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Article

Can we trace biotic dispersals back in time? Introducing backward flow connectivity

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Abstract

Connectivity in ecology deals with the problem of how species dispersal will happen given actual landscape and species presence/absence over such landscape. Hence it can be considered a forward (ahead in time) scientific problem. I observe here that a backward theory of connectivity could be of deep interest as well: given the actual species presence/absence on the landscape, where with the highest probability such species is coming from? In other words, can we trace biotic dispersals back in time? Recently I have introduced a modelling and theoretical approach to ecological connectivity 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. In this paper, I introduce a new theoretical and modelling approach called “backward flow connectivity”. While flow connectivity predicts future species dispersal by minimizing at each step the potential energy due to fictional gravity over a frictional landscape, backward flow connectivity does exactly the opposite, i.e. maximizes potential energy at each step sending back the species to higher levels of potential energy due to fictional gravity on the frictional landscape. Using backward flow connectivity, one has at hand a new tool to revert timeline of species dispersal, hence being able to trace backward biotic dispersals. With few modifications, the applications of backward flow connectivity can be countless, for instance tracing back-in-time not only plants and animals but also ancient human migrations and viral paths.

Keywords backward simulation; biotic flows; dynamical GIS simulation; flow connectivity; gene flow; human migrations; partial differential equations; past dynamics; viral paths.

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1 Introduction

Predicting ecological connectivity across landscape is pivotal for understanding a large number of ecological processes, for environmental management aims (such as preserving plant and animal populations), for predicting infectious disease spread and for conserving biodiversity (Crooks et al., 2006; McRae, 2007). Hence, there is a demand for reliable models that relate landscape composition and pattern to connectivity of ecological processes and biotic dispersals.

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). 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). 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).

Recently, I have introduced 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 (Ferrarini, 2013a). 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. In addition, in a recent paper (Ferrarini, 2014a) I have proposed an advance to flow connectivity, named reverse flow connectivity, that is able to assign realistic resistance (frictional) values to landscape categories. Thanks to the conceptual and operative framework proposed in that paper the subjectivity in ecological connectivity is minimized.

In this paper, I face another important topic for the comprehension of biotic dispersals: given the actual species presence/absence on the landscape, where with the highest probability such species is coming from? In other words, can we trace biotic dispersals back in time? To this aim, I introduce a new theoretical and modelling approach called “backward flow connectivity”.

Using backward flow connectivity, I show here that one has at hand a new tool to revert timeline of species dispersal, hence being able to trace backward biotic dispersals. Besides species dispersals, the applications of backward flow connectivity are countless, for instance tracing back-in-time not only plants and animals but also ancient human migrations and viral paths.

2 Backward 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 $T_{0,}$

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

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,

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

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. Barriers (structural or functional) can be simulated using very elevated friction values. True-to-life coefficients for landscape friction can be calculated as 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 prediction bias B between P and P^* is hence calculated as

$$B = \mathrm{mod}\left(\int P dx - \int P^* dx\right) \tag{3}$$

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

$$B = \begin{cases} \int P dx - \int P^* dx & \text{where } P > P^* \\ \int P^* dx - \int P dx & \text{where } P^* > P \end{cases} \tag{4}$$

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

set B to 0 (5)

or, at least,

minimize B (6)

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 (Ferrarini et al., 2008; 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, 2014b). At time T_0,

$$L_{s0} = L_s(x, y, \varphi(L_0)) \tag{7}$$

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,

$$S_0 = S(x, y, t_0) \tag{8}$$

Now I define the backward flow over the fictional landscape L_s as follows

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

with initial conditions S_0 at time T_0, where $t \to -\infty$ indicates that time is going backward.

I further define I_x and I_y as two intervals around the generic pixel <x,y> so that

$$I_x = [x - \partial x, x + \partial x]$$

(10)

and

$$I_y = [y - \partial y, y + \partial y]$$

(11)

Now, I define here the back-in-time biotic flow as:

$$\frac{\delta S}{\delta x}=\begin{cases} 0 \;\; if \quad S_{xyt}=1 \;\; and \;\; I_{x-}=0 \\ \qquad or \; (S_{xyt}=0 \;\; and \;\; I_{x-}=0) \\ \qquad or \; (S_{xyt}=1 \;\; and \;\; I_{x-}=1) \\ \\ 1 \;\; if \quad S_{xyt}=0 \;\; and \;\; I_{x-}=1 \end{cases} \tag{12}$$

and

$$\frac{\delta S}{\delta y}=\begin{cases} 0 \;\; if \quad S_{xyt}=1 \;\; and \;\; I_{y-}=0 \\ \qquad or \; (S_{xyt}=0 \;\; and \;\; I_{y-}=0) \\ \qquad or \; (S_{xyt}=1 \;\; and \;\; I_{y-}=1) \\ \\ 1 \;\; if \quad S_{xyt}=0 \;\; and \;\; I_{y-}=1 \end{cases} \tag{13}$$

