Species resistance and community response to wind disturbance regimes in northern temperate forests

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Summary

1 Severe winds are the predominant cause of natural disturbance in temperate forests of north-eastern and north-central North America. Conceptual models of the effects of wind disturbance have traditionally focused on the impacts of catastrophic disturbances and have painted a simple picture of how disturbance acts to maintain tree species diversity. These models ignore variation among species characteristics that could have important consequences for both resistance to and recovery from disturbance.

2 We integrated an empirically parameterized, mechanistic model of windstorm mortality (WINDSTORM) and a seed-mass-based dispersal and recruitment model into a spatially explicit, individual tree model of forest dynamics (SORTIE) in order to create simulated long-term 'experiments' designed to explore the sensitivity of forest composition and structure to species-specific resistance to and recovery from disturbance.

3 We found that species-specific variation in resistance to wind mortality interacted strongly with: (i) shade tolerance characteristics, (ii) the medium-term history of disturbances, (iii) the long-term average severity of the disturbance regime and (iv) seedbed substrate dynamics to influence tree population dynamics and successional trajectories.

4 We also examined how local and long-distance dispersal affect response to wind disturbance. Ignoring differences among local dispersal characteristics overestimates the importance of dispersal-limited species. Our results show that long-distance immigration maintains species coexistence only if the immigration rate is very high relative to local dispersal. Despite this, stand-scale models that ignore long-distance dispersal can underestimate population dynamics of dispersal-limited species.

5 Our results indicate that landscape-scale heterogeneity in structure and species composition in these forests is facilitated by synergisms between the stochastic nature of wind disturbance and complex interactions between species traits that govern: (i) resistance to disturbance, (ii) local dispersal and seedling establishment and (iii) competitive (i.e. growth/survival) traits that do not adhere to strict tradeoffs.

6 We conclude that wind disturbance has much more complex and variable effects on long-term dynamics of forest structure and composition than suggested by previous models. In particular, non-catastrophic disturbances can generate important variation in forest dynamics that can either lead to dominance by a single or small number of species, or facilitate species coexistence.

Key-words: community dynamics, competition, disturbance, forerst ecology, local and long-distance seed dispersal, resistance to disturbance, seedling establishment, simulation model, succession, wind disturbance.

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Introduction

Disturbance is a major force influencing the species composition and structure of ecosystems throughout the world (Pickett & White 1985). Disturbances (particularly catastrophic disturbances) promote diversity

at the landscape scale by maintaining populations of shade-intolerant and early-successional species (Loucks 1970; Bormann & Likens 1979). The effects of natural disturbances can be difficult to characterize, however, because disturbances operate over such a wide range of spatial and temporal scales. Historically, disturbance theory has relied on two key concepts, resistance to disturbance and community resilience after disturbance, to describe how ecosystems react to and recover from disturbances (e.g. Attiwill 1994). These concepts are difficult to quantify because, among many other reasons, they require specification of a reference, predisturbance or equilibrial condition. Recently, however, empirical approaches have been developed that allow us to estimate directly the species-specific resistance of trees to disturbance as a function of disturbance severity (e.g. Canham *et al*. 2001). Together with the development of spatially explicit, individual-based forest simulation models (e.g. Pacala *et al*. 1996), we can directly explore the consequences of key processes that determine community susceptibility to and recovery from disturbance.

Severe winds are the predominant cause of natural disturbance in temperate forests of north-eastern and north-central North America (e.g. Lorimer 1977; Canham & Loucks 1984; Frelich & Lorimer 1991b). Both theoretical and empirical studies of wind disturbance in temperate forests have generally focused on the effects of catastrophic storms (e.g. Loucks 1970; Lorimer 1977; Bormann & Likens 1979; Canham & Loucks 1984) that create a landscape-scale mosaic of patches of various sizes and ages (Canham & Loucks 1984) in which the species composition of each patch is assumed to be largely a result of successional processes (e.g. Loucks 1970). In effect, these studies assume that catastrophic wind disturbances simply reset stands to an earlier successional stage.

Non-catastrophic disturbances may also have important, underappreciated ecological consequences. The susceptibility of canopy trees to damage or death as a result of severe winds varies as a function of species, size, and a host of other individual traits and site-specific factors (e.g. Foster & Boose 1992; Canham *et al*. 2001). Catastrophic disturbances overwhelm the abilities of trees to resist disturbance, rendering differences among species moot. In the far more frequent non-catastrophic storms, however, variation in resistance to disturbance among trees has a profound effect on both the immediate and the long-term effects of any given storm, and may have pervasive impacts on forest composition and structure, at both the stand and the landscape scales (e.g. Lorimer & Frelich 1989; Frelich & Lorimer 1991a; Foster & Boose 1992; Canham *et al*. 2001). Despite awareness that species composition influences the severity of the effect of a given storm, there has been little explicit consideration of species-specific differences in resistance to disturbance as a factor in determining post-disturbance community development.

Post-disturbance colonization is also strongly dependent on differences among species in local and long-distance dispersal, and subsequent seedling establishment (i.e. recruitment). Highly localized dispersal patterns are an important feature of seedling recruitment patterns in forest trees (Janzen 1970; Connell 1971; Ribbens *et al*. 1994) and many theoretical studies have shown the importance of dispersal for finding suitable germination and establishment substrates (Levin *et al*. 2003; Levine & Murrell 2003). Windthrows create gaps that increase light and free other resources for understorey tree and seedling growth (Mladenoff 1987; Canham *et al*. 1990). As they decay, fallen trees become a favourable seedbed germination substrate for small-seeded species such as yellow birch (*Betula alleghaniensis* Britton) and hemlock (*Tsuga canadensis* L.) moreso than larger seeded species (Godman & Lancaster 1990; Peterson & Pickett 1995; McGee 2001). These pulses of rotting coarse woody debris (CWD) combined with higher understorey light levels in large windthrow gaps (Peterson & Pickett 1995) could have long-term impacts on subsequent community dynamics.

Long-distance dispersal (LDD) also presumably plays an important role in post-disturbance colonization. The importance of long-distance dispersal is clear in studies of island colonization and in the reconstruction of post-glacial plant migrations (e.g. Clark 1998; Higgins & Richardson 1999; Cain *et al*. 2000). Recent studies have shown that our ability to predict the effects of climate change critically depends on high-quality information and on models of long-distance dispersal (Cain *et al*. 2000). Historically, diffusion spread models have underestimated spread rates (e.g. Weinberger 1982), in part because they assumed that the spread rate was constant and exponentially bounded (Weinberger 1982). Current empirical approaches to estimating LDD have made progress in approximating the spread of populations, but have proved sensitive to assumptions of constant mean reproductive rates and the proportion of seeds that disperse long distances (Clark *et al*. 2001). Thus, the importance of long-distance dispersal for community dynamics following wind disturbance remains an open question.

In the absence of suitable long-term empirical studies, models parameterized using field data can be used to improve our understanding of how natural ecosystems function (Levin *et al*. 2003; Levine & Murrell 2003); they are a powerful alternative to purely empirical studies (Pacala *et al*. 1996); they can bridge the gap between the theoretical and empirical literature (Levine & Murrell 2003); and they can be used to choose between alternative hypotheses generated by different theories (DeAngelis & Mooij 2003). In this paper, we use SORTIE (Pacala *et al*. 1996), a spatially explicit model of forest dynamics, to undertake long-term, simulation 'experiments' to explore the sensitivity of forest composition and structure, to the resistance of individual trees to wind disturbance and the roles of local and long-distance

dispersal and seedling establishment in community recovery. Specifically, we address five questions:

1 How does variation in the severity of a wind disturbance regime affect long-term patterns of composition, structure and diversity of canopy tree species?

2 How important is species-specific resistance to windthrow for patterns of relative abundance and diversity in forests subject to storms with a broad range of severity?

3 How does variation among species in local dispersal of seeds affect patterns of relative abundance and species coexistence in forests subject to recurrent wind disturbance?

4 Are forest composition and structure sensitive to species-specific responses to and spatial and temporal variation in recruitment opportunities (particularly seedbed substrates) created by wind disturbance?

5 How important is long-distance dispersal for patterns of succession and tree species diversity in forests subject to wind disturbance?

