Do small spores disperse further than large spores?

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Abstract. In species that disperse by airborne propagules an inverse relationship is often assumed between propagule size and dispersal distance. However, for microscopic spores the evidence for the relationship remains ambiguous. Lagrangian stochastic dispersion models that have been successful in predicting seed dispersal appear to predict similar dispersal for all spore sizes up to ~40 µm diameter. However, these models have assumed that spore size affects only the downwards drift of particles due to gravitation and have largely omitted the highly size-sensitive deposition process to surfaces such as forest canopy. On the other hand, they have assumed that spores are certain to deposit when the air parcel carrying them touches the ground. Here, we supplement a Lagrangian stochastic dispersion model with a mechanistic deposition model parameterized by empirical deposition data for 1–10 µm spores. The inclusion of realistic deposition improved the ability of the model to predict empirical data on the dispersal of a wood-decay fungus (aerodynamic spore size 3.8 µm). Our model predicts that the dispersal of 1–10 µm spores is in fact highly sensitive to spore size, with 97–98% of 1 µm spores but only 12–58% of 10–µm spores dispersing beyond 2 km in the simulated range of wind and canopy conditions. Further, excluding the assumption of certain deposition at the ground greatly increased the expected dispersal distances throughout the studied spore size range. Our results suggest that by evolutionary adjustment of spore size, release height and timing of release, fungi and other organisms with microscopic spores can change the expected distribution of dispersal locations markedly. The complex interplay of wind and canopy conditions in determining deposition resulted in some counterintuitive predictions, such as that spores disperse furthest under intermediate wind, providing intriguing hypotheses to be tested empirically in future studies.

Key words: Basidiomycetes; boreal forest; deposition; Lagrangian stochastic models; species traits; wind dispersal.

INTRODUCTION

Knowledge of species’ dispersal rates is necessary for addressing a number of both basic and applied questions in population dynamics, nature conservation, and environmental risk assessment. Species-specific differences in dispersal ability influence which species spread, decline, or invade other ecosystems following anthropogenic changes in the environment. They also affect species coexistence and thus community-level phenomena such as succession (Hovestadt et al. 2000) and the diversity and stability of communities (Levine and Murrell 2003, Ives and Carpenter 2007).

In species that are dispersed passively as airborne propagules, atmospheric conditions dominate the movement process while the organisms can control only the aerodynamic properties of the propagules and when and where to produce them (Nathan et al. 2008). Considerable advances have been made in the past decade in the mechanistic modeling of airborne dispersal (Kuparinen 2006, Nathan et al. 2011). These models, particularly the complex and realistic Lagrangian stochastic dispersion models, have been very useful for studying the sensitivity of the dispersal process to factors of interest, including species traits (Soons et al. 2004, Schippers and Jongejans 2005, Bohrer et al. 2008, Wright et al. 2008, Savage et al. 2010, 2012, Nathan et al. 2011, Reynolds 2011).

For plant seeds, models have shown that the probability distribution of dispersal distances (dispersal kernel) is the result of a complex interplay between species traits, most importantly propagule settling velocity and release conditions, and external factors such as atmospheric conditions, topography and vegetation (Soons et al. 2004, Schippers and Jongejans 2005, Wright et al. 2008, Savage et al. 2010, Nathan et al. 2011). All else being equal, small seeds disperse further than large seeds due to their lower settling velocity and thus longer expected airborne time. The effect of settling velocity on seed dispersal kernels has been confirmed by empirical measurements (Jongejans and Telenius 2001, Muller-Landau et al. 2008).

For microscopic particles such as the spores of fungi, the effect of size is less clear. Settling velocity of particles...
below ~20 µm is proportional to the square of particle size according to Stokes’ law. However, when settling velocity is low enough, particle flight trajectories are almost completely dominated by the movements of the air. According to the Lagrangian stochastic dispersion model by Kuparinen et al. (2007), the dispersal kernel is no longer sensitive to settling velocity when it is small enough (below 0.04 m/s under the typical boreal forest conditions simulated by Kuparinen et al. (2007), corresponding to aerodynamic diameter below ~40 µm). As the downwards drift of particles through gravitational settling is the only size-dependent process in most Lagrangian stochastic dispersion models used so far, they predict that size does not matter in the dispersal of microscopic particles.

