BIODIVERSITY RESEARCH

Long-distance biological transport processes through the air: can nature's complexity be unfolded *in silico*?

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ABSTRACT

Understanding and predicting complex biological systems are best accomplished through the synthesis and integration of information across relevant spatial, temporal and thematic scales. We propose that mechanistic transport models, which integrate atmospheric turbulence with information on relevant biological attributes, can effectively incorporate key elements of aerial transport processes at scales ranging from a few centimetres and fractions of seconds, to hundreds of kilometres and decades. This capability of mechanistic models is critically important for modelling the flow of organisms through the atmosphere because diverse aerial transport processes — such as pathogen spread, seed dispersal, spider ballooning and bird migration — are sensitive to the details of small-scale short-term turbulent deviations from the mean airflow. At the same time, all these processes are strongly influenced by the typical larger-scale variation in landscape structure, through its effects on wind flow patterns. We therefore highlight the useful coupling of detailed atmospheric models such as large eddy simulations (LES), which can provide a high-resolution description of turbulent airflow, with regional atmospheric models, which can capture the effects of landscape heterogeneity at various scales. Further progress in computational fluid dynamics (CFD) will enable rigorous exploration of transport processes in heterogeneous landscapes.

Keywords

Atmospheric models, biological transport, computational fluid dynamics (CFD), large-eddy simulations (LES), long-distance dispersal, turbulence.

INTRODUCTION

In the first 106 s of the film, 'Forrest Gump', the camera follows a feather flying erratically through the air, abruptly changing speed and direction. Because seemingly random small-scale and short-term events govern airflow and thus the feather's flight trajectory, we do not know when and where its flight will end. Remarkably, the feather ends up exactly on the tip of the shoe of a strange-looking man sitting in the park. In this first time we see Forrest Gump, director Robert Zemeckis gently but powerfully illustrates that vanishingly improbable things just happen to this unusual person.

Small-scale, short-term turbulent deviations from the mean airflow not only dictate the flight of a feather but also profoundly influence the transport of a variety of organisms through the air (Edmonds, 1979; Isard & Gage, 2001). Turbulence affects the onset, propagation and termination of a diverse array of biological transport phenomena, such as pathogen spread, seed dispersal, spider ballooning and bird migration. At the same time, these processes occur over a wide range of spatial and temporal scales, and are strongly affected by structural changes in the landscape.

These features of aerial transport processes — the high level of uncertainty as a result of the critical role of turbulence, the wide range of relevant spatial and temporal scales and the profound effect of structural heterogeneity — along with non-linear inter-dependence among multiple influential factors, are typical characteristics of a complex biological system (Michener *et al.*, 2001). Scaling rules — which are defined by the mean properties of the flow field and are calculated by averaging over long intervals — have been claimed to be sufficient for understanding and predicting airflow patterns (Raupach *et al.*, 1996). However, short-term turbulent gusts are obscured by averaging wind velocity over long intervals, and the effects of landscape heterogeneity are often neglected. Despite long recognition of their importance for

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aerial transport processes (Edmonds, 1979), these complexities have not been addressed in previous models of aerial transport.

The main goal of this article is to draw the attention of ecologists to recent advances in atmospheric models, and to highlight the opportunity for unravelling biological transport processes through the air. This complements the growing importance of developing a quantitative understanding of biological transport processes as a prerequisite for successful management of many ecosystems (Isard & Gage, 2001; Reiners & Driese, 2004). While insights from studies of long-term, large-scale atmosphere–biosphere interactions have recently been reviewed (Greenland *et al.*, 2003; Moorcroft, 2003), many ecologists remain unaware of emerging tools that can provide detailed description of atmospheric flows, especially turbulent eddy motion, and that can also incorporate the effects of landscape heterogeneity at much larger spatial scales. We first point out which modelling tools have become available and then we provide an overview of ecological processes for which application of these tools is expected to advance our quantification and understanding of biological transport processes.

ADVANCES IN MODELLING TURBULENT AIRFLOWS

The stability of a flow is characterized by the dimensionless Reynolds number: low values are typical for laminar, stable flows, whereas high values characterize turbulent, unstable flows. Atmospheric airflows are characterized by high Reynolds numbers. The velocity of the turbulent deviations from the mean airflow is at least as important for the transport of organisms as the mean airflow itself. We refer to the 'mean airflow' as airflow averaged over a period of 1 h, over an area of at least 1 km^2, adhering to the meteorological literature and the relevant scale for the processes discussed here. Atmospheric flows occur over a very wide range of spatial scales ranging from meteorological pressure systems (hundreds of km), through the height of the atmospheric boundary layer (approximately 1–2 km), down to the scale of viscous dissipation (approximately 1 mm). At every scale, transfer of momentum, energy and mass through the air involves a complex set of turbulent transport processes in which eddies — vortex-like coherent fluid structures — are produced, transported and dissipated.

