



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.

$$Q = \frac{-kA\Delta P}{\mu L} \quad (1)$$

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 $A = w \times h$. 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:

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

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:

$$k_{av} = \frac{\sum_{j=1}^n L_j}{\sum_{j=1}^n (L_j/K_j)} \quad (3)$$

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 .

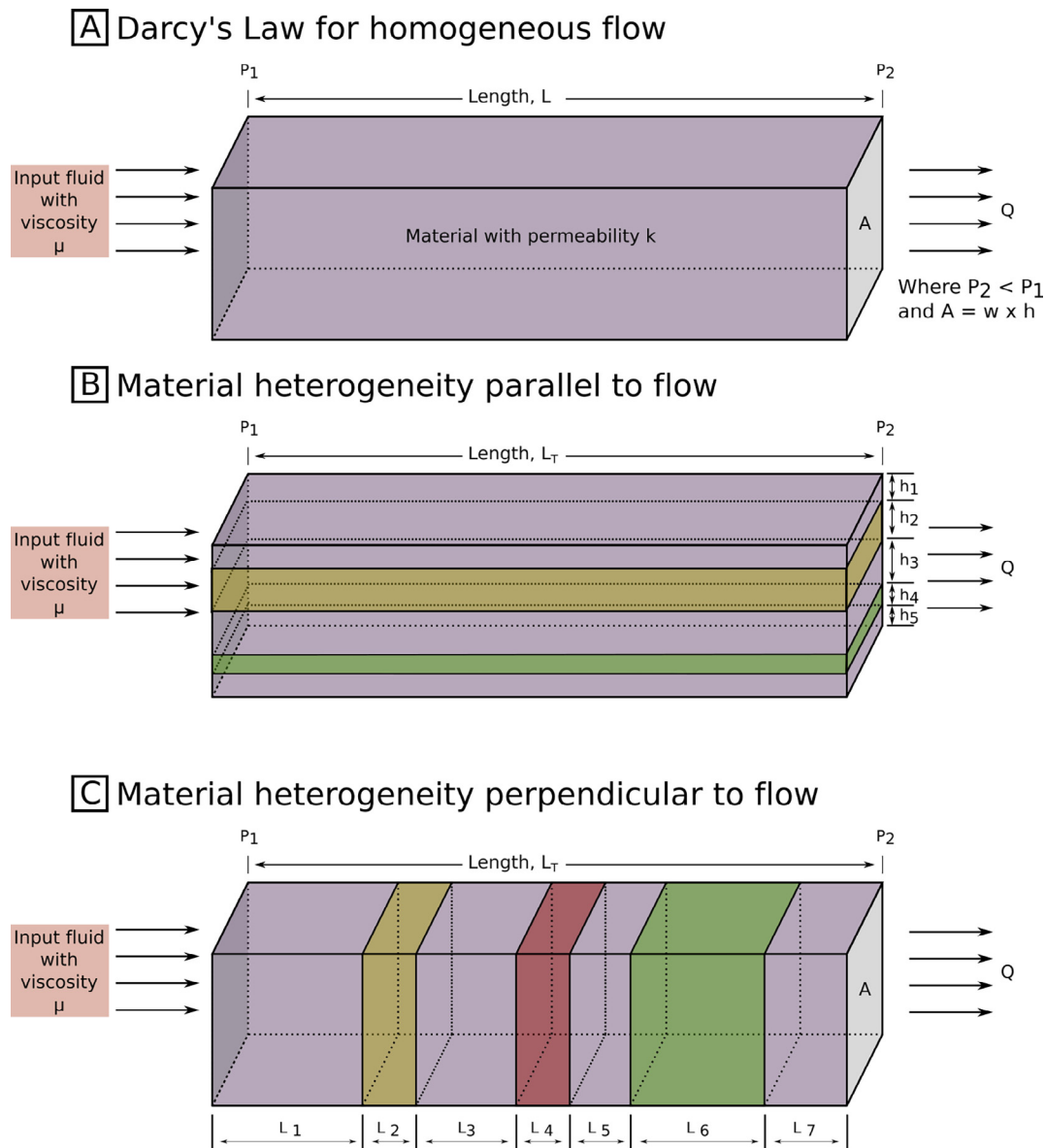


Fig. 1. Schematic of one-directional fluid flow through porous media. (a) Darcy flow through a homogeneous porous layer. (b) Darcy flow through a system with heterogeneous permeability parallel to the flow direction. (c) Darcy flow through a system with heterogeneous permeability perpendicular to the flow direction.