Air movement combined with the downwards drift through gravitation can be sufficient for describing the airborne transport of seeds, but for microscopic particles, the aerosol dynamic processes of deposition should also be considered (Seinfeld and Pandis 1998, Kuparinen 2006). Deposition is likely to be especially important when dispersal is initiated within dense vegetation such as a forest. So far, most Lagrangian stochastic dispersion models have accounted for deposition by simply assuming that once an air parcel containing particles reaches the ground, all particles within it land (Kuparinen et al. 2007, Bohrer et al. 2008, Reynolds 2011, Savage et al. 2012; but see Aylor and Flesch 2001). However, not all particles that are transported close to a surface will cross the boundary layer of quasi-laminar flow of air surrounding it. For particles in the 1–10 µm size range, transport across the boundary layer can occur through several mechanisms, including inertial impaction, interception, and gravitational settling—all of which are sensitive to particle size (Petroff et al. 2008a). The effect of particle size on deposition has been measured for nonliving particles in a number of aerosol physical studies (e.g., Rannik et al. 2000, Petroff et al. 2008a, Pryor et al. 2008), and several models have been formulated to describe the process (e.g., Lai 2005, Petroff et al. 2008b, Hussein et al. 2012). In a recent laboratory study we found a strong effect of spore size on the deposition rate of fungal spores, both through gravitational settling and other mechanisms (Hussein et al. 2013) (Fig. 1).

In this study, we supplement a Lagrangian stochastic dispersion model (essentially as in Kuparinen et al. 2007; henceforth called “Model LS”) with a mechanistic deposition model (Petroff et al. 2008b) fitted to empirical deposition data for 1–10 µm fungal spores (Hussein et al. 2013). We validate the Lagrangian stochastic dispersion model including deposition (henceforth called “Model LSD”) by comparing its predictions to independent empirical data on the dispersal of Phlebia centrifuga (see Plate 1), a corticioid wood-decay fungus with an aerodynamic spore size of 3.8 µm (Norros et al. 2012). We compare the fit of Model LSD to that of Model LS and two semi-empirical models (quasi-mechanistic following the classification of Kuparinen [2006]) used in Norros et al. (2012). Furthermore, we compare scenario simulations of Models LSD and LS to investigate how deposition affects the dispersal of 1–10 um spores released within a forest. More specifically, we assess how spore size affects the dispersal kernel and the height at which spores are expected to deposit, and how the effect of size is influenced by atmospheric conditions, spore release height and canopy type.

**Material and Methods**

Implementing deposition in a Lagrangian stochastic dispersion model

To account for deposition on canopy foliage and ground vegetation, we adopted the model developed by Petroff et al. (2008b), as it includes inertial impaction, interception, and gravitational settling, which are the most relevant particle deposition mechanisms for the studied size range (1–10 µm). Furthermore, the model requires few and simple input parameters. To obtain a realistic parameterization of particle collection in a forest, we estimated the characteristic needle dimension $d_{n}$ from experimental laboratory data on the deposition of fungal spores to spruce needles (Hussein et al. 2013) (Fig. 1). To assess the sensitivity of predictions to the adopted $d_{n}$, we used three different $d_{n}$ values in the dispersal simulations (3.2, 2.0, and 4.6 µm), corresponding to the parameter estimates obtained for different subsets of the deposition data. More details on the deposition model and its fit to the laboratory data are given in Appendix A.

Lagrangian stochastic dispersion models describe the diffusion of particles (here spores) by a stochastic differential equation that determines the particle trajectory in space and time as the sum of deterministic drift and random terms. For the drift term we used the

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**Fig. 1.** The effect of spore size on deposition. The green dots and line show deposition velocity on spruce needles under flow speed 3.2 m/s as a function of spore size, as measured in a laboratory experiment and predicted by the model of Petroff et al. (2008b). For comparison, we show the gravitational settling velocity of spores as measured (black dots) and predicted by Stokes’ law (black line), and the deposition velocity of spores on a metal mesh (blue points; the blue line shows a regression model fitted to the points). The data are from Hussein et al. (2013) and represent almost exclusively fungal spores.
stationary turbulence model by Thomson (1987). The model was parameterized with Gaussian turbulence both within and above the canopy. Two different leaf-area distributions were considered to represent spruce and pine forests (Appendix A). The leaf-area distributions define the vertical profiles of turbulence statistics within the canopy according to the model by Massman and Weil (1999). For above the canopy we assumed neutral atmospheric boundary layer (ABL) parameterizations for horizontal wind speed and dissipation rate of turbulent kinetic energy. The vertical profiles of wind variances and momentum flux were assumed to decay with height inside the ABL according to a commonly used parameterization (Stull 1988).