Methods

ADAPTING SORTIE TO THE STUDY OF WIND DISTURBANCE

SORTIE is a spatially explicit, individual-based forest simulator that forecasts long-term changes in the abundance and spatial distribution of tree species as a function of the competitive dynamics of individuals in a stand (Pacala *et al*. 1996). Each of the component models of SORTIE, which include light (Canham *et al*. 1994), growth (Canham *et al*. 1994; Pacala *et al*. 1994), mortality (Kobe *et al*. 1995), fecundity and local dispersal (Ribbens *et al*. 1994), have been empirically parameterized and validated. SORTIE has been parameterized for three regions where wind is a major natural disturbance agent: the transition oak – northern hardwood forests of the north-eastern USA (Canham *et al*. 1994; Pacala *et al*. 1994; Ribbens *et al*. 1994; Kobe *et al*. 1995), the interior cedar–hemlock forests of north-western British Columbia, Canada (Kobe & Coates 1997; Wright *et al*. 1998; Canham *et al*. 1999; LePage *et al*. 2000), and the tropical forests of the Luquillo Mountains of Puerto Rico (Uriarte *et al*. 2004, 2005).

For the purposes of the present study, we focus our simulations on the transition oak – northern hardwood forests where SORTIE was originally developed (Pacala *et al*. 1996). There are a variety of forest types in this region, with a transition from oak-dominated forests on the drier and more southern and eastern sites, to northern hardwood species on more mesic and northern sites. The six species used in our simulations include the most common northern hardwood species found in mid- and late-successional stands across the region. The species are (in approximate decreasing order of shade tolerance; Kobe *et al*. 1995): American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* L.), yellow birch (*Betula alleghaniensis*

Britton), sugar maple (*Acer saccharum* Marsh), red maple (*A. rubrum* L.) and black cherry (*Prunus serotina* Ehrh).

None of the previous studies using SORTIE has explicitly considered the role of canopy disturbance. Incorporating disturbance in the model required that we develop two new submodels and we adopt a new approach for estimating fecundity. First, we have developed a wind disturbance submodel, WINDSTORM, which is based on our previous work (Canham *et al*. 2001) to parameterize species-specific functions for the susceptibility of canopy trees to windthrow as a function of tree size and storm severity. The submodel also allows us to specify the characteristics of the regional, long-term disturbance regime. Second, we have incorporated a new submodel for the dynamics of seedbed substrates (Papaik *et al*. 2005) that allows us to track the effects of windstorms on the availability of tip-up mounds and rotted logs as substrates for seedling establishment. Third, we are using an alternative approach to estimating seedling establishment to that developed by Ribbens *et al*. (1994). This approach is based on work by Greene & Johnson (1994, 1998), and uses seed mass as a basis for estimating fecundity and substrate-dependent seedling establishment. These additions to SORTIE allow us to explore how species-specific variation in: (i) resistance to a wide range of windstorm severity, and (ii) dispersal characteristics (both local and long-distance) and seedling recruitment following disturbance can shape the structure and composition of forested landscapes.

THE DISTURBANCE SUBMODEL

Integrating the new WINDSTORM submodel into SORTIE requires specifying: (i) parameters that define species-specific resistance to windthrow and (ii) the wind disturbance regime.

Resistance of trees to windthrow

Canham *et al*. (2001) developed a method of simultaneously estimating an index of local (i.e. stand-scale) storm severity and the parameters of functions that quantify species-specific variation in probability of windthrow (i.e. defined as either uprooting or stem break) as a function of storm severity and tree size. The method follows directly from the principles of likelihood estimation and takes advantage of the fact that most severe (i.e. landscape-scale) windstorms contain considerable variation in severity. The model calculates the log of the odds ratio of mortality as a function of species, individual tree size and the estimated index of local storm severity (Canham *et al*. 2001):

$$\log\left(\frac{p_{isj}}{1 - p_{isj}}\right) = a_s + c_s S_i DBH_{isj}^{b_s} \qquad \text{eqn 1}$$

where p_{isj} is the probability of windthrow for the jth individual of species s in plot i; S_i is the estimated storm
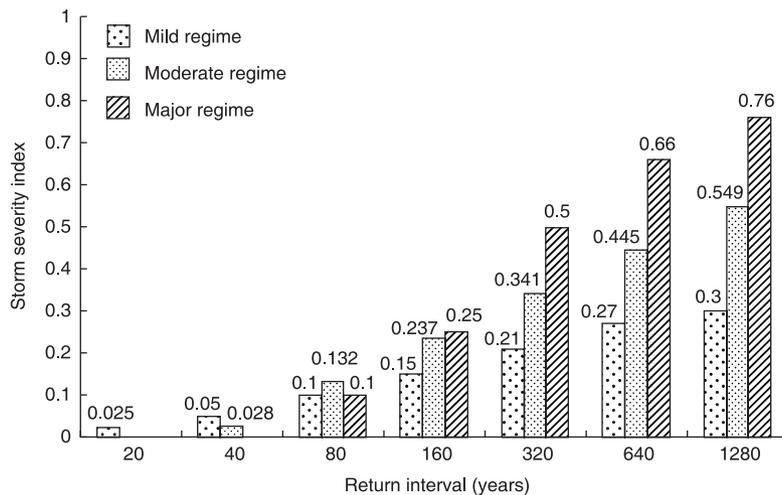
Fig. 1 Wind disturbance regimes used in simulations. Height of the bar is the expected probability of mortality from a single storm with the given return interval in a well-mixed stand in which all species are present with a broad size distribution of trees. The numbers at the top of the bars indicate the expected long-term average probability of mortality from storms of a given return interval. The total annual percentage mortality for each regime is the sum of these numbers (0.6%). Actual mortality in any given storm will vary depending on the composition and size structure of the stand at the time of the storm. The moderate disturbance regime is adapted for use in SORTIE from Frelich & Lorimer (1991a).

severity for plot *i* (on an arbitrary scale of 0–1); DBH_{isj} is diameter at breast height (d.b.h.; in cm at 1.35 m height) of the *j*th individual of species *s* in plot *i*; and a_s, b_s and c_s are estimated, species-specific parameters (see Canham *et al*. 2001). The resulting probability of mortality is a response surface that is expected to increase with both d.b.h. (i.e. $b_s > 1$) and storm severity index (i.e. $c_s > 0$). For our analyses of wind disturbance in temperate forests, we do not consider damage that results in only partial loss of the crown. In tropical forests, crown damage is far more common than outright mortality (Walker 1991), and our empirical methods have been extended to predict levels of damage rather than simply survival vs. mortality as a function of storm severity (e.g. Uriarte *et al*. 2004).

The wind disturbance regime

A disturbance regime is typically defined in terms of four characteristics: spatial extent, severity (i.e. the amount of tree and plant mortality in a disturbed area), return frequency and type of disturbance (Frelich 2002). In this study, we hold spatial extent (i.e. the SORTIE stand size) and disturbance type (wind) constant. The disturbance regime is characterized by variation in the frequency and severity of individual windstorms. We use a synthetic index of storm severity (ranging from 0 to 1) representing the approximate proportion of trees killed in a well-mixed plot with broad size distribution of trees of all species (Canham *et al*. 2001). There are a number of benefits to using an index rather than more operational measures such as wind speed, not the least of which is the scarcity and difficulty of obtaining direct local measurements of severe winds during storms. Storms are episodic and occur with a frequency equal to the inverse of their return interval (Fig. 1).

We use three different disturbance regimes in our simulations (mild, moderate and major) (Fig. 1). Each regime has the same expected long-term, average annual mortality from wind (0.6%). The moderate storm regime is equivalent to the historical regime derived by Frelich & Lorimer (1991a); the mild storm regime specifies more frequent, less severe storms; and the major storm regime specifies less frequent but more severe storms (Fig. 1). The sum of all other sources of stochastic mortality of canopy trees is set to 1% per year for each species. All non-disturbance simulations are set to 1.6% per year, keeping the long-term expected mortality equal for all disturbance and non-disturbance simulations.

