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Mechanistic modeling of seed dispersal by wind over hilly terrain

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ABSTRACT

Seed dispersal is the main movement mechanism used by plants. The last decade saw rapid progress in understanding the underlying processes, especially for dispersal by wind, in part due to new mechanistic modeling approaches that account for turbulent fluctuations. Yet, current wind dispersal models stop short of explicitly incorporating the effects of landscape topography on the main transporting vector – wind, so that the effects of wind variability over hills on dispersal patterns remain by and large unstudied.

A new mechanistic model was developed that combines Eulerian wind statistics derived from a simplified analytical approach of flow over gently sloped forested hills with a Lagrangian seed trajectory model. Model runs were used to explore the effects of seed release location along the hill on dispersal kernels predicted by the new model in relation to their flat-terrain counterparts. The model was parameterized for a *Pinus taeda* plantation, and a range of seed motion capacities represented by terminal velocity and release height, and realistic topographic variation were then explored.

To evaluate model performance, computed kernels were compared to kernel measurements collected in a large flume for spherical ‘seeds’ released near the top of a rod canopy covering gentle cosine hills. The evaluation showed that the model reproduced the key experimental differences in dispersal patterns for releases at the hill crest and bottom.

The simulations revealed several novel findings. For seeds released within the canopy, both median and 99th percentile dispersal distances on the hill upwind side were up to two times longer than on flat terrain for the same motion capacity. Seeds released on the lee side traveled mostly toward the hill crest – following the local within-the-canopy wind direction. This direction was contrary to the ‘regional’ wind direction set by the flow conditions above the canopy. There, the directionality of the long-distance dispersal was additionally dependent on uplifting probability, affected by seed motion capacity.

It was demonstrated that neglecting the effects of even gentle topography in mechanistic seed dispersal models can lead to biased estimates of dispersal distances and directionality on hilly terrain. These results are pertinent to plant population demography, connectivity and spread on hills. More broadly, the approach developed here can be extended to movement of pollen and various airborne organisms over hills.

1. Introduction

Seed dispersal, or the transport of seeds away from a parent plant, is the main movement mechanism in plants (Ridley, 1930; van der Pijl, 1982; Levin et al., 2003; Nathan et al., 2008b). As such, seed dispersal is central to a broad array of ecological processes. Short-distance dispersal (SDD) generates the spatial template for subsequent demographic processes (e.g. establishment) and plays a role in species coexistence. The inherently rare long-distance dispersal (LDD) is crucial for landscape-scale processes such as colonization of new sites or re-colonization after a local extinction, inter-population connectivity and gene flow, and community assembly from the metacommunity (Levine and Murrell, 2003; Trakhtenbrot et al., 2005; Nathan et al., 2008b).

On the individual and the population level, the spatio-temporal dispersal patterns result from the intricate interplay of the plant traits determining the seed dispersal ability (motion capacity *sensu* Nathan et al., 2008a) and the vector characteristics, such as its seed load (Nathan et al., 2008b; Cousens et al., 2008). In the transportation phase of the dispersal event, factors affecting the movement of the dispersal vector(s) are of the utmost importance

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(Nathan et al., 2008b). The movement of both biotic and abiotic vectors is well known to be affected by landscape heterogeneity (e.g. Mack, 1995; Levey et al., 2005, 2008; Belcher et al., 2012). Topography is a widespread heterogeneity defining natural landscapes. Yet, while the effects of topography on dispersal were previously studied on a wide range of spatial scales – from microtopographic effects on seed deposition (e.g. Reader and Buck, 1986) to the possible role of mountain ranges as dispersal barriers (e.g. Rupp et al., 2001; Gugger et al., 2008), only a few studies have examined mechanistically and systematically the effects of complex topography on the movement of seed dispersal vectors and on its consequences to dispersal distances and directionality. One exception is the Mack (1995) study showing that *Aglaia aff. flavida* seeds dispersed by dwarf cassowaries (*Casuarius bennetti*) were moved predominantly uphill, mainly due to cassowary-preferred resting sites on ridgetops and level bluffs; while seeds contained in fruit falling from the trees and not treated by cassowaries were deposited mainly downhill from the source due to gravity.

Studying the effects of topography on the movement of biotic dispersal vectors may be extremely challenging and species-specific, as exemplified by Mack (1995). On the other hand, since wind is a dispersal vector common to many species and ecosystems (Willson et al., 1990; Ozinga et al., 2004), and because wind dynamics can be predicted from physical principles, wind dispersal is a logical starting point to disentangle the possible effects of topography on seed dispersal kernels.

