

# Large-scale spatial synchrony and the stability of forest biodiversity revisited

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## Abstract

### Aims

Mechanisms contributing to species coexistence have at least one of two modes of action: (i) stabilization of populations through restoring forces and (ii) equalization of fitness across individuals of different species. Recently, ecologists have begun gleaning the relative roles of these by testing the predictions of neutral theory, which predicts the properties of communities under pure fitness equalization. This null hypothesis was rejected for forests of southern Ontario based on large-scale (~100 km) spatial synchrony evident in the fossil pollen record over the entire Holocene, and the argument that a species' relative abundance would instead vary independently at such distances in the absence of stabilizing mechanisms. This test of neutral theory was criticized based on the idea that the synchrony might be produced by dispersal alone. Here, I revisit this test of neutral theory by explicitly calculating the synchrony expected in these forests using a novel simulation method enabling examination of the distribution of a species over large spatial and temporal scales.

### Methods

A novel neutral simulation algorithm tracking only the focal species was used to calculate the neutral expectation for spatial synchrony properties examined empirically by Clark and MacLachlan [(2003) Stability of forest biodiversity. *Nature* **423**:635–8] using fossil pollen data from eight lake sites. The coefficient of variation (CV) in a species' relative abundance across the eight sites (initiated at about 10% with a small CV) was calculated for 10 runs over a 10 000 year time interval. The CV reflects the level of spatial synchrony in that less synchronous dynamics should lead to more variation across space

(a higher equilibrium CV), and in particular, a greater increase in the CV over time from a small initial value. A 'two dimensional  $t'$  fat-tailed dispersal kernel was assumed with parameters set to the median derived from seed trap data for deciduous wind-dispersed trees. Robustness of results to assumed dispersal distance, density of trees on the landscape, site sizes, age at maturity and starting spatial distribution were checked.

### Important Findings

In contrast to the prediction of Clark and MacLachlan that, in the absence of stabilization, the CV across the sites should increase over time from levels observed at the beginning of the Holocene, under fat-tailed dispersal my neutral model robustly predicted only a brief (50 years) and small increase in the CV. I conclude that purely fitness-equalized species coexistence cannot be rejected based on the observed lack of increase in the CV across the eight sites in southern Ontario over the Holocene. Synchronous variation in environmental factors could alternatively explain the observed synchrony without the need for stabilization. However, neither dispersal nor environmental synchrony seems likely explanations for the quick wide-spread recovery of *Tsuga* in the Holocene after its seeming decimation, likely due to a pest outbreak.

**Keywords:** neutral theory • community dynamics • turnover

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## INTRODUCTION

A question that has important implications for the resilience of ecological communities under global change is how the coexistence of competing species arises. One hypothesis is that

'stabilizing mechanisms' cause species to rebound from low abundances and hence stave off extinctions (Adler *et al.* 2007; Chesson 2000a). Examples are when species are subject to frequency-dependent predation (Harms *et al.* 2000), providing a rare-species advantage, or when species differ in their

response to the environment and the environment fluctuates so as to be favorable for different species at different points in time and species' have a means to buffer their populations through rough periods, such as a seed bank (Chesson 1994, 2000b). The alternative is that the path to eventual extinction is slowed down by 'equalizing mechanisms' that cause species to be similar in per capita fitness but do not induce a tendency to rebound. Where species differ in important traits, fitness equalization is thought to arise through interspecific trade-offs that balance the advantages of one species against those of the others (Hubbell 2001). The result is that species' abundances undergo random 'ecological drift' brought about by chance birth, death and dispersal events.

Traditionally ecologists have focused on stabilizing species coexistence mechanisms, but the hypothesis of equalized species coexistence has gained more interest recently due to the development, preliminary successes and potential use as a null model of a 'neutral theory' predicting the properties of communities under this hypothesis of coexistence (Alonso *et al.* 2006; Bell 2001; Caswell 1976; Chave 2003; Hubbell 1979; Hubbell 2001; Leigh 1981; McGill *et al.* 2006; Rosindell *et al.* 2011). However, Clark and MacLachlan (2003) have claimed that fitness equalization can be rejected as the explanation for the coexistence of competing species in forests in southern Ontario, on the basis of the large-scale spatial synchrony in species' relative abundances observed there over the Holocene. Clark and MacLachlan argue that under equalizing mechanisms alone, a forest species' abundance would instead vary independently at sites separated by the large distances in their study (~100 km).

Large-scale spatial synchrony has been observed in the population fluctuations of many types of species (see Kendall *et al.* 2000 for references). The work of Clark and MacLachlan (2003) is unique in that it shows that populations can remain synchronous for very long time scales (hundreds of generations), over which the effects of ecological drift would be more pronounced. However, as pointed out by Volkov *et al.* (2004) one possible driver of large-scale spatial synchrony consistent with fitness equalization and ecological drift is dispersal (Kendall *et al.* 2000). Although in response Clark and MacLachlan (2004) argue that dispersal is unlikely to be the cause of synchrony over the large distance scale of their study, no quantitative analysis has been performed to determine whether dispersal alone could produce the synchrony they observed.

The purpose of this study is to carry out that analysis. I present a novel algorithm for keeping track of just one of the species in a community undergoing ecological drift, the key ecological process shaping communities under fitness equalization. This algorithm saves on computational time and memory compared with evolving an entire community to equilibrium, enabling the calculation of large-scale properties of the spatial distribution of a species within a community shaped by ecological drift. I use this algorithm to simulate the region studied by Clark and MacLachlan (2003). In particular, I ask if 'fat-tailed' dispersal (i.e. dispersal probability

decaying with distance slower than an exponential), which is necessary to explain the high rate of expansion of these forests upon the retreat of the glaciers at the end of the Pleistocene (Clark 1998), can also provide an explanation for the spatial synchrony observed by Clark and MacLachlan (2003).

