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Short Note

Using fluid dynamic concepts to estimate species movement rates in terrestrial landscapes

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ABSTRACT

Habitat loss and fragmentation threatens biodiversity and ecosystem function. ‘Permeability’ and ‘connectivity’ indices are used to estimate how individuals, populations or genes move spatially through a landscape. Yet, despite the analogies between landscape permeability and the physical definition of permeability (the ability for a porous media to transport a fluid), there have been few attempts to apply the physical concepts of permeability and fluid flow to problems in landscape movement ecology beyond some simple examples in the early literature. Here, we present a conceptual model linking physical principles to ecological terms and illustrate how concepts from Darcy’s Law of fluid flow through porous media could be used to quantify species movement rates through a heterogeneous terrestrial landscape. Although further refinement is needed to take this concept to two dimensions and into a full predictive model, the approach presented shows promise for quantifying the relative impacts of landscape change (e.g. habitat fragmentation or creation) on species movement rates.

1. Introduction

Reversing habitat loss and fragmentation is a global conservation priority (Fahrig, 2003; Haddad et al., 2015), and there is an increasing focus on improving and conserving landscape 'permeability' through targeted habitat restoration and creation (Doerr et al., 2011). Several indices are available to estimate how individual organisms, populations or genes might be expected to move through heterogeneous landscapes (with differing degrees of permeability), with such information being used to inform land-management decisions. Examples include adaptations of established mathematical concepts such as least-cost path, circuit theory, graph theory and variations thereof (Adriaensen et al., 2003; McRae et al., 2008; Minor and Urban, 2008; Pinto and Keitt, 2009; Zeller et al., 2012; Watts and Handley, 2010; Saura and Pascual-Hortal, 2007) and stochastic, individual-based models that can incorporate a large number of biologically realistic processes (Bocedi et al., 2014). However, there has been considerable debate in the literature over the relative value of these approaches in terms of ecological realism and the balance between metric performance and data requirements (Calabrese and Fagan, 2004; Baranyi et al., 2011; Zeller et al., 2012).

Landscape ‘connectivity’ can broadly be defined as “the ease with which individuals can move about within the landscape” (Merriam, 1984), although this can be further refined into structural (i.e. landscape structure) and functional definitions (i.e. behavioural responses to landscape patterns) (Kindlmann and Burel, 2008). Landscape ‘permeability’ can be considered a functional definition, which acknowledges that different land-use types can either impede or facilitate movement (Kindlmann and Burel, 2008). Most existing permeability or connectivity indices fall into two broad categories that either comprise or combine (1) raster based approaches that subdivide the landscape into a uniform grid, and (2) vector-based approaches that use nodes to represent habitat patches and edges to represent links between patches (Minor and Urban, 2008). Perhaps the most widely used index is least-cost path analysis (Adriaensen et al., 2003; Etherington, 2016), which combines both techniques to identify the path of least resistance between two points (nodes) in a landscape using a cost-surface derived from raster data. Least-cost models have also been developed for use within triangulated irregular networks (TIN) instead of raster grids (Etherington, 2012). One of the main limitations to least-cost approaches is that they can be computationally challenging in very large landscapes and the method has been criticised for assuming that individuals have prior knowledge of the study landscape (Sawyer et al., 2011). More recently, there have been significant advances in applying physical concepts from ‘circuit theory’ to estimate landscape connectivity, which uses the analogy of the flow of electrons through an electrical circuit (Leonard et al., 2016). This method has also proven particularly useful for estimating connectivity between two points of

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Table 1
The relationship between physical fluid dynamic terms and their ecological analogue.

Parameter	Symbol	Units	Ecological analogue
Average intrinsic permeability of porous material j.	k	m^2	Permeability of land-cover type to individual movement (landscape specific).
Pressure differential across length, L, of interest.	ΔP	Pa	Held directionally constant from east to west in our example but can be modified to represent a driving force to movement, such population size or propagule pressure.
Viscosity of the fluid.	μ	Pa s	Mobility/dispersal ability of a particular species.
The length (L) and cross-sectional area (A) of the system considered.	L, A	m, m^2	Landscape dimensions
Bulk volumetric flow rate through material within the geometry considered.	Q	$m^3 s^{-1}$	Species movement rate: the higher the flow rate, the greater number of individuals able to transit though an area in a given time.

interest (e.g. protected areas) in a landscape.

Although these recent models (McRae et al., 2008; Leonard et al., 2016) represent significant advances in our modelling capabilities, they are commonly limited to pairwise connectivity (i.e. the connectivity between two discrete landscape locations). However, if the research question is to model transport starting from a designated region (e.g. an entire coastline, or a woodland patch) through a large connected terrestrial landscape without a pre-determined "end destination" then pairwise connectivity becomes limited. To overcome this, it is possible to iteratively quantify pairwise connectivity between random start and end locations (e.g. Theobald et al., 2012; Leonard et al., 2016), but it would also be valuable to view the landscape as continuum where the movement of organisms, populations or genes are not 'directed' between two or more specific points of interest. Basic fluid flow concepts, presented in this work, can provide a framework to access these broader species movement challenges.