We simulated the flight trajectories of air parcels containing particles, and particle deposition was treated as a probabilistic absorption process according to Kurbanmuradov et al. (2001). When the air parcel passed a medium with surface elements either in the canopy or at the forest floor, some portion of the contained particles deposited according to the deposition submodel and the particle concentration within the air parcel decreased correspondingly. In the canopy, we assumed randomly oriented needles with the surface area density given by the assumed vertical distribution. Deposition to the ground was modeled by including a horizontal surface with unit area at height interval 0–0.01 m and a vegetation layer with randomly oriented needles at 0.01–0.02 m (ground vegetation; Appendix A: Table A1), where h is the assumed canopy height.

To compare predicted dispersal with and without realistic deposition, we used the same model with the deposition submodel (Model LSD) and without it (Model LS). In Model LS we assumed complete particle absorption when an air parcel intersected with the forest floor but no deposition to canopy (as in Kuparinen et al. [2007]). After model validation (described in the next section), we used Models LSD and LS to simulate the dispersal of 1-μm, 3.8-μm and 10-μm particles under different scenarios of wind conditions (friction velocity \(u^* = 0.2\) or 0.5 or 1.5 \(m/s\)), spore release height (0.02 h or 0.75 h) and canopy type (spruce or pine). In the parameterization of turbulent statistics, friction velocity determined both the average wind speed and the variances of wind speed components, which were proportional to friction velocity. For more details on the model and the calculation of the dispersal kernel from the simulations, see Appendix A. The C language and MATLAB (MathWorks, Natick, Massachusetts, USA) codes used for the model simulations are provided as Supplement 1.

**Model validation and comparison**

To examine the performance of Models LSD and LS we used a set of measurements of the dispersal of the corticoid wood-decay fungus *Phlebia centrifuga* (see Plate 1; spore aerodynamic diameter 3.8 μm) (Norros et al. 2012). The data consist of seven dispersal experiments conducted at mature forest sites dominated by spruce (experiments 1–6) or pine (experiment 7) (Appendix B).

The data were collected using species-specific mycelial spore traps (Adams et al. 1984, Williams and Todd 1984) that detect viable spores, allowing distinction between occupied and unoccupied traps but not the quantification of the number of spores in occupied traps. Thus, the raw data are numbers of occupied and unoccupied traps for each sampling location and time. Spore trapping was carried out over a period of 5–24 hours in each experiment, up to 1000 m around a single spore source, a group of spore-producing fruit bodies of *Phlebia centrifuga*. Horizontal wind speed and direction were monitored with at least 1-min resolution at the source. The spore production rate of the fruit bodies was sampled at 1–3 hour intervals.

We simulated the dispersal of *P. centrifuga* spores under the conditions observed during the experiments assuming hourly varying spore production rates calculated from the spore-production measurements. Friction velocities (\(u^*\)) above canopy were deduced by matching the measured and modeled wind speeds at the measuring heights. Leaf-area profiles were obtained by combining the spruce and pine profiles according to the approximate proportions of the tree species at the study sites and estimates of their total leaf-area index. We used four of the seven experiments in Norros et al. (2012) in this study (experiments 1, 3, 4, and 7), including a total of 8024 individual traps (most typically 25 but up to 100 at a single trapping point) out of which 3268 became occupied.

To account for possible biases in the spore-production estimates, as well as for the fact that only viable spores were detected by our trapping method, we multiplied the predicted spore rain (i.e., the number of deposited spores per unit area and time) by an experiment-specific level correction parameter \(f_i\) where \(i\) indicates the experiment number. The resulting four \(f_i\) parameters were estimated using a Bayesian Markov chain Monte Carlo approach (as in Norros et al. [2012] but omitting background spore rain and overdispersion in the data model; see the section “Connecting the LSD and LS models to *P. centrifuga* dispersal data” in Appendix A for details). The deviance from 1 of the estimated values of the \(f_i\) parameters can be interpreted as a measure of how well the overall level of spore rain could be predicted from first principles, including the (unrealistic) assumption of 100% viability and mating compatibility. The Mathematica (Wolfram Research, Champlain, Illinois, USA) code used for model fitting is provided as Supplement 2.