Hence, an averaged volumetric flow rate (Q_{av}) for the pathway (L_T) can be written as:

$$Q_{av} = \frac{-k_{av} A \Delta P}{\mu L_T} \quad (4)$$

In ecology, a cost surface is commonly created from a variety of input variables (e.g. land cover type, terrain gradients, habitat quality etc.). We propose that these cost surfaces could be easily inverted for permeability. For example, dense, urban areas have a high cost associated with them, and therefore in our analogue will have a low ecological permeability.

The timescale in which the fluid is able to travel through the porous material is also dependant on the fluid viscosity, μ , where higher viscosity fluids will take longer to flow through the material. In the ecological sense the viscosity term relates to the species' mobility, where viscous species (those with high viscosity values) are less mobile, or have a lower dispersal potential, for example. This is an important parameter that will make fluid dynamical models species-dependent and merits further consideration. We suggest that one possible way to quantify the viscosity of a particular species is to consider its dispersal

ability. For example, insectivorous birds that occupy the understory are known to have a lower capacity to disperse than omnivores, frugivores and other feeding guilds (e.g. Şekercioğlu et al., 2002; Uezu et al., 2005). Thus, even though several species may share the same general habitat preferences (i.e. forest) at the landscape-scale, they can have radically different dispersal rates in any given landscape. Thus, for a given set of species an ecologist could use a single landscape permeability raster and change the viscosity term to compare relative landscape-permeability for multiple species that have similar broad habitat requirements but have very different dispersal capacities.

The pressure difference is the driving force for flow, or species movement, so if this term is zero, there will be no movement. In ecology, this parameter can be related to seasonal migration, population size or propagule pressure (density dependent-dispersal). Higher values represent a greater pressure for the species to move through the system. Given that the population pressure, by its very definition, is a sum of numerous factors, we note that this parameter may be difficult to quantify in ecological models. However, it also could provide great strength to a model; the pressure gradient (or population pressure) will often change in time as species movement occurs. Therefore, this term

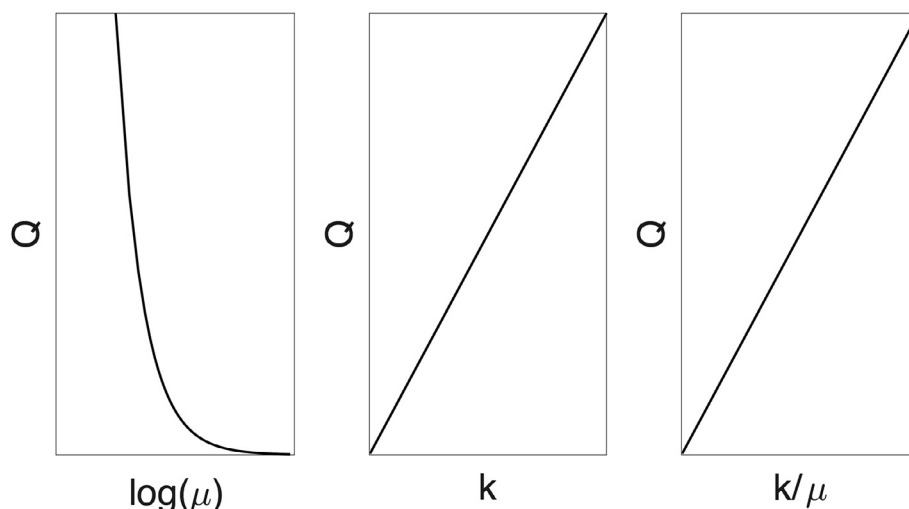


Fig. 2. Relationships between the species movement rate, Q , (the amount/number/volume of individuals able to transit through a landscape per unit time) and other key parameters (mobility, permeability, effective permeability) when assessing movement through an ecological landscape.

could allow for a time dependant population pressure as individuals disperse, for example.

