FECUNDITY AND DISPERSAL IN PLANT POPULATIONS: IMPLICATIONS FOR STRUCTURE AND DIVERSITY

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Abstract.—Demographic models of tree populations assume that seed availability does not depend on the populations themselves. We develop models to assess the consequences of fecundity and dispersal for population structure and diversity. Results show that population structure and reproductive success are importantly affected by seed production and dispersal for realistic parameterization of time scales describing thinning, disturbance, maturation, and longevity. Maturation age affects mean and variance in seed rain. Populations with well-dispersed seed have a structure that is most sensitive to maturation age when disturbance is frequent. With restricted dispersal, delayed maturation means increased variability in seed rain, maximized when half of all patches support reproductive individuals. Density-dependent thinning compensates for the initial variability conferred by limited dispersal but not enough to permit the neglect of fecundity and dispersal at the disturbance frequencies and thinning rates typical in many forests. Longevity matters most when it is short and disturbance rare. To assess the effects of dispersal on reproductive success, we partition the contributions of seed-rain mean and variance. Fecundity and population structure affect both the mean and the variance in seed rain, albeit in different ways. Dispersal affects only the variance. The partitioned contribution of mean and variance are used to consider two cases: how dispersal consequences for reproductive success depend on life-history schedules and disturbance regime, and boundary growth rates of a globally dispersed population invading a resident population with restricted dispersal. In both cases, restricted dispersal has important consequences on the scales observed in many real forests. This assumption leads to two opposing (offsetting?) consequences for species diversity: artificially high diversity due to continuous seed supply and artificially low diversity due to lack of sites where good competitors with restricted dispersal should be absent.

Recruitment represents a potentially significant, yet poorly described, aspect of tree population dynamics. Fecundity schedules may affect the success of a population in competition and when the environment varies in time (e.g., because of weather or disturbance). Dispersal governs spatial variance in seed rain. That variability can determine whether offspring locate suitable sites and the importance of density- and frequency-dependent interactions (e.g., pathogens, herbivores, competition with parent, siblings, other species). These relationships affect, in turn, species diversity and rates at which species ranges respond to changing environments (Watts 1973; Baker 1974; Payette and Gagnon 1985). Fecundity and dispersal are difficult to parameterize in closed stands, because seed production can vary with age, size, stand characteristics, and across time scales.
Estimation difficulties are largely responsible for the neglect of fecundity and dispersal in tree population models. Forest simulators (Botkin et al. 1972) have for 20 yr provided a tool for analysis of life-history consequences, plant competition, disturbance, environmental change (app. A), nutrient cycling (Pastor and Post 1986), and harvest (Aber et al. 1979). These models simulate populations on a collection of small plots within which individuals are recruited, grown, and killed. Most are nonspatial and have a constant seed pool. At least one of these models has light availability that is affected by neighboring plots (Urban et al. 1991), and another has a switch (on/off) that makes seed available if mature adults are likely to be nearby (Shugart and Noble 1981). Several related models (see, e.g., Kohyama 1993) have bath seed pools that respond to adult trees but global dispersal. Thus, although fundamentally demographic in nature, most of these models lack reproduction in the usual sense of seed production, dispersal, and germination. Because fecundity and dispersal data are hard to obtain, the recruitment process is simplified to random draws from a pool of potential recruits that does not depend on seed production by the populations contained in the models. We refer to this assumption as the constant seed pool (CSP) assumption. Models based on this assumption (CSPMs) have been validated numerous times (see, e.g., Shugart 1984; Pastor and Post 1986).

Success of CSPMs might be viewed as contrary to theory that predicts population, community, and evolutionary consequences of fecundity and dispersal (Hamilton and May 1977; Levin et al. 1984; Shmida and Ellner 1984; Comins and Noble 1985; Pacala and Silander 1985; Geritz et al. 1988) and empirical observations suggesting that seed production and dispersal strategies importantly influence population dynamics and species composition (Heinselman 1973; Marks 1974; Houle 1992; Johnson 1992). Indeed, many authors have argued that the recruitment phase is among the most limiting for a species’ success (Marks 1974; Grubb 1977; Harper 1977; Alvarez-Buylla and Garcia-Barrios 1991). If fecundity and dispersal are as important as many theoretical treatments and empirical studies suggest, then why do models that ignore any link between the existing population and the seed pool give the right answers?

Unfortunately, there is no real basis for assessing effects of seed production and dispersal on the dynamics of “shifting mosaic populations” such as forest trees (Watt 1947; Peet 1981; Clark 1991a). Constant seed pool models assume this kind of mosaic structure, with local thinning governed by interactions within a prescribed neighborhood. But, because they do not include fecundity and dispersal, they cannot be used to evaluate those processes. They also contain too many parameters and functional forms to permit much analysis (see, e.g., Alvarez-Buylla and Garcia-Barrios 1993; Pacala and Hurtt 1993). Simpler population models are more analyzable, but they generally do not assume the appropriate structure or the kinds of parameters that would permit direct application to trees (Huston et al. 1989). These more analyzable models lack one or more of the following processes that appear critical in forest tree populations: both within-(i.e., thinning) and among- (i.e., dispersal) patch dynamics, episodic recruitment
tied to some mortality processes (i.e., "disturbance" and/or "senescence"), but not to others (i.e., thinning), and differential responses of thinning rates and recruitment to density.

We provide here a middle ground for analysis of recruitment processes in a tree population. We develop and analyze models of fecundity and dispersal in a population that is structured by disturbance on a landscape scale and by competition or thinning on a local scale. Recognizing that the role of recruitment is likely to change with other life-history and environmental factors, we devote some attention to understanding consequences of maturation age, seed production, longevity, and dispersal within the context of structure imposed by thinning and disturbance. Our efforts complement existing numerical and analytical models by assuming a reasonable spatial structure for tree life histories while incorporating recruitment in a tractable fashion. Because our models contain parameters that can be estimated directly from real forests, we then use published values to demonstrate some dangers of CSPM assumptions in forest models and the instances for which these assumptions appear reasonable. We analyze the consequences of fecundity and dispersal for population structure and the interaction between temporal (disturbance, thinning, life-history schedules) and spatial (dispersal) scales to demonstrate some contributions to species coexistence.

SCALES OF VARIABILITY IN FOREST STANDS

The importance of seed dispersal depends on the spatial scales of variability in forest stands, including dispersal area and the distribution of recruitment sites. The importance of spatial variability depends, in turn, on temporal scales. If recruitment sites become available on an episodic basis (e.g., disturbances such as canopy gaps), then the effect of dispersal may depend on how frequently those opportunities occur. Relationships between spatial and temporal aspects of recruitment have been shown to affect coexistence in the simplest types of lotteries (Shmida and Ellner 1984; Comins and Noble 1985). Our analysis will show those relationships to be the key to understanding recruitment in forest mosaics.

We focus on two spatial and four temporal scales. Spatial scales are the area over which propagules are dispersed and the area of patches within which conditions are suitable for recruitment. We summarize these two scales by a dimensionless dispersal parameter,

$$\tau = (\text{mean dispersal distance})^2 / \text{patch area},$$

the average number of patches within the dispersal area of a seed-bearing individual. Time scales include thinning rates that prevail in crowded stands $\rho$ (1/age), disturbance frequency $\lambda$ (1/age), maturation age $t_i(\text{age})$, and longevity $t_l(\text{age})$. Typical parameter ranges for three different woody plant assemblages are listed in table 1.

MODEL DESCRIPTION

Relationships among Three Types of Models

In order to isolate the effects of fecundity and dispersal we develop gap models at three levels of complexity (table 2). Level I is an analytical model that mimics
<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>Forest Canopy Gap</th>
<th>Fire in Dry Woodland</th>
<th>Fire in Boreal Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maturation age, ( t_1 ) (yr)</td>
<td>10–60 (Powell 1965; Loehle 1988)</td>
<td>4–8 (Nieuwenhuis 1987)</td>
<td>10–60 (Powell 1965; Loehle 1988)</td>
</tr>
<tr>
<td>Longevity, ( t_2 ) (yr)</td>
<td>( 10^2 - 10^3 ) (Powell 1965; Loehle 1988)</td>
<td>( 10^1 - 10^2 ) (Keeley 1991)</td>
<td>( 10^2 - 10^3 ) (Powell 1965)</td>
</tr>
<tr>
<td>Disturbance frequency, ( \lambda ) (yr(^{-1}))</td>
<td>( .005 - .01 ) (Runkle 1982; Barden 1989)</td>
<td>( .05 - .2 ) (Keeley 1983)</td>
<td>( .005 - .02 ) (Zackrisson 1977; Johnson 1979; Foster 1982)</td>
</tr>
<tr>
<td>Average dispersal distance (m)</td>
<td>( 10^1 - 10^2 ) (Coweeta, N.C., J. S. Clark, unpublished manuscript; Okubo and Levin 1989)</td>
<td>( 10^2 - 10^3 ) (Keeley 1991; Yacuton and Bond 1991; others bird dispersed [Bond et al. 1988])</td>
<td>( 10^1 - 10^2 ) (Johnson 1992)</td>
</tr>
<tr>
<td>Average patch size (m(^2))</td>
<td>( 10^3 ) (Runkle 1982)</td>
<td>( 10^1 - 10^2 ) (Minnich 1983; Bond et al. 1988)</td>
<td>( 10^3 - 10^8 ) (Foster 1982; Eberhart and Woodard 1987; Payette et al. 1989)</td>
</tr>
</tbody>
</table>