To compare the predictive power of the mechanistic models with semi-empirical models, we re-fitted the power law (Model L) and diffusion (Model D) models used in Norros et al. (2012) using exactly the same data as for Models LS and LSD, and omitting background deposition and overdispersion. Note that while the
parameterizations of Models LSD and LS were independent of the spore-trapping data (except for the level parameter \( f_i \)), all parameters of Models L and D were fitted to those data.

We assessed model fits based on the Bayesian information criterion (BIC; Schwarz 1978) and by visual examination of the patterns in the residuals. To compare the predictive power of the mechanistic and semimechanistic models, we also tested the ability of Models L and D fitted to a part of the data (denoted \( y_1 \)) to predict the rest of the data (denoted \( y_2 \)). Here, we estimated the shape parameters (those describing the distance and wind dependency of deposition around the source) based on \( y_1 \) and then fixed them to the obtained posterior median values. The models with the fixed shape parameters are denoted by \( \text{L} \mid y_1 \) and \( \text{D} \mid y_1 \). We then fitted \( \text{L} \mid y_1 \) and \( \text{D} \mid y_1 \) to \( y_2 \) by estimating only the experiment-specific level parameters (those describing the overall level of deposition around the source, similar to \( f_i \)) and compared the resulting model fit to that obtained with the mechanistic models using BIC and the patterns in the residuals. We used posterior medians instead of the complete posteriors for better comparability with the mechanistic models in which no uncertainty in the process model parameters was included.

**RESULTS**

Model LSD (a Langrangian stochastic dispersion model (Model LS) with mechanistic deposition) with the fitted level parameters \( f_i \) was able to reproduce the overall pattern of the measured dispersal data, and the inclusion of the deposition submodel improved model fit (Fig. 2; Appendix B). Both Models LSD and LS underestimated spore rain at the first 7 m and underestimated it further away, especially at 7–55 m, but the bias was stronger in Model LS. The accuracy of the predictions of Model LSD improved towards higher wind speeds and larger angles between the trapping transect and the wind direction (Fig. 2B). The observed level of colonization was generally higher than predicted by Model LSD (posterior median values of the level
correction parameter $f_1 = 18.2$, $f_3 = 2.91$, $f_4 = 3.62$, $f_7 = 0.603$; Appendix B), but lower than predicted by Model LS ($f_1 = 0.150$, $f_3 = 0.057$, $f_4 = 0.048$, $f_7 = 0.005$). The ability of Model LSD to predict the measured data was not sensitive to the deposition model parameterization (Appendix B).

Both semi-empirical models used by Norros et al. (2012) and especially the diffusion model D reproduced the data better than Model LSD (Fig. 2; Appendix B). Model LSD performed as well or better than the semi-empirical models only when the angle between the trapping transect and the wind direction was larger than $67.5^\circ$. When fitted to experiments 4 and 7, both semi-empirical models predicted experiments 1 and 3 better than Model LSD (maximum log likelihood $C_0 = 303$, $C_0 = 414$, and $C_0 = 601$ for Models D, L, and LSD, respectively; Appendix B). However, data incorporating different wind conditions was needed for the parameterization of the semi-empirical models. Without including experiment 7, in which the wind was faster and less variable in direction, no combination of experiments 1, 3, and 4 enabled the successful identification of the parameter values (Appendix B).

The inclusion of the deposition submodel dramatically altered the sensitivity to spore size of the predicted dispersal kernel (Fig. 3). While Model LS predicted almost identical dispersal distances for 1-µm, 3.8-µm and 10-µm spores, Model LSD predicted an order-of-magnitude difference between the different sizes. Due to their higher deposition velocity and thus higher probability of deposition, larger spores tend to get stuck closer to the source and have shorter expected dispersal distance. At the simulated range, the difference was obvious in the level of the kernel, i.e., the proportion of spores dispersing to a given distance, whereas the shape of the kernel was very similar for all spore sizes (Fig. 3). The predictions of Model LSD were generally not sensitive to the deposition model parameterization (Appendix B).

