

Article

Where do diaspores come from? Reverse wind modelling unveils plant colonization trajectories

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Received 1 August 2015; Accepted 10 September 2015; Published online 1 December 2015



Abstract

In alpine habitats, wind is the predominant dispersal vector of diaspores (seeds and spores). The wind flow field in mountain areas depends on the interaction of wind with topography which creates very complex patterns for both wind directions and speeds. Most alpine species utilize wind transport for diaspore dispersal, and more than 90% are anemochorous. The transport of diaspores is to date considered a forward (ahead in time) problem, i.e. from actual diaspore locations to future ones. I argue here that, using appropriate reverse mathematical modelling, the problem can be reversed: starting from actual locations of plants and diaspores, one can evince the trajectories that led to actual positions. So doing, one can reconstruct the trajectories followed by plant species to reach actual niches. A particular application of this approach is the individuation of corridors followed by exotic plant species. The ad-hoc software *Wind-Lab* has been realized which incorporates both forward and backward wind modelling. The model described here might be of importance in geobotany, climatic ecology and plant conservation biology.

Keywords evolutionary modelling; GIS; partial differential equations; plant colonization; reverse modelling; seeds; spores; wind flow.

Proceedings of the International Academy of Ecology and Environmental Sciences
ISSN 2220-8860
URL: <http://www.iaees.org/publications/journals/piaees/online-version.asp>
RSS: <http://www.iaees.org/publications/journals/piaees/rss.xml>
E-mail: piaees@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

In mountain areas, wind is the predominant dispersal vector of diaspores (van der Pijl, 1982). Most alpine species utilize wind transport for diaspore (seeds and spores) dispersal, and more than 90% are anemochorous (van der Pijl, 1982). Species colonizing alpine-nival summits are likely to be anemochorous rather than zoochorous or autochorous (Holzinger et al., 2008). Stocklin and Baumler (1996) demonstrated that most colonizing species on glacier forelands possess wind dispersed seeds. Tackenberg and Stockling (2008) showed that more than 50% of alpine species have a good chance of being dispersed by wind over long

distances. Vittoz et al. (2009) classified alpine summit colonizers into good and weak colonizers and most of the good colonizers were wind-dispersed.

The transport of diaspores is to date considered a forward (ahead in time) problem, i.e. from actual plant placements to future diaspore locations. I argue here that, using appropriate reverse mathematical modelling, the problem can be reversed: starting from actual locations of plant species and diaspores, one can evince the trajectories that led to actual positions. So doing, one can reconstruct the trajectories followed by plant species to reach actual niches.

The ad-hoc model *Wind-decoder* for both forward and backward wind flow modelling upon (real or simulated) topographic surfaces is presented here. The software *Wind-Lab* (Ferrarini, 2009) has been realized to apply *Wind-decoder*.

2 Forward and Backward Modelling of Wind Flows: Mathematical Formulation

The forward option of *Wind-Lab* makes use of a mass-consistent wind flow model, similar to that of Davis et al. (1984) and Ross et al. (1988), which explicitly incorporates the law of conservation of mass. The model minimizes the change from an initial wind field while conserving mass as

$$F(u, v, w) = \int_{\Phi} [(u - u_0)^2 + (v - v_0)^2 + (w - w_0)^2] d\Phi \quad (1)$$

where u, v, w are the velocity components in the x (positive to the east), y (positive to the north) and z (positive upward) directions; u_0, v_0 and w_0 are the initial values of wind velocity; Φ is the spatial domain of wind simulation; $F(u, v, w)$ is the equation to minimize.

Under the conservation of mass equation

$$H(u_x, v_y, w_z) = \frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0 \quad (2)$$

the minimum of $F(u, v, w)$ is achieved through the Euler-Lagrange equations

$$u = u_0 + 0.5 * \frac{\partial \lambda}{\partial x} \quad (3)$$

$$v = v_0 + 0.5 * \frac{\partial \lambda}{\partial y} \quad (4)$$

$$w = w_0 + 0.5 * \frac{\partial \lambda}{\partial z} \quad (5)$$

subject to the boundary condition

$$\lambda \vec{\nabla} * \vec{n} = 0 \quad (6)$$

where $\lambda(x, y, z)$ is a Lagrange multiplier, \vec{n} is the outward unit vector normal to the surface of the domain Φ , and $\partial\vec{V}$ is the first variation of the velocity on Φ .