Composite parameters:

| \( \lambda_t \)            | \(.3 (.05-.6)\) | \(.25 (.2-1.6)\) | \(.5 (.05-1.2)\) |
| \( \lambda_t \)            | \(.15 (.5-10)\) | \(.1 (.5-20)\) | \(.2 (.5-20)\) |
| \( U(t_1, t_2) \)           | \(.67\) | \(.65\) | \(.55\) |
| \( \tau \)                  | \(.1 (.25-25)\) | \(.00002-.02\) | \(.00005-.05\) |

Thinning rate, \( p \) (yr\(^{-1}\)) 10\(^{-2}\)–10\(^{-4}\) (Buchman 1983; Clark 1990; Kohyama 1993)

* Values in parentheses are ranges.
TABLE 2
COMPARISON AMONG MODEL ASSUMPTIONS AT THREE DIFFERENT LEVELS

<table>
<thead>
<tr>
<th>Level I</th>
<th>Level II</th>
<th>Level III</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fecundity</strong></td>
<td><strong>Seed production per patch</strong></td>
<td><strong>Seed production per patch</strong></td>
</tr>
<tr>
<td>Fixed number of seeds completely fills patch following disturbance</td>
<td>Seed is constant once patch reaches age of tree maturation</td>
<td>Seed depends on tree sizes and densities</td>
</tr>
<tr>
<td><strong>Dispersal</strong></td>
<td><strong>Seeds are dispersed evenly over neighboring patches</strong></td>
<td><strong>Seeds are dispersed evenly over neighboring patches</strong></td>
</tr>
<tr>
<td>Effectively global</td>
<td>As in Level I plus crowding effect</td>
<td>As in Level I plus crowding effect</td>
</tr>
<tr>
<td><strong>Thinning</strong></td>
<td><strong>As in Level I</strong></td>
<td><strong>As in Level I</strong></td>
</tr>
<tr>
<td>Proportional to plant growth rate</td>
<td>Random</td>
<td>Random</td>
</tr>
<tr>
<td><strong>Disturbance</strong></td>
<td><strong>Random</strong></td>
<td><strong>Random</strong></td>
</tr>
</tbody>
</table>

The CSP assumption of a seed pool that does not respond to seed production by the population. This model assumes a metapopulation stochastic on a regional scale and deterministic on the local scale (Hastings and Wolin 1989; Clark 1991a). “Local” refers to conditions within a patch. “Regional” or “landscape” refers to the ensemble of patches or metapopulation. A disturbance process affects patches at random, killing trees, resetting patch age to zero, and initiating a new round of local dynamics. Newly disturbed patches start at a fixed density of new recruits representing an even-aged cohort. That cohort thins deterministically as a consequence of plant growth. Patch location is irrelevant, a feature this model shares with CSPMs. Analysis shows consequences of shifting mosaic demography at a fixed level of crowding and in the absence of the variability conferred by seed dispersal.

The second level of complexity (Level II) is represented by analytical approximations to the process that admits both regional and local stochasticity. Recruitment depends on age structure and dispersal area. This model retains the simplicity necessary for analysis with the addition of spatial effects. Limiting cases collapse to the Level I model. Comparisons between Levels I and II permit partitioning of several dispersal effects and the roles of time scales.

The third level of complexity (Level III) is represented by a numerical model that assumes a spatially explicit grid of sites. This model is used to assess the biases introduced by approximations of Level II.

**Shifting Mosaic Population Structure**

Common to all three models is the assumption of a mosaic of patches each the size of a mature individual tree, that is, 10^2 m^2 (fig. 1A), although we deal with dimensionless quantities to the extent possible. Patches are identical in kind, differing only in their individual disturbance histories. The degree of interaction among patches depends on seed dispersal. Individuals become established on a patch following disturbance and grow (fig. 1A). Each patch supports a cohort of age identical individuals. Growth results in crowding and hence thinning (fig. 1B). As a measure of within-patch crowding, we use total canopy area (area occupied per tree x cohort density), which can vary with time since disturbance.
FIG. 1.—Dynamics of a shifting mosaic population. Disturbances on individual patches reset patch age to zero and permit recruitment of small individuals (A) at high density (B). Crowding (C) results in thinning (B) as a consequence of growth (A). In this numerical example, increase in crown area (A) is sigmoid, disturbance probability increases with patch age, and the importance of density-dependent mortality decreases with patch age as crowding levels decline (C). Landscape density (summarized by mean and standard deviation on crowding levels in D) remains rather constant once the patch ages achieve an equilibrium distribution.
on the local (within-patch) scale (fig. 1C). Population density can be described statistically on the regional scale, for instance, by means and variances (fig. 1D). Dynamics are summarized by

\[
\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = - \left[ \sum_{i=0}^{q} m_i(\cdot) \right] n(a, t)
\]  

(1a)

for the density of cohorts \( n(a, t) \) of age \( a \) at time \( t \) exposed to \( q \) mortality agents characterized by rates \( m_i \), at least one of which (thinning) can be density-dependent. Recruitment constitutes the boundary condition

\[
n(0, t) = \int_{t_1}^{t_2} u(a, t)n(a, t)b(a, t)da
\]  

(1b)

for a distribution of patch ages \( u(a, t) \), fecundity schedule \( b(a, t) \), initial age distribution \( n(a, 0) = n_0(0) \), maturation age \( t_1 \), and longevity \( t_2 \). Equation (1b) is termed "seed" or "initial density," which can assume a distribution of values that depend on population structure and dispersal. The landscape density is

\[
E[N(t)] = \int_{0}^{t_2} u(a, t)n(a, t)da.
\]

In all subsequent analyses we consider only the equilibrium behavior (i.e., as time \( t \) becomes large). The next sections outline assumptions common to all three models. We then distinguish among the three model types.

**Disturbance Process: The Regional Scale**

Levels I, II, and III assume the same type of disturbance process (table 2). Each patch realizes a different (stochastic) sequence of identically distributed waiting times between disturbances (fig. 1A–C). Let \( \lambda(a) \) be the age-specific probability of disturbance on a patch \( a \) years since the last disturbance occurred. The probability that the elapsed time between disturbances on a patch is at least \( a \) years is

\[
S_j(a) = \exp \left[ - \int_{0}^{a} \lambda(x)dx \right],
\]

with equilibrium density of patch ages

\[
u(a) = S_j(a)/\mu,
\]

where \( \mu \) is the average disturbance interval:

\[
\mu = \int_{0}^{\infty} S_j(a)da.
\]

The fraction of all patches older than age \( a \) is

\[
U(a) = \int_{a}^{\infty} u(x)dx.
\]
Here we assume a disturbance rate that is independent of patch age $\lambda(a) = \lambda$, but deterministic longevity permits the view of a single disturbance process having probability that increases rapidly near maximum age $t_2$. By varying the relationship between $\lambda$ and $t_2$ we can address both limiting cases of constant probability and periodic disturbance processes. Relevant details for the competing disturbance agents considered here are given in appendix B.

Three Types of Mortality

Plants can die by any of three agents: cohort thinning, senescence, and disturbance. Thinning within a cohort depends on patch density, individual size, and growth rate. Initial density on a patch $n(0, t)$ follows different assumptions in the three models (see below). Thinning rate, $dn/da$, is determined by plant growth rate and by the degree of crowding within a patch. Tree size is summarized by its "zone of influence" or "crown area" $A(a)$ (Yoda et al. 1963; Hara 1985; Zeide 1987; Norberg 1988; Tait 1988; Valentine 1988). The value $A(a)$ increases with age $a$ according to a deterministic rate equation $p(a) = (1/A)(dA/da)$ (fig. 1A). The level of crowding within a cohort is (to a constant) the product of cohort density and crown area of individual plants:

$$F(n, A) = n(a)A(a)$$

(fig. 1C). "Complete canopy coverage" is defined as $F = 1$. Cohort thinning rate

$$\frac{1}{n(a)} \frac{dn}{da} = -F(n, A)\rho(a)$$

is equal to the rate of crown-area increase when $F = 1$ and greater (less) than this value when coverage is greater (less) than complete.

The second mortality agent is senescence. Age-specific mortality rates appear to increase with age permitting rough estimates of longevity (reviewed in Loehle 1988). All three model levels (table 2) assume a deterministic longevity $a = t_2$. Plants not killed by thinning or by disturbance by age $t_2$ are removed, and patch age is reset to zero. The rationale is that death of a large individual produces a canopy gap. Finally, the disturbance process is a mortality agent. We assume for simplicity that disturbance removes all individuals from a patch (app. B).