Finally, the output of Darcy's Law is the volumetric flow rate that describes the ability of the system to transport a certain volume of fluid per unit time. The ecological analogue is the species movement rate. A numerical value, not a probability, that describes the number of individuals passing through a landscape per unit time.

Finally, Fig. 2 illustrates the control that these key landscape variables have on the species movement rate, Q . In this example, the value of Q is arbitrary, but if all other landscape factors remain constant, decreasing the species mobility has an exponential relationship with species movement rate such that: $Q \propto 1/\mu$. Using this framework, we can estimate that a species with a lower mobility (higher μ) will have a drastically lower species movement rate relative to a more mobile species transiting the same landscape. The permeability, k , and the effective permeability, k/μ both exhibit a linear dependency on Q such that higher permeability values lead to a higher species movement rate. Despite these two terms having the same dependency on Q , it is more intuitive to consider the effective permeability when calculating model values; the effective permeability is sensitive to both species (viscosity) and landscape (permeability) changes.

3. Using Darcy's law in an ecological landscape

We now relate Darcy's Law terms to a landscape in order to illustrate how these physical concepts and their ecological analogues could give insight into species movement rates. We stress that this is a conceptual model, which should not be applied to ecological problems in its current form, and it is deliberately presented in a simplified way to demonstrate the analogies between physical and ecological concepts. In particular, further work is needed to understand how this model can be parameterised (see Discussion).

3.1. Creation of rasterised landscape

Landscape-scale ecological studies of fragmented habitats often use land-cover data to create cost surfaces in raster format, and these data are used to quantify permeability and connectivity for a given taxa. To demonstrate how Darcy's Law can be applied to such data, we used an example landscape (Fig. 3) from Watts et al. (2010), who hypothetically modified the landscape in three ways by adding additional woodland habitat in different configurations (clumped, targeted and random woodland creation; see Table 2 in Watts et al., 2010) to compare the relative effectiveness of alternative management options for improving

landscape permeability. The width and length of the raster form the geometrical dimensions of the network, length and area (L, A ; Table 1).

3.2. Choosing model parameters

Once a raster image file has been created, each habitat and corresponding cell is assigned a permeability value (Table 2). In this example, broadleaf woodland is the most favourable habitat for the example species group and therefore has the highest permeability, whereas unfavourable land-cover such as roads, urban areas and water have the lowest permeability (Watts et al., 2010). The values in this example are inverted cost values from Watts et al. (2010), which gives permeability. Next, the viscosity of the model fluid (i.e. species; see Table 1) is chosen. The driving pressure head is the last parameter in our conceptual model that could be changed. In this example, we keep the magnitude of the pressure difference constant with a direction left – right in the landscape (i.e. west – east), which would be relevant for studying directional migration. Lastly, the model output, Q is the species movement rate, which represents the number of individuals passing through a given landscape per unit time.

3.3. A 1-D transport example

Now let us use concepts from for one-directional transport through porous media to estimate permeability in a west – east direction across the model landscape. Firstly, permeability values based on the land cover type are assigned to the landscape raster grid (cf. Section 3.2). Darcy's law (Eq. (1)) is only valid for 1-D flow (i.e. transport in one direction) so the 2-D raster grid must be collapsed down by one dimension for illustrative purposes. Here, we consider transport only in a west-east vector, therefore, following Eq. (2) we perform a weighted average to each landscape permeability column (i.e. north–south) to create an average west-east permeability profile for the model landscape. We stress that this is not intended to produce quantitative results and is a large over-approximation only designed for concept illustration (Fig. 3). Permeability profiles for the three-management options show that targeted woodland creation resulted in the greatest improvements to landscape permeability and therefore species movement rate for the model species. Importantly, the profiles also show which sections of targeted woodland creation have the greatest impact on permeability. This result agrees with the more complex analysis using least-cost path models on the same landscapes presented in Watts et al. (2010). However, again, we stress that for robust conclusions the analyses presented here should be expanded to 2-D. In the future, this could