I find that it can, and in particular that fat-tailed dispersal might even lead to a higher degree of spatial synchrony than Clark observed. This study contributes to the growing awareness of the importance of including the details of the dependence of dispersal on distance in neutral models if we are to use them as null models whose rejection indicates the importance of stabilizing mechanisms as well as of the additional predictions that can be derived through explicit inclusion of space (Chave and Leigh 2002; Chisholm and Lichstein 2009; Condit *et al.* 2002; Etienne and Rosindell 2011; O'Dwyer and Green 2010; Rosindell and Cornell 2007, 2009). In fact, the details of the dependence of dispersal on distance are just one aspect of what in the population genetics context is called 'demographic complexity' (Ackey *et al.* 2004; Strasburg and Rieseberg 2010; Wakeley 2004). This means essentially dependencies of birth and death rates on various system-specific details that do not necessarily involve stabilization or selection of a particular allele or species. Other examples in the community context include the presence of interspecific life history trade-offs that do not induce stabilization (Allouche and Kadmon 2009; Etienne *et al.* 2007; Lin *et al.* 2009; Ostling 2004, 2011), size structure (O'Dwyer *et al.* 2009; Ostling *et al.* unpublished results). Complexities of the speciation process (Etienne and Haegeman 2011; Etienne *et al.* 2007; Haegeman and Etienne 2009; Rosindell *et al.* 2010) are other aspects of 'demographic complexity' that must be considered, where the relevant demographic process is the birth of species. An important avenue of research is to identify which aspects of demographic complexity influence expectations under equal fitness, and where needed formulate system-specific neutral models that factor in these aspects of complexity, that can then be confidently applied as null models whose rejection indicates the presences of other mechanisms.

## MATERIALS AND METHODS

Using simulation, Clark and MacLachlan (2003) demonstrated that for independent communities undergoing ecological drift and initialized with approximately the same abundance of a given species, the coefficient of variation (CV) of the abundance of that species across the communities increases with time for hundreds of generations. To test for this pattern in real communities, Clark and MacLachlan used data on fossil pollen in lake sediments available from the North American Pollen Database at NOAA to determine the relative abundance of dominant tree taxa across eight distant sites over the Holocene (the past 10 000 years). The locations of the eight lakes they used, as well as their areas, and citations of original papers presenting data used are listed in Table 1. They are spread over a region of size 100 000 km<sup>2</sup> in southern Ontario. For each

of seven dominant tree families, Clark and MacLachlan calculated the variance and CV of the percentage of the total pollen coming from that tree family at each site. The CV was calculated for variation across the eight lake sites and plotted over time. As shown in Fig. 1, they found no consistent increase in the CV and increases in the variance arising only from increases in the mean pollen percentage. Hence Clark and MacLachlan rejected ecological drift as the primary shaper of the forest communities surrounding each one of these eight lakes over the Holocene and rejected fitness-equalized species coexistence in favor of stabilized species coexistence in these communities.

The CV reflects the degree to which the spatial dynamics of the large-scale forest community are synchronous in the following sense. The less synchronous the spatial dynamics are the higher the equilibrium CV should tend to be. In particular, if the CV starts out small, the more spatially independent the dynamics are the higher the CV should rise before reaching equilibrium. (Note, however, that a high CV and lack of decline in it may in itself not reflect in itself a lack of synchrony. In the presence of dynamics that are spatially synchronous due to mechanisms that do not involve dispersal, the CV could be initially large due to some inherent differences between sites and remain large due to those differences.) Note that Clark and MacLachlan mainly emphasized the lack of consistent increase in the CV calculated from the fossil pollen data and did not consider the observed magnitude of the CV. Here, I will consider both the trend and the equilibrium magnitude of the CV under neutrality in comparison to observations.

To determine if the observed lack of consistent increase in the CV could arise under ecological drift through dispersal and compare values of the CV predicted at equilibrium to those observed, I considered these eight sites as part of a forest metacommunity linked by dispersal. I used a single species simulation method based on the same dynamics of the community as the simulation method of Clark and MacLachlan, but with

dispersal through space explicitly included. Specifically, individuals in the metacommunity die at random with equal probability and are replaced by an offspring of an individual in the surrounding community. Clark and MacLachlan assumed that establishing offspring are from a parent individual within the same local site around the lake. I instead choose parent individuals from the metacommunity according to a dispersal probability that depends on distance.

Below I describe the details of the single species simulation algorithm I used and the parameter choices I made for the dependence of dispersal on distance, the density of trees on the landscape, the size of the community contributing to the fossil pollen at each lake, the time to reproductive maturity and the initial spatial distribution. Overall, my parameter choices were aimed at obtaining an upper bound prediction of the spatial variation expected under ecological drift. I performed additional simulations to determine the sensitivity of predictions to these parameter choices and verify that an upper bound was obtained. I used the simulation method described below to calculate the CV in a species' abundance across the eight lake sites, over time.

Because these simulations are computationally time consuming (~12 h per 10 000 years), I performed a limited number of them (10 runs with the main parameter choices for each type of dispersal, additional single or multiple runs to study sensitivity to parameter choices). In order to obtain a measure of the average spatial variation on the landscape with less statistical variability than the eight-site CV, I also calculated mean and confidence interval of the CV of a species' abundance across pairs of sites at large distances from one another, where the mean was taken over 100 pairs.