By taking the partial derivatives with respect to x , y , and z , the result is an elliptic partial differential equation for $\lambda(x, y, z)$ as follows

$$\frac{\partial^2 \lambda}{\partial x^2} + \frac{\partial^2 \lambda}{\partial y^2} + \frac{\partial^2 \lambda}{\partial z^2} = -2\left(\frac{\partial u_0}{\partial x} + \frac{\partial v_0}{\partial y} + \frac{\partial w_0}{\partial z}\right) \quad (7)$$

that is solved with respect to $\lambda(x, y, z)$ on the terrain grid using the finite element method.

This dynamical model takes into account the interaction of wind with topography which creates very complex patterns for both wind directions and speeds. Diaspore deposition occurs when seeds are released due to lack of kinetic energy (Nathan et al., 2002). Hence, a deposition area is a site with lower wind speeds than those of outside areas. The cut-off velocity below which diaspores are released (velocity of release) by winds is called here V_{rel} and depends almost exclusively on the weight and the structure of seeds or spores. Deposition areas are defined here as A_d , while source areas for diaspores are named here A_s .

In order to reverse wind flow modelling, *Wind-Lab* makes use of genetic algorithms (GA; Holland, 1975). GA 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, 2011b; Ferrarini, 2013a; Ferrarini, 2013b; Ferrarini, 2013c; Ferrarini, 2013d; Ferrarini, 2014a; Ferrarini, 2015a; Ferrarini, 2015b). *Wind-Lab* employs the optimization algorithm for point sampling developed in Ferrarini (2012b) which reads as follows

$$S_{bs} = \frac{\alpha * \left(1 + \sum_{i=1}^n \left(- \frac{\sum_{j=1}^{k_i} p_{ij} * \ln p_{ij}}{\ln k_i} \right)\right)}{\beta * \left(1 + \left(n * \frac{s}{s_{max}} * \frac{D_s}{D_{smax}}\right)\right)} \quad (8)$$

that must be maximized using GA under the constraint that

$$D_{AB} \geq D_{min} \quad (9)$$

and

$$s \leq S_{max} \quad (10)$$

and where:

p_{ij} is the proportion of sampling points that falls in the j -th interval of the i -th variable;

s is the number of candidate sites for A_{sour} ;

S_{max} (maximum number of sampling points) is chosen at the beginning of sampling;

D_{smax} is the maximum possible distance within the study area (diameter of the study area);

D_{min} is the minimum distance among sampling points;

D_{AB} is the geographical distance between two generic sampling points A and B;

D_s is just a function of the s points and their correspondent coordinates;

n and k are two parameters that must be chosen at the beginning of the sampling algorithm;

α and β are two different weights given to numerator and denominator.

The equation in (8) is used by *Wind-Lab* to detect a minimum number of candidate points for A_s . In fact, without this step the goal to find all the possible candidates for A_s would be computationally prohibitive, at least for standard computers. Starting from the candidate sites chosen through eq. (8), *Wind-Decoder* calculates forward wind flows and detects for which candidate sites the deposition areas exactly correspond to A_d with at maximum a tolerance distance (for example, 10 meters) that can be set by the user. These are the areas from which diaspores can come from. Then the process is repeated, so that the full trajectory of diaspores in the study area is detected.

It should be noted here how much the task computed by *Wind-Decoder* and *Wind-Lab* is difficult. The wind flow over terrain depends on the strict and continued interaction of wind with topography which creates very complex patterns for both wind directions and speeds. If forward modelling of wind flows over terrain is complex, backward modelling is much more. The goal has been solved in *Wind-decoder* using an optimization approach based on optimal sampling. In fact, using eq. (8) the model selects a minimum number of potential candidate points for A_s . Then forward wind modelling is applied, and only the points leading to deposition areas close to A_d are maintained. Then, using GA, new points close to the most promising ones are created and forward modelling is repeated. The loop is replicated until the areas individuated by forward wind modelling perfectly correspond to A_d (with eventually a tolerance distance).

The software *Wind-Lab* has been first realized in June 2009 (Ferrarini, 2009). The 2.0 version has been realized on April 2010. The most recent version (which comprises the reverse modelling option) is the 5.0 one, realized on July 2013. It has been already used in Ferrarini et al. (2014b).