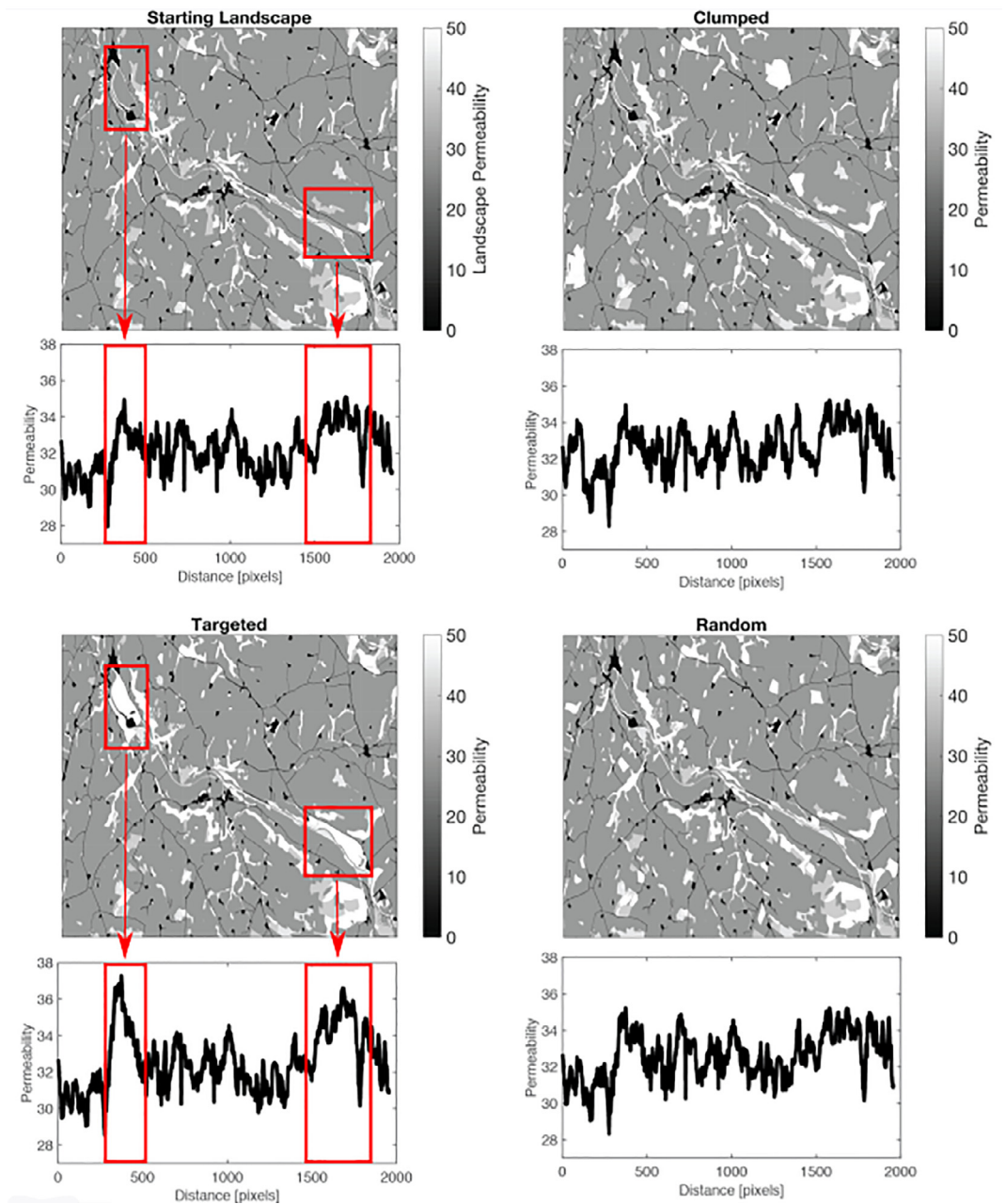


Fig. 3. Raster grid of landscapes (not to scale) from Watts et al. (2010), colour coded here for permeability. Permeability profiles are shown beneath each landscape raster. Red boxes on the starting landscape and post targeted woodland creation illustrate regions of high permeability.

involve a much more sophisticated computational fluid dynamics simulation.