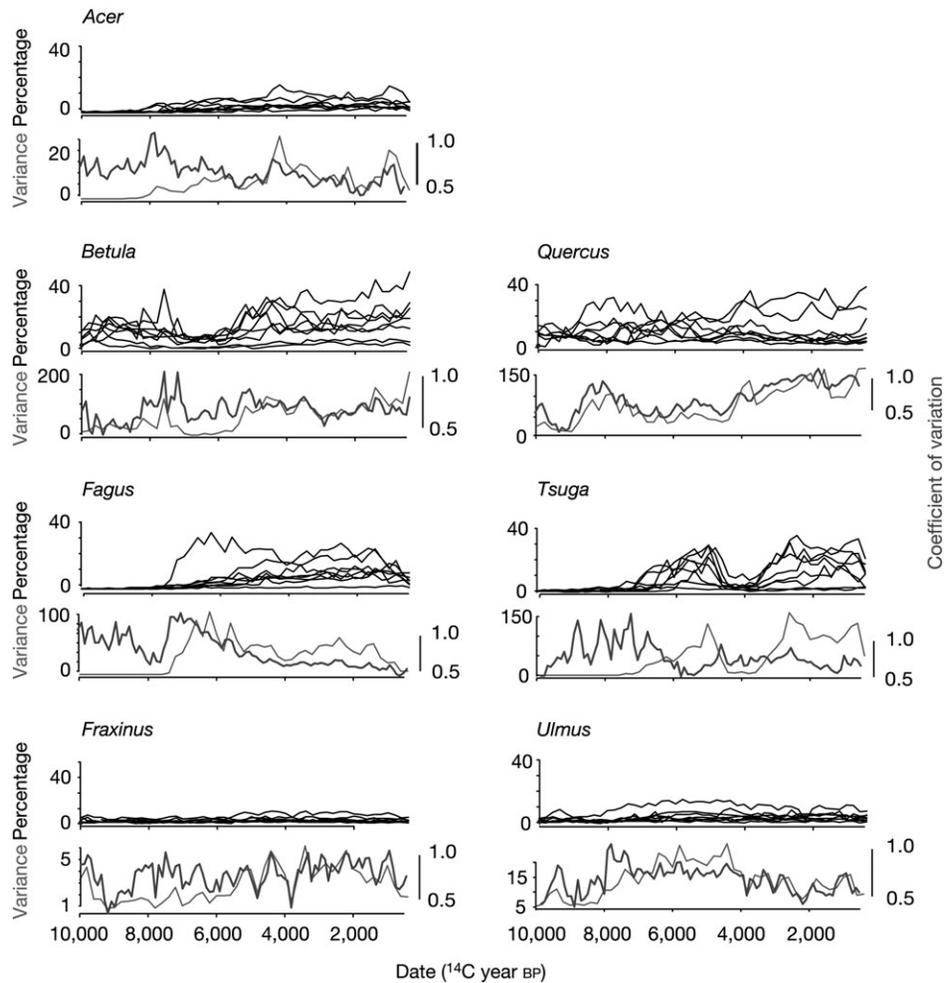
### Single species simulation algorithm

Neutral theory in ecology is intended to describe groups of species that are tropically similar, and hence, it is based on a model in which species are competing for resources. In particular, current neutral models are typically based on a 'lottery'

**Table 1:** location, area, pollen source area and citations for fossil pollen data for each lake in this study

Site	Latitude (°N)	Longitude (°W)	Area (ha)	Pollen source area (ha)	Citation
Lac Bastien	46.24.00	78.55.00	80	1840	Bennett (1987)
Decoy Lake	43.14.00	80.22.00	0.42	2	Szeicz and MacDonald (1991)
Graham Lake	45.11.00	77.21.00	2.5	33	Fuller (1995, 1997, 1998)
Hams Lake	43.14.12	80.24.48	24	820	Bennett (1987) and McAndrews and Campbell (1993)
High Lake	44.31.00	76.36.00	2.5	33	Fuller (1995, 1997, 1998)
Nutt Lake	45.13.00	79.27.00	80	1840	Bennett (1987)
Second Lake	44.51.00	79.58.48	40	33	Burden (1978) and Burden <i>et al.</i> (1986a, 1986b)
Tonawa Lake	44.51.00	77.10.30	??	33	McAndrews and Campbell (1993)

The location and area of the lakes from which Clark and MacLachlan (2003) used fossil pollen data (listed in alphabetical order) are shown. Also listed is the pollen source area I estimated for each lake based on a model of catchment length by Jacobson and Bradshaw (1981). The source areas in parentheses are conservative guesses I used in carrying out my simulations before I could track down information on the area of those lakes. I have as yet been unable to track down the area of Tonawa Lake. Finally listed are citations of the original papers presenting the fossil pollen data for each lake. All fossil pollen data can be obtained from the North American Pollen Database (<http://www.ngdc.noaa.gov/paleo/pollen.html>).



**Figure 1:** observed percentage, variance and CV for tree taxa across eight lake sites over Holocene. Percent pollen (in upper graphs) and (in lower graphs) variance (in red or gray) and CV (in blue or black) of percent pollen across the eight lake sites in Table 1 over the Holocene are shown for seven dominant tree taxa. Note in particular the widespread decimation and recovery of *Tsuga*. Reprinted by permission from Macmillan Publishers Ltd.: Nature, Clark and MacLachlan (2003).

competition model in which competition occurs at replacement events, i.e. offspring compete to fill in sites that become vacant upon death events. Another way of putting this is that most current neutral models assume ‘zero-sum dynamics’, in which the total community size stays fixed (Etienne *et al.* 2007). This assumption is essentially one of ‘contest’ competition, meaning that individuals either have all the resources they need or no resources at all. This contrasts with ‘scramble’ competition, in which high densities cause decreased reproduction and survival of all individuals. ‘Scramble’ competition is the same thing as what some neutral theorists call ‘community-level density-dependence’. So far this mode of competition has not been fully incorporated into neutral models (but see Haegeman and Etienne 2008 and Haegeman and Loureau 2011 for some progress toward this end). Here, I also consider a neutral model based on ‘lottery’ competition. However, it seems unlikely that this detail would have more than a small influence expected patterns of spatial synchrony.

Specifically, the community dynamics I consider are as follows (note that a novel algorithm for calculating the consequences of these dynamics for a particular species is presented below). There are a fixed number  $N$  of individuals in the community laid out in space on a grid. In each time step:

- (i) individual at a randomly chosen location  $\bar{x}$  dies, then
- (ii) that individual’s location is colonized by either:
  - a. a new species (the occurs a fraction  $v$  of the time, where  $v$  is the speciation rate) or
  - b. the offspring of an individual at location  $\bar{y}$  according the probability  $p(|\bar{x} - \bar{y}|)$

where  $p(r)$  is called the ‘dispersal kernel’ and describes the probability that an offspring disperses a distance  $r$  from its parent. In this model, individuals of different species are ecologically equivalent—the rules governing an individual do not depend on species identity. The commonly used method for calculating the predictions of this model is to evolve the

community from some starting point to equilibrium (as defined by no consistent directional changes in community-level properties like the number of species and the species-abundance distribution) multiple times and then calculate the average properties of the equilibrium community configurations obtained (Bell 2001; Chave *et al.* 2002; Hubbell 2001).

To calculate predictions of spatial synchrony under these neutral dynamics, Clark and MacLachlan (2003) essentially used a spatially implicit version of this model in which each of the eight lake sites mentioned above are independent local communities, completely isolated from one another. This assumption vastly saved on computation time. Since they were interested in the properties of a particular species over a limited time frame, Clark and MacLachlan also ignored the speciation process and did not need to evolve the community in time all the way to equilibrium but instead just track the community over the time period of interest. This further saved on computation time.

The novel computational method used here draws on the latter part of the approach of Clark and MacLachlan (simply looking at the dynamics over some particular time frame) but not the former, since the aim is to explicitly account for dispersal. To further save on computation time so that dispersal could be explicitly accounted for, the algorithm here takes advantage of the realization that when one evolves through time the whole community, the distribution of one particular species will change only some of the time and what happens to the rest of the species in the intervening time is irrelevant.