Recruitment

Recruitment is episodic, occurring with canopy gap formation or disturbance (fig. 1B). Thus, recruitment is associated with two of the three types of mortality, senescence and disturbance. Thinning does not result in open space and so does not allow for seedling establishment.

The fecundity schedule consists of three components: maturation age, when reproduction begins; longevity, when seed production stops because of death; and seed production rate between these two ages. Per capita seed production is assumed proportional to crown area once a tree achieves maturation age $t_1$:

$$b(a) \propto \begin{cases} \beta A(a) & t_2 \geq a \geq t_1 \\ 0 & \text{otherwise}. \end{cases}$$
Here $\beta$ is seed production per unit of crown area. It can be viewed as a recruitment parameter that summarizes density-independent processes that operate from the time of seed set through seedling establishment. Seed production of an entire patch of age $a$ is

$$B(a) = b(a)n(a).$$

(5)

Scaling this value by the fraction of patches of age $a$, $u(a)$ and integrating over patch age return us to boundary condition (1b), the expected seed rain. This is the seed density all patches receive if dispersal is global (Level I).

**LEVEL I: DISTURBANCE AND POPULATION STRUCTURE**

*Crowded Landscapes and Global Dispersal*

In this section we analyze a simple model of population structure for effects of four time scales—maturation age, longevity, disturbance frequency, and thinning rate—and the three components of the fecundity schedule (eq. [4]) on the distribution of cohort densities. This simplest “Level I” assumes that each patch is fully occupied by seed following disturbance ($n(0) = 1$ in fig. 2A); that is, dispersal is global (table 2). This section serves as a baseline for subsequent analysis of thinning and dispersal.

Complete canopy coverage requires that thinning rates compensate for variability in initial seedling densities in a way that makes density rapidly converge to a common thinning equation. Setting $F = 1$ in equation (2) and substitution in equation (3) yields the thinning equation

$$\frac{1}{n(a)} \frac{dn}{da} = -\rho(a).$$

(6)

Equation (1a) tends to

$$n(a) = n_0 \exp \left[ -\int_0^a \rho(x) dx \right]$$

as $t$ becomes large (fig. 2B).

Seed production by an entire patch is relatively constant once trees that occupy the patch achieve maturation age. With complete occupancy ($F = 1$), equation (2) implies that $n(a)A(a)$ is constant. Substitution in equation (5) gives patch seed production

$$B(a) \propto \left\{ \begin{array}{ll} \beta & a \geq t_1 \\ 0 & \text{otherwise} \end{array} \right. $$

(7)

(fig. 2C), and boundary condition (1b) becomes

$$n_0 \propto \int_{t_1}^{t_2} \beta u(a) da \propto \beta U(t_1, t_2).$$

(8)

The value $U(t_1, t_2)$ is the fraction of patches that support reproductive individuals (app. B). Population structure can be summarized by a distribution of densities
FIG. 2.—Some assumptions and predictions of the three levels of models summarized in table 1. Levels I (A-C) and II (D-F) assume constant seed production per patch once plants achieve maturation age $t_1$ (C and F). They differ in that Level I assumes all patches are continuously crowded from the time of initial seed germination (A) and throughout stand development (B). Level II allows for a range of initial densities (D), depending on the dispersal of seed from nearby patches, that result in a distribution of thinning trajectories (E). These trajectories (summarized by mean [solid line] ± 1 SD [dashed line] in E) tend toward a single thinning trajectory because of crowding effects on thinning rates. Level III is a numerical model of the process in which seed production responds to crowding levels in addition to tree size (I). The resultant distributions of initial seed densities (G) have modes corresponding to those of the Level II model (compare D and G). Thinning trajectories are well described by statistics derived from the Level II model (compare E and H). The distributions in time of thinning (H) and seed production (I) have circles proportional to the density at a particular density level. For instance, in H, the initial broad distribution of densities at age zero (corresponding to distribution G) shows several modes that converge with age. The broad scatter of small circles converges to fewer large circles as patches with a range of initial densities converge to similar values. Parameter values are $\lambda = \rho = 0.05$, $t_1 = 7.6$, $t_2 = 42$, $\pi = 9$. 
or by their moments (Hastings and Wolin 1989; Clark 1991a).

**Effects of Seed Density and Time Scales on Metapopulation Structure**

Equations (8) and (9) provide a basis for understanding how the time scales, represented by rate parameters, affect population structure, summarized by distributions. If disturbance risk $\lambda$ and thinning rate $p$ are relatively constant, the distribution of densities is solved using equations (6), (8), (B2), and (9):

$$f(n) = \frac{\Phi n^{\phi-1}}{n^\phi - n_{12}^\phi}, \quad n_{12} \leq n \leq n_0,$$

where $\Phi = \lambda/p$, $n_0 = n(0)$, and $n_{12} = n(t_2)$. This distribution has $k$th moment

$$E(N^k) = n_0^k(t_1, t_2, \lambda) C_k(t_2, \lambda, p),$$

where $n_0$ is given by equation (8) and

$$C_k = \left(\frac{\lambda}{\lambda + kp}\right) \left(1 - e^{-(\lambda + kp)t_2}\right) \left(1 - e^{-\lambda t_2}\right).$$

The mean and coefficient of variation are, respectively,

$$E(N) = n_0 C_1$$

and

$$CV(N) = \frac{1}{C_1} \sqrt{C_2 - C_1^2}.$$
class contribute seed. A CSP assumption would predict excess representation of young, high-density cohorts, failing to accommodate the declining seed rain produced by a population dominated by immature individuals. Expected density is maximized at intermediate disturbance rates (fig. 3B).

The distribution of density classes (eq. [10]) depends on time scales. A large seed rain that is caused by early maturation produces a broad range of high-

Fig. 3.—Effect of maturation age and disturbance frequency on expected density \( E(N) \) calculated from the Level I model (eq. [13]). The two components in A are seed density (descending) and \( C_1 \), which increases with disturbance frequency. Their product is expected density (B), maximized at intermediate frequencies. Density-dependent thinning ("with") reduces sensitivity to disturbance regime (B), and it reduces variability for any given disturbance regime (C). Shading in (B) represents ±1 SD from eq. (14) ("without") and eq. (20) ("with"). Parameterizations for fig. 4 are shown in C.
density patches (curves 1 and 3 have \( t_1 = 0 \) in fig. 4A–C). Delayed maturation \( (t_1 \gg 0) \) has the largest effect on structure when disturbance is frequent (e.g., curve 2 in fig. 4A). Longevity \( (t_2) \) has little effect on population structure if the probability of surviving to that age is low. There are no observable differences between curves 1 and 3 in figures 4A and B, because disturbance (fig. 4A) or thinning (fig. 4B) removes most individuals before they reach age \( t_2 \). Figure 4C demonstrates how reduced longevity removes the left-hand side of the distribution (curve 3) when other mortality risks are low. Seed densities are independent of thinning rates (corresponding to growth rate \( \rho \)), because the canopy remains crowded (this assumption is relaxed in Level III). Thus, a CSP assumption would be most importantly wrong when disturbance is frequent and maturation is delayed.

LEVEL II: VARIABILITY WITHIN AND AMONG PATCHES

Density-Dependent Thinning and Restricted Dispersal Distance

Restricted dispersal affects several aspects of mosaic population structure. Here we allow for variable seed densities arriving at newly opened patches, depending on the fraction of nearby patches producing seed and on the dispersal area. We first establish some rules regarding how seed arrival at a newly opened patch affects subsequent dynamics (i.e., thinning) on that patch. We then describe the dispersal process.

Seed production and dispersal determine initial patch crowding \( F(0) = n(0)A(0) \) and, consequently, subsequent thinning. The simplest assumption for this density dependence is equation (3). Cohorts on patches with initially high densities thin more rapidly than do those at low densities (fig. 2E, F) (see, e.g., Harper 1977). At complete canopy coverage \( (F(a) = 1) \), the patch is fully occupied, and thinning simplifies to equation (6). Equation (3) implies a sigmoid approach to complete canopy coverage with stand age, \( dF/da = \rho F(1 - F) \) (Clark 1992). The first-order approximation, \( dF/da = \rho (1 - F) \), is a close estimate on patches that remain near complete canopy coverage \( (F = 1) \). For simplicity we assume a constant rate of canopy increase \( \rho \), which, combined with the rate equation for crowding, \( dF/da \), yields crowding on a patch of age \( a \)

\[
F(a) = 1 + [F(0) - 1]e^{-\rho a}.
\]  

(15)
The density on a patch of age \( a \) can be written in a way that facilitates subsequent analysis,

\[
n(a) = n_e(a)F(a),
\]  

(16)
where \( n_e(a) \) is the density that prevails when canopy coverage is complete (i.e., eq. [6]). Equations (15) and (16) yield cohort density in terms of patch age

\[
n(a) = e^{-\rho a}[1 + (F(0) - 1)e^{-\rho a}].
\]  

(17)