Now consider the starting landscape in Fig. 3; we calculated an

effective permeability based upon the species mobility, or viscosity. Specifically, the effective permeability is defined as: k/μ . Fig. 4 shows the original raster landscape colour-coded for effective permeability,

Table 2
Permeability cost of land-cover types as given in Watts et al. (2010). These values were inverted for use in our model, which uses the physical definition of permeability where higher values are more permeable.

Land cover type	Movement cost (Watts et al., 2010)	Permeability (this study)
Semi-natural broadleaved woodland	0	50
Planted/felled broadleaved woodland & mixed woodland, scrub, bracken	1	20
Heathland, marshy grassland	3	10
Unimproved grassland, mire	5	5
Planted/felled coniferous woodland, semi-improved grassland, swamp	10	3
Improved amenity grassland, arable, water	20	1
Roads, buildings, water	50	0

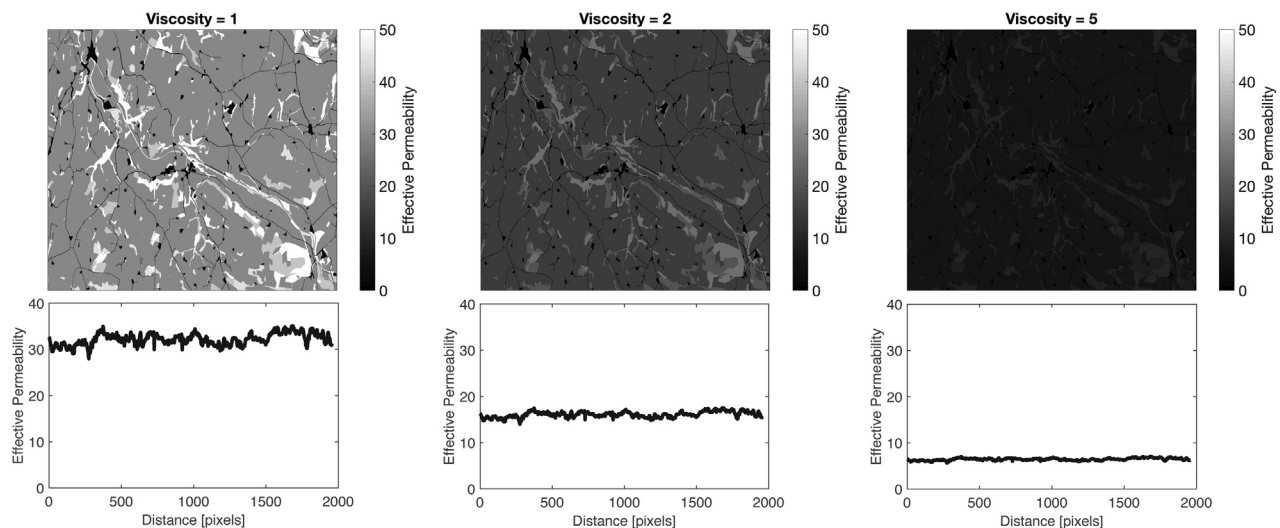


Fig. 4. Raster grids of original landscape (not to scale) coloured for the effective permeability of three different hypothetical, woodland species that share the same large-scale habitat requirements (e.g. forest or woodland), but which have different mobility (represented by the viscosity parameter: 1, 2 or 5) through the model landscape. High effective permeability values result in fast transport through the landscape.