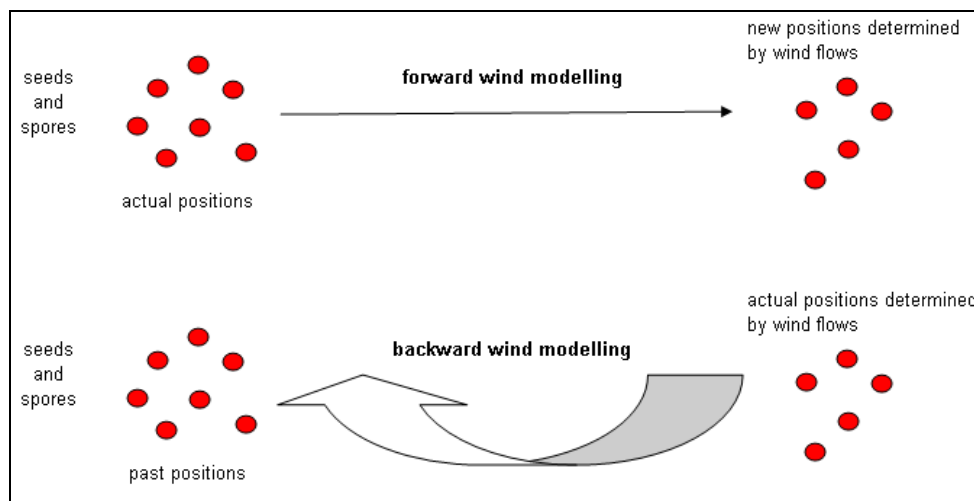


Fig. 1 The idea behind *Wind-decoder*: wind flows over terrain can be modelled both forward and backward.

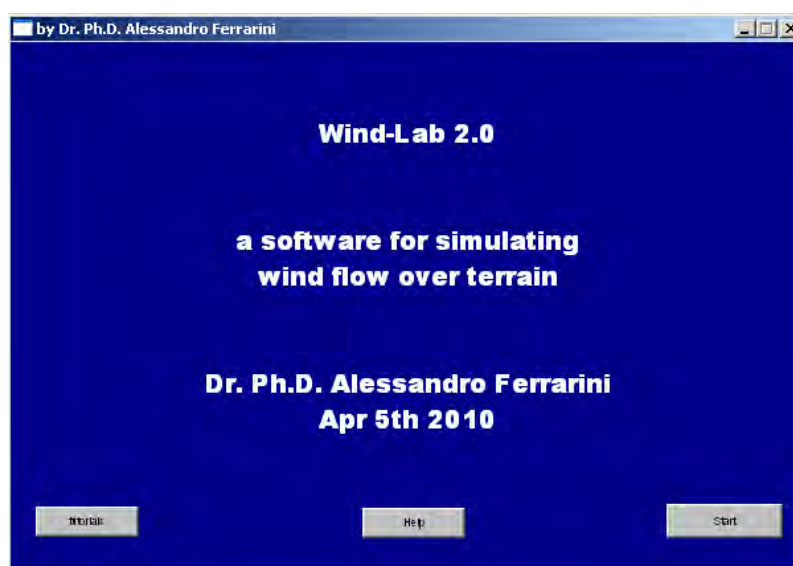


Fig. 2 The splash screen of the software *Wind-Lab* (version 2.0) which incorporates both forward and backward wind modelling upon topographic surfaces.

3 An Applicative Example

Let's consider the study area depicted in Fig. 3. It's a virtual square area of 25 *15 sq. km, generated using the software DTM-Lab that builds virtual topographic surfaces with desired properties (Ferrarini, 2007).

First, using *Wind-Lab* I'll simulate dominant wind flows with average wind speed = 5 m/s (measured at 2 m above terrain) from East, and V_{rel} for diaspores = 3 m/s. So doing, I'll individuate future A_d .

Second, using Wind-Lab I'll reverse wind flow modelling. The process is repeated backward, until the full trajectory that can be followed by diaspores is detected within the study area.