Seed production is assumed to operate as in the Level I model (eq. [7]), but now the dispersal area is limited. The relationship between growth and thinning
Fig. 4.—Distributions of cohort densities for different combinations of thinning rates and disturbance frequencies for Level I (left) and II (right) models. Each graph contains three curves having maturation age, longevity combinations \( (t_1, t_2) \) of 1: \( (0, \infty) \), 2: \( (7.6, \infty) \), and 3: \( (0, 41) \). \( \beta = 1.0 \). Curves 1 and 3 are indistinguishable in A and B, which reflects the fact that longevity has little effect on population structure when growth, and thus thinning, is rapid relative to other time scales. Level II distributions in D, E, and F show effects of fecundity \( \beta \) on the distributions of densities, when thinning rate responds to crowding levels. Distributions are \( f(n|a) = \lambda e^{-\lambda a} \rho (1 - e^{-\lambda a})[F(a)]^2 \) having limits \( (n_1, n_0) \), solved from eq. (10). Maturation age, longevity combinations are \( (7.6, 41) \).
means that seed production per patch remains relatively constant at rate $\beta$ once the trees it supports achieve reproductive age $t_1$ (eq. [7]) (fig. 2F). An individual's $b(a)$ seeds (or, equivalently, a patch's $\beta$ seeds) are evenly distributed among all patches within “dispersal area” $\pi$ of the resident patch: each of $\pi$ patches receives $b(a)/\pi$ seeds from this individual. The arrival rate of seeds at a given patch depends on the production of seeds on all patches within the dispersal area (app. C). Because only patches sufficiently old to support reproductive individuals produce seeds, the probability that a patch supports reproductive individuals is $U(t_1)$ (app. B). The distribution of the number of patches within the dispersal area producing seed at any given age is binomial with parameters $U(t_1)$ and $\pi$ (fig. 2D).

The Importance of Density-Dependent Thinning:
The Global Dispersal Case

How does seed production rate affect landscape structure when initial crowding determines subsequent thinning rates? Analyses for the global dispersal case are straightforward. The $k$th moment of landscape density is

$$E(N^k) = \int_0^{\infty} n^k(a)u(a)da = \int_0^{\infty} n^k_i(a)[E[F(a)]]^k u(a)da .$$

In contrast to the Level I model, the expected density now consists of two terms,

$$E(N) = C_1 + (n_0 - 1)C_2,$$

where $n_0$ is given by equation (8), and $C_k$ is given by equation (12). The second term depends on the extent to which average initial density deviates from full occupancy (i.e., $n_0 = 1$). This term can be positive or negative, depending on whether the birth rate $\beta$ is sufficiently high to offset the negative effects of delayed maturation on the reproductive fraction $U(t_1)$. We refer to the situation where $\beta > 1/U(t_1)$ as “recruitment limitation” (Alvarez-Buylla and Garcia-Barrios 1991; Pacala and Tilman 1994). Variance, solved from equation (18), is quadratic in initial densities

$$\text{var}(N) = C_2 - C_1^2 + 2(n_0 - 1)(C_3 - C_1C_2) + (n_0 - 1)^2(C_4 - C_2^2).$$

For $\beta = 1/U(t_1)$, average seed rain fills the patch, and results simplify to the Level I case; that is, $E(N)$ is given by equation (13) and $\text{CV}(N)$ by equation (14).

The effect of seed density on population structure is constrained by the way in which thinning rates respond to density. Figure 4D–F shows the effects of seed rain on the distributions for parameter combinations used in Figure 4A–C. The upper limit of these distributions is seed rain $n_0$, which is increased either by increasing the fraction of seed-bearing patches $U(t_1)$ (fig. 4D vs. 4E and 4F) or by increasing fecundity $b$ (three levels shown on each plot). Density-independent thinning rates in the Level I model (fig. 4A–C) cause expected density to scale directly with fecundity (eqq. [8], [13]). The density dependence in equation (19) makes the distribution less sensitive to fecundity. Unlike Level I, low initial density means a low rate of thinning away from this upper boundary, and density "piles up" at $n_0$ (fig. 4D–F). The three curves in figure 4D become less steep as
TREE POPULATION RECRUITMENT

Level II

Level III

Distribution of
seed densities

Distribution of
thinning trajectories

Distribution of
seed densities

Distribution of
thinning trajectories

\[ \pi = 25 \]

\[ \pi = 9 \]

\[ \pi = 2 \]

\[ f(n(0)) \]

\[ n \]

\[ \text{Age} \]

\[ \text{Age} \]

\[ f(n(0)) \]

Fig. 5.—Analytical distributions of initial (seed) densities (left) and subsequent thinning \( n(a) \), summarized by expectation (eq. [C3]) and standard deviation (eq. [C5]) for three different dispersal areas \( \pi \) as predicted by the Level II model (app. C). Reduced dispersal area (\( \pi = 2 \)) results in a wide variance on initial densities. This variance diminishes with patch age at a rate determined by growth rates of trees. On the right are distributions generated by the numerical model (Level III) for the same parameter values. Symbolism for thinning trajectories is described in fig. 2.

Fecundity increases. High seed rain means higher thinning rates and less tendency to pile up at the \( n_0 \) boundary; the upper part of the distribution tends to be rather flat. Low growth rate (contrast fig. 4E vs. 4F) means decreasing thinning rate at all densities, but densities can still pile up at the upper limit when seed rain is low (\( \beta = 1 \)). This compensating effect of thinning rates for initial density means an overall lower variability in density (fig. 3C).

Dispersal Affects Variability among Cohorts

Allowing for variable seed rain means that patches of the same age support a distribution of densities (fig. 2E). Several consequences are gleaned from results in appendix C. First, limited dispersal does not change the mean seed density—the expected density from limited dispersal (eq. [C1]) is the same as that from global dispersal (eq. [8]). Figure 5 (left side) presents three examples of initial densities, \( f(n(0)) \), and thinning trajectories, \( E[n(a)] + \sigma(a) \), for three populations that differ only in the area \( \pi \) over which they disperse seed. Expected values are the same in all cases.
Second, variance on seed density \( n(0) \) in the Level I model was zero (fig. 2A), a result that also follows from the global dispersal case (\( \lim \pi \to \infty \)) in this model (eq. [C6]). With large dispersal, all initial densities tend to the expected value (fig. 5, upper left). Variance is large when maturation age and disturbance frequency combine to make \( U(t_i) \) near 0.5. Thus, Level I can be viewed as a special case of the Level II model with regard to dispersal effects on seed density.

Third, variability among patches decreases with patch age as initial crowding levels converge to full canopy coverage, \( F(a) = 1 \) (app. C). The per-area rate of crown-area increase, the per capita thinning rate, and the rate of percentage decrease in variability are all equal:

\[
\frac{-1}{A} \frac{dA}{da} = \frac{1}{n} \frac{dn}{da} = \frac{1}{\sigma} \frac{d\sigma}{da}.
\]

The rate of decrease in among-patch variance is given by the growth rates of the plants themselves. High growth rates result in low variability among patches of the same age. This result places the damping effect of thinning on variability within the context of other time scales.

**Dispersal and the Fraction of Unoccupied Space**

The equilibrium fraction of unoccupied patches is approximated by

\[
\int_0^\infty f(t) dt \times [1 - U(t_i)]^{\pi - 1} = [1 - U(t_i)]^{\pi - 1}.
\]

For constant disturbance rate \( \lambda \), the fraction of unoccupied patches diminishes as a power function of dispersal area.

**LEVEL III: COMBINED FECUNDITY AND DISPERAL EFFECTS**

A numerical model of this process was constructed to test predictions of fecundity and dispersal effects on population structure under less confining assumptions (table 2). We produced a spatially explicit landscape of patches 100 \( \times \) 100 grid cells in size. Each patch is exposed to constant disturbance risk \( \lambda \) at each time step. Disturbances remove all trees from the patch and reset patch age to zero. Patches not hit by disturbance by patch age \( a = t_2 \) are also reset to age zero.

Seeds colonize open patches at age \( a = 0 \). Seed density is determined by the number of trees within dispersal area \( \pi \) of the patch and by their age-specific
fecundities (eq. [4]). A given mature individual contributes $b(a)/\pi$ seeds to each of the $\pi$ patches within its dispersal area. Landscape edges are reflecting boundaries for seeds. Subsequent thinning on the patch depends on tree growth rates ($dA/da$) and on crowding (eq. [3]) as set by seed densities. The model was initialized for a time interval of the order $10 \times \lambda t_1$, by which time stationarity of population structure was achieved. Indexes of population structure, including means, variances, and distributions, were determined from subsequent dynamics spanning an interval of equal duration. The parameter space delimited by table 2 was explored.

In general, the analytical model of Level II accurately predicts the behavior of the numerical model. The close agreement between the two rests with the fact that patch seed production by the time trees reach reproductive maturity is not highly sensitive to initial seed densities. Initial densities on newly opened patches and subsequent thinning trajectories have mean values predicted by the Level I model (fig. 2), and they show scatter about the distributions predicted by the Level II model (compare fig. 5). With large dispersal area ($\pi = 25$), seed densities are normal with small variance. With decreasing dispersal, spatial variability increases. As dispersal area falls below the nine adjacent patches, a noticeable zero-density class begins to develop. Density-dependent thinning rates (fig. 2H) cause tree and therefore seed densities to converge with age (figs. 2I, 5).