where bright colours (white) represent regions capable of high movement rates. The three grids illustrates three example species that have viscosity values of 1, 2 and 5 respectively (e.g. ranging from a highly mobile species to a relatively immobile species; see examples of typical model species in Synes et al., 2016). Conceptually, these species might be forest birds that have the same general habitat requirements (i.e. forest or woodland), but which have different dispersal capacities (e.g. Şekercioğlu et al., 2002; Uezu et al., 2005), as discussed in Section 2.1. Thus, Fig. 4 shows that reducing the species mobility by increasing the viscosity term lowers the landscape's effective permeability and the species movement rate, assuming that the driving pressure for movement remains constant. The viscosity or mobility term can therefore be thought of as a scaling factor to account for species that have the same general habitat preferences but are able to disperse at different speeds. This allows for a more generic model to be produced based on landscape permeability (e.g. for woodland birds) and then subsequently 'fine-tuned' for different species' mobility within that group.

4. Discussion

Estimating how individuals, populations and genes move through heterogeneous landscapes is an important theme in ecology (Zeller et al., 2012), particularly when quantifying the relative value of alternative conservation actions (Watts et al., 2010). Here, we use a simple example to demonstrate how Darcy's empirical law for fluid flow through porous media has ecological analogues. Using fluid dynamical relationships and concepts, we illustrate that the areas with highly permeable land cover (Fig. 3: red boxes) can be directly correlated with higher species movement rates (Fig. 2).

To more effectively apply these physical concepts to ecological problems we recommend that a 2-D model is produced, since our illustrative example is designed to be informative for ecologists but at the cost of trading off accuracy. A simple example is shown in Fig. 5, wherein a hypothetical permeable landscape (Fig. 5a) facilitates movement of a single species purely in a left – right vector, with a constant driving pressure. The calculated magnitude of the species movement is shown in Fig. 5b and can be clearly correlated to the landscape permeability.

However, problems with this fluid flow approach exist, and satisfying ecological assumptions is not trivial. Selecting the appropriate permeability values is one of the largest challenges with this approach. Since permeability is highly scale dependant, the scale (i.e. raster cell

size) at which the analysis is conducted needs careful thought and where possible, ground-truthing. For instance, if the ecologist wants to quantify country-wide species movements rates a permeability grid that considers tree to tree connectivity (i.e. a small pixel size) is unlikely to be representative. Rather a pixel size of 10's of km² that broadly accounts for landcover type would be more representative. One solution to accurately quantify permeability values for a given species group would be to use existing field data (e.g. GPS trackers on migratory birds). These data could help assign permeability values to particular land cover types at the regional scale.

Furthermore, as with other permeability and connectivity indices, the total domain size (i.e. length and width of landscape) can impact the results. Therefore, like the selection of permeability values, the dimensions of the landscape under investigation require careful selection. As a guide, the landscape width and length should be considerably larger than the maximum expected dispersal distance of the study species (e.g. more than double this distance) to prevent boundary effects, and the landscape should be sufficiently large to reflect the spatial distribution of habitat patches within the study area. Thus, as with any modelling approach, care should be taken to use ecologically relevant scales based on the study species' or taxa of interest.

Additionally, unlike in our simple illustrations, the driving pressure term is in reality likely to evolve over time as a population disperses or migrates through a landscape. The origin of the population dispersal could also be changed, in our examples we considered entry from the edge of the landscape, but in 2-D space this could be changed to a singular, central habitat patch of interest, for example.

5. Conclusion

In physics, the properties of fluid flow through porous media are well understood, and we conclude that these concepts could prove valuable for developing indicators of species movement rates in terrestrial landscape ecology. In particular, the species-specific mobility term (viscosity) allows for models to be easily adapted when considering movement of different species that have similar habitat requirements through the same landscape, but which differ in dispersal capacity, such as different guilds of forest birds. Future work should involve the expansion of our simple 1-D concepts to a 2-D model, which could overcome some of the limitations of existing techniques that rely on estimating pairwise connectivity to quantify regional landscape permeability.