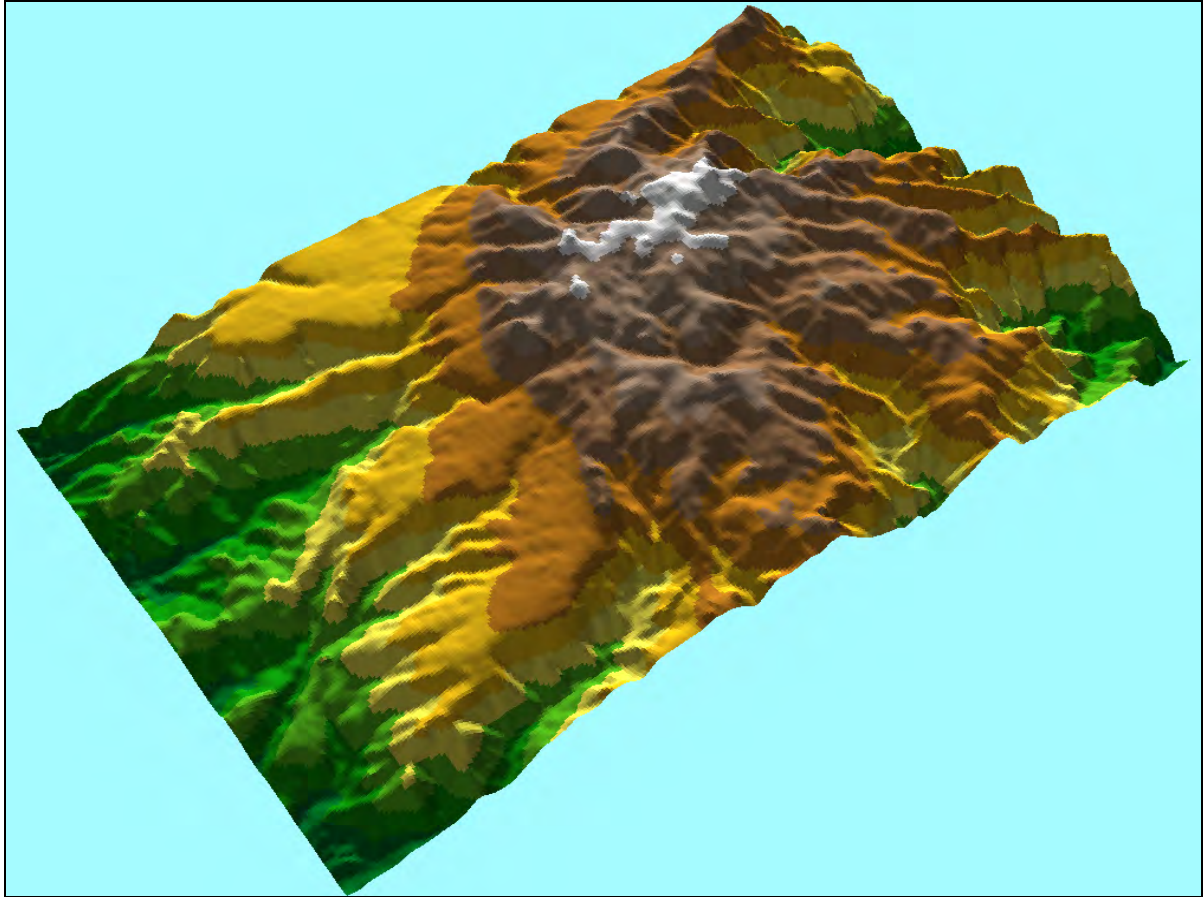


Fig. 3 The virtual 3D study area (25 * 15 sq. km) generated through the software model DTM-Lab (Ferrarini, 2007).

Results provided by the *Wind-decoder* model are shown in Fig. 4. Five possible routes for diaspores in the study area have been individuated. There are no further possible routes under the simulated wind profile (average wind speed = 5 m/s from East).

All routes avoid the most elevated portion of the study area which acts as a barrier. Eleven diaspore A_d are present. Routes 2 and 4 have three A_d for diaspores, route 3 just 1. If diaspores are detected in site 2, they can only come from site 1. Diaspores in site 1 can only come from outside the study area. Diaspores of site 4 can only shift to site 5, and so on.

It is important to note that there are many other points in the virtual study area where wind speed falls below 3 m/s when interacting with the topographic surface of Fig. 3, but this is not enough to determine an A_d for diaspores since only vectors of wind flows that transport seeds or spores along the study area must be considered.