In addition, it takes advantage of the fact that when something does happen to the species of interest, it will either lose an individual or gain one and that these will occur with about equal probability (i.e. each with probability about 1/2) (see online supplementary material, Appendix 1). Losing an individual happens slightly more often because it can occur through speciation as well as normal death and replacement events. That tiny difference can be ignored for our purposes here (but could be included for more general purposes). Furthermore, when the species loses an individual, the individual lost will essentially be a randomly chosen one of the species' individuals. (See online supplementary material Appendix 2 for information on why this is an approximation and the exact algorithm used here for choosing the individual that is lost. But note that there seems to be little difference in the results here when this simpler version is used.) When it gains an individual, the location at which the individual is gained can be chosen essentially by choosing the parent of the new offspring at a random location  $\bar{x}$ , where the species is already present and then choosing another location  $\bar{y}$  according to the dispersal probability  $p(|\bar{x} - \bar{y}|)$  with the constraint that  $\bar{y}$  cannot be a location, where the species is already present. (See online supplementary material Appendix 2 for the slight modification to this needed to make it an exact representation of the spatial dynamics.)

In summary, algorithm for the dynamics of a single species within a community undergoing ecological drift is as follows. In each time step, there are two choices as to what happens to the species' distribution, each with the same probability (1/2):

- (i) the species loses a randomly chosen individual or
- (ii) the species gains an individual at site  $\bar{y}$  chosen with probability  $p(|\bar{x} - \bar{y}|)$ , where  $\bar{x}$  is the location of a randomly chosen individual of the species and  $\bar{y}$  is a location at which the species is not already present.

This algorithm saves on both computational time and memory for the problem at hand compared with simulation of the full community. For a species whose relative abundance is 10%, it means ~90% less computation since one need not worry about what is happening to the rest of the community. It also means lower memory requirements, since one need not keep track of the species identity at each location on the landscape, just the presence or absence of the species, requiring only one bit per location. This algorithm is well suited to the consideration of properties changing over or influenced largely by processes acting on ecological time scales. If one is concerned with the properties of a neutral community for which longer time scale processes such as speciation play an important role, a coalescence computational approach (Rosindell *et al.* 2008) is much more appropriate and efficient.

Note that this algorithm assumes the distribution of the species of interest changes in some way in each simulation time step. Due to this assumption, the amount of real time that a simulation time step corresponds to depends on the abundance of the species. Specifically, the length of a time step  $\Delta t$  in units of 'turnovers' of the community (the amount of time it takes for  $N$  individuals to die and be replaced, where  $N$  is the metacommunity size) should on average be

$$\Delta t = \frac{p_{\text{same}}^k}{1 - p_{\text{same}}^k} \frac{1}{N} \quad (1)$$

In Equation (1)  $p_{\text{same}}^k$  is the probability that the distribution of species  $k$  would not change in a death and replacement event, given its current configuration.  $N$  is the total number of individuals in the community. The rationale behind Equation (1) is as follows. The probability  $p_{\text{same}}^k$  can be thought of as the rate of death and replacement events for which species  $k$ 's distribution does not change, divided by the total rate at which death and replacement events occur. The probability  $1 - p_{\text{same}}^k$  can similarly be thought of as the rate at which death and replacement events for which species  $k$ 's distribution does change, divided by the total death and replacement rate. (Note these interpretations arise from thinking of the discrete time formalism as essentially the Gillespie algorithm (van Kampen 2007) for a continuous time formulation of the model involving rates at which different types of death and replacement events occur.) Given this interpretation, for every death and replacement event that changes the distribution of species  $k$ , there will be on average  $p_{\text{same}}^k / (1 - p_{\text{same}}^k)$  events that do not change the distribution of species  $k$ , since this ratio can be thought of as just the ratio of the rates at which these two types of death and replacement events occur. Hence, the amount of time between death and replacement events that change the distribution of species  $k$  should be equal to

the average time between each death and replacement events ( $1/N$ ) times this factor reflecting the number of events that must have occurred on average while waiting for an event that actually changes the distribution. Technically,  $p_{\text{same}}^k$  depends on both the number of individuals of the species present and their spatial locations (see online supplementary material Appendix 1 for an exact expression for  $p_{\text{same}}^k$ ), but in practice, I found little difference (5%) between its exact value and the following global dispersal approximation:

$$p_{\text{same}}^k = \left(1 - \frac{n_k}{N}\right)^2 + \left(\frac{n_k}{N}\right)^2 \quad (2)$$

(the probability no individuals of species  $k$  die and none have their offspring replace the individual that did die, plus the probability that an individual of species  $k$  does die but is simply replaced by another individual of species  $k$ ). Using this expression allowed for faster computation. Since the only effect of error in the value of  $p_{\text{same}}^k$  is to make the actual time corresponding to simulation time be greater or lower by that error—a difference of little consequence for the goals here—I used the global dispersal approximation.

### Dispersal kernels

I ran simulations with two possible descriptions of the dependence of dispersal on distance—(i) Gaussian and (ii) fat tailed—and compared with the case of independent local sites. The specific ‘dispersal kernels’ I used are shown in Fig. 2. Information on Gaussian dispersal kernel fit parameters for temperate species was not directly available in the literature. I used a mean dispersal distance  $\sigma = 40$  m, which is the average  $\sigma$  across species of fits to seed trap data for a tropical forest plot in Panama (Condit *et al.* 2002). Based on fits to the fat-tailed dispersal kernel, tropical forest species’ mean dispersal distances fall in the mid range of those for temperate deciduous and conifer species, and hence, this choice provides a reasonable central-tendency description of those species.

To model fat-tailed dispersal, I used a ‘two-dimensional  $t'$  ( $2Dt$ ) distribution, which combines the concave shape of a Gaussian at small distances with the ‘fat-tailed’ shape of dispersal kernels typically used to describe the large-scale dispersal relevant to population spread. The form of this distribution is shown in Fig. 1. It arises from the Gaussian distribution if  $\sigma$  is allowed to vary according to a particular distribution described by two parameters labeled  $u$  and  $P$  (see Clark *et al.* 1999 for details). Clark *et al.* (1999) have shown that this distribution provides a better fit to seed trap data than either a Gaussian or an exponential for most of the temperate and tropical forest tree species examined. In addition, Clark (1998) has argued that the rapid rates of tree migration ( $10^2$ – $10^3$  m/year) are unexplainable unless dispersal has a ‘fat’ tail that decays slower than an exponential. I used  $u = 300$  m<sup>2</sup> and  $P = 0.5$ , the median value for deciduous wind-dispersed species obtained from fits of the  $2Dt$  model to seed trap data (Clark *et al.* 1999). Animal dispersal is not captured well by seed trap data, and hence, good estimates of the parameters describing animal-dispersed species are not