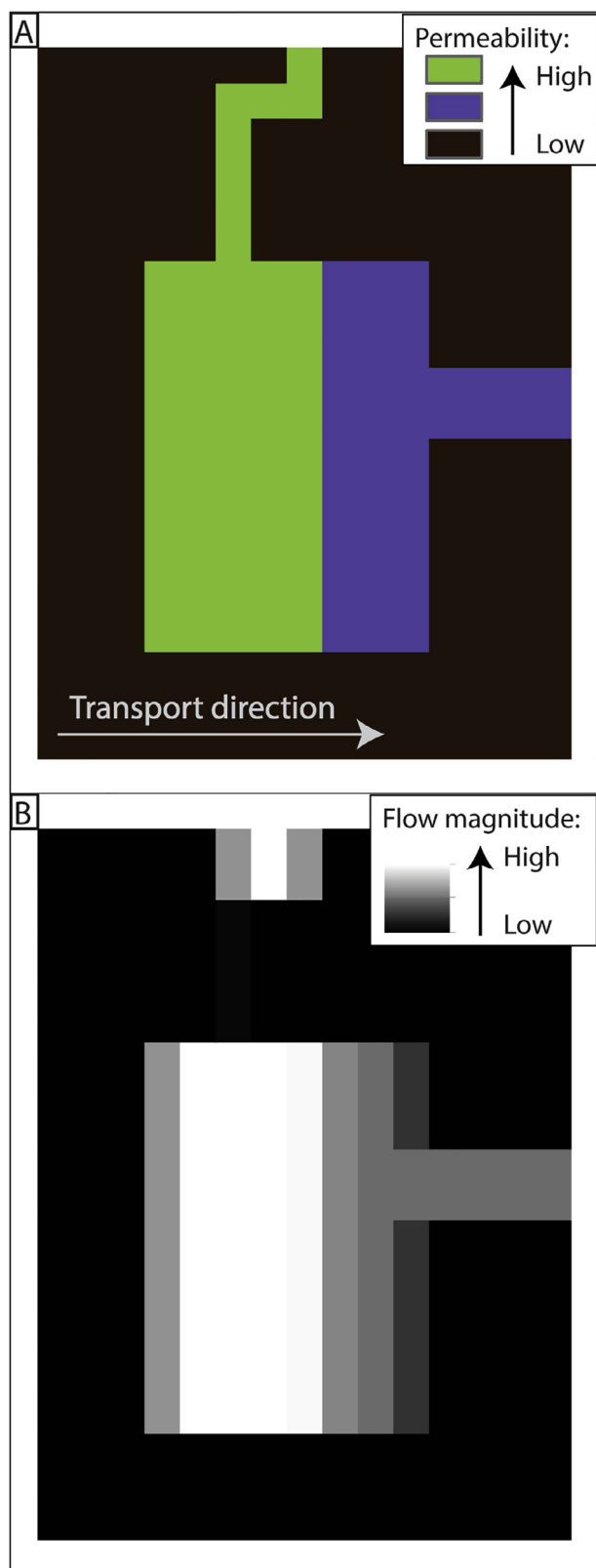


Fig. 5. (a) A hypothetical landscape with variable permeability. (b) The relative magnitude of Darcy flow through the hypothetical landscape. Where lighter colours represent a greater amount of flow from left to right.

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Conflict of interest

None.

