and 3) depict safety corridors that take into account not only the supposed ecological requirements of the study species while shifting over the landscape, but also the uncertainty of our knowledge about its requirements.

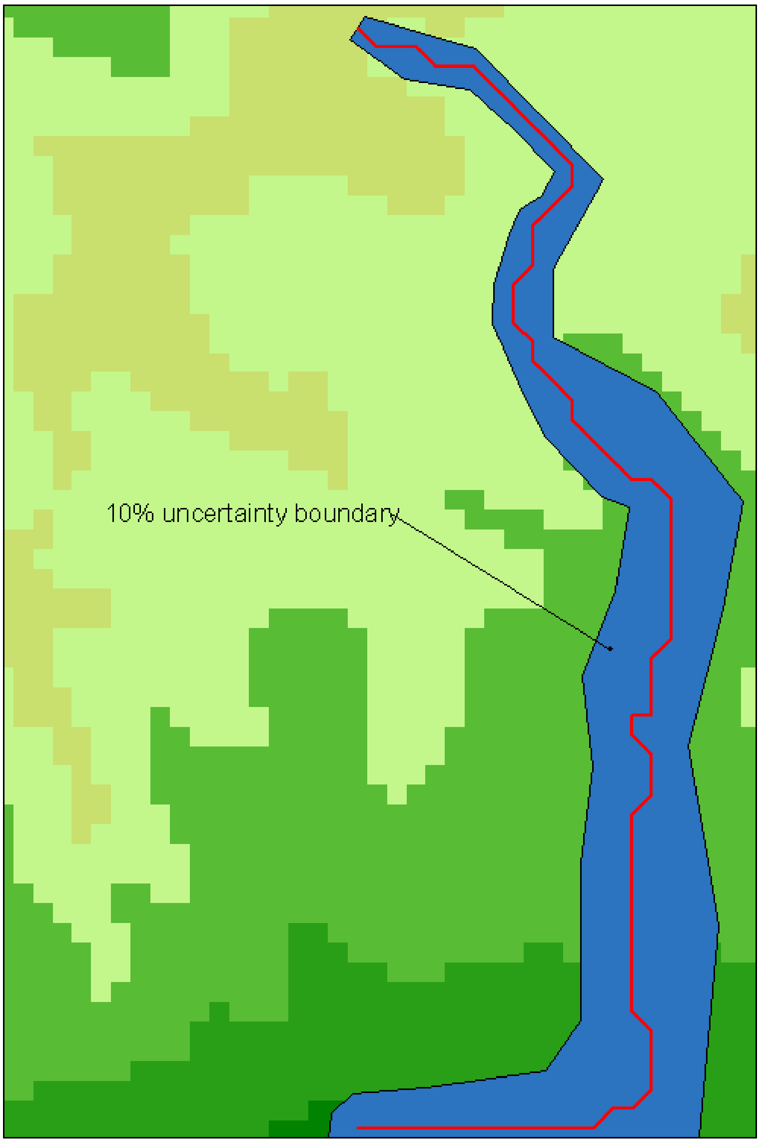

Fig. 2 Application of stochastic Flow Connectivity to one of the two predicted dispersal routes of Fig. 1. For each pixel of the frictional landscape, a 10% uncertainty has been simulated using 1000 random values in a 10% uncertainty interval, and each time the resulting biotic flow has been recalculated. Last, the minimum circumscribed polygon around path simulations has been detected using the *ad hoc* software Connectivity Lab (Ferrarini, 2013f).

The minimum width around the predicted flows is 15.78 m in Fig. 2 and 16.78 m in Fig. 3 respectively, while the maximum width of the uncertainty boundary is 78.45 m in Fig. 2 and 82.87 m in Fig. 3.