CHANGES TO THE SORTIE RECRUITMENT
SUBMODEL

Seedling establishment

The original recruitment submodel in SORTIE (Ribbens *et al*. 1994) predicts the number and spatial locations of new seedlings produced by a parent tree of a given species as an increasing function of parent tree size and a decreasing function of distance from a parent (Ribbens *et al*. 1994):

$$F_x = STR \times (DBH/30)^2 \times R(x) \qquad \text{eqn 2}$$

where F_x is the number of seedlings per m^2 at distance *x* from the parent tree, STR is the number of first-year seedlings produced by a tree of 30 cm d.b.h. and $R(x)$ is the Weibull dispersal kernel function that describes how seeds are dispersed as a function of distance *x* from the source tree (Ribbens *et al*. 1994). Ribbens *et al*. (1994) based their estimates of STR on only a few

Table 1 Fecundity and substrate favourability parameters used in the model. (a) Calculating standard total recruitment of seedlings (STR) from seed mass using eqn 6 and parameters from Green & Johnson (1998). (a) Seed mass (m_s) in grams (Greene & Johnson 1994); μ is the number of established seedlings per 2×2 m quadrat per year. The parameter μ creates the same number of seedlings for a 16-ha stand as STR. (b) Values for α and β are derived from Greene & Johnson (1994; D. Greene, personal communication), all others from Greene & Johnson (1998)

(a) Species	m_s	$f_1(m_s)$	$f_2(m_s)$	STR	μ
Betula alleghaniensis	0.0010	167767.0	0.0386	458.3	0.0054
Tsuga canadensis	0.0024	100811.8	0.0552	393.3	0.0046
Acer rubrum	0.0149	35246.2	0.1113	277.2	0.0033
Acer saccharum	0.0484	17767.8	0.1686	211.7	0.0025
Prunus serotina	0.1070	11212.8	0.2165	171.6	0.0020
Fagus grandifolia	0.2835	6371.4	0.2817	126.8	0.0015

(b) Fecundity		Substrate favourability			
α	3067	g_L	1.83	g_H	0.33
β	0.58	d_L	0.43	d_H	0.76
m_g	0.43				

years of field data. Without longer-term data, their approach does not capture the high interannual variability of seed production in these forests, nor generate reasonable estimates of mean fecundity (Ribbens *et al.* 1994; Clark *et al.* 2004).

Many studies have shown that seed production, subsequent seedling germination and seedling establishment are all influenced by seed mass (e.g. Westoby *et al.* 1992, 1996; Greene & Johnson 1994, 1998). Our approach estimates the number of 1-year-old seedlings produced by a parent tree as a function of seed mass, seedbed substrate characteristics and the basal area of the parent tree (Greene & Johnson 1994, 1998; Greene *et al.* 2002; D. Greene, personal communication). Mean annual fecundity is calculated as:

$$f_1(m_s) = \alpha m_s^{-\beta} B \qquad \text{eqn 3}$$

(Greene & Johnson 1994) where α and β are empirically derived parameters (reproduced in Table 1), m_s is seed mass in grams and B is the basal area of the tree. Seed germination and 1-year seedling survival is determined by:

$$f_2(m_s) = m_g w \left(1 - e^{-\gamma_L m_s^{\delta_L}}\right) + m_g (1 - w)\left(1 - e^{-\gamma_H m_s^{\delta_H}}\right) \qquad \text{eqn 4}$$

where m_g is mortality from granivory, w is the proportion of favourable seed bed area, and γ_L, δ_L, γ_H and δ_H are empirical coefficients for favourable and unfavourable substrates, respectively (Greene & Johnson 1998) (parameter values are reproduced in Table 1b). The product of $f_1 \times f_2$ is the number of 1-year seedlings per

unit basal area of source tree. The result when multiplied by 0.0707 (the basal area of a 30-cm d.b.h. tree) is equivalent to STR in eqn 2 (Fig. 2).

Substrate model

The substrate model used in this investigation is derived from LePage *et al.* (2000) and described in detail in Papaik *et al.* (2005). The model is composed of four different seedbed substrate types: fresh CWD, rotting CWD, mineral soil from pit-mound complexes and litter, where substrate creation is driven by tree mortality, and substrate change is driven by eqn 5. Each substrate type has a species-specific 'favourability' that is determined empirically (Greene & Johnson 1998; LePage *et al.* 2000). Substrates are either favourable for establishment (e.g. mineral soil, humus, rotted logs, see Table 4), where a high proportion of seeds germinate and establish, or unfavourable for establishment (e.g. undisturbed sites, freshly fallen trees, see Table 4), those on which many fewer seeds germinate and establish. Favourable substrates are considered to be equally favourable. The favourability index of an unfavourable substrate (Table 4) is determined by eqn 2 and is defined as the ratio of seedling establishment on an unfavourable substrate to the ratio of seedling establishment on a favourable substrate. Substrate creation occurs when a tree dies. A specified proportion of trees that die are uprooted, creating new mineral soil substrate as a function of tree size (Papaik *et al.* 2005). Fallen trees, whether uprooted or not, create fresh CWD that is also a function of tree size (Papaik *et al.* 2005). The area of fresh CWD and mineral soil substrates 'decay' as a logistic function of time since creation in 5-year timesteps:

$$S(t) = e^{-\nu t^{\eta}} \qquad \text{eqn 5}$$

where $S(t)$ is the proportion of the area of the original substrate remaining at t, 5-year timesteps since the creation of fresh CWD, and ν and η are substrate-specific decay parameters. Fresh CWD is transformed to rotting CWD (ν = –0.5 and η = 2.6; Papaik *et al.* 2005), which in turn decays to litter, and mineral soil is transformed to the background litter layer (ν = –1.0 and η = 4.4; Papaik *et al.* 2005). A constant proportion of rotting CWD (0.45; Papaik *et al.* 2005) transforms to forest litter at each timestep, completing the cycle of substrate dynamics.

The substrate model also defines the species-specific probabilities of successful germination and seedling establishment for each substrate type (eqn 4). Establishment of large-seeded species at our study sites (e.g. *Quercus*, *Acer*, *Fagus*) is relatively insensitive to substrate conditions (Ribbens *et al.* 1994; our personal observations), and all substrates are considered uniformly favourable. Rates of establishment of the smallest-seeded species, particularly *T. canadensis* and *B. alleghaniensis*, however, are sensitive to substrate
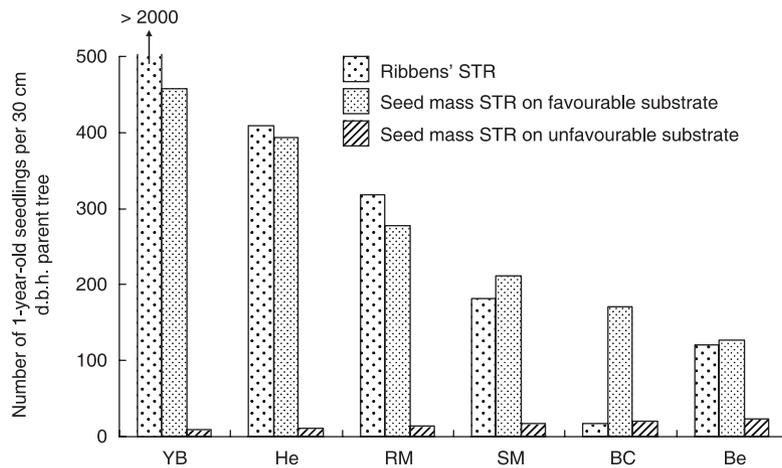
Fig. 2 Validation of values for STR calculated as a function of seed mass. The validation data are the empirical results of Ribbens *et al.* (1994). STR is the number of 1-year-old seedlings produced by a tree of 30 cm d.b.h. Variation in the number of seedlings that establish in the seed mass model is highly sensitive to the relative amount of favourable substrate present (eqn 4).

Table 2 Overview of research questions and the specification of the simulation treatments designed to address them. Blank cells are the same as control

Question/hypothesis	Disturbance regime (parameters in Fig. 1)	Regeneration (parameters in Table 3)	Initial abundances (parameters in Table 4)
0 Control	None	Dispersal: local, spatially explicit seedbed favourability: species-specific	25 per sp. ha^{-1}
1 How does variation in the severity of a wind disturbance regime affect long-term patterns of composition, structure, and diversity of canopy tree species?	Mild; moderate; major		25 per sp. ha^{-1} vs. seed-mass based
2 How important is species-specific variation in resistance to windthrow for patterns of relative abundance and diversity in forests subject to storms with a broad range of severity?	Mild; moderate; major		
3 How does variation among species in local dispersal of seeds affect patterns of relative abundance and species coexistence in forests subject to recurrent wind disturbance?	None; moderate	Local dispersal: spatially explicit vs. non-spatial 'bath'	
4 Are forest composition and structure sensitive to species-specific responses to, and spatial and temporal variation in, recruitment opportunities (particularly seedbed substrates) created by wind disturbance?	None	Seedbed favourability: control vs. all substrates favourable	
	Moderate	Control vs. no substrates favourable vs. all substrates favourable	
5 How important is long-distance dispersal for patterns of succession and tree species diversity in forests subject to wind disturbance?	Moderate	Dispersal local: control vs. long-distance: κ varies ∝ 0.1%, 1% and 10% total fecundity (for 10 m^2 ha^{-1} per species in landscape)	Field data

conditions. They require either bare mineral substrates or elevated seedbeds on well-rotted logs, with little effective establishment on either litter or fresh CWD (Godman & Lancaster 1990; McGee 2001).