For both Lagrangian stochastic dispersion models, the proportion of spores that was lifted above the forest canopy was a fair indicator for the proportion of spores that disperse beyond the simulated range (2 km when the assumed canopy height was 20 m) (Fig. 3). In the case of a low release height, Model LS (with certain deposition if reaching the ground) predicted a low probability of escaping the canopy, whereas Model LSD (with a more realistic deposition model) predicted that especially the smallest spores are very likely to be lifted above the canopy and thus reach a long dispersal distance (Fig. 3). With realistic deposition, the probability of long-distance dispersal was predicted to be high regardless of release height, while according to Model LS long-distance dispersal is very sensitive to release height (Fig. 3). Model LSD predicted that the effect of release height is the greatest, though still not dramatic, for the largest particles.

Perhaps surprisingly, Model LSD predicted a non-monotonic relationship between dispersal distance and wind speed and turbulence (as described by $u^*$) for the larger spore sizes (Fig. 3). The probability of long-distance dispersal increased for 3.8-µm and 10-µm spores when $u^*$ increased from 0.2 to 0.5 m/s but decreased when $u^*$ increased further to 1.5 m/s. In fact,
FIG. 3. Comparison of the dispersal kernels and deposition profiles predicted by Models LSD and LS (with and without a realistic deposition submodel, respectively) under different wind and release-height scenarios. The dispersal kernels are shown in cumulative form. The deposition profiles show the distribution of deposition heights among those spores that deposited to the canopy as opposed to the ground; they are omitted for Model LS as it only describes deposition to the ground. The deposition profiles are shown in differential form, i.e., as a density function that integrates to 1. The horizontal dashed line in the deposition profile plots shows the height of spore release. For each scenario, we show also the proportion of spores that were lifted above the canopy at least once, the proportion of spores that deposited within the simulated domain (<2 km from source), and the proportion of spores that deposited on the ground out of all deposited spores. The different colors correspond to different aerodynamic spore sizes ($D_a$). Blue, $D_a = 1 \mu$m; green, $D_a = 3.8 \mu$m; red, $D_a = 10 \mu$m. All scenarios assume a spruce canopy of 20 m height but differ in the assumed friction velocity ($u^*$) and release height ($h_0$). (A) and (B) $u^* = 0.5$ m/s, $h_0 = 0.4$ m. (C) $u^* = 0.2$ m/s, $h_0 = 0.4$ m. (D) $u^* = 0.5$ m/s, $h_0 = 15$ m. (E) $u^* = 1.5$ m/s, $h_0 = 0.4$ m. (F) $u^* = 0.5$ m/s, $h_0 = 15$ m.

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10-μm spores had a higher probability of long-distance dispersal under the lowest than the highest \( \mu^* \). For the smallest spores, probability of long-distance dispersal always increased with \( \mu^* \), but only very slightly.

Wind speed and turbulence (\( \mu^* \)) as well as spore size were the most important determinants of the height at which spores deposited in the canopy as predicted by Model LSD (Fig. 3). Under low \( \mu^* \), spores deposited more in the lower parts of the canopy, the largest spores the lowest. Conversely, under higher \( \mu^* \), the larger spores deposited higher than the smallest spores, while overall the differences between spore sizes were less prominent. The deposition profile of the smallest spores was remarkably robust to wind and release conditions. Release height had only a small effect on the deposition profile within the canopy, except for a small local peak in deposition around the release height. Deposition to the ground instead of the canopy decreased with increasing wind speed and turbulence, and generally increased with spore size.

The results described above were obtained assuming dispersal in a spruce forest. The overall patterns in the results concerning dispersal distances were similar for pine canopies, whereas the deposition profiles were clearly different (Appendix B), following the different leaf area density distributions assumed for the two canopy types (Appendix A). Further, the deposition profiles for pine were not as sensitive to wind conditions as those for spruce. Interestingly, Model LSD predicted a slightly smaller probability of long-distance dispersal in pine than in spruce canopies, although the assumed total leaf area was larger for the spruce canopy.

**Discussion**

In most previous Lagrangian stochastic dispersion models (e.g., Kuparinen et al. 2007, Bohrer et al. 2008, Reynolds 2011, Savage et al. 2012; but see Aylor and Flesch 2001), propagule size has been assumed to affect dispersal only through gravitational downwards drift, resulting in similar dispersal for all small propagules (Kuparinen et al. 2007). In our present study we have shown that including a realistic description of the deposition process makes a major difference. Deposition is very sensitive to particle size, especially in the studied 1–10 μm range, with larger particles having a higher probability of deposition when they encounter a surface (Fig. 1). As a result, large spores tend to deposit closer to the source than do small spores. Further, including realistic deposition means that spores do not necessarily deposit when the air parcel carrying them touches the ground, resulting in increased dispersal distances for all spore sizes in the 1–10 μm range. According to our predictions, the dispersiveness of especially the smallest spores is so high that landing may in fact be a bigger challenge for them than flying.