Turbulent flows are traditionally described by the Navier-Stokes equations, a set of nonlinear partial differential equations that represent the conservation of momentum in fluids and whose analytical solution has eluded mathematicians and physicists for centuries. To date, only numerical approximations can be calculated for the Navier-Stokes equation system. Yet, numerically solving the Navier-Stokes equations for all relevant spatial scales up to 1 km in three dimensions, requires at least 10^{18} grid nodes, which remains well beyond the range of modern computing (approximately 10^{10}).

To avoid the impossibly high computational costs of numerical calculations, the large eddy simulation (LES) technique, introduced in the early 1970s (Deardorff, 1970, 1972), restricts the numerical integration of the Navier-Stokes equations only to large eddies, which contribute most of the energy and momen-

tum transfer and are sensitive to the specific settings of the simulated flow (Mason, 1994). The smaller eddies, which contribute significantly to the total turbulent kinetic energy, are assumed to exhibit universal statistical characteristics (such as local isotropy and constant power-law scaling) thereby, permitting simpler techniques at a smaller-scale level to be used instead of directly resolving them through the Navier-Stokes equations. While some debate remains as to whether such smaller eddies truly retain universal characteristics (Katul *et al.*, 2001), the LES technique has recently been shown to be a powerful tool for the study of fluid turbulence for a wide range of flow systems (Friedrich & Rodi, 2002).

One of the major advantages of the LES technique lies in its ability to incorporate high spatial (down to the centimetre scale for spatial domains of up to few km^3) and temporal (fractions of seconds) resolution. This allows expression of rare short-term deviations from the mean airflow, which, as we explain later on, can be of paramount importance for aerial transport processes. However, the high resolution of LES also entails a major limitation — high demands on a computer's central processing unit (CPU) — which restricts its application to relatively small spatial and temporal domains (few km, few hours). To provide realistic atmospheric forcing conditions to the LES, it is conceivable to 'nest' it within a low-resolution regional model such as the regional atmospheric model system (RAMS) (e.g. Baidya Roy & Avissar, 2000). This hierarchical setup may consist of several levels of nested grids, which zoom in from large-scale meteorological phenomena, where only the mean properties of the airflow are simulated, to a small focal area of interest, where the details of turbulent airflow is resolved by higher-resolution (few metres, fraction of second) LES. A nested LES interacts with larger-scale levels, thus accounting for the impact of large-scale changes in meteorological systems on turbulence within the focal area, and vice versa. The result is a hierarchical model of multiscale computational fluid dynamics (CFD). While widespread application of detailed hierarchical atmospheric models such as LES and other CFD techniques is still limited by their complexity and high CPU demand, the rate of improvement of CPU capabilities, the assemblage of large computer clusters and new high performance numerical methods are rapidly pushing back this limitation.

Another limitation stems from the chaotic nature of turbulence: important extreme events predicted by atmospheric models typically involve a great deal of uncertainty that complicates our understanding and reduces predictability. This is typically addressed by resolving and comparing the higher statistical moments of airflow by statistical descriptions of the flow, rather than by attempting to reconstruct the turbulent flows explicitly. Future breakthroughs in modelling turbulence may rise from new conceptual approaches to turbulence, such as the one suggested by Chen *et al.* (2003). Their technique replaces the assumption of a continuum employed in the Navier-Stokes equations by the assumption of discrete molecular-like motion of eddies inherent in the Boltzmann equations. It gains high computational efficiency by adopting a hierarchical lattice approach, and it claims accuracy well beyond anything conceivable with LES (Chen *et al.*, 2003).

Such detailed flow models, combined with advanced computational capabilities, can play a key role in quantifying and understanding transport processes.