We tested sensitivity of forest dynamics to seedbed favourability, both with and without disturbance. In both cases, we tested the control, in which only the small-seeded species find decaying CWD and mineral soil a favourable substrate, against all substrates being favourable for all species. In the disturbance tests, we also determined the case in which all substrates are unfavourable for all species (Table 2).

Table 3 Species parameters used in the model. Species are listed in order of increasing seed mass. 'F' denotes favourable substrate; 'U' denotes unfavourable substrate; NA denotes not applicable

| Species | STR | LDD | | | Mean local dispersal* | Substrate favourability | | | Index of unfavourable substrate‡ | Windstorm resistance† | | |
		Low κ (0.1%)	Mid κ (1%)	High κ (10%)		Litter/ fresh log	Decaying CWD	Mineral soil		a	b	c
Betula alleghaniensis	15.28	0.0153	0.153	1.53	1.0×10^{-7}	U	F	F	0.0386	−3.302	0.193	2.341
Tsuga canadensis	13.11	0.0131	0.131	1.311	6.87×10^{-3}	U	F	F	0.0552	−1.599	1.470	0.015
Acer rubrum	9.24	0.0092	0.092	0.924	3.62×10^{-4}	U	U	F	0.1113	−2.261	0.426	1.140
Acer saccharum	7.06	0.0071	0.0706	0.706	7.44×10^{-4}	U	U	F	0.1686	−1.960	0.679	0.190
Prunus serotina	5.72	NA	NA	NA	7.75×10^{-4}	U	U	F	0.2165	−2.752	0.680	0.663
Fagus grandifolia	4.23	NA	NA	NA	1.96×10^{-3}	U	U	F	0.2817	−3.057	0.941	0.231

*From Ribbens *et al.* (1994).

†From eqn 1 (reproduced from Canham *et al.* 2001).

‡From eqn 2. This is the ratio of STR for unfavourable substrate to STR for favourable substrate.

Local and long-distance bath dispersal

The default dispersal model in SORTIE disperses seeds from each parent tree according to spatially explicit dispersal functions (Ribbens *et al.* 1994). In order to isolate the role that spatially explicit dispersal has in these forests and to explore the consequences of omitting the effects of long-distance dispersal for forest succession following windthrow, we added a submodel to SORTIE that generates stochastic seedling establishment with a uniform mean across the plot (i.e. without respect to the locations of parent trees). This mode of dispersal and seedling establishment can be termed 'bath' recruitment by analogy with the settling of invertebrate larvae in marine intertidal zones. We divide the plot up into 2 × 2 m quadrats and disperse the calculated number of seedlings as a uniform random process within each quadrat. Bath recruitment is assumed to follow a Poisson distribution with the expected mean number of seedlings of a given species for each quadrat (λ) specified as a linear function of the basal area (BA) of the species in the plot:

$$\lambda = \mu(BA) + \kappa. \qquad \text{eqn 6}$$

In effect, eqn 6 contains two components: (i) adult biomass-dependent (but non-spatial) local dispersal, which is determined by parameter μ; and (ii) input that is independent of local adult abundance (presumably primarily due to long-distance dispersal), which is determined by parameter κ.

The basal area coefficients, μ, are calculated (Table 1a) to construct a density-dependent, non-spatial model of local dispersal that is quantitatively equivalent to the default spatial dispersal model, but which distributes seeds independently of the locations of parent trees. We used μ to explore the importance of spatially explicit local dispersal in these forests (Table 2, question 3), both with and without disturbance.

Both the default spatially explicit dispersal model and the local bath dispersal model will disperse seedlings only if there are adult trees of that species present in the plot. The intercept term in eqn 6, κ, represents LDD from source trees outside the plot. Thus, even if there are no adult trees of a given species in the plot, there will be immigration via LDD if κ is non-zero. In order to examine the relative importance of LDD vs. local dispersal, we kept track of locally dispersed individuals separately from LDD-dispersed individuals. To set κ, we assume a constant matrix of species across the landscape outside of our simulation plot at an abundance of 10 m² ha⁻¹. We made this assumption to constrain the boundary conditions of these simulations, and to provide tests that render the simulation results interpretable in biological terms. We look for thresholds regarding the ability of the four wind-dispersed species to persist in or invade already existing forested stands by taking advantage of the fact that where the tail is flat (i.e. far from the parent), the density of propagules scales with fecundity (Clark 1998). We tested three levels of LDD by setting κ to approximate 0.1%, 1% and 10% of the total fecundity of each wind-dispersed species (given the assumed constant landscape-level abundance of 10 m² ha⁻¹) (Table 3).

SET-UP OF THE SIMULATION EXPERIMENTS

Parameters for our simulated 'experiments' are detailed in Table 3. All other parameters used in these simulations are from Pacala *et al.* (1996). The 'experimental' set-ups are detailed in Table 2. Each of the tests varied one or more of the features of our control simulations. All simulations used a 400 × 400 m (16 ha) plot and ran for 1000 years. There were 10 replicate runs of each test. Initial conditions for the control runs had 25 trees ha⁻¹ per species distributed randomly between 0 and 1 cm d.b.h. and dispersed randomly throughout the stand. The test for sensitivity to initial conditions apportioned initial abundances among species proportionately by seed mass (Table 4). We calculated the initial conditions for the LDD tests from field data (Table 4). All other simulations used the same

Table 4 Initial abundances (no. ha⁻¹). Even abundance initial conditions and seed-mass-weighted initial conditions both sum to 150 trees ha⁻¹ between 0 and 1 cm d.b.h. Field demographics calculated from pooled plot data that were used in the long-distance dispersal runs

	Betula alleghaniensis	*Tsuga canadensis*	*Acer rubrum*	*Acer saccharum*	*Prunus serotina*	*Fagus grandifolia*
Even	25	25	25	25	25	25
Seed-mass	41.9	36.0	25.4	19.4	15.7	11.6
Initial abundances for LDD test from field data by d.b.h. class (cm)						
0–10	6.0	0.2	33.2	45.0	1.4	44.6
10–20	3.2	0.7	39.8	27.3	9.3	10.8
20–30	2.8	2.2	17.3	23.9	20.1	5.2
30–40	5.2	1.5	6.9	4.5	14.5	2.4
40–50	3.6	0.9	1.7	3.1	3.5	0.9
50–60	4.0	0.4	0.4	0.4	0.7	0.2
70–80	2.0	0.2	0.4	0.7	0.4	0
80–90	0.6	0	0	0.2	0.3	0

initial conditions as the control. The three disturbance regimes were set according to Fig. 1. Bath dispersal parameters for the long-distance tests are shown in Table 1 (μ) and non-spatial local dispersal tests are shown in Table 2 (κ).

Results and discussion

THE EFFECTS OF WIND DISTURBANCE ON TREE POPULATION DYNAMICS
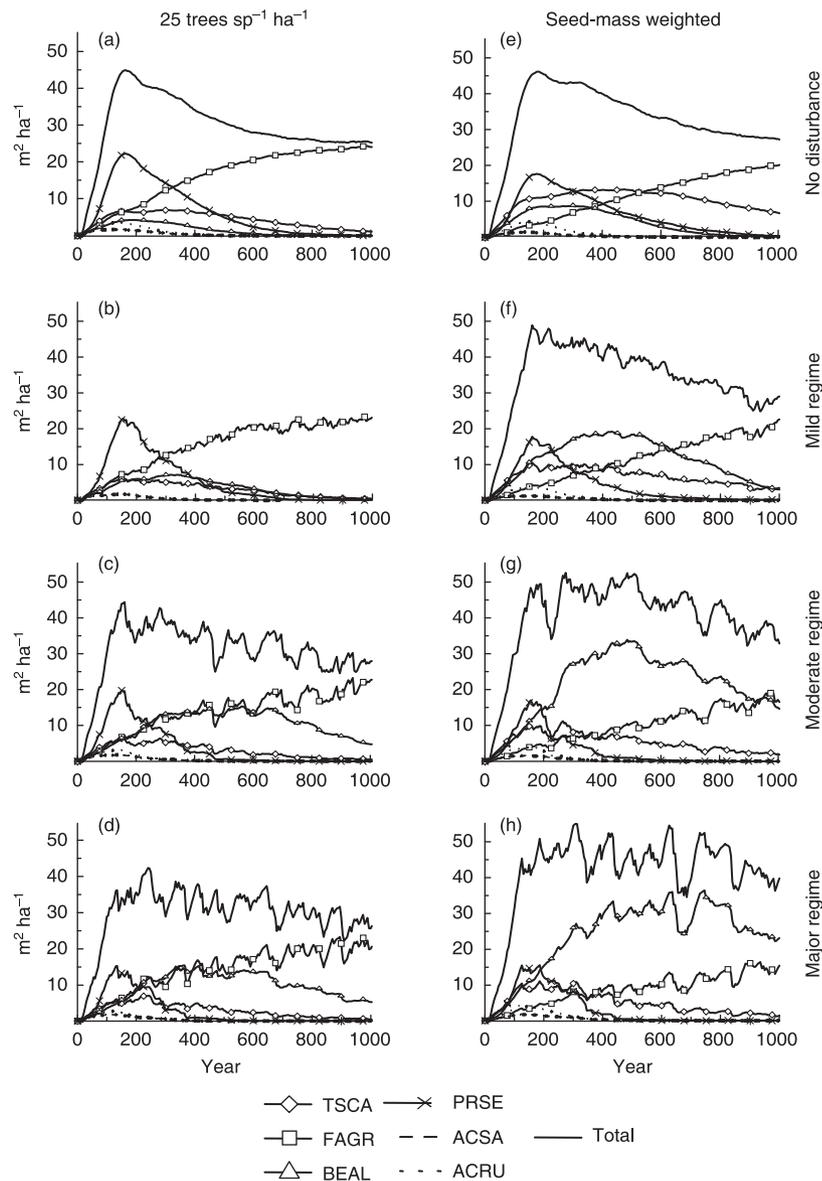
Sensitivity to initial conditions