While Model LSD (the Lagrangian stochastic dispersion model including deposition) predicted that small spores disperse further, the predicted slope of the dispersal kernel at log-log scales was not visibly size dependent at the simulated distance range. There are only a few published empirical studies that have measured the dispersal of different-sized spores simultaneously (Stepanov 1935, Sreeramulu and Ramalingam 1961, Gregory 1973 citing Stepanov [1962], Sundberg 2005). In agreement with our predictions, in these studies the slope of the dispersal kernel was similar for species with different-sized spores, but a greater proportion of the larger spores deposited within the monitored range. To be useful in model validation, future empirical studies of the dispersal of small spores should especially strive to quantify out of all released spores the proportion of spores that reach a given distance.

Including deposition affected the predicted sensitivity of dispersal distances to other factors, too. The effect of spore release height became much less dramatic when a realistic deposition model was included, suggesting that the sensitivity of airborne dispersal to release height may be less severe for small propagules than for large propagules such as plant seeds (Soons et al. 2004, Gomez 2007, Nathan et al. 2011). The reason is probably the relatively weak deposition of small spores, which means that they are not deposited immediately around the release point but have sufficient airborne time and distance to spread throughout the canopy.

Some of the predictions of Model LSD are not immediately intuitive. Intermediate wind speed and turbulence led to a higher probability of long-distance dispersal of 3.8-μm and 10-μm spores than higher wind speed and turbulence. Further, a higher proportion of spores escaped the spruce than the pine canopy even though the total leaf area of the spruce canopy was higher. These results arise from the interaction of wind speed and canopy density on deposition. Increasing wind speed increases deposition rate more than linearly and differently for different spore sizes (Appendix A); at the same time, wind speed linearly decreases the residence time of an air parcel within a section of the canopy. Thus, while higher wind speed transports spores faster to long distances and higher turbulence tends to lift spores above the canopy, these effects are countered by the nonlinear increase in deposition rate. In the pine canopy the leaf area is concentrated higher than in the spruce canopy, where faster wind promotes deposition. Concentration of foliage in the upper part of the canopy also results in the absorption of momentum there and lower turbulence intensity within the canopy, increasing the residence time of flight trajectories in the canopy. Even though these results remain hypotheses that should be confirmed empirically, they illustrate the value of mechanistic modeling in studying the dispersal of small propagules that interact with their environment in complex and sometimes surprising ways.

Gilbert (2005) measured patterns in the density of fungal spores in the air in a tropical forest and found that spores were much more abundant in the understory than
higher in the canopy. It is interesting to note that our Model LSD produced such a distribution of deposition heights for 10-μm spores under low turbulence. Given sufficient documentation of spore sizes and wind conditions, such data could be used to validate the deposition profiles predicted by this or other dispersal models. As our results agree with previous findings that uplifting above the canopy is a good surrogate for long-distance dispersal (Nathan et al. 2002), data on the vertical distribution of spores in the air could also be used to estimate the otherwise-elusive long-distance dispersal.

Reynolds (2011) and Savage et al. (2012) found that the atmospheric conditions at the time of spore release greatly affect the dispersal kernel of plant pathogenic fungi as predicted by Lagrangian stochastic dispersion models. In our study, including realistic deposition made the dispersal kernel perhaps surprisingly robust to different wind and canopy scenarios, particularly for the smallest spores. However, our results still suggest that by adjusting spore size, release height, and the timing of spore release, fungi and other organisms with microscopic spores can change the expected distribution of dispersal locations drastically, giving the species some navigation capacity in the evolutionary sense (Nathan et al. 2008). Small spores disperse the furthest; large spores deposit low in the canopy when produced under low wind speed and turbulence, but high in the canopy when produced under high wind speed and turbulence. Deposition height could be of consequence, e.g., for wood-decay fungi that infect living trees through wounds in the branches.