Significant effort was devoted to mechanistic treatment of wind mediated dispersal over the last decade (see review in Nathan et al., 2011b). Indeed, there is wide agreement (e.g. Cousens et al., 2010) that currently mechanistic modeling is more advanced for wind than for other dispersal vectors. Physical models provide insights on possible causal links between the movement of this vector and its interaction with environmental factors and the dispersal patterns (Nathan et al., 2001, 2002a,b; Tackenberg, 2003; Soons et al., 2004; Katul et al., 2005; Nathan and Katul, 2005; Nuttle and Haefner, 2005; Kuparinen et al., 2007; Bohrer et al., 2008; reviewed in Kuparinen, 2006 and in Nathan et al., 2011b). A major advancement in recent years was in incorporating into the mechanistic models some of the main features of turbulent vertical velocity fluctuations whose coherency and vertical gradients were shown to be necessary to the onset of LDD (Nathan et al., 2002b; Tackenberg, 2003; Soons et al., 2004; Kuparinen et al., 2007; Bohrer et al., 2008; Wright et al., 2008).

Hilly terrain changes the basic balance of forces driving wind flow as compared to flat terrain (Stull, 1988; Finnigan and Belcher, 2004). These fundamental differences are expected to alter seed dispersal kernels, yet have rarely been considered in present mechanistic models or in empirical studies. A recent laboratory study in a flume demonstrated that dispersal distances of heavy spherical particles released from the top of a rod canopy situated on top of a gentle cosine hill were considerably larger than their counterpart releases at the bottom of the hill for the same canopy (Katul and Poggi, 2012). Yet, most mechanistic models of seed dispersal by wind to date were developed for flat terrain with perhaps some exceptions (Tackenberg, 2003; Horn et al., 2012). In one previous effort, incorporating some effects of topography into mechanistic seed trajectory calculations was attempted (PAPPUS model, Tackenberg, 2003), though this treatment was primarily an alignment of the mean flow streamlines along the topography using a pre-defined angle between the mean flow and topography. Thus, a mean vertical velocity component, resulting from the inclination of the wind vector direction to follow the terrain, was added (in contrast to a mean zero vertical component on flat terrain). PAPPUS did not explicitly model or treat spatial (i.e. horizontal and vertical) variations in wind flow dynamics generated by non-flat topography.

The lack of mechanistic seed dispersal models by wind for hilly terrain is not surprising given that simplified theories for turbulent wind flow over a hill covered by a uniform vegetated canopy, as opposed to a bare hill (Jackson and Hunt, 1975), was only developed in the last decade (Finnigan and Belcher, 2004, reviewed in Belcher et al., 2008, 2012). Analytical models of flow over a gentle hill covered by uniformly vegetated canopy were tested in flumes and via Large Eddy Simulations (LES) runs for isolated and train of gentle hills (Finnigan and Belcher, 2004; Poggi and Katul, 2007a,b,c; Dupont et al., 2008; Poggi et al., 2008; Patton and Katul, 2009). Good agreement between analytical models and observed mean flow patterns was reported in several cases (Poggi et al., 2008) – at least for the case of gentle hills and dense yet tall canopies. The relative simplicity of these analytical approaches is advantageous for incorporating them into seed dispersal models, since they enable computing dispersal patterns over large temporal (up to yearly) and spatial (up to tens of kilometers) domains that are the most relevant for many ecological processes.

Building on these previous efforts, a model is constructed so as to examine, for the first time, the effects of topography-induced variability in wind dynamics on seed dispersal by wind, as referenced to the flat terrain scenario. Our main goal was proposing a model that enables both to test hypotheses about the topographically induced modifications of the dispersal patterns and, more importantly, to generate new hypotheses on dispersal patterns. Specifically, for SDD, our hypothesis was that variations in dispersal distances and direction across the hill will follow patterns of within-the-canopy mean terrain-following wind velocity established in vicinity of the release site. The complex interaction of the mean terrain-following and normal-to-terrain velocities and the turbulent wind parameters (both within and above the canopy) that governs LDD prevents formulation of specific hypotheses on LDD patterns. It follows that the model runs serve here to generate novel hypotheses on LDD in complex terrain and its potential role in inter-population connectivity in terms of dispersal directionality. It is envisaged that these new hypotheses and model runs will guide the planning of future field experiments intended to explore the role of topography on dispersal patterns.

2. Methods

2.1. Overview of wind flow over hills

The main factors affecting wind flow over a hill are the hill slope, surface roughness, and the atmospheric stability parameter, a dimensionless variable that dictates whether the flow is dominated by mechanical or by convectively produced turbulence (Stull, 1988; Finnigan and Belcher, 2004). The key features of a flow over a bare hill under a nearly neutral stability regime (where mechanically produced turbulence is dominant) are the acceleration of the mean terrain-following velocity component on the upwind side, and its deceleration on the lee side due to pressure gradients produced by the hill surface (Jackson and Hunt, 1975; Stull, 1988; Finnigan and Belcher, 2004; Poggi and Katul, 2007b). This spatial variability in the longitudinal dimension is in contrast with the planar-homogeneous mean horizontal velocity characterizing the flow over flat terrain with uniform vegetation cover. Canopy cover on a hill further complicates the flow regime by imposing additional drag opposing the flow in both longitudinal and vertical directions (Finnigan and Belcher, 2004).