In the absence of disturbance, SORTIE forecasts of forest dynamics are very sensitive to initial conditions (both abundance and size structure) (Pacala *et al.* 1996). Initial conditions influence stand development well beyond the age of most stands in north-eastern North America, indicating the importance of understanding the processes controlling colonization following disturbance (Pacala *et al.* 1996). We tested how disturbance influences sensitivity to initial conditions by keeping total plot abundance the same (150 trees ha⁻¹) between 0 and 1 cm d.b.h., but distributing the relative abundance among species in two ways: uniformly among species (25 trees ha⁻¹ per species), and proportionally according to seed mass (Table 4). In the absence of disturbance, relative and absolute basal area changed in a manner that follows from the initial advantages in abundance given to the smaller seeded species in the proportional seed-mass-weighted initial conditions (Fig. 3a,e). The higher initial abundance ratio (~3 : 1) of *T. canadensis* relative to *F. grandifolia* was sufficient to make *Tsuga* the dominant species for a 200-year period from about 350 to 550 years stand age, and delayed *F. grandifolia* dominance by ~100 years (Fig. 3a,e). Basal area increases of the smaller seeded species (*T. canadensis* and *B. alleghaniensis*) in the seed-mass-weighted runs were offset by decreases in the larger seeded species (*P. serotina* and *F. grandifolia*) such that there was only a modest increase in total basal area throughout the duration of the simulation

(Fig. 3a,c). These changes were all moderate, reflecting the modest differences in initial conditions, and were consistent with previous studies (Pacala *et al.* 1996).

Incorporating wind disturbance complicates the role that initial conditions play. The modest advantage in the initial abundance of *B. alleghaniensis* relative to *F. grandifolia* (~3.5 : 1 per ha, see Table 4) was amplified by the superior wind resistance of *B. alleghaniensis* (Fig. 4). As a result, there was a sustained increase in total stand basal area and a 400-year delay in the time it took for *F. grandifolia* to become the dominant species (Fig. 3c,g). The reverse is true for *T. canadensis*. Low resistance to mild and intermediate-severity storms of medium and large *T. canadensis* (Canham *et al.* 2001; Fig. 4) virtually offsets the early abundance advantage such that there was only a minimal increase in the basal area of *T. canadensis* (Fig. 3c, g). The two heavier-seeded species, *P. serotina* and *F. grandifolia*, became less important in relative and absolute basal area when wind disturbance was included. Their greater susceptibility to wind, relative to *B. alleghaniensis*, increasingly prevented them from becoming more important as the disturbance regime increased toward major storms (Fig. 3). As the severity of the disturbance regime increased, the peak basal area and persistence of *B. alleghaniensis* increased significantly and delayed succession to *F. grandifolia* (Fig. 3f–h). In addition, total basal area increased significantly as the disturbance regime increased owing to the response of *B. alleghaniensis* (Fig. 3f–h). Consequently, if a wind-resistant species (e.g. *B. alleghaniensis*) has even a slight initial advantage, it can persist virtually indefinitely because of disturbance.

Species-specific resistance to disturbance

Species-specific resistance to non-catastrophic disturbances interacted strongly with shade tolerance of the species, the medium-term history of disturbances (time scales of 1–3 centuries) and the long-term average severity of the disturbance regime to influence the

Fig. 3 Sensitivity of stand dynamics to initial conditions (left vs. right column) and to variations in the disturbance regime (rows) as a result of species-specific resistance to disturbance. See Fig. 1 for disturbance regime specifications and Table 4 for initial abundances.

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relative importance of species throughout succession. For example, the abundance of *B. alleghaniensis* was positively correlated with the severity of the disturbance regime (Fig. 3) because it is the most resistant species across a broad range of tree sizes and wind severities (Fig. 4). Conversely, *P. serotina* is highly susceptible across all tree sizes (Canham *et al*. 2001; Fig. 4), and its importance was inversely related to the severity of the disturbance regime (Fig. 3). However, resistance to disturbance is not a trait by which all species can be simply ordered as being more or less resistant. For instance, *T. canadensis* is the most susceptible species in low-severity storms for all tree sizes but becomes more windfirm, relative to other species in the same size range, as storm severity increases (Fig. 4, and see Canham *et al*. 2001). Therefore, milder storms act as a bottleneck limiting the long-term abundance of

T. canadensis in all disturbance regimes (Fig. 3). As a second example, large *F. grandifolia* are highly susceptible to wind disturbance (in part because of the presence of beech bark disease; Papaik *et al*. 2005), but small *F. grandifolia* have the highest resistance (Canham *et al*. 2001; Fig. 4). Thus, *F. grandifolia* persisted as an abundant understorey species (Fig. 3) because of the resistance to wind disturbance of small trees (Fig. 4) and its shade tolerance (Kobe *et al*. 1995). In effect, species-specific resistance to disturbance adds variance to community dynamics that cannot be predicted by models that ignore it.

Intermediate-severity windstorms do not simply reset succession to an earlier state or advance it to a later state as is often assumed. The response of the community in our simulations depended on the temporal pattern of storms over an extended period and
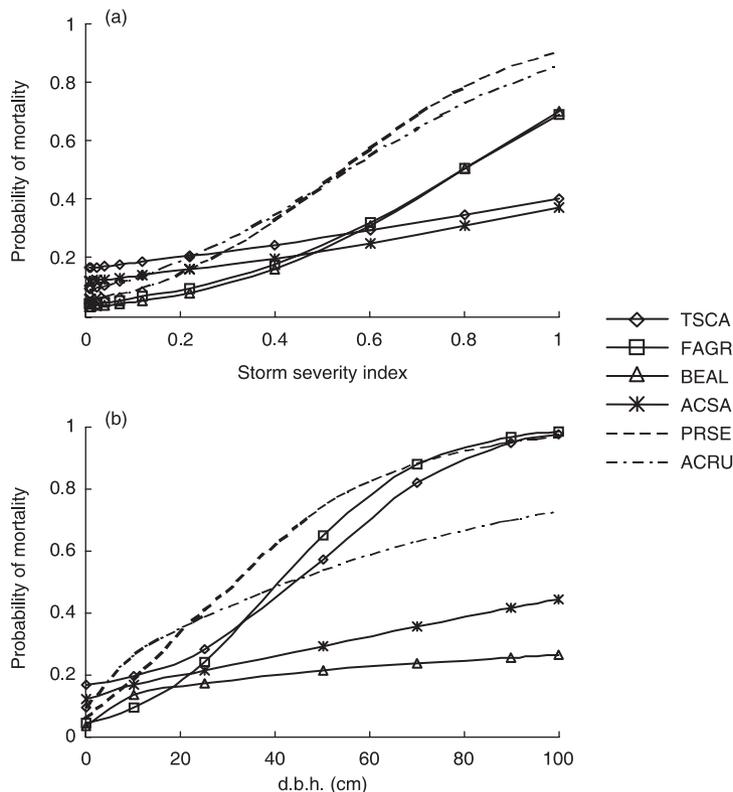
Fig. 4 Expected probability of mortality: (a) of a 20-cm d.b.h. tree as a function of storm severity index; and (b) as a function of d.b.h. for storm severity = 0.4. (Figure adapted from Canham *et al.* 2001.)

the relative importance of wind-susceptible vs. wind-resistant species. Succession of young stands was accelerated in the moderate disturbance regimes (Fig. 3) because the less shade-tolerant *P. serotina* is more susceptible to low- and moderate-severity disturbances than later successional species (Canham *et al.* 2001; Fig. 4). However, the most important intermediate successional species predicted in the disturbance-free simulations changed from the more shade-tolerant *T. canadensis* to the more disturbance-resistant *B. alleghaniensis* as the severity of the disturbance regime increased (Fig. 3).