Comparisons of distributions of densities from the numerical model with the Level II predictions identify some clear effects of dispersal on population structure (fig. 6). When disturbance is frequent (left side of fig. 6), distributions are sensitive to dispersal area. The fraction of patches at densities greater than one (i.e., complete canopy coverage) declines as dispersal area falls below $\pi = 9$. Many patches are recruitment limited, receiving fewer than the average seed density because of few seed-producing patches being within dispersal area: the landscape is no longer "full." The "empty" fraction is represented by development of a second mode at zero, which becomes evident at dispersal areas less than or equal to nine. The bimodal distribution has a zero-class fraction that is approximated by equation (21) of the Level II model (fig. 7C). The analytical predictions for mean and variance closely approximate numerical results until dispersal area falls below $\pi = 6$ (fig. 7A, B). With the rise in open patches at low dispersal area, expected densities fall. This development at low dispersal range begins to affect the entire landscape structure (fig. 6).

When disturbance is moderately rare (right side of fig. 6), dispersal area has little effect on density structure. The high frequency of low-density stands results from a bias toward older stands, because thinning dominates. Dispersal has its greatest effects on representation of young, high-density stands and so is less important as initiation of new stands becomes increasingly rare.

**IMPLICATIONS FOR LIFE HISTORY AND DIVERSITY**

Spatial and temporal heterogeneity of the sort considered here is sufficient to permit coexistence of alternative life histories if dispersal is global, species are
Fig. 6.—Comparison of distributions of densities under assumptions of constant seed production per patch once trees reach maturity (Level II) vs. the numerical model that permits production to vary with crowding and tree size (Level III) for two combinations of rate parameters and six dispersal areas. This variable recruitment has the greatest effect when disturbance is frequent and dispersal is limited (graphs toward the lower left). Parameter values are $b = 2$, $(t_1, t_2) = (7.6, 41)$, the same as in fig. 4E and F. The fraction of open patches is given in fig. 7C. The first two moments of these distributions are shown in fig. 7A, B.
iteroparous, but recruitment is variable and species are not highly correlated in terms of recruitment requirements (Chesson 1982; Comins and Noble 1985); if dispersal is global, but stochastic (Geritz et al. 1988); or if dispersal is deterministic and partly local, species are iteroparous, and species are negatively correlated in terms of loss rates within a patch (determined by growth, competition, or density-independent mortality) versus recruitment rates (fecundity, dispersal, and/or "colonization") (Hastings 1980; Shmida and Ellner 1984; Caswell and
Cohen 1991; Kohyama 1993; Tilman 1994). If fecundity and growth are positively correlated (as is implicit in Tilman’s [1988] ALLOCATE model), spatial variability may still promote some degree of coexistence among competitors provided they are not too similar in how they exploit environmental resources (Pacala and Tilman 1994). Iteroparity and dispersal of competing species permit temporal and spatial integration across the recruitment opportunities that occur episodically. If gains during those recruitment opportunities exceed the mortality losses that ensue at intervening times and places for several species, then coexistence is possible. Results of previous studies broadly apply here, so there is no need to reproduce them; we do not present another demonstration that variability can promote coexistence. Rather, we provide an interpretation of coexistence in shifting mosaic populations, and we determine parameter ranges in which invasion is easy, in order to place shifting mosaic populations, in general, and the CSP assumptions, in particular, within the context of these previous results.

Our argument uses two relationships: how reproductive success depends on the different levels of crowding an invader encounters in the mosaic produced by a resident population, and the distribution of those crowding levels across a landscape. Together, these two functions permit approximation of expected reproductive success of a population with a given life-history schedule invading the mosaic produced by a resident population, as analyzed in the previous section. We first summarize our notion of an “optimal” life-history schedule given the foregoing definitions of a shifting mosaic population. This definition is a straightforward extension of previous mosaic population models, using net reproductive rate as the index of success (Clark 1991b). This optimal maturation age assumes a genotype pitted against an abiotic opponent (i.e., a “disturbance regime”). Dispersal determines (the distribution of) initial patch densities. Competition enters through its effect on thinning. Our principal results bear on how dispersal affects reproductive success as life histories diverge from this optimum and how the net reproductive rate of an invading population is affected by the population structure of a resident population.

**Net Reproductive Rate in the Average Patch**

Previous models of tree life history (Clark 1991b) and patch age structure (Clark 1991a) can be generalized to examine reproductive success on the mosaic landscape. These previous approaches adopt a simplistic analysis of the timing of reproduction relative to disturbance. Although size is probably a better index of reproductive effort (reviewed in Caswell 1989), relating life history to disturbance requires that both be measured in common units, and most forest disturbance data are temporal. Let $S_p(a)$ and $S_f(a)$ be survivor functions associated with stand thinning and the disturbance process, respectively. Although some correlation between the two is expected, that correlation might often be low. For simplicity we take them as independent. The average net reproductive rate across a large landscape mosaic with global dispersal and constant disturbance probability is

$$R_0 = \int_{t_1}^{t_2} S_f(a) S_p(a, n_0) \lambda b(a) da .$$  \hspace{1cm} (22)
One definition of persistence is that this quantity exceeds unity (i.e., net increase) when density is low. Birth rate is the product of the fecundity schedule from equation (4) and the fraction of open patches (resulting from disturbance) $\lambda \cdot b(a) = \lambda \beta A_0 e^{pa}$. Disturbance survival rate is $S_d(a) = e^{-\lambda a}$. Together with equation (17), thinning survival rate on a patch receiving the average seed rain $bU$ is approximately

$$S_p(a, \beta U) = \frac{n(a)}{n(0)} = e^{-\beta a} \left[ \frac{1}{\beta U} + \left( 1 - \frac{1}{\beta U} \right) e^{-\beta a} \right],$$

where $U = U(t_1, t_2)$, and $A_0$ is, for convenience, equal to unity. These relationships imply a net reproductive rate approximated by

$$R_0 = \frac{\lambda_0}{U} + \left( \beta - \frac{1}{U} \right) \Lambda_1,$$

where

$$\Lambda_j = \frac{\lambda}{\lambda + jV} (e^{-(\lambda + j)\tau} - e^{-(\lambda + j)\tau}).$$

The Optimum Is an Environmentally Stable Strategy When Dispersal Is Uncorrelated with Maturation Age

The best time to reach reproductive maturity has been determined (Clark 1991b) under the assumption of correlated maturation age and longevity (Harper and White 1974; Loehle 1988). Define

$$I(a) = S_d(a) S_p(a) \lambda b(a).$$

For a population growing at constant per capita rate $r$ we have Lotka’s equation

$$1 = \int_{t_1}^{t_2} e^{-ra} I(a) da.$$

At equilibrium $r = 0$, and

$$1 = R_0 = \int_{t_1}^{t_2} I(a) da.$$

The optimal maturation times satisfies $R_0(t_1) = R_0(t_1 + \tau)$ for some small age increment $\tau$. The correlation between maturation age and longevity is summarized by the dimensionless parameter

$$\alpha = t_2 / t_1,$$

which has values ranging from about four to 10 for most tree species (Loehle 1988). For the equilibrium case, we write the optimality criterion as

$$\int_{t_1}^{t_1 + \alpha t_1} I(a) da = \int_{t_1 + \alpha t_1}^{t_1 + \alpha t_1 + \tau} I(a) da.$$
Infrequent disturbance

Frequent disturbance

High dispersal $z_1 = 40$

Low dispersal $z_1 = 9$

Maturation strategy played by opponent (age)

Fig. 8.—Numerical simulations of the relative abundances of phenotypes having a range of maturation ages competing against the phenotype playing the optimal maturation age (arrow). Phenotypes do as well as the optimal strategy only when they, too, play the optimum.

Manipulate limits,

$$\int_{t_1}^{t_1+\tau} I(a) \, da = \int_{a(t_1)}^{a(t_1+\tau)} I(a) \, da,$$

divide by $\tau$, and take the limit $\tau \to 0$ to yield the solution

$$I(t_1) = \alpha I(a(t_1)).$$

This optimum is achieved where half the population is reproductively mature. The earlier result (Clark 1991b) is a special case of equation (25).

The “optimal strategy” given in equation (25) satisfies one definition of an evolutionarily stable strategy (ESS) under the constraints we have imposed. The net reproductive rate for a strategy $i$ invading $r$ is optimal at

$$\frac{\partial}{\partial t_1} R_{0[i,r]} = 0.$$

By extensive simulation of a two-species version of the Level III model, we find that an invading population cannot improve on the optimal strategy through changes in dispersal area (fig. 8). Even if the resident’s dispersal area is too narrow to permit persistence (see below), the maturation time satisfying equation
(25) still describes the maturation age at which extinction is least rapid. The trade-off between dispersal in space versus time predicted by some dormancy/dispersal models (see, e.g., Levin et al. 1984; Comins and Noble 1985) results from assumptions that dispersers encounter a different set of risks than do nondispersing seeds. Because we assume here that all seeds are equally susceptible to risks, we do not predict such a trade-off. A relationship between temporal and spatial scales is observed below, but dispersal supplements, rather than substitutes for, well-timed life-history schedules.