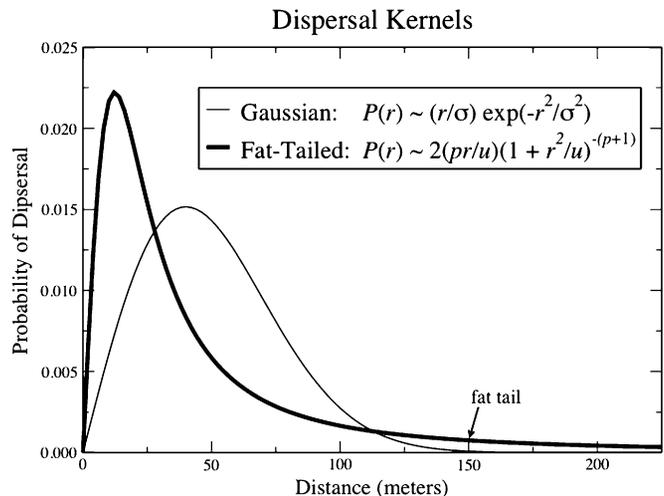
available. Figure 2 shows that for these choices of dispersal parameters, the  $2Dt$  distribution produces higher probabilities at local scales and at large scales, whereas the Gaussian yields a higher probability of dispersal distances 30–120 m. To study the sensitivity of the results to the value of  $u$ , I also performed a simulation with  $u = 30$  m<sup>2</sup>.

### Landscape size and density

I simulated an  $\sim 3.5^\circ$  latitude  $\times$   $4^\circ$  longitude (or  $390 \times 325$  km) area in which the eight lake sites used by Clark and MacLachlan are contained as a contiguous metacommunity. I used a density of 49 adult trees/ha, leading to a spacing of 1 tree per 14.3 m. This density is about an order of magnitude lower than the observed canopy density (400 trees/ha) in mature forests of this type (namely mixed broadleaf–coniferous) (Frelich *et al.* 1993), and hence, my simulations are of a coarse-grained version of the landscape in which each simulated individual represents 10 actual trees. One could argue that such coarse graining will produce an upper bound on the expected variation across space because it ignores the correlations that arise from repeated dispersal at distances less than the tree spacing modeled. To verify this trend, I performed simulations at even lower densities (12 trees/ha and 3 trees/ha) to uncover the trend of predicted spatial variation with simulated density.

### Site sizes and site coordinates

I put the origin of the grid in my simulation at  $43.00.00^\circ\text{N}$ ,  $80.30.00^\circ\text{W}$  and fixed the location of the eight lake sites



**Figure 2:** dispersal kernels used: Gaussian versus fat-tailed. Spatially explicit simulations of ecological drift were carried out using the two dispersal kernels shown, namely a Gaussian model and a particular fat-tailed model called the ‘ $2Dt$ ’ distribution. The parameters for the kernels used in simulations (and plotted here) are as follows (see text for justification):  $\sigma = 40$  m,  $u = 300$  m<sup>2</sup>,  $P = 0.5$ . Note that the Gaussian produces higher probabilities of intermediate dispersal distances 30–100 m, whereas the fat-tailed distribution produces higher probabilities of both local and long-distance dispersal.

according to their latitude and longitude in Table 1. In my simulation, each 'lake site' was a contiguous square region equal in area to the pollen source area of the particular lake. Hence, I ignored the fact that the trees at a particular lake site are actually positioned around the lake. Hence, I disregarded any patchiness caused by the lake itself. I used a conservatively small estimate for the pollen source area for each of the eight lake sites in study of Clark and MacLachlan. The distance range from which most pollen in a lake sediment travels is sensitive to the size of the lake as well as the tree taxa. I used a model of catchment length that is based on the transport of pollen through runoff and dry and wet deposition (Jacobson and Bradshaw 1981). Specifically, I used 50 m for Decoy Lake (~50 ha); 250 m for Graham and High Lakes (each 2.5 ha), 1500 m for Hams Lake (~25 ha) and 2000 m for Lac Bastien and Nutt Lake (each ~80 ha). For Second Lake and Tonawa Lake, I used a conservatively small area of 2.5 ha, while I awaited information on the actual areas (which was not readily available) and hence used a catchment length of 250 m for these lakes. The source area for each lake was modeled as a square region equal in area to a ring around each lake, with ring width set to the catchment length just listed. The resulting source area estimates are shown in Table 1. The catchment lengths I used are conservatively small compared to what has been measured in empirical studies (Davis 2000), however, one would expect variation across sites to decrease with site sizes, and hence for this choice to lead to an upper bound on that variation. To verify this, I also performed simulations with all source areas set to the second smallest source area and to the largest source area.

### Turnover time and time to maturity

To calculate the amount of real time corresponding to simulation time, I assumed a turnover time of 50 years. Longer turnover times would lead to fewer turnovers in a given time frame, and hence less likelihood for a species' relative abundance to diverge at distant sites within that time frame. The time it takes for individuals to reach reproductive age can have important effects on the rate of population spread under fat-tailed dispersal (Clark 1998). To account for the potential effects of time to maturity on the degree of spatial synchrony, I incorporated an age cut-off, below which an individual could not be chosen as a parent, into my simulation algorithm. I performed simulations with this age cut-off set to 0, 10 and 20 years.

### Initial spatial distribution

Allowing the species to evolve from a one individual (its abundance at speciation) to an abundance high enough that the species populates most of the lake sites took too much computation time for calculations on this large region. Instead I initialized the abundance of the species at 10% of the individuals in the region, large enough for the species to be one of the most dominant and the same as the initial value at each site Clark and MacLachlan used in their simulations. In order to assess the potential effects of initial spatial aggregation on predictions