STAND VS. LANDSCAPE DYNAMICS

We are able to parse out the general trends described above because we have been considering the average response of replicate runs for a given disturbance regime. This is analogous to a landscape-scale analysis. Consider, however, that averaging eliminates important information by masking the effects of transient events. The temporal patterns of storms are stochastic, and individual runs have distinct histories that vary considerably within each disturbance regime. Individual runs within one regime can resemble those in other regimes and the average response of another regime (Fig. 5). Thus, individual runs are analogous to stand-scale dynamics. To illustrate how specific temporal patterns of storm events (i.e. disturbance history) shape community composition and succession at the stand

scale, we selected three runs from the moderate disturbance regime (Fig. 5). Plot 10 is similar to the mild storm disturbance regime (Fig. 3b), plot 7 is similar to the mean of the moderate storm disturbance regime (Fig. 3c) and plot 9 is similar to the mean of the major storm regime (Fig. 3d).

First, note that although individual, non-catastrophic storms change structure, they had minimal effect on succession when compared with the disturbance-free simulations, despite substantial differences among species in resistance to disturbance (Fig. 4, based on Canham *et al.* 2001). A series of storms were necessary to alter succession and the length of time to the onset of old growth conditions. For example, consider early in succession when *P. serotina* dominated. The importance of *P. serotina* was extended when this period was relatively quiet (Fig. 5b), whereas it was curtailed by a series of storms that occurred at or near the peak abundance of *P. serotina* (Fig. 5d) and we see a similar pattern shortly later in succession. *P. serotina* and *F. grandifolia* were the most important species when two mild storms with a combined severity index of 0.369 occurred in plot 10 in year 360 (Fig. 5b). The more susceptible species (*P. serotina*) was effectively removed from the stand, but *F. grandifolia* recovered because, being shade-tolerant, it had established abundant saplings in the understorey. The major storm (index 0.445) that occurred 100 years later knocked back *F. grandifolia*. However, in this case, *F. grandifolia* recovery was forestalled because one major and four
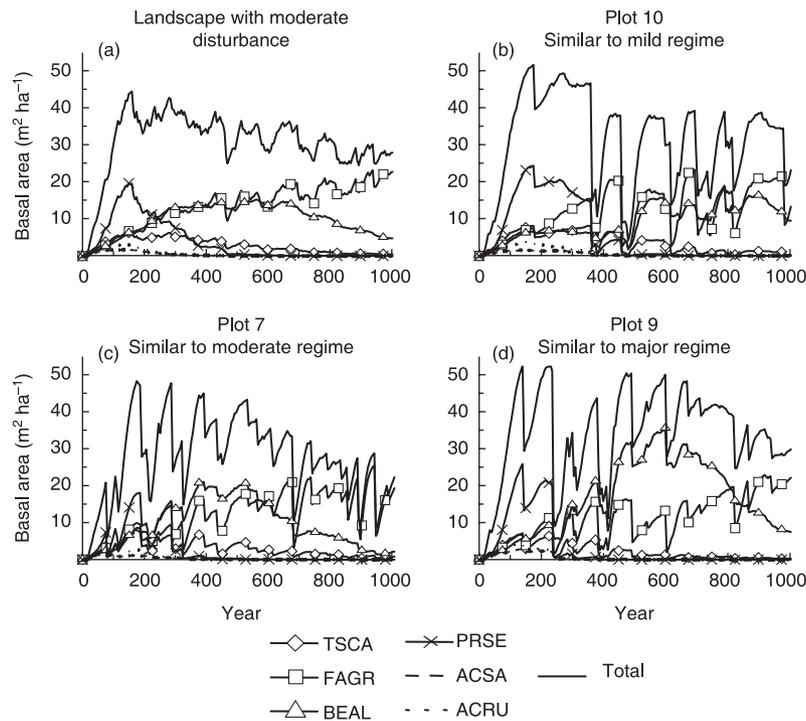
Fig. 5 Plot vs. landscape effects of disturbance. The average response of the 10 replicate runs of the moderate disturbance regime is analogous to the average variation across the landscape, whereas individual runs are analogous to individual stand histories. Three individual runs were selected because they most resembled the averages of the three disturbance regimes. This figure illustrates how viewing forest dynamics from (a) the landscape scale masks important variation at the stand scale, and (b–d) the stand scale masks evidence of long-term trends in disturbance regimes (see also Fig. 3).
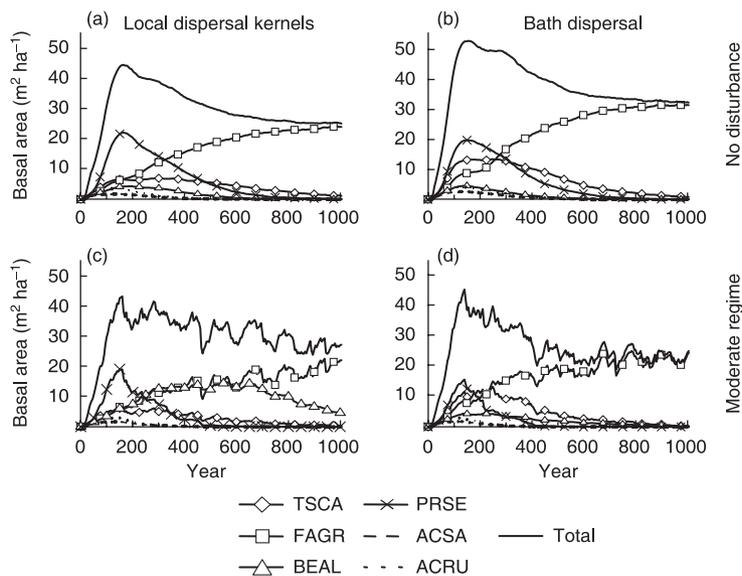
mild storms quickly followed the major storm. This sequence of storms, which occurred later in succession, created suitable sustained conditions (i.e. gaps and decaying CWD from previous storms) for *B. alleghaniensis* to establish and increase, but not become dominant. By contrast, a similar series of storms that occurred earlier in succession in plots 7 and 9, before *F. grandifolia* became fully established, led to the dominance of *B. alleghaniensis* (Fig. 5). It took sustained quiet periods in both plots for *F. grandifolia* to regain dominance (Fig. 5). A substantial understorey of *F. grandifolia* developed during these periods, and it remained the dominant species regardless of the subsequent pattern of storms.

Thus, quiet periods in excess of 100–150 years allowed the most shade-tolerant species (*F. grandifolia*) to increase in all regimes. Periods during which storms occurred more frequently allowed the more wind-resistant species (*B. alleghaniensis*) to increase. In effect, resistance to disturbance dominated competitive ability as a trait determining relative abundance during stormy periods. Lasting differences in succession among the regimes were a result of changes in the probability of relatively disturbance-free periods of at least 100–150 years. This cannot be inferred from the aggregated runs showing the differences among the average landscape responses to the disturbance regimes (Fig. 5a). We can only infer stand-scale processes by examining individual plot histories. By contrast, variation among individual stand histories masks important

differences in expected successional trajectories that are only revealed by a landscape-scale analysis. In summary, species-specific resistance to disturbance interacts with the stochasticity of disturbance events and initial conditions to have dramatic and long-lasting effects on the patterns of community development (Fig. 3) at both the stand and the landscape scales.