**Dispersal Aids Persistence for the Nonoptimal Phenotype**

Reproductive success is spatially variable, depending on the local level of competition. The optimal maturation age derived above assumes global dispersal. But an optimal life history with respect to maturation age need not yield an $R_0$ that exceeds unity, and it can fail within a mosaic population if dispersal is so restricted as to preclude finding opportunities for successful establishment. Thus, before considering coexistence, it is necessary to determine the effects of mosaic structure on net reproductive rate. Here we consider how time scales contribute to the way in which dispersal increases the probability of persistence in the face of the "wrong" (i.e., suboptimal) maturation age. Appendix D derives expected reproductive success on the basis of the distribution of seed densities and its effect on reproductive success (eq. [D2]).

Reproductive success can be approximated as the sum of contributions from the mean and the variance in seed densities (eq. [D4]):

$$R_0 \text{ at the level} = \text{mean crowding} + \left( \frac{1}{\pi} \times \text{curvature} \times \text{constant} \right).$$

Provided dispersal is not too small and the population is not declining, the expected seed density is $E[n(0)] = \beta U(t_1)$, and the contribution of the variance is small, proportional to the inverse of dispersal area.

The advantage of dispersal is realized primarily by "nonoptimal" phenotypes, having $R_0$ values less than unity, consistent with the conclusions of Comins and Noble (1985). We use plots of total density to demonstrate our result (fig. 9), as this is maximized at the ESS (numerical results from our model and Hastings 1978). At the optimum (eq. [25]) there is no real advantage to large dispersal area (fig. 9B), because the close match between maturation age and new recruitment opportunities provided by disturbance makes distant dispersal unnecessary. As the fraction of reproductive individuals falls below one-half, however, reproductive success is greatly improved by dispersal (fig. 9C, D). Although the population is heading to extinction in figure 9D ($R_0 < 1$), the decline is much more rapid at low dispersal rates. The variance term makes a large contribution to reproductive success, whereas the mean contributes little. Reproductive success is highly dependent on the individuals that encounter low-density sites. Thus, little is to be
Dispersal benefits the suboptimal life histories in C and D, when disturbance is too rare, but it is of benefit at neither the optimum (B) nor the late maturation age (A).

gained by dispersal, unless the reproductive age is too short relative to disturbance frequency. Alternatively, dispersal cannot save the life history that errs in the direction of delayed maturation (fig. 9A). If disturbances are too frequent, enhanced dispersal is of little benefit.

**Consequences for Species Coexistence**

Where populations compete for new sites, the dispersal area of a resident can affect invasibility of an invader, which does best in sites in which the resident is at low density. Consider a population $i$ invading from low density a resident
Assume that population \( i \) is well (globally) dispersed. How restricted must the dispersal area of the resident be to allow the invading population to realize a positive expected growth rate? The approximation (D6) gives the expected reproductive success of the invader assuming that the density dependence in the thinning survival rate is set by the resident population, because the invader is "rare." The derivation makes use of the conditional net reproductive rates \( R_0\{i,r\} \mid m \), where \( m \) is the number of nearby patches contributing seed, together with the distribution of crowding levels \( p(m) \) (fig. 10).

The expected \( R_0\{i,r\} \) of an invader can exceed unity in the figure 10 example if at least two necessary conditions are met: the response of the invader's reproductive success to crowding \( (R_0) \mid m \) in fig. 10) is nonlinear, and seed rain of the resident is variable (dispersal is not global). Neither by itself is sufficient. If reproductive success is a linear function of crowding, the potentially large gains on uncrowded sites are offset by the losses on crowded sites. Then the "curvature" in equation...
(26) is zero. If seed rain is everywhere the same, reproductive success does not vary. When both are present, the nonlinear response of net reproductive rate to crowding means that great success in patches of low crowding can more than outweigh poor success in crowded patches.

Figure 10 shows how the two components contribute to invasibility. To highlight the effect of variability conferred by dispersal, the mean seed density is the same in figure 10A and B. With broad resident dispersal (fig. 10A), the great successes possible on uncrowded patches are never realized, because such patches are rare. As resident dispersal declines, invasion becomes easier (fig. 10B). Variability adds a positive term to reproductive success, decreasing to zero as resident dispersal area becomes large and as disturbance becomes rare (fig. 11A). This term has the greatest impact on reproductive success as the reproductive fraction of both species falls below one-half (fig. 11B).

We simulated a two-species version of the Level III model to assess whether dispersal had the predicted effect on invasion by inferior life histories. As predicted, invasion by a well-dispersed species is easy if the disturbance regime matches its life-history traits and the resident population is not too well dispersed (lower right-hand region of fig. 12). Recruitment opportunities become rare as disturbance becomes infrequent (left-hand side of fig. 12) or as dispersal of the resident becomes large (upper part of fig. 12). The converse side of this relationship is that it is harder to be a "good disperser" in the lower right-hand side of figure 12, because \( \pi \), can be small in part because of large patch size.

CONCLUSIONS

Can we continue to ignore recruitment processes if we are to use models to help us understand forest dynamics? Analyses here provide a basis for evaluating the assumption of a constant seed pool—that is, that seed falling on the ground is independent of the populations that presumably should be responsible for producing that seed. By relaxing this assumption in simplified models, we found that the effects depend critically on several spatial and temporal scales, all of which are described by parameters with simple biological interpretations. These parameters are measurable and available in an approximate way from existing literature (table 2). Three parameters related to fecundity schedules are maturation age, seed production rate per unit of crown area, and dispersal area. Additional time scales include plant longevity, thinning rate, and disturbance frequency. Mean population density and variance consist of two components: seed density, which depends on types of mortality that open the canopy and affect the fraction of reproductive individuals; and coefficients that scale the contribution of different density classes. Distributions of densities (figs. 4, 5, 8) can likewise be viewed as consisting of a boundary condition set by seed densities and frequencies within classes that reflect effects of several time scales on representation of density classes.

The Contribution of Time Scales to Seed Rain

Products of this analysis include relationships showing how spatial variability depends on the dominant time scales that operate in a shifting mosaic population.
The fraction of the population that is reproductively mature depends, in a non-linear way, on time scales that include thinning, maturation age, longevity, and disturbance (app. B). This fraction determines the average seed rain, and it has a strong effect on seed-rain variance (app. C). This variability in turn affects diversity by contributing to the probability of success of competitors (app. D).

Disturbance plays a unique role in shifting mosaic dynamics, because the dual consequences for mortality and regeneration affect structure in opposing ways. Density is maximum at intermediate disturbance frequency, because frequent disturbance means increased young, high-density stands but decreased seed rain
Fig. 12.—Results of numerical simulations of competing species over the parameter space from table 2. Contours are relative abundances of the invading population, depending on disturbance and the dispersal area of the resident.

(fig. 3B). Constant seed pool models accommodate only one of these effects (fig. 3A) and so do not permit seed rain to respond to population structure as disturbance frequency changes. The example we used shows an overestimate of density as disturbance increases (fig. 3). Parameter values for the time scales represented by disturbance rates, maturation ages, and longevities fall within ranges that imply sensitivity to environmental change. The quotient \( t_d / t_1 \) is roughly 4–10 (table 1). The product \( \lambda t_1 \) ranges from \( 10^{-1} \) to \( 10^{9} \), and \( \lambda t_2 \) from \( 10^{9} \) to \( 10^{1} \). At these parameter values roughly half of the population is reproductive, and density is importantly constrained by seed rain. Predictions of how composition will respond to increasing disturbance in the future (see, e.g., Overpeck et al. 1990) might consider consequences of ignoring the declining seed rain that attends reduction in the pool of reproductive individuals.

**Thinning as the Mediator of Other Effects**

All sources of variability, be they fecundity, dispersal, or disturbance, have their effects damped by density-dependent thinning. Variability among patches at any given age depends on initial variability, set by dispersal area and secondarily by plant growth rates (fig. 5). Our results predict that damping in among-cohort variance proceeds at the same rate as the proportionate increase in crown
area. Although that result depends on the particular form of the density dependence assumed in equation (3), we expect this rate of convergence to depend on some straightforward relationship with individual plant growth. The predicted decrease in cohort variability with age is consistent with forestry yield tables that allow reasonable predictions of density as a function of stand age and “site index,” an index that summarizes fertility effects on growth rate. Seedling densities have high variance, while those of older trees are more predictable. Our predictions for the rate of change in variance among stands of the same age is a new result and one that is potentially testable. It applies to the phase when density-dependent thinning is dominant, and so it is not intended to hold for seedlings and senescent stands, in which density-dependent thinning is not the dominant mortality agent (Clark 1992). Knowledge of tree growth rates should therefore aid interpretation of the extent to which thinning might damp out the effects of ignored recruitment processes in CSPMs.