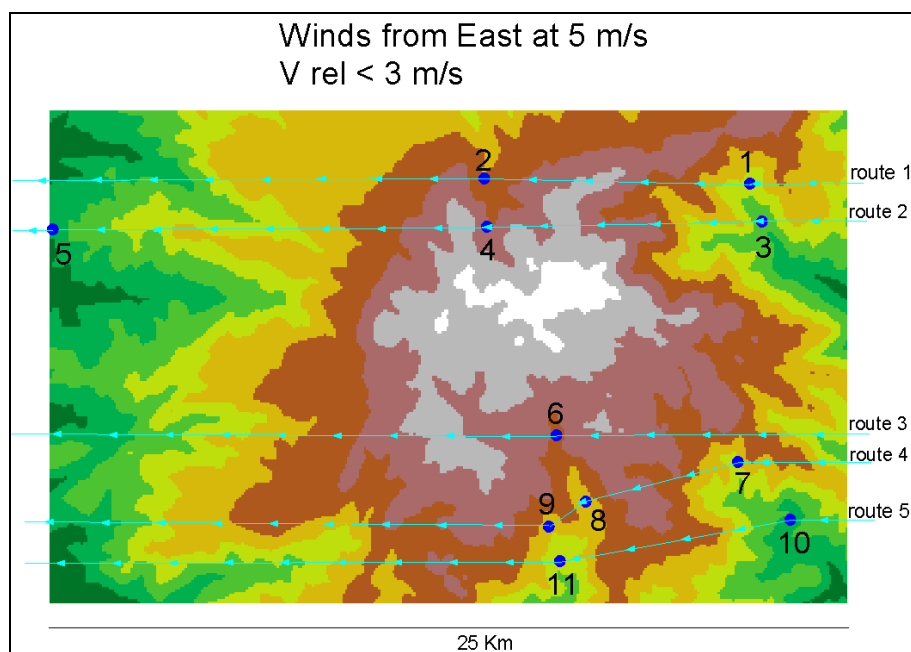


Fig. 4 Diaspore trajectories (detected through *Wind-Decoder*) generated by dominant winds flowing from East at an average speed = 5 m/s. The velocity of release for diaspores is set to 3 m/s.

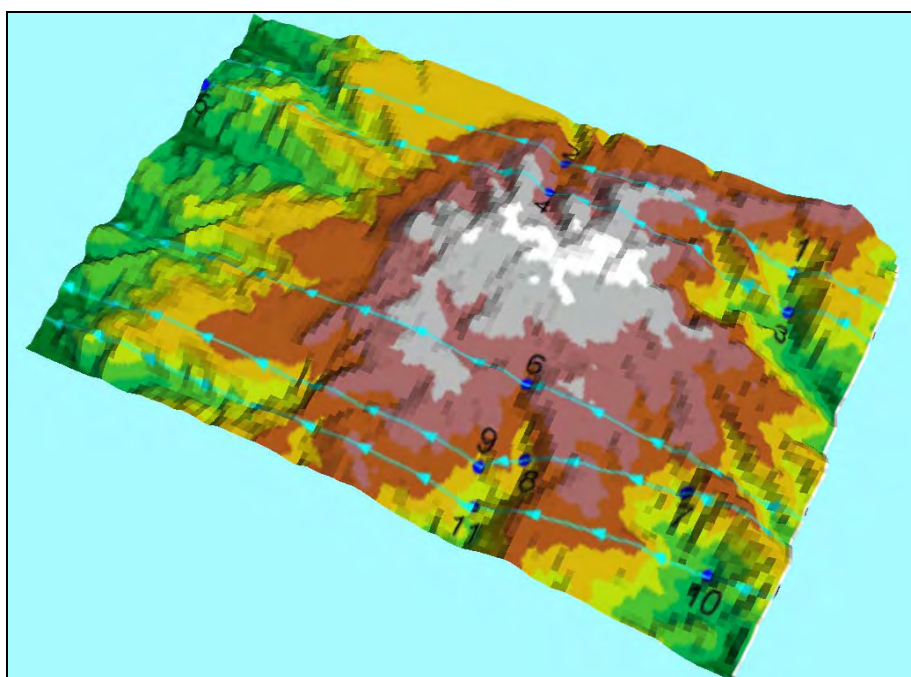


Fig. 5 Diaspore trajectories (detected through *Wind-Decoder*) upon the 3D surface.

Fig. 5 shows the detected diaspore routes and A_d upon the 3D surface of Fig. 3. It results clear that A_d correspond to kinetically steady areas where winds are decelerated below 3 m/s by particular local topographic morphologies.

Of course, the coupled forward-backward wind simulation used by *Wind-decoder* must be repeated in case further dominant wind directions are present in the study area. For instance, Ferrarini et al. (2014b) individuated several directions of dominant winds in a study area close to Himalaya.

A particular application of *Wind-decoder* and *Wind-Lab* is the individuation of corridors followed by exotic plant species. In fact, only the knowledge of such spatial corridors could allow for the eradication of undesired species.

4 Conclusions

The colonization of mountain areas by plant species is almost exclusively driven by winds.

To date, the transport of diaspores (seeds and spores) by winds has always been considered a forward scientific problem (i.e. from actual plant stations to future locations). In this paper, I have proposed that diaspore dispersal could also be thought as a backward process, and that this novel vision can lead to reconstruct the past trajectories followed by plant species to reach actual niches. I have then developed the necessary math to reverse diaspore transport by winds. A particular application of *Wind-decoder* and *Wind-Lab* is the individuation of corridors followed by exotic plant species, which could allow for the eradication of such undesired plant species.

The ad-hoc software *Wind-Lab* has been realized which incorporates such math. It might be of interest in geobotany, climatic ecology and plant conservation biology.

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