INTERACTIONS BETWEEN LOCAL DISPERSAL AND SPECIES-SPECIFIC RESISTANCE TO DISTURBANCE

The importance of modelling local dispersal as a spatially explicit process is made clear in Fig. 6a & b. In the absence of disturbance, bath recruitment resulted in higher total stand basal area than spatially explicit, local dispersal (Fig. 6a,b). This was due almost entirely to increases in the basal areas of the most dispersal-limited species of this community (i.e. *T. canadensis* and *F. grandifolia* – Table 3) when dispersal was modelled as a bath process (Fig. 6a,b). Limited local dispersal of the shade-tolerant species (*T. canadensis* and *F. grandifolia*) led to an increase in establishment opportunities for more broadly dispersed, less competitive species and fostered coexistence in the absence of disturbance. Disturbance interacted with spatially explicit dispersal to facilitate a shift in composition to *B. alleghaniensis* from *T. canadensis* early in succession (Fig. 6c,d) and, later, resulted in co-dominance between *B. alleghaniensis*

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Fig. 6 Spatially explicit local dispersal vs. 'bath' dispersal. Ignoring variation in local dispersal characteristics among species overestimates the abundance of dispersal-limited species.

and *F. grandifolia* (Fig. 6c). Given equal dispersal characteristics, the superior competitive ability of *T. canadensis* relative to *B. alleghaniensis* (Pacala *et al*. 1994; Kobe *et al*. 1995) was more advantageous than the superior windthrow resistance of *B. alleghaniensis* (Canham *et al*. 2001). We conclude that: (i) abundance of *B. alleghaniensis* was strongly dependent on broad dispersal relative to the other later successional species (e.g. *T. canadensis* and *F. grandifolia*), (ii) *T. canadensis* was strongly dispersal limited and (iii) *F. grandifolia* eventually overcame both dispersal limitation and relatively lower resistance to windthrow because of superior competitive ability (i.e. shade tolerance) in this community. Our results support theories that suggest localized dispersal improves species coexistence (Chave *et al*. 2002) and delays competitive exclusion (Bolker & Pacala 1999; Murrell & Law 2003) (Fig. 6a,b), but argues against the need for strict tradeoffs between dispersal traits and competitive ability. Tilman (1994) showed that by including variation in resistance to disturbance, coexistence could occur without strict competition-dispersal trait tradeoffs. Our results support this and suggest that species-specific resistance to windthrow obviates the need for strict trait tradeoffs between mean dispersal and competitive ability (Fig. 6c,d).

*Interactions between windstorms and dispersal – a caveat*

It is tempting to use the model to assess how disturbance and dispersal interact. Dispersal is clearly a factor in community response to wind disturbance, as strong winds will disperse seeds much further, and in addition, smaller seed will disperse further than large seeds. But the focus of our analysis was to explore those factors that govern the community response to wind

disturbance for which we have good empirical measures (e.g. growth as a function of light, regeneration as a function of seedbed). We do not address specific 'disturbance–dispersal' interactions because we do not have the appropriate data to support modelling dynamics of dispersal changes as a function of wind disturbance severity (i.e. is the kernel shape sensitive to wind intensity? How much does the mean dispersal increase as a function of disturbance severity?).

INTERACTIONS BETWEEN SEEDLING RECRUITMENT AND SPECIES-SPECIFIC RESISTANCE TO DISTURBANCE

Effects of substrate limitations

When substrate limitation was removed the initial basal area of all species increased relative to the control (Fig. 7a,b). This was most dramatic for *P. serotina* and *B. alleghaniensis*. This is largely an artefact of the absence of density-dependent seedling mortality in SORTIE and the initial conditions of the test (Pacala *et al*. 1996). As the initial cohort of saplings matured (150 ha⁻¹) they dispersed a dense carpet of seedlings that is ~10-fold greater than when substrate limitation was included. All these seedlings grew in this open environment and led to very high basal areas early in succession. After approximately 100 years, the canopy closed and all species declined (Fig. 7b). Subsequently, with the exception of *B. alleghaniensis*, community dynamics followed the same pattern as the control (Fig. 7a). However, *B. alleghaniensis* maintained a very high basal area well after the canopy closed, and shading effects on seedling and small sapling mortality came to dominate. The dramatic increase in *B. alleghaniensis* at this time was due to its considerable advantage over other species in finding suitable
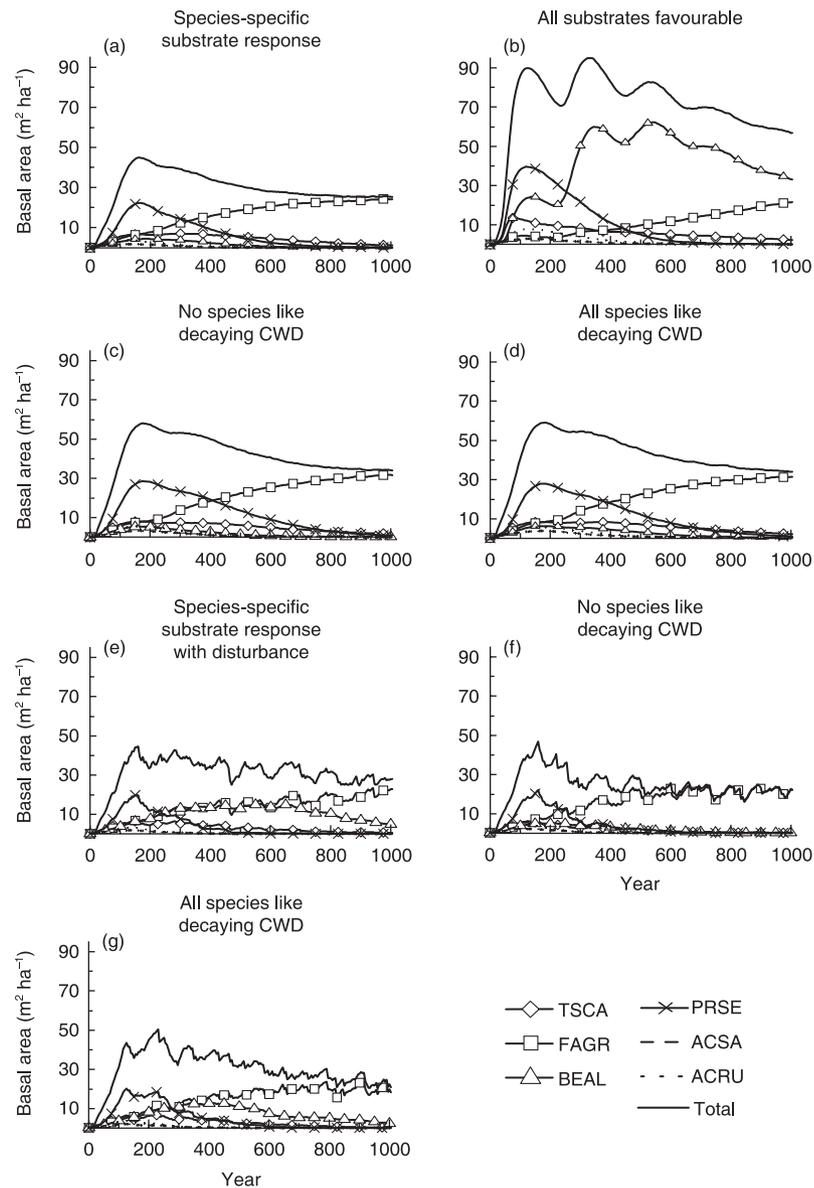
Fig. 7 Effects of substrate limitation without disturbance (a–d) and with disturbance (i.e. the moderate disturbance regime) (e–g). Establishment limitation as a function of variation among species responses to substrate interacts strongly with species-specific dispersal and disturbance history (see text for details).

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establishment sites that resulted from its broad dispersal. Without strong substrate limitations on establishment, the broad dispersal ability of *B. alleghaniensis* enabled its establishment throughout the plot. *T. canadensis*, for which establishment is limited by the same factors as *B. alleghaniensis*, does not experience a similar secondary peak in basal area because it is dispersal limited in these simulations (Table 3). As a cautionary note regarding our model predictions, Greene *et al.* (2004) have pointed out that Ribbens *et al.* (1994) probably underestimated mean dispersal for *T. canadensis*. We tested whether our predictions were sensitive to the precise estimate of the local dispersal characteristics of *T. canadensis* by removing all establishment limitation for this species (Fig. 7g). In this case, extremely dense, light-limited, fine-scale patches of *T. canadensis* regeneration occurred such that

canopy recruitment by *T. canadensis* was self-limiting. This was the reason *T. canadensis* failed to replace *B. alleghaniensis* in our simulations and was not a result of underestimating the mean dispersal for this species.