where

$$I_{x-}=\begin{cases} 0 \;\; if \quad \varphi(L)_x<\varphi(L)_{x\text{-}\partial x} \;\; and \;\; \varphi(L)_x<\varphi(L)_{x+\partial x} \\ \qquad or \;\; (\varphi(L)_x>\varphi(L)_{x\text{-}\partial x} \;\; and \;\; S_{x\text{-}\partial x}=0) \\ \qquad or \;\; (\varphi(L)_x>\varphi(L)_{x+\partial x} \;\; and \;\; S_{x+\partial x}=0) \\ \\ 1 \;\; if \quad \varphi(L)_x\geq\varphi(L)_{x\text{-}\partial x} \;\; and \;\; S_{x\text{-}\partial x}=1 \\ \qquad or \;\; (\varphi(L)_x\geq\varphi(L)_{x+\partial x} \;\; and \;\; S_{x+\partial x}=1) \end{cases} \tag{14}$$

and

$$I_{y-}=\begin{cases} 0 \;\; if \quad \varphi(L)_y<\varphi(L)_{y\text{-}\partial y} \;\; and \;\; \varphi(L)_y<\varphi(L)_{y+\partial y} \\ \qquad or \;\; (\varphi(L)_y>\varphi(L)_{y\text{-}\partial y} \;\; and \;\; S_{y\text{-}\partial y}=0) \\ \qquad or \;\; (\varphi(L)_y>\varphi(L)_{y+\partial y} \;\; and \;\; S_{y+\partial y}=0) \\ \\ 1 \;\; if \quad \varphi(L)_y\geq\varphi(L)_{y\text{-}\partial y} \;\; and \;\; S_{y\text{-}\partial y}=1 \\ \qquad or \;\; (\varphi(L)_y\geq\varphi(L)_{y+\partial y} \;\; and \;\; S_{y+\partial y}=1) \end{cases} \tag{15}$$

Hence, I obtain that

$$\frac{\delta S}{\delta t}=\begin{cases} 0 \quad if \quad \dfrac{\delta S}{\delta x}=\dfrac{\delta S}{\delta y}=0 \\ \\ 1 \quad if \quad (\dfrac{\delta S}{\delta x}=1 \; and \; \dfrac{\delta S}{\delta y}=0) \\ \qquad\quad or \; (\dfrac{\delta S}{\delta x}=0 \; and \; \dfrac{\delta S}{\delta y}=1) \\ \qquad\quad or \; \dfrac{\delta S}{\delta x}=\dfrac{\delta S}{\delta y}=1 \end{cases} \tag{16}$$

While flow connectivity predicts future species dispersal by minimizing at each step the potential energy due to fictional gravity over a frictional landscape, backward flow connectivity does exactly the opposite, i.e. maximizes potential energy at each step sending back the species to higher levels of potential energy due to fictional gravity on the frictional landscape.

In order to apply equations from (1) to (16), I wrote the *ad hoc* software Connectivity Lab (Ferrarini, 2013f).

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 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. For the sake of simplicity, I applied my backward 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.

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 backward flow-connectivity model provides the results of Fig. 2. Red scattered lines represent the expected back-in-time dispersal paths P_i of *Canis lupus* populations from simulated actual presences (black points; S_0=1). Almost all the expected backward paths are directed toward North, i.e. toward the higher part of the valley. This is in agreement with recent observations of wolf (forward) shifts toward the lowland.

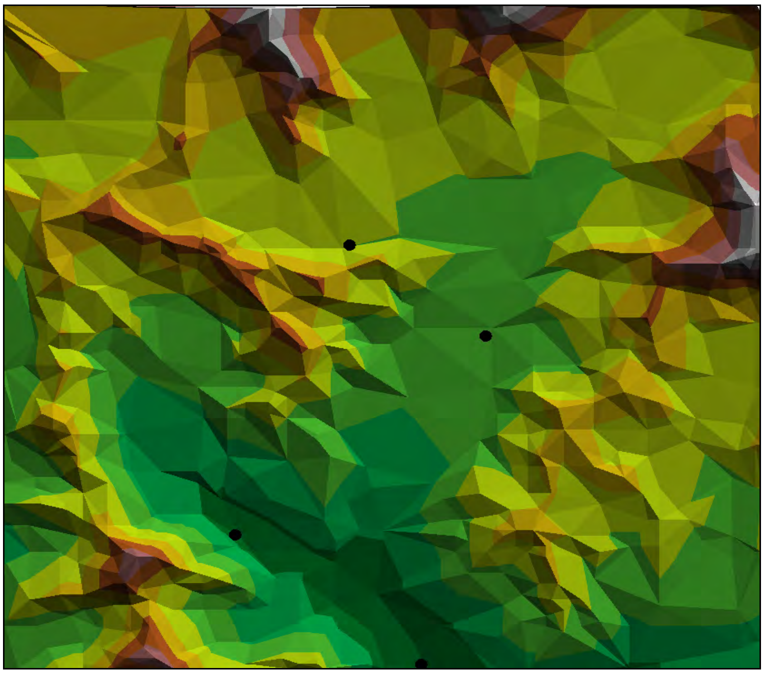

Fig. 1 The fictional landscape *Ls* has been built for wolf upon a portion of the Ceno Valley (province of Parma, Italy) that represents here the real landscape *L(x,y,z,t)*. The elevation represents for each pixel the landscape friction $\varphi(L)$ for the species under study: the higher the elevation, the higher the friction to the species. Black points represent sites where the species is simulated to be present at time T_0 (S_0=1).