Although Model LSD was better than Model LS (the Lagrangian stochastic dispersion model, as in Kuparinen et al. 2007) in predicting the dispersal data of Norros et al. 2012, the fit was clearly not perfect. Further, these models did not succeed in predicting from first principles the overall level of deposition to the spore traps. Although the level predicted by Model LSD was closer, the discrepancy was still great, especially for experiment 1. It is difficult to assess whether the discrepancy was caused by structural shortcomings of the model (description of deposition mechanisms, turbulence structure and canopy geometry), by inaccurate parameter values, or by biased estimates of the spore production rate. The contrasting level of the correction parameter values obtained for experiment 7, in which a different method was used to monitor spore production, suggests that biased spore-production estimates are at least a part of the story. Both empirical models (L and D) used by Norros et al. 2012 performed better than the mechanistic models (LS and LSD), even when model parameterization was based on an independent part of the data. However, this is not surprising since, unlike the mechanistic models, the empirical models are essentially statistical fits to the data, and thus good at predicting similar data but less reliable for making predictions for new conditions (Kuparinen 2006). To improve the fit with empirical data, Model LSD could be improved in several ways (see Appendix A, section “Areas for improvement in Model LSD”). However, we find that the lack of sufficiently large and controlled data sets currently limits our understanding of the dispersal of small spores more critically than does the shortcomings of modeling techniques.

Previous studies have found that size matters for active dispersal (Jenkins et al. 2007) and through settling velocity, also for the dispersal of plant seeds, although other traits than size are also important in determining seed settling velocity (e.g., Skarpaas et al. 2011). In this paper we have shown that aerodynamic size is likely to be important also for the smallest propagules. Our results are in agreement with the idea of microscopic organisms as potentially stupendously efficient dispersers (Finlay 2002, Wilkinson et al. 2012). However, it should be borne in mind that the transport of spores does not equal colonization. Mortality during dispersal, e.g., due to sensitivity to solar radiation, can place limits to effective dispersal distances (Rotem et al. 1985, Bonte et al. 2012). Furthermore, as the number of spores deposited per unit area is strongly distance dependent even for small spores, colonization can be much more likely near the source if the establishment probability of individual spores is low. This seems to be the case at least in some specialist wood-decay fungi (Norros et al. 2012). Thus, while long-distance transport is probably common in species with small spores, dispersal may still limit their occurrence. Jenkins et al. 2007 did not find a general relationship between propagule size and dispersal distance in passive dispersers. Apart from the sparseness of data for small spores, one likely reason for this result is that species-specific differences in establishment probability as well as other factors affecting dispersal (e.g., typical wind conditions at the time of spore release) can mask the effect of spore size (Soons et al. 2004, Wright et al. 2008, Skarpaas et al. 2011). Another point is that while we have assumed that spores appear directly into dispersive airflow, real species rely on a variety of mechanisms for launching their spores into the air (Gregory 1973). Spore size is likely to play a role in most of these mechanisms and could make the relationship between spore size and dispersal more complex.

Our main finding is that the dispersal distances of small spores are larger and less sensitive to environmental conditions than those of large spores. From the evolutionary point of view, this indicates that there are likely to be correlations and trade-offs between dispersal and other size-related life-history traits such as fecundity and mortality (Jakobsson and Eriksson 2003, Bruun and ten Brink 2008, Kauserud et al. 2008, 2011, Muller-Landau et al. 2008). For relatively well-known groups such as basidiomycete fungi, analysing the relationships between spore size, other morphological traits, and ecological features among species and larger groups could give interesting insight into their ecology and evolution. For instance, do fungi that infect trees
through wounds in the canopy produce spores predominantly under high turbulence, when most spores are expected to deposit high in the canopy? Many wood-decay fungi are characterized by very small spores (down to 1 μm; Parmasto and Parmasto 1992, Fischer et al. 2010). One evolutionary factor behind this could be that small spore size is beneficial in species occurring in forests where the deposition to the canopy makes dispersal especially size sensitive.

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LITERATURE CITED


Supplemental Material

Appendix A
Details of the deposition and dispersal modeling and model fitting (Ecological Archives E095-140-A1).

Appendix B
The design of the dispersal experiments, plus supplementary result tables and figures (Ecological Archives E095-140-A2).

Supplement 1
C and MATLAB code used for the model simulations (Ecological Archives E095-140-S1).

Supplement 2
Mathematica code used for model validation (Ecological Archives E095-140-S2).