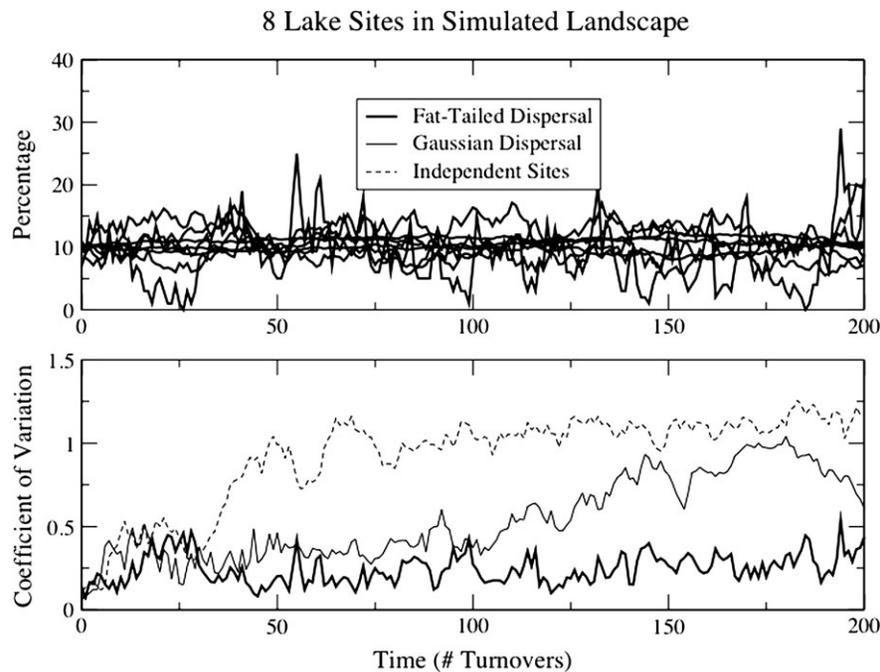
of spatial synchrony, simulations were performed with two extreme possibilities for the starting spatial distribution: (i) a statistically uniform distribution created by randomly placing individuals and (ii) a tightly clumped distribution created using the Poisson cluster process. The Poisson cluster process distributes individuals into  $\rho$  clusters per unit area with distance from the center of the cluster following a Gaussian distribution with mean  $\alpha$  (see Plotkin *et al.* 2000 for details). I picked values of  $\rho$  and  $\alpha$  that provided a spatial distribution that was visually much more clustered than randomly placed individuals when ~10 km<sup>2</sup> of the region were viewed, specifically  $\rho \approx 5$  km<sup>2</sup> and  $\alpha \approx 100$  m. The initial CV across the lake sites was determined by the initial spatial distribution.

## RESULTS

### The CV over time under different dispersal assumptions

Figure 3 shows the results of single simulations of the 10 000 years (or 200 community turnovers) of the Holocene for the eight lake sites, using the estimated pollen source areas in Table 1. The upper panel shows the percent abundance of the species at each of the eight sites under one run of 10 000 years with fat-tailed dispersal. The lower panel shows the CV across the eight sites under fat-tailed dispersal, Gaussian dispersal and the case where the eight lake sites are modeled as independent local entities with no linkage to a metacommunity, each for one run of 10 000 years. As shown by Clark and MacLachlan (2003), in the case of independent sites, the CV increases substantially with time from its starting value (generated by the random spatial distribution). The CV also increases with time, although to a lesser degree, under Gaussian dispersal. However, under fat-tailed dispersal, the CV does not increase substantially with time from its low starting value. The equilibrium value of the CV in this case is not much higher than the starting CV, and it is approached very quickly, both presumably due to the high degree of spatial mixing under a fat-tailed dispersal kernel. In fact, throughout all of the 10 simulations performed under fat-tailed dispersal, the CV across the eight sites rarely achieved values as high as those observed in Fig. 1.

Figure 4 shows the trend of the average spatial variation with time from a single simulation under each of the descriptions of dispersal. Specifically, it shows the mean and the 95% confidence interval of the mean CV of pairs of sites of size 200 ha separated by ~150 km. Figure 4 indicates that if the pairs of sites are taken to be independent local communities, the CV of the abundance across the two sites will on average increase steadily and substantially over a time period of 200 community turnovers when it begins at a value created by a random spatial distribution. A steady but shallower increase with time in this paired-site CV also occurs in a metacommunity linked by Gaussian dispersal. In contrast, under fat-tailed dispersal, the paired-site CV increases over its value for the initial randomly placed species distribution for only a brief time, arriving



**Figure 3:** effect of dispersal on the temporal trend of the CV across the eight lake sites. The upper panel shows the percent abundance of the species at each of the eight lake sites over time under one simulation run of ecological drift with fat-tailed dispersal. The lower panel shows the CV of the species' abundance across the eight lake sites over time from single simulation runs of ecological drift with fat-tailed dispersal, Gaussian dispersal and for the case where the eight lake sites are taken to be independent local communities, as in Clark and MacLachlan (2003). Time is measured in the number of turnovers of the community that have occurred. Results shown are for the age cut-off set to 10 years.

at what appears to be an equilibrium value of about 0.13 by no later than 50 turnovers of the landscape.

The results just described were consistent across the simulation runs performed with each type of dispersal (results shown in Figs S1–S3, see online supplementary material). In addition, the paired-site CV is fairly insensitive to the distance chosen between the two sites in the pair, with only an  $\sim 15\%$  difference between the mean for 2 km and the mean for 150 km. All of the values plotted in Figs 3 and 4 were from simulations with a landscape density of 49 individuals/ha and in which the species was initialized with a statistically uniform distribution (i.e. a 'random' spatial distribution).

### Robustness to dispersal distance, density, site size, time to maturity and initial spatial distribution

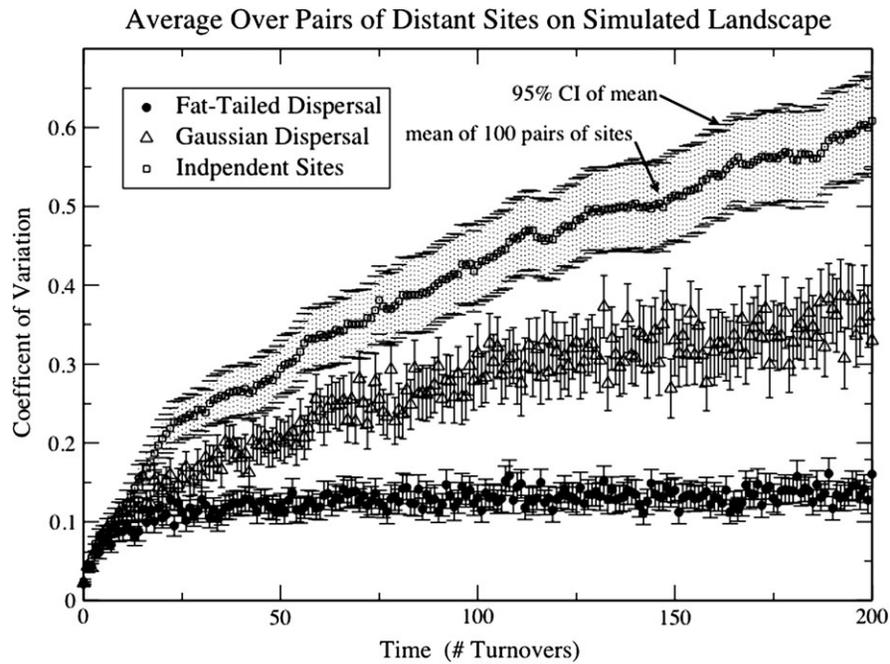
The same basic result of a lack of substantial increase with time in the CV in a species' abundance across distant sites under fat-tailed dispersal is obtained in simulations with  $u = 30 \text{ m}^2$  or with lower model densities or with smaller and larger site sizes. The CV ends up only slightly higher with  $u = 30 \text{ m}^2$  than with  $u = 300 \text{ m}^2$  (average CV over pairs after 10 000 years was 0.17 vs. 0.12), and hence, there is still only a small increase through time as compared with the Gaussian and independent site cases. The CV was found to decrease with increasing density and increasing site sizes, indicating that the results presented above (for a coarse-grained landscape with conservatively small site sizes) provide an upper bound on this measure of