TURBULENT FLOWS AND BIOLOGICAL TRANSPORT PROCESSES

The description of turbulent flows made possible by high-resolution modelling approaches is important for quantifying, understanding and predicting biological transport processes for two main reasons. First, the details of turbulent deviations from the mean airflow can constitute the key requirement for various transport processes. Second, small-scale landscape heterogeneity, resulting from small-scale variation in environmental conditions, can critically affect airflow patterns at larger scales, and hence determine biological transport processes. In the next two sections we discuss these two topics. While focusing on the importance of turbulence for large-scale (hundreds of meters to thousands of kilometers) transport processes, we wish to emphasize that proper and detailed description of turbulence is necessary for modelling biological transport processes, but is not sufficient. Coupling detailed description of turbulence with coarser description of large-scale atmospheric phenomena is essential to encompass the entire spectrum of spatial and temporal scales over which these biological processes operate.

Effects of turbulence on large-scale transport processes

Seeds of many plant species are equipped with morphological structures that slow down their rate of descent, in particular their terminal velocity in still air. However, despite such sophisticated wind dispersal adaptations, seeds of many plant species, especially trees and lianas, are much heavier than spores, pollen and pathogens, and many seeds have terminal velocities on the order of 1 m/s. In forests, winds are typically weak: their vertical velocities are usually $\ll$ 1 m/s and their horizontal velocities are much weaker than winds outside or above the forest (Nathan *et al.*, 2002a). Thus, the vast majority of seeds of forest trees encounter very weak vertical and horizontal air movements, and are doomed to travel relatively short distances. Nevertheless, a small proportion of seeds may travel much longer distances via rare, prolonged turbulent updrafts that lift them up from the forest interior to the atmospheric layer above the forest canopy, where horizontal winds are much stronger (Nathan *et al.*, 2002b). Recent studies of seed dispersal in open landscapes such as grasslands and heathlands have reached a similar conclusion (Tackenberg, 2003; Soons *et al.*, 2004). Long-distance dispersal of seeds by wind thus requires organized eddies that are sufficiently long and energetic to lift seeds up high. Therefore, simulation of long-distance seed dispersal must properly describe these eddies. The strong vertical winds characterizing occasional intense events such as thunderstorms and more extreme events such as tornadoes and hurricanes may lift up seeds, including heavy seeds that do not possess any special adaptations for wind dispersal (Higgins *et al.*, 2003), resulting in long-distance dispersal

events. Future advances in the development of atmospheric models may resolve the challenge of modelling such weather events, thus providing the means to simulate extreme long-distance dispersal.

Lighter biological particles such as spores, pollen or pathogens may be passively transported in the atmosphere over thousands of kilometres (Campbell *et al.*, 1999; Brown & Hovmoller, 2002). Yet, the onset of such long journeys depends critically on the relatively infrequent occurrence of small-scale local gusts that are stronger than a certain threshold wind velocity required for launching a small particle from the land surface (Burrows, 1986; Aylor & Flesch, 2001). Spider ballooning provides one of the most fascinating examples of such long-distance aerial transport, which is also of practical importance as a result of the role of spiders as generalist predators of insect pests in agriculture. Spiders exhibit a specialized preballooning behaviour of climbing to a height, hanging suspended or raising their bodies ('tiptoeing'), then releasing a silk thread into the air to facilitate take-off. Spider launching was found to correlate with meteorological conditions of high turbulence, vertical updrafts and relatively weak horizontal winds (Suter, 1999; Thomas *et al.*, 2003).

Results from recent manipulative experiments indicate an important role for airflow in transporting aquatic invertebrates over relatively short distances (Brendonck & Riddoch, 1999; Caceres & Soluk, 2002; Cohen & Shurin, 2003). Detailed atmospheric models can help explain how their dispersal units launch from the surfaces of pools and ponds. The significance of wind as a long-distance dispersal vector for aquatic invertebrates has been questioned, mostly resulting from the seemingly inherent inefficiency of random deposition by wind, as compared to directed (targeted) dispersal by waterfowl and other animal vectors (Bilton *et al.*, 2001; Bohonak & Jenkins, 2003; Green & Figuerola, 2005). However, as explained in the next section, we suggest that wind-dispersed aquatic invertebrates may disproportionately deposit in suitable habitat patches (ponds) in forested landscapes as a result of organized turbulent flows. A detailed atmospheric model can also help evaluate this hypothesis.