The fact that seed rain sets the degree of density dependence means that it determines the mortality that will result from “thinning” relative to density-independent factors. This result follows Harper’s (1977) argument that variability in local densities, beginning with seed rain, could be largely damped by density-dependent thinning rates. Our results do not predict that sib competition is high in juvenile stages; they merely assume that it can be high if crowding becomes intense. Indeed, our results suggest little advantage to high seed production that would lead to such levels of crowding.

In addition to effects among cohorts of the same age, thinning also reduces variability across the entire population (fig. 3C), and it reduces sensitivity of population processes to changes in disturbance frequency (fig. 3B). Again, consequences of the CSP assumption depend on the relationship among time scales.

Dispersal, Population Structure, and Diversity

Our treatment of “limited” dispersal differs from previous ones in that it is not defined by the fraction of seeds apportioned to each of two pools, local, which remains in the resident patch, versus regional, which is evenly distributed across the domain of nonresident patches. Some models do this deterministically (Levin et al. 1984; Shmida and Ellner 1984), others stochastically (Geritz et al. 1988; Pacala and Tilman 1994). “Limited dispersal” in our model means that seeds are evenly distributed across a finite area surrounding the resident patch. It contains a stochastic component produced by stand history but is otherwise deterministic. Because dispersal is treated differently than in previous models, and because we have not rigorously explored coexistence criteria, results from previous studies should be applied with caution. Persistence is not strictly the “stochastic boundedness” interpretation of Chesson (1982), because our species are strongly correlated in terms of recruitment—they exploit the same gaps. Despite the different type of stochasticity explored by us, it is interesting that, like previous studies (see, e.g., Shmida and Ellner 1984; Comins and Noble 1985; Pacala and Silander 1985; Geritz et al. 1988), we found its effects on some aspects of population structure to be minimal provided it is not too restricted. By identifying the rela-
tionships among temporal and spatial scales that affect structure and coexistence, however, we determine that dispersal effects can be extremely important on dispersal scales observed in real forests.

When realistic dispersal areas (table 1) are applied in our model, local recruitment limitation is common and reflected in population structure. Dispersal matters when disturbance rates are similar to or greater than thinning rates (fig. 6), as can prevail with "gap-phase" dynamics in temperate forests and fire in boreal forests (table 1). The time scales of real forests fall in the range that makes sensitivity to dispersal important. Limited dispersal is predicted to result in many areas that will not be reached by seed of a given species following disturbance.

In contrast to some previous studies of dispersal, our results suggest potentially important consequences of dispersal for diversity. The view of invasibility we adopt in this analysis rests solely with spatial and temporal scales. The two key elements, variable crowding coupled with crowding-dependent reproductive success, both depend on time scales describing life history and disturbance. Dispersal represents a way out for the "wrong" life histories (i.e., those that are ill suited to the disturbance regime). This "way out" exploits spatial variability as the potential for success when success at the mean crowding level is limited. For species having maturation well timed to take advantage of new disturbances, dispersal adds almost nothing to reproductive success (fig. 9). Comins and Noble (1985) argued that dispersal did not add to the reproductive success of *Eucalyptus* populations that burn every 50 yr. Using their parameter values with the optimization of net reproductive rate in equation (25) puts *Eucalyptus* close to the optimum life-history schedule for that environment. Our results agree that dispersal adds little in this case. It is the "wrong" life histories that can greatly increase their success by exploiting distant recruitment opportunities.

In many environments, the assumption of global dispersal is importantly wrong. Dispersal area has little effect on mean population density (fig. 9). population structure (fig. 6), reproductive success (fig. 10), and invasibility (fig. 12) so long as it exceeds values of 5–10 patches. The dispersal area of a resident must similarly fall below 5–10 patches before seed-rain variability begins to contribute importantly to invasibility by other species (fig. 11A). Real-world parameterizations place many of the dominant species from boreal forest, sclerophyllous woodland, and canopy gap assemblages far below this range, in a parameter space in which dispersal may be critical (fig. 12). In boreal forest tree seeds are wind dispersed over distances that can often be small relative to the size of average burns. Cone serotiny and root suckering of conifers and hardwoods, respectively, allow for the recolonization by progeny of cohorts occupying the same piece of ground before fire. For these parameter values, our model predicts that limited dispersal could be among the dominant influences on population dynamics. In northwestern Ontario, where individual burns have been dated for the past several decades, burns that revisit jack pine (*Pinus banksiana*) stands before regenerating cohorts achieve maturation age can result in barren ground for extended intervals (J. S. Clark, personal observation). The large fraction of open area predicted in figure 7C results from dispersal distances that are small relative to patch size combined with disturbance effects on seed availability. The poor match
of spatial scales in many sclerophyllous woodlands is also consistent with the importance of vegetative reproduction and animal seed dispersal there (see, e.g., Keeley 1991).

Temperate forests contain some canopy gap species that would qualify as global dispersers in our model and others that would not. Yellow birch (Betula alleghaniensis), for instance, has light seeds released in winter that blow across the snow spanning combined areas of many tree-fall gaps (Houle 1992). Many bird-dispersed seeds are likewise widely dispersed relative to mean disturbance size. Other species have the vast majority of seed remaining within tens of meters of the parent (table 1). Seed rain studies in closed forest of the southern Appalachians show average dispersal distances for most species near or below the average canopy gap diameter (J. S. Clark, unpublished manuscript). Even for the relatively fine scale of a gap disturbance regime, these distances are sufficiently restricted to affect structure (fig. 6) and invasibility (fig. 11) in our models, especially if disturbance rates are of the same order as thinning rates.

Dual Effects of CSPMs

Constant seed pool models have two opposing effects on species diversity, both of which bear scrutiny for forest trees. First is an effect of the mean seed rain, an external pool of immigrants that continues to prop up inferior competitors otherwise doomed to failure (Pacala and Hurtt 1993). The most obvious unrealistic effect resulting from our analysis is the collapse of the seed rain that develops as disturbance increases and the reproductive fraction of the population declines (fig. 3A, B). Parameterizations from table 1 can make this an important source of error (fig. 12).

The second, opposing CSPM effect on diversity comes from global dispersal, which reduces the success of potential good colonists in a sea of better competitors. Limited dispersal by competitive dominants may be critical to coexistence in many sessile populations. The global bath in CSPMs means that diversity is artificially low and must be maintained by some other mechanism (the unrelenting supply of "immigrant" seed?). It is possible that, even with global dispersal, the randomness in seed rain in which the global bath is small can promote coexistence (see, e.g., Geritz et al. 1988; Pacala and Tilman 1994). Whether this stochasticity is a factor maintaining diversity in CSPMs appears to be unexplored, but it is unlikely given that the landscape remains essentially full.

Neither of the two components we identify as necessary components for coexistence are contained in CSPMs. Realistic parameterizations strongly indicate that variable seed rain and nonlinear reproductive success (fig. 10) can be important contributors to diversity in real forests. Lack of these components in CSPMs raises questions regarding predictions of species diversity. The balance between the effects of global dispersal and an unlimited immigrant seed pool might explain the "right" diversity predicted in CSPM studies.

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APPENDIX A

TABLE A1

SOME USES OF GAP MODELS TO ANALYZE POPULATION AND COMMUNITY ASPECTS OF FOREST DYNAMICS

<table>
<thead>
<tr>
<th>Population processes:</th>
<th>References</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Diversity:</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pathogens</td>
<td>Shugart and West 1977*; Alvarez-Buylla and Garcia-Barrios 1991*</td>
</tr>
<tr>
<td>Herbivory</td>
<td>Busing and Clebsch 1987*; Patterson and Aizen 1989*; Alvarez-Buylla and Garcia-Barrios 1991*</td>
</tr>
<tr>
<td>Climate change</td>
<td>Davis and Botkin 1985*; Solomon 1986*; Bonan et al. 1990*; Overpeck et al. 1990*; Shugart 1990*</td>
</tr>
</tbody>
</table>

Note.—We do not include studies of monocarpic plants (see, e.g., Pacala and Silander 1985; Tilman 1988), because such life histories are an exception for trees.

* Studies with constant seed pools (no seed production, i.e., CSPMs).
† Studies with a global seed bath that responds to populations.