spatial variability. Interestingly, the time to maturity had no noticeable effect on the large-scale CV.

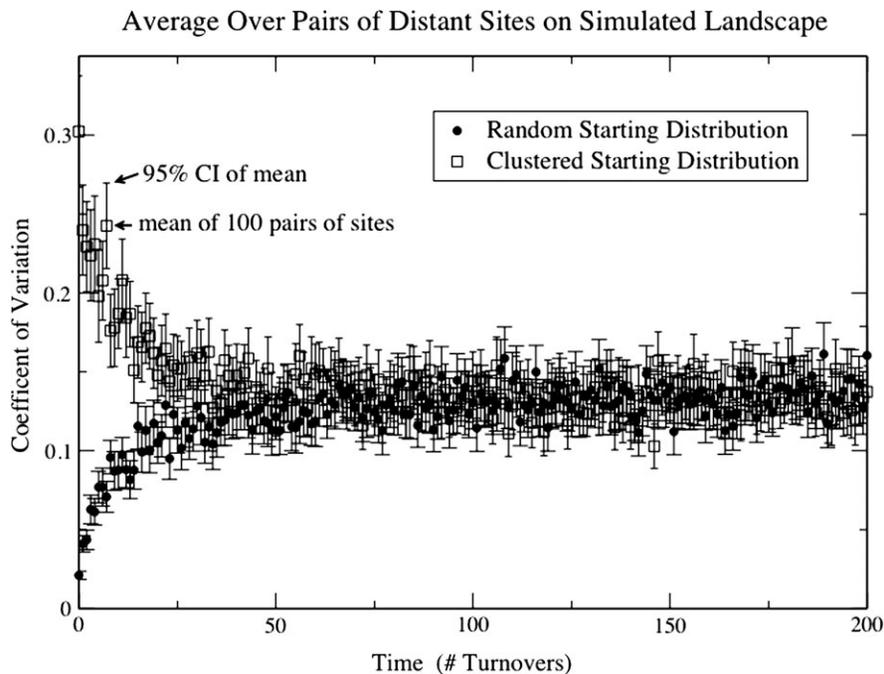
The results presented above are also robust to the initial spatial distribution of the species. Figure 5 compares the average spatial variability over time in the clustered and random starting distribution cases under fat-tailed dispersal. After about 50 turnovers, the mean CV at a scale of 150 km is independent of the starting configuration. In the case of an initial spatial distribution with intraspecific clustering, the CV decreases with time at first. In addition, despite an initial contrast, after 40 turnovers the spatial distribution with these two different starting conditions appeared indistinguishable upon visual inspection (see Fig. S4, online supplementary material). Hence, it appears that under fat-tailed dispersal the spatial distribution of the species quickly arrives at an equilibrium that is independent of its starting point.

## DISCUSSION

An understanding of the fundamental dynamics shaping communities is pivotal to predicting how they will behave under global change. Mechanisms that contribute to the coexistence of competing species have at least one of two possible modes of action (Adler *et al.* 2007; Chesson 2000a): (i) stabilization and/or (ii) fitness equalization. On the basis of the large-scale spatial synchrony in species' abundances observed in southern Ontario forests over the Holocene, Clark and MacLachlan



**Figure 4:** effect of dispersal on the average spatial variation on the landscape and its trend in time. The trend with time under ecological drift of the mean CV of a species' abundance across pairs of sites of size 200 ha separated by 150 km, from landscapes simulated with fat-tailed dispersal, Gaussian dispersal and assuming that the two sites in the pair are independent local communities. Again results are shown for age cut-off 10.



**Figure 5:** robustness of average spatial variation at equilibrium to initial spatial distribution. This figure shows the mean CV of a species' abundance across pairs of sites of size 200 ha separated by 150 km under fat-tailed dispersal and two extremes of the initial spatial distribution: randomly placed and clustered. Although the initial CV is quite sensitive to the starting distribution, after about 50 turnovers of the landscape it is independent of the starting spatial distribution.

(2003) argued that community dynamics there could not be governed by fitness equalization alone. In contrast, the results presented here indicate that this synchrony could have arisen

under purely fitness-equalized species coexistence if dispersal is fat tailed. Specifically, using a novel method for simulating the dynamics of one species in a fitness-equalized community

that enables the calculation of large-scale spatial properties, I have shown that the CV in a tree species' abundance across sites separated by ~100 km could maintain a constant average value over a time frame the length of the Holocene under pure fitness-equalization with fat-tailed dispersal.

Contrary to the implication by Clark and MacLachlan (2003), trade-offs between species are an important component not only of stabilizing species-coexistence mechanisms but also of fitness-equalizing coexistence mechanisms. The recent development of theory of fitness-equalized communities (i.e. 'neutral theory' in ecology) has focused on the case where individuals of different species are completely ecologically equivalent (Bell 2001; Hubbell 2001). However, in many communities, species do differ in important traits, and when they do fitness-equalization can only occur through an interspecific trade-off. An example of a trade-off that exists in many plant communities and can lead to fitness-equalization, but not stabilization, is a trade-off of per capita recruitment with per capita survival (Moles and Westoby 2004a, 2004b; Ostling 2011).