While it is widely recognized that airflow profoundly affects migrating birds and insects, little is known about these effects. Large birds such as geese and ducks that are capable of powerful active flight exhibit small-scale changes in flight direction, probably resulting from turbulent fluctuations in wind direction, which increase the time of the migratory journey by up to 10% (Desholm, 2003). Frigate-birds are evidently capable of precisely tracking small-scale turbulent updrafts to ride up high in the boundary layer (up to 2.5 km above the ground) while searching for food resources with minimal energy expenditure (Weimerskirch *et al.*, 2003). A large-scale study using satellite-based tracking data of migrating raptors and wind data estimated by National Oceanic and Atmospheric Administration-Cooperative Institute for Research in Environmental Science (NOAA-CIRES) Climate Diagnostics Center revealed that juvenile birds are strongly drifted by crosswinds, while adults are able to compensate and reduce the drift to a third of that of juveniles (Thorup *et al.*, 2003). We emphasize, however, that the relatively coarse grid resolution applied in this study (2.5 latitude/longitude degrees) precludes conclusions on the role of the smaller scale fluctuations
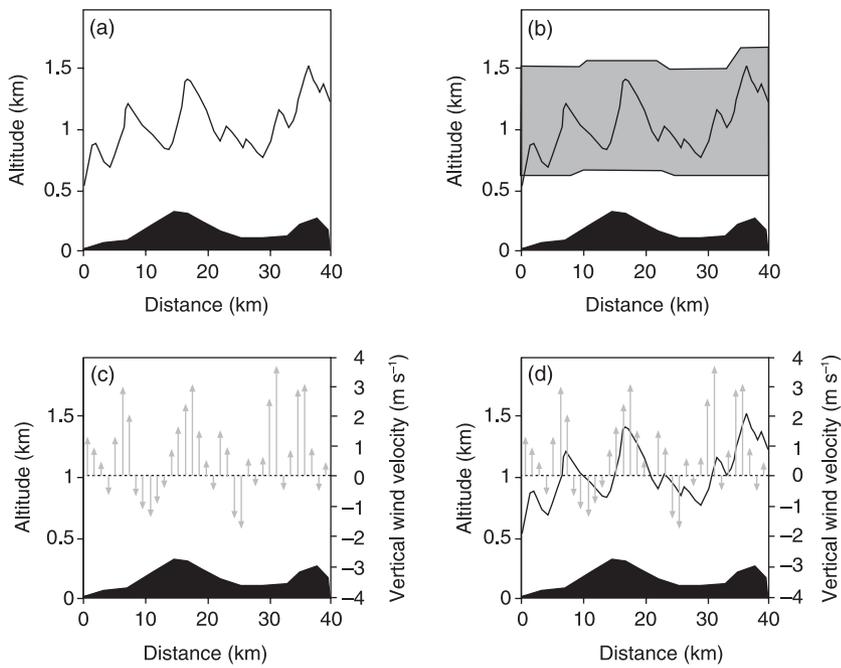
Figure 1 Bird flight can be measured these days in very high resolution (a; only vertical movements are shown, but horizontal movements can also be measured), and can be coarsely explained as spanning the region where thermals are present (b; e.g. Shamoun-Baranes *et al.*, 2003). Atmospheric models capable of simulating airflow in greater detail can provide more accurate information of airflow patterns in three dimensions (c; again, only vertical wind velocity is shown, but the two other components of wind velocity can also be calculated). Coupling this information with bird flight trajectories can promote our understanding on how birds respond to and possibly utilize the variation in airflow at various spatial and temporal scales (d). Filled area represents topography.

that directly affect the birds. Two other recent studies (Shannon *et al.*, 2002; Shamoun-Baranes *et al.*, 2003) used different types of atmospheric models and have related bird flight trajectories to coarse properties of atmospheric conditions (e.g. the depth of the vertical column where thermals are present). Rigorous assessment of bird migration in response to variation in atmospheric conditions necessitates modelling of wind flow patterns in much greater detail, to grasp the spatial scale at which the birds actually sense, and respond to, wind conditions. In Fig. 1, we hypothetically illustrate the merits of describing airflow patterns over complex terrain in finer details than those applied in these recent studies, for addressing questions of optimization of bird migration.

Effects of landscape heterogeneity on transport processes

A second major advantage of high-resolution atmospheric models for studying transport processes lies in their ability to incorporate small-scale landscape heterogeneity, which can strongly affect airflow patterns, and hence biological transport processes. As a result of the nonlinear nature of atmospheric flows, interactions between processes in small scales can propagate on, and even initiate, large-scale patterns. Recent LES studies revealed strong effects of small-scale landscape heterogeneity on air temperature (Albertson *et al.*, 2001), heat and moisture fluxes (Kustas & Albertson, 2003) and particle dispersion (Gopalakrishnan & Avissar, 2000). High-resolution atmospheric models are therefore particularly useful in studying transport processes in naturally patchy environments or anthropogenically fragmented habitats.