References

- Adriaenssens, F., et al., 2003. The application of least-cost modelling as a functional landscape model. *Landscape Urban Plann.* 64 (4), 233–247.
- Aziz, K., Settari, A., 1979. *Petroleum Reservoir Simulation*. Chapman & Hall.
- Baranyi, G., et al., 2011. Contribution of habitat patches to network connectivity: redundancy and uniqueness of topological indices. *Ecol. Ind.* 11 (5), 1301–1310.
- Bear, J., Braester, C., 1972. On the flow of two immiscible fluids in fractured porous media. *Dev. Soil Sci.* 2, 177–202.
- Bocedi, G., et al., 2014. RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods Ecol. Evol.* 5 (4), 388–396.
- Calabrese, J.M., Fagan, W.F., 2004. A comparison-shopper's guide to connectivity metrics. *Front. Ecol. Environ.* 2 (10), 529–536.
- Darcy, H., 1856. *Les fontaines publiques de la ville de Dijon: exposition et application*. Victor Dalmont.
- Doerr, V.A.J., Barrett, T., Doerr, E.D., 2011. Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson, et al. *J. Appl. Ecol.* 48 (1), 143–147.
- Drever, M.C., Hrachowitz, M., 2017. Migration as flow: using hydrological concepts to estimate the residence time of migrating birds from the daily counts. *Methods Ecol. Evol.* <http://dx.doi.org/10.1111/2041-210X.12727>.
- Etherington, T.R., 2012. Least-cost modelling on irregular landscape graphs. *Landscape Ecol.* 27 (7), 957–968.
- Etherington, T.R., 2016. Least-cost modelling and landscape ecology: concepts, applications, and opportunities. *Curr. Landscape Ecol. Rep.* 1 (1), 40–53.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Ann. Rev. Ecol. Evol. System.* 34 (1), 487–515.
- Green, D.G., 1994. Connectivity and complexity in landscapes and ecosystems. *Pacific Conserv. Biol.* 1 (3), 194–200.
- Haddad, N.M., et al., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1 (2), e1500052.
- Kindlmann, P., Burel, F., 2008. Connectivity measures: a review. *Landscape Ecol.* 23 (8), 879–890.
- Leonard, P.B., et al., 2016. gflow: software for modelling circuit theory-based connectivity at any scale. *Methods Ecol. Evol.*
- McIntyre, N.E., Wiens, J.A., 1999. Interactions between habitat abundance and configuration: experimental validation of some predictions from percolation theory. *Oikos* 129–137.
- McRae, B.H., et al., 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89 (10), 2712–2724.
- Merriam, G., 1984. Connectivity: a fundamental ecological characteristic of landscape pattern. In: Brandt, J., Agger, P. (Eds.), *Proceedings of First International Seminar on Methodology in Landscape Ecology Research and Planning*, vol. I. Roskilde Universitetsforlag GeoRue, Roskilde, Denmark, pp. 5–15.
- Minor, E.S., Urban, D.L., 2008. A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conserv. Biol.* 22 (2), 297–307.
- Pinto, N., Keitt, T.H., 2009. Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. *Landscape Ecol.* 24 (2), 253–266.
- Saura, S., Pascual-Hortal, L., 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. *Landscape Urban Plann.* 83 (2), 91–103.
- Sawyer, S.C., Epps, C.W., Brashares, J.S., 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? *J. Appl. Ecol.* 48 (3), 668–678.
- Şekercioğlu, Ç.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Sandí, R.F., 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proc. Natl. Acad. Sci.* 99 (1), 263–267.
- Synes, N.W., et al., 2016. Emerging opportunities for landscape ecological modelling. *Curr. Landscape Ecol. Rep.* 1 (4), 146–167.
- Theobald, D.M., et al., 2012. Connecting natural landscapes using a landscape permeability model to prioritize conservation activities in the United States. *Conserv. Lett.* 5 (2), 123–133.
- Uezu, A., Metzger, J.P., Vielliard, J.M., 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biol. Conserv.* 123 (4), 507–519.
- Watts, K., et al., 2010. Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. *Landscape Ecol.* 25 (9), 1305–1318.
- Watts, K., Handley, P., 2010. Developing a functional connectivity indicator to detect change in fragmented landscapes. *Ecol. Ind.* 10 (2), 552–557.
- Zeller, K.A., McGarigal, K., Whiteley, A.R., 2012. Estimating landscape resistance to movement: a review. *Landscape Ecol.* 27 (6), 777–797.
- Zheng, C., Bennett, G.D., 2002. *Applied Contaminant Transport Modeling*. Wiley-Interscience, New York.