APPENDIX B

DISTRIBUTION OF PATCH AGES

This appendix derives the equilibrium distribution of patch ages given both stochastic and deterministic disturbance agents. Assume patches are reset to age zero by a disturbance process, characterized by constant probability λ and by tree senescence, which occurs without exception at age $a = t_2$. The distribution of waiting times between events is discontinuous:

$$f_s(a) = \begin{cases} \lambda e^{-\lambda a} & a < t_2 \\ e^{-\lambda t_2} & a = t_2 \\ 0 & \text{otherwise} \end{cases} \quad (B1)$$

with the bulk of patch turnovers at $t_2$ constituting all those patches that managed to avoid disturbance until that age. The survivor function is obtained by integrating across this distribution:

$$S_s(a) = \int_0^a f_s(a) da + S_s(t_2) = \begin{cases} e^{-\lambda a} & a \leq t_2 \\ 0 & a > t_2 \end{cases} \quad (B2)$$

By integration we have an expected patch age of
**TREE POPULATION RECRUITMENT**

\[ \mu = \int_0^\infty S_i(a) da = D/\lambda \]

for the constant \( D = 1 - e^{-\lambda t} \) and distribution of patch ages

\[ u(a) = S_i(a)/\mu = \frac{\lambda e^{-\lambda a}}{D}. \] (B2)

The fraction of patches greater than age \( a \) is

\[ U(a) = \frac{e^{-\lambda a} - e^{-\lambda t}}{D}. \] (B3)

For instance, the fraction of patches that support reproductive individuals is \( U(t_i) \).

**APPENDIX C**

**MEAN AND VARIANCE FOR THE LEVEL II MODEL**

This appendix contains approximations to the mean and variance of metapopulation densities for the Level II model. Assuming the disturbance process is independent of patch location, the probability that \( M \) patches within dispersal area \( \pi \) of a given patch contribute seed to that patch is binomial,

\[ p(m) = \Pr\{M = m\} = \binom{\pi}{m} \left[U(t_i)\right]^m \left[1 - U(t_i)\right]^{\pi - m}, \]

having expectation \( \pi U(t_i) \). Expression \( U(t_i) \) is the fraction of patches supporting reproductive individuals (eq. [B3]). The initial density on a patch (i.e., at age \( a = 0 \)) is the product of the number of patches contributing seed to that patch and the number of seeds contributed by each patch:

\[ n(0) = n_m(0) = m \times \frac{\beta}{\pi}. \]

On the average, this density is

\[ E[n(0)] = \sum_n np(n) = \sum_m m^2 p(m) = \frac{\beta}{\pi} \sum_m mp(m) = \beta U(t_i). \] (C1)

This result makes use of the fact that \( p(m) \) is a density function with expectation \( \pi U(t_i) \). This is the same result we obtained for the Level I model (eq. [8]), where dispersal is effectively global.

Changes in expected density with patch age are estimated to first order using equation (16). Average crowding level on an age \( a \) patch is \( E(F(a)) = 1 + \{E[F(0)] - 1\} e^{-\rho a} \). Let \( F_m(0) \) be the initial crowding level on a patch that received seeds from \( M \) nearby patches. A patch starting out with crowding level \( F_m(0) \) thins along the trajectory

\[ F_m(a) = 1 + [F_m(0) - 1] e^{-\rho a}. \] (C2)

Substitution in equation (15) gives the change in expected density with patch age

\[ E[n(a)] = \sum_n n(a) p[n(a)] = \sum_m [n(a)|m] p(m). \]

Using equation (C2), we see that density at age \( a \) given that the patch initially received seeds from \( M \) nearby patches is

\[ n(a)|m = e^{-\rho a} \left[1 + \left(\frac{m^2 \beta}{\pi} - 1\right) e^{-\rho a}\right]. \]
Substitution and some manipulation yields

\[ E(n(a)) = e^{-p\alpha} \left( \sum_m p(m) + \left[ \frac{\beta}{\pi} \sum_m mp(m) - \sum_m p(m) \right] e^{-p\alpha} \right). \]

Again, noting that \( p(m) \) is a density function, this simplifies to

\[ E(n(a)) = e^{-p\alpha}[1 + (\beta U(t) - 1)e^{-p\alpha}] \]

where \( E[F(a)] \) is the expected crowding level on a patch of age \( a \) with expected initial crowding from equation (8)

\[ E[F(0)] = \beta U(t). \]

The variance on densities at patch age \( a \) is

\[ \sigma^2_{n(a)} = \sum_m (\{n(a) - E(n(a))\}^2|p(m)). \]

With equation (C3) and the argument used to arrive at that result, we find

\[ \sigma^2_{n(a)} = e^{-2p\alpha} \sum_m \left[ \frac{m\beta}{\pi} - \beta U(t) \right]^2 p(m). \]

The series expression is the variance on densities of age \( a = 0 \). We can therefore write the variance as

\[ \sigma^2_{n(a)} = \sigma^2_{n(0)} e^{-2p\alpha}. \]

The variance on initial crowding levels can be determined using

\[ \sigma^2_{n(0)} = E[n(0)^2] - \{E[n(0)]\}^2. \]

The second moment is

\[ E[n(0)^2] = \frac{\beta^2}{\pi^2} \sum_m m^2 p(m) = \frac{\beta^2 U(t)}{\pi} \{\pi U(t) + 1\}. \]

Upon substitution, then,

\[ \sigma^2_{n(0)} = \frac{\beta^2 U(t)[1 - U(t)]}{\pi}. \]

This expression constitutes the variability in seed rain across a landscape having reproductive fraction of patches \( U(t) \) and dispersal area \( \pi \).

APPENDIX D

REPRODUCTION WITH DISPERSAL

This appendix approximates reproductive success from the distribution of crowding levels and the effect of crowding on the net reproductive rate. The net reproductive rate of an individual that finds itself established in a patch that received \( m = n_m(0)/\pi/\beta \) seeds (app. C) is

\[ R_0|m(0), m > 0 = \beta \left[ \frac{\Lambda_0}{n_m(0)} + \left( 1 - \frac{1}{n_m(0)} \right) \Lambda_1 \right], \]

a simple extension of equation (24). This approximation breaks down for the case of totally
empty patches, because it is based on a first-order approximation to thinning rate in the neighborhood of full canopy coverage (i.e., eq. [15]). Empty patches are better approximated by

\[ R_0[m = 0] = \Lambda_{-1}. \]

The expected reproductive rate across this landscape is

\[ E(R_0) = \sum_{m=0}^{\infty} [R_0|m]p(m), \quad (D2) \]

where \( p(m) \) is the (binomial) distribution of crowding levels (app. C). An approximation to the solution of equation (D2) in the neighborhood of the mean crowding level can be obtained by expanding about the mean,

\[ R_0|m = \sum_{k=0}^{\infty} \left( \frac{mB}{\pi} - U(t)B \right)^k \frac{k!}{k!} R_0^{(k)}, \]

where

\[ R_0^{(k)} = \frac{d^k R_0}{dn_k^k} \bigg|_{U(t)} \]

is the \( k \)th derivative of \( R_0 \) evaluated at the mean crowding level \( U(t) \) and \( n_0 = n_m(0) \).

Substitution into equation (D2) and switching the order of summations (because \( R_0^{(k)} \) is evaluated at a constant) gives the expectation

\[ E(R_0) = \sum_{k=0}^{\infty} R_0^{(k)} \frac{\mu_k}{k!} \quad (D3) \]

for the \( k \)th central moment of the distribution of crowding levels

\[ \mu_k = \sum_{m=0}^{\infty} \left( \frac{mB}{\pi} - U(t)B \right)^k p(m). \]

These first few moments are \( \mu_0 = 1, \mu_1 = 0, \) and \( \mu_2 = \sigma_m^2 \), the variance on initial densities (i.e., eq. [C6]). Upon substitution,

\[ E(R_0) = R_0(U(t)B) + \frac{\sigma_m^2}{2} \frac{d^2 R_0}{dn_k^k} \bigg|_{U(t)} + \cdots \quad (D4) \]

This approximation expresses the expected reproductive success as the sum of two terms, treating as independent the contributions by mean crowding level, \( \bar{n}_0 = U(t)B \), and variance in crowding, \( \sigma_m^2 \), determined by dispersal area. This result is

\[ E(R_0) \approx \beta \Lambda_1 + \frac{1}{U(t)} (\Lambda_0 - \Lambda_1) + \frac{1 - U(t)}{\pi U(t)^2} (\Lambda_0 - \Lambda_1), \]

the last term being the contribution of the variance.

This general approach can be applied to the case of a species \( i \) invading a resident population \( r \) that is at equilibrium (on a landscape scale). Locally, net reproductive rates depend on crowding level \( m \),

\[ R_{0|m} \bigg|_{[n_{r,m}(0), m > 0]} = \beta_1 \left\{ \frac{\Lambda_{0,i}}{n_{r,m}(0)} + \left[ 1 - \frac{1}{n_{r,m}(0)} \right] \Lambda_{1,i} \right\}. \quad (D5) \]
Here \( n_{\text{res}}(0) = \frac{\beta_{\text{res}}}{\pi} \) is seed density for the resident population. Subscript \( i \) denotes life-history parameters for the invading life history. Using equation (D4), we find this result is

\[
E(R_0(\sigma_i)) = \beta_i \left( \Lambda_{1,i} + \frac{\Lambda_{0,i} - \Lambda_{1,i}}{\beta_i U_0(t_i)} \left( 1 + \frac{1 - U_i(t_i)}{\pi U_0(t_i)} \right) \right).
\]  

(D6)

**LITERATURE CITED**


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