We demonstrate the importance of interactions between wind flows at different scales by LES simulation of the wind field in a small gap within a forested landscape during a hot day with strong (10 m/s) regional-scale winds (Fig. 2). In this example, the interaction between regional-scale winds and the small-scale structural change (the forest gap) amplifies turbulent eddy production within and around the gap. Consequently, although turbulence remains chaotic and unpredictable, zones where vertical turbulent eddies are significantly more frequent can be distinguished. The production of turbulent eddies is enhanced between the centre of the gap and the upwind forest edge, generating updrafts that are sufficiently strong to uplift a propagule (e.g. a plant seed or a ballooning spider) above the forest canopy (Fig. 2). The production of more energetic downdrafts at the opposing half of the gap can lead to disproportionate deposition of seeds and other airborne organisms into canopy gaps (Fig. 2). Although further LES simulation work should be done to develop a general rule governing the effects of gaps of different size under a range of environmental conditions, such gaps typically offer favourable light conditions for the establishment of various tropical tree species (Augspurger & Franson, 1988). Vernal pools within a forested landscape may generate gaps in the forest canopy and affect wind flow patterns in a similar manner. Therefore, they are likely to accumulate a disproportionate number of wind-dispersed aquatic invertebrates, as compared to nearby forested patches. Detailed atmospheric models thus provide the means to assess the hypotheses of non-random departure and arrival of wind-dispersed trees and aquatic invertebrates from and to suitable habitats in forested landscapes.

Landscape heterogeneity at larger scale can also affect transport processes. A recent RAMS study, for example, showed that regional scale (approximately 5–200 km) deforestation in the Amazon triggers the generation of thunderstorms and induces notable changes in local and regional precipitation patterns (Baidya Roy & Avissar, 2002). Thunderstorms may raise the scale
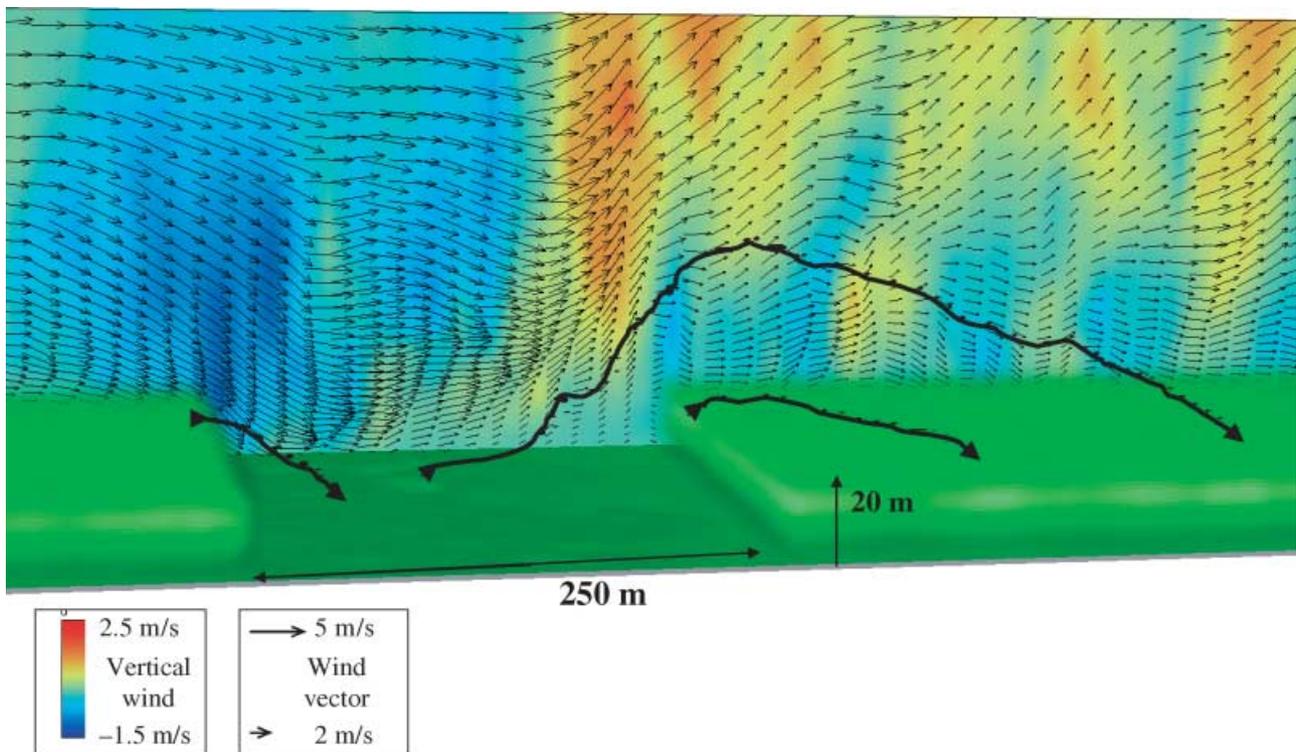
Figure 2 Large eddy simulation of a gap in a 20-m high mid-latitude forest during noontime in a cloudless day with strong western winds (10 m/s aloft, 3 m/s at the top of the canopy), illustrating enhanced production of eddies induced by structural change in the landscape. Arrows indicate the wind velocity vector; colour surface shows the velocity of the vertical wind component. The flight trajectories of three propagules (e.g. plant seeds or ballooning spiders), all with a terminal velocity of 1.0 m/s, are shown by thick lines with arrowheads indicating release and deposition points. The notable differences between the three sample flight trajectories demonstrate the critical role of small-scale turbulence generated by landscape heterogeneity in determining aerial transport processes. Indeed, a propagule could ride out of the picture if it caught a sequence of small-scale eddies leading to the region of frequent, strong updrafts on the right of the gap.