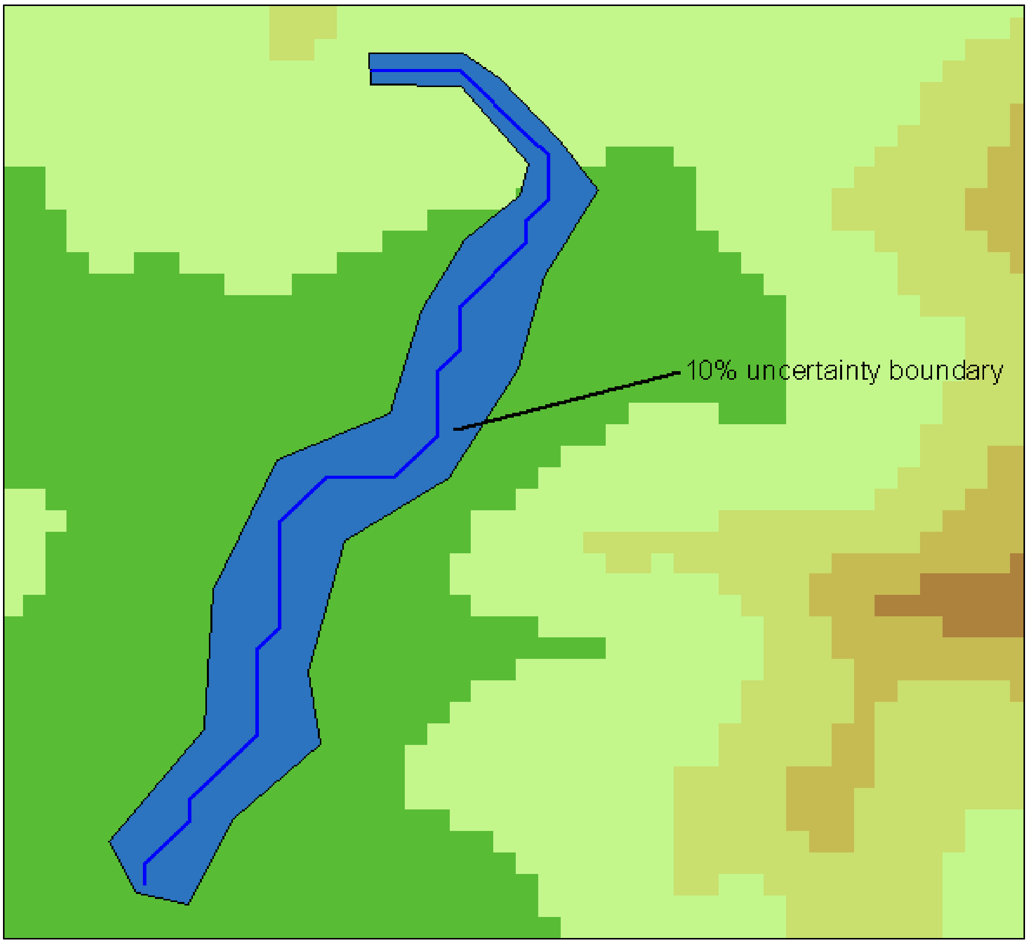

Fig. 3 Application of stochastic Flow Connectivity to one of the two predicted dispersal routes of Fig. 1. For each pixel of the frictional landscape, a 10% uncertainty has been simulated using 1000 random values in a 10% uncertainty interval and each time the resulting biotic flow has been recalculated.

An important result emerges from previous simulations: all other things being equal, the uncertainty about how species dispersals happen is much higher when the surrounding frictional landscape is homogeneous, i.e. landscape friction varies slowly. In Figs. 2 and 3 it can be seen that at the beginning of the dispersal paths the landscape friction varies quickly and the uncertainty polygon is narrow. Instead, in the middle and ending parts of the paths, friction varies little and slowly and the uncertainty boundary becomes much larger. This suggests that Stochastic Flow Connectivity is particularly useful for hilly and mountain landscapes where the land cover is very homogeneous, and the uncertainty about biotic corridors increases.

In order to apply stochastic FC modelling to real landscapes, I wrote the *ad hoc* software Connectivity Lab (Ferrarini, 2013f).

4 Conclusions

To date, corridors to biotic flows have been thought as deterministic outputs emerging from some kind of model. Uncertainty about the individuation of biotic corridors has never been considered.

In this work, Flow Connectivity has been extended to find a solution to the problem of calculating the uncertainty associated to the prediction of biotic flows. The output of this method is an "uncertainty polygon" (e.g., 5% or 10% uncertainty) around the predicted biotic flow.

Together with previous variants, stochastic Flow Connectivity represents a further contribution to the realistic forecast of biotic and gene flows over real landscapes with application to landscape genetics, landscape ecology and species conservation.

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