The lack of substantial increase in the CV under fitness equalization with fat-tailed dispersal found in this paper is obtained from a model in which fitness equalization arises through ecological equivalence of individuals. The novel simulation method employed might be generalizable to cases where fitness equalization arises through a trade-off but that was not carried out here. However, one can qualitatively argue that the same result would also arise under at least one other case of fitness equalization and probably more. Under the recruitment-survival trade-off just discussed, the same lack of substantial increase in the CV with time would be expected. This is because for species with low recruitment and high survival rates, the spatial dynamics would essentially be slowed down and for those with high recruitment and low survival, they would be sped up. But there is no obvious reason why the value of the CV eventually obtained for either type of species would be any different than that found in the simulations here. Hence, the possibility of pure fitness equalization demonstrated here would not necessarily involve the total absence of interspecific trade-offs but instead would mean the absence of the sort of interspecific trade-offs that stabilize (as well as the absence of other types of stabilizing mechanisms).

Note that in this study the forests of southern Ontario were modeled as a contiguous metacommunity. The patchiness of habitats on the landscape could have important effects on the spatial variability of a species' relative abundance at large scales. It is known that sizable areas of the forests in southern Ontario were replaced by Oak savanna in the mid-Holocene (about 4000–6000 years ago) (Szeicz and MacDonald 1991). It is possible that if one factored in this and other patchiness that may have existed in southern Ontario forests in the Holocene, one would in fact expect an increase in the CV under fitness equalization. Furthermore, one might be able to reject the hypothesis of fitness equalization based on the association of different tree taxa with the values of abiotic hab-

itat variables. In fact, one might even be able to uncover some interesting dynamical habitat associated range structure over the Holocene, adding an interesting new dimension to the types of range structure patterns recently reported for only one point in time for South America (Graves and Rahbek 2005). Such patterns indicate some degree of niche differentiation and likely stabilization at play, at least at landscape scales (Ostling 2005). However, rejecting the possibility of fitness equalization on this basis of an expectation of an increasing CV due to patchiness of forest habitat would require information about the structure of the landscape over the Holocene at a level of detail not currently available. Rejecting it on the basis of habitat associations through time would additionally require information on key abiotic variables at large spatial scales over the Holocene.

Volkov *et al.* 2004 also disputed rejection of Clark and MacLachlan of fitness-equalized coexistence in southern Ontario forests based on even simpler grounds than that linkage through the metacommunity could stabilize the CV. They argued that even if distant sites could be modeled as independent, the variance and CV of a species' abundance would not increase perpetually under fitness-equalization but instead would eventually fluctuate around an equilibrium value. This is true, and indeed, the independent site simulations that I performed do not provide a clear sense that the observations could not be explained under that scenario. When the CV is initialized using a random spatial distribution, the mean CV across two independent sites continues to increase for the full length of the 1000 community turnovers or 50 000 years examined (see Fig. S5, online supplementary material). The tree species only began expanding into southern Ontario with the recession of the glaciers beginning at the end of the Pleistocene (about 15 000 years ago), so this makes it seem unlikely that the large-scale CV for species would have reached equilibrium by 10 000 years ago. However, the CVs observed starting at 10 000 years ago (see Fig. 1—for many of the taxa the CV is 0.5 or higher) are typically much higher than the initial CVs in my simulation. So the time it would take for the CV to become close to its equilibrium value would actually be shorter than the 50 000 years. Furthermore, my simulation used conservatively small site sizes, so the equilibrium CV under independent site may actually be larger than that seen in these simulations, and hence the time to equilibrium under that scenario shorter. So the observations may not indicate large-scale spatial synchrony at all.

Besides fat-tailed dispersal, there is another possible explanation for large-scale spatial synchrony, if it is present, that is consistent with 'unstable' coexistence. Large-scale spatial synchrony could arise because species' relative abundances are affected by environmental conditions and there is large-scale spatial synchrony in the environment. This provides an explanation for spatial synchrony that involves large changes in a species' relative abundance like some of those observed over the Holocene. In my simulations, a species' relative abundance

simply does not fluctuate all that much over a time scale comparable to the Holocene under fat-tailed dispersal. If a given set of regional environmental conditions favors one species over others (i.e. leads to unequal fitness), that species will have synchronous increase in its relative abundance. The difference in fitness may be small enough that other species can persist with this superspecies for a long period of time, long enough for their regional environment to change and for species' relative fitnesses to change again. These types of changes can occur without their being a consistent means by which a species' population size is buffered (or 'stabilized') through the rough times in the region (i.e. without the existence of the 'storage mechanism' studied by Chesson 1994). Furthermore, if the dispersal of these tree taxa is indeed fat tailed with parameters comparable to those I used here (chosen based on fits to seed trap data in Clark *et al.* 1999), some kind of responses to the environment and some degree of spatial asynchrony in the environment must be invoked to explain observed CVs across the eight sites substantially higher than simulated values (compare Figs 1–3).

Either fat-tailed dispersal or large-scale synchrony in key abiotic variables could explain the observed patterns of spatial synchrony in abundance for most of the tree taxa in Fig. 1 but not all. *Ulmus* and *Fraxinus* exhibited fairly constant relative abundance, consistent with fitness equalization maintained throughout the Holocene and fat-tailed dispersal. The abundance of *Acer*, *Betula*, *Quercus* and *Fagus* slowly increased, fairly consistently across sites, perhaps due to a change in a key environmental variable at large scales. However, *Tsuga* (or Hemlock) exhibited dramatic changes in relative abundance, being just about decimated at all sites about 5000 years ago and then recovering at all of the lake sites soon after. This decimation and recovery of a species would happen very infrequently under fitness-equalized species coexistence. Furthermore, there is no obvious change in the abiotic environment that occurred at large scales to explain these changes in fitness of Hemlock. Other lines of evidence (macrofossils showing insect damage) (Bhiry and Filion 1996) support the hypothesis that a pest outbreak and crash caused the Hemlock's decline and eventual recovery. The most plausible explanation at hand for its quick recovery is indeed some sort of 'stabilizing mechanism', in which Hemlock was able to reclaim the niche that became empty in its absence.

An interesting future line of research is to quantify just how unlikely such decimation and recovery is under fitness equalization, in order to provide a quantitative measure by which to reject this hypothesis for the interaction of Hemlock with other tree taxa over the Holocene. Another potentially important line of future research is to employ the approach developed here of incorporating system-specific details and realistic dispersal, as well as the novel simulation algorithm, for re-evaluating and providing more strength to other recent tests of neutral theory involving large scale spatial and temporal dynamics (e.g. McGill *et al.* 2005; Wootton 2005), as well as for testing neutral theory in other contexts.

## SUPPLEMENTARY MATERIAL

Supplementary Figs S1–S5 and Appendices are available at *Journal of Plant Ecology* online.

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