of influence of turbulent updrafts by several orders of magnitude. Detailed atmospheric models can also help elucidate the role of dispersal barriers in a landscape. Tree lines, buildings and other large objects are often considered barriers to wind dispersal of seeds and small animals, but effects of their size, structure and composition have not yet been quantified, and under certain conditions they may enhance dispersal rather than retard it.

THE WAY FORWARD

The findings discussed in this paper belong to diverse fields of research; they all imply that knowledge of turbulence, i.e. the deviations from the mean airflow, is important for unveiling biological transport processes. This approach contrasts with the strong motivation to define broadly applicable 'scaling rules', which would imply that the mean properties of a flow, which are relatively simple to measure, could be sufficient for understanding and predicting the biologically relevant characteristics of flow patterns (Raupach *et al.*, 1996). Yet, many biological transport processes are sensitive to short-term turbulent variability in airflow, which is obscured by averaging over long intervals that inappropriately smooth out the strong nonlinearity involved in transport mechanisms. The importance of deviations from the mean flow has

already been demonstrated for wind dispersal of seeds of forest trees and grassland forbs (Nathan *et al.*, 2002b; Soons *et al.*, 2004) and it is also increasingly recognized in studies of transport processes of abiotic particles through the sea and air (e.g. Namikas *et al.*, 2003).

Successful application of detailed atmospheric models can advance the study of biological transport processes in four main directions. First, it will provide new insights and better understanding of the mechanisms underlying these processes, and how they are affected by key environmental factors. It will provide the means to examine, for example, whether spiders select turbulent eddies with particular attributes, whether birds select their migratory flight paths in response to specific features of the environment that are associated with turbulent fluctuations (Pennycuick, 1998), why birds increase wing-beat frequency in headwinds and why and when they intersperse continuous wing-beat flapping with gliding phase (Cochran & Wikelski, 2004). Second, it can help quantify the basic features of many hard-to-track transport processes, such as frequency and magnitude of long-distance seed and insect dispersal (Nathan *et al.*, 2003). The diagnostic capability of these models should be evaluated. Then verified models could efficiently predict the outcome of long-distance transport. Third, better understanding of the mechanisms and improved quantification of patterns of transport will

resolve outstanding questions about the impact of aerial biological transport. Predictive transport models could help evaluate, for example, the role of extreme long-distance dispersal events in pathogen spread (Edmonds, 1979; Brown & Hovmoller, 2002), in regional species survival (Soons & Ozinga, 2005) and in shaping the genetic structure of populations in fragmented habitats (Trakhtenbrot *et al.*, 2005). Finally, detailed atmospheric models can help explore hypotheses about the evolution of traits for sensing and utilizing turbulence in order to optimize the cost-benefit balance of long-distance movements. Among the huge variety of traits involved with movement of organisms through the air (Edmonds, 1979; Vogel, 1981; Isard & Gage, 2001), which traits can be considered as those selected for sensing and utilizing turbulence? Candidate traits may include, for example, abscission tissues in seeds and spore capsules, aerodynamic structures of seeds, tipping behaviour of spiders and flexibility in switching flying modes (e.g. flight altitudes, wing-beat frequencies, wing-beat-to-gliding ratios) in migrating birds.

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