In physics, permeability is defined as the ability for a porous medium to transport a fluid (Bear and Braester, 1972). Furthermore, the volumetric flow rate (the amount of material transported per unit time) through a permeable medium also depends on the physical properties of the fluid itself, such as its viscosity. The fluid viscosity is defined as the resistance to flow; when the same stress is applied, high viscosity fluids (e.g. honey) flow over much longer timescales compared to low viscosity fluids (e.g. water). Although there were some early attempts to apply physical laws of fluid movement to estimate ecological movement (percolation theory; Green, 1994; McIntyre and Wiens, 1999), these were relatively simple and represented probabilistic passive flow. More recently, Drever and Hrachowitz (2017) have applied concepts from hydrology to estimate length of stay at stop over sites (or reservoirs) during bird migration. Despite the analogies between the physical definition of permeability, viscosity, transport rate and the movement of organisms or populations through a landscape, there have been few attempts to apply fluid dynamic concepts to problems in landscape ecology.

2. Estimating landscape permeability using a fluid dynamical model

Here, we illustrate how the principles of basic fluid flow through porous media could be applied to assess species movement in fragmented landscapes, taking into account species-specific mobility values. The strengths of using fluid dynamical concepts are (1) species movement rate through all cells can be considered – not just the connectivity between two discrete points; (2) the model can be quickly applied to entire landscapes from a raster environment; (3) parameters can be changed independently to compare transport rates between species which differ in their mobility yet share similar habitat requirements, and (4) fluid flow, a surrogate for species movement across a landscape, is an intuitive concept – it is easy for end users to visualise the concept.

In Physics, Darcy's Law (Eq. (1); Darcy, 1856) is commonly used to describe one-dimensional or one-directional fluid flow through porous media.

$$Q = \frac{-kA\Delta P}{\mu L} \tag{1}$$

where Q ($m^3 s^{-1}$) is the volumetric flow rate; k (m^2) the permeability; A (m^2) is the cross-sectional area; ΔP (Pa) is the pressure gradient; μ (Pa s) is the fluid viscosity and L (m) is the transport length. Major applications include the prediction of groundwater flow and contaminant transport (Zheng and Bennett, 2002), and petroleum reservoir modelling to estimate production rates (Aziz and Settari, 1979).

The purpose of this paper is to conceptually illustrate how a fluid dynamical approach could be used to quantify landscape permeability and transport rate (species movement), with the aim of stimulating further discussion and development of the proposed ideas and methods. We do this by (1) demonstrating how parameters such as fluid viscosity have an ecological analogue in Section 2.1, and (2) in Section 3, we relate Darcy's Law in a conceptual way to a landscape taken from the literature. This is done with the hope of stimulating future research and the production of robust 2-D models.

2.1. Linking physics terms to their ecological analogue

We now relate each of the terms in Darcy's Law (Eq. (1)) to their ecological analogue (Table 1). Firstly, consider a layer of porous material (the landscape) (Fig. 1a) of length (L) and a cross sectional area (A), where A = w × h. The fluid at entry has pressure P_1 and is subject to a gradient with the pressure at the end of the layer being P_2. To achieve a pressure balance the fluid will attempt to flow through the material, which is governed by its permeability. Permeability is specific to the material and is defined as the ability of the porous network to allow a fluid to pass through it. Note the difference here between the physical definition of permeability and some previous interpretations in ecology, which can be specific to the species and not solely the material (landscape).

Permeability is dependent on both material type and, in the case of anisotropic materials, the flow direction. If the material, and therefore permeability changes along a flow path the volumetric flow rate will be altered. The average permeability can be calculated by weighting the permeability values. If the layers or varying landcover patches are parallel to flow (Fig. 1b) the average permeability is calculated as:

$$k_{av} = \frac{\sum_{j=1}^{n} k_j h_j}{\sum_{j=1}^{n} h_j} \tag{2}$$

where k_{av} is the *arithmetic* mean permeability along the entire transport length and k_j is the permeability of a specific layer/ landscape patch, j with thickness h_j. Whereas if the layers or varying landcover patches are perpendicular to flow (Fig. 1c) the average permeability is calculated as:

$$k_{av} = \frac{\sum_{j=1}^{n} L_j}{\sum_{j=1}^{n} (L_j/K)_j} \tag{3}$$

where k_{av} is the *harmonic* mean permeability along the entire transport length and k_j is the permeability of a specific layer/habitat zone, j with length L_j.