Effects of differences among species in favourability of CWD substrates

Many studies have shown that decaying CWD is a more favourable establishment substrate for small-seeded species (i.e. *B. alleghaniensis*, *T. canadensis*) than large seeded-species (e.g. LePage *et al.* 2000; McGee 2001). However, empirical evidence suggests that recruitment into the sapling stage and canopy may be more dependent on light than favourable seedbed substrates (McGee 2001). The population dynamics of
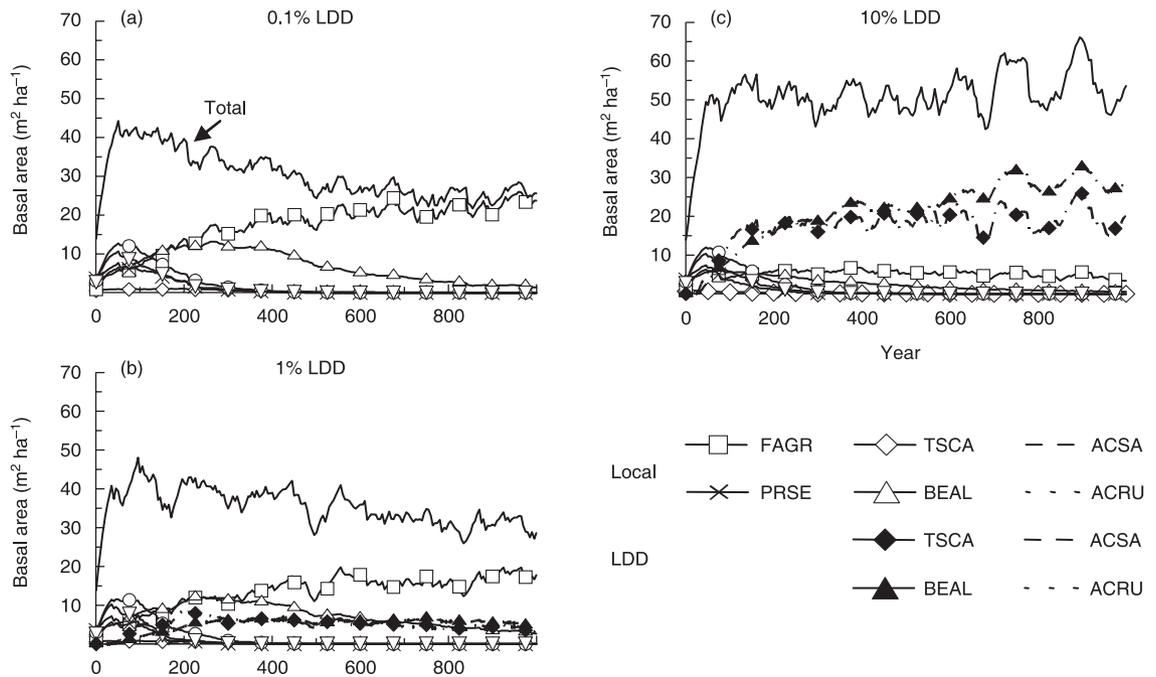
Fig. 8 Relationship between long-distance dispersal (LDD) and forest dynamics. The four smaller seeded species [BEAL (*Betula alleghaniensis*), TSCA (*Tsuga canadensis*), ACSA (*Acer saccharum*) and ACRU (*Acer rubrum*)] were assigned three different levels of LDD to test the importance of LDD to forest dynamics in forests with an established community (see text). (a) Low levels of LDD had no effect on local forest dynamics; (b) the abundance of LDD immigrants of the two establishment-limited species is approximately equal to the abundance from local dispersal; (c) at high levels of LDD relative to local dispesal, canopy dominance is defined by LDD dispersal ability and not shade tolerance. Initial conditions are described in Table 4. Values for LDD are defined by the assumption that the surrounding landscape matrix consists of a uniform distribution of 10 m² ha⁻¹ of each species. Values of κ refer to the percentage of seeds that are dispersed from the surrounding landscape into the plot. For clarity, only those species for which there was a noticeable contribution from LDD are shown.

small-seeded canopy tree species are thought to be more dependent on light, because seeds that land in the moist litter layer in canopy gaps are able to germinate and subsequently grow faster and survive better through the sapling stage than seedlings on decaying logs and other more favourable germination sites. We examined the influence of decaying CWD on canopy tree dynamics, both with and without disturbance, by removing the species-specific advantage of decaying CWD for the small-seeded species (i.e. *T. canadensis* and *B. alleghaniensis*; Table 3). This was undertaken in two ways: (i) decaying CWD was first made equally favourable for all species, then (ii) equally unfavourable. In the absence of disturbance, the results are consistent with empirical findings and show that the advantage given to establishment of small-seeded species on decaying CWD does not have a noticeable effect on canopy dynamics (Fig. 7c,d). Including disturbance, however, changes this. The ability of small-seeded species to establish on decaying CWD had a noticeable influence on successional dynamics (Fig. 7e–g). *B. alleghaniensis*, in particular, appears to be limited by establishment rather than light.

INTERACTIONS BETWEEN LDD AND SPECIES RESISTANCE TO DISTURBANCE

The LDD model is non-spatial and generates a species-specific, constant annual rate of seed rain (defined by

the parameter κ in eqn 5). There are precious little data on LDD in forest stands to guide us in setting reasonable values for κ. However, one modelling study found that as little as 0.1% of total fecundity dispersing further than 1 km increased the population dispersion rate 10-fold (Higgins & Richardson 1999). Our model and the dispersion model of Higgins & Richardson (1999) have different goals. Higgins & Richardson (1999) were interested in how rapidly trees can spread across a landscape and establish new populations; however, we are exploring how LDD influences the establishment and dynamics of a species within an existing community.

Our results clearly show an absence of an effect of LDD near the rates (0.1%) responsible for a 10-fold increase of geographical dispersion found by Higgins & Richardson (1999) (Fig. 8a). That is, none of the four LDD species established significant numbers of individuals via LDD. By contrast, long-distance immigrants of two of the wind-dispersed species (i.e. *T. canadensis* and *B. alleghaniensis*) quickly swamped the high LDD stand (10%, Fig. 8c). There was a noticeable and persistent increase in the abundance of *B. alleghaniensis* and *T. canadensis* in the 1% LDD stands over the 0.1% LDD conditions (Fig. 8b). There is no evidence that either of the maples benefited from LDD even at the 10% level (Fig. 8c). This suggests a spatial mass effect (Shmida & Ellner 1984) for *B. alleghaniensis* and *T. canadensis* somewhere between 0.1% and 1% LDD, but not for the two maple species,

which are present but uncompetitive at this site because of soil nutrient limitations (Kobe *et al*. 1995).

In our simulations, density independence of the LDD seed pool leads to one of two consequences (Clark & Ji 1995). Either diversity is high, because a continuous seed supply maintains less competitive species, or it is low, because more dispersal-limited, competitive species become more broadly established. Our simulations do not allow the latter as neither *F. grandifolia* nor *P. serotina* have effective LDD, and support the former only for extremely high LDD (Fig. 8c). In general, our results support the hypothesis that increased dispersal results in increased recruitment and abundance (see Turnbull *et al*. 2000), but they do not support the hypothesis that long-distance immigration maintains species coexistence (Hubbell *et al*. 2001) unless the immigration rate is very high (Fig. 8b). They are also consistent with predictions of lottery models (Chesson & Warner 1981) and Janzen–Connell escape hypotheses (Janzen 1970; Connell 1971) for *T. canadensis* and *B. alleghaniensis* because the high colonization rates of these species allow them to dominate the system (Fig. 8c, and less so for Fig. 8b). Nevertheless, for these effects to be important, the proportion of LDD relative to local dispersal must be very high.

Conclusions

Conceptual models of the effects of wind disturbance (e.g. Loucks 1970; Bormann & Likens 1979) have traditionally focused on the impacts of catastrophic disturbances and have painted a simple picture of how disturbance acts to maintain tree species diversity. Our results suggest that wind disturbance has much more complex and variable effects on long-term dynamics of forest structure and composition. In particular, non-catastrophic disturbances can generate important variations in forest dynamics that can either lead to dominance by a single or small number of species, or facilitate species coexistence. We have also shown that there are important scale-dependent characteristics of wind disturbance that depend at the landscape scale on the disturbance regime, and at the stand scale on the particular history of disturbances. Furthermore, our results fail to show evidence of simple tradeoffs between the effects of traits related to resistance to disturbance vs. colonization following disturbance. Diversity of structure and species composition is maintained by the stochastic nature of disturbance and complex interactions between: (i) species traits that govern resistance to disturbance, (ii) local dispersal and seedling establishment and (iii) competitive (i.e. shade tolerance) traits that strongly influence community responses to disturbance.

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