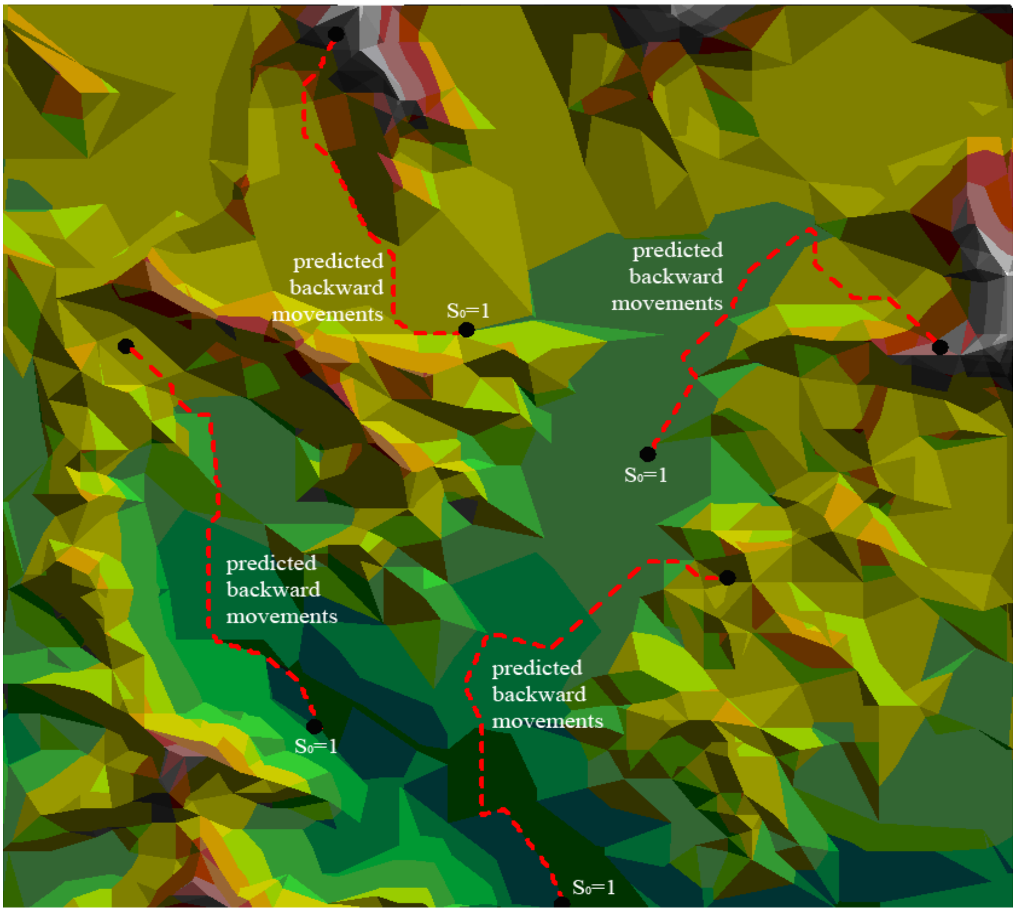

Fig. 2 Predicted backward dispersal paths of *Canis lupus* are depicted using red scattered lines. Each line represents a predicted back-in-time biotic path from actual presences (black points; S_0=1).

In situ GPS efforts to detect paths followed by wolf populations and to compare them with results of backward flow connectivity modelling have been already planned.

Attention should be paid to a possible weak point of backward flow connectivity: it relies on the hypothesis that landscape has not changed, or at least only slightly, in the past. Hence, it can be successfully applied to brief or mid-term periods (weeks or months) in the past, or to landscapes that have a strong inertia. For instance, hill and mountain landscapes change very slowly (in the order of years or decades) because they follow natural dynamics instead of human ones. As opposite, lowland landscapes have very fast dynamics (Ferrarini et al., 2000; Ferrarini et al., 2003; Rossi et al., 2003). In the latter case, backward flow connectivity should be applied to predict only recent species dispersals.

4 Conclusions

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

In this paper, I have faced another important topic for the comprehension of biotic dispersals: can we trace biotic dispersals back in time? To this aim, I have introduced a new theoretical and modelling approach called “backward flow connectivity”. While flow connectivity predicts future species dispersal by minimizing at each step the potential energy due to fictional gravity over a frictional landscape, backward flow connectivity does exactly the opposite, i.e. maximizes potential energy at each step sending back the species to higher levels of potential energy due to fictional gravity on the frictional landscape.

Using backward flow connectivity, I have showed here that one has at hand a new tool to revert timeline of species dispersal, hence being able to trace backward biotic dispersals. With few modifications, the applications of backward flow connectivity can be countless, for instance tracing back-in-time not only plants and animals but also ancient human migrations and viral paths.

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