Forest Dynamics, Differential Mortality and Variable Recruitment Probabilities

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Abstract. Both spatial and temporal variability in recruitment probabilities can lead to coexistence in gap-phase regenerating forests which would otherwise tend to be dominated by fewer species. Using modified Markov models, the potential roles were examined of temporal variability and differential mortality rates among species in the dynamics of a forest for which spatial variability has been rejected as a strong factor leading to coexistence. Differential longevity modifies results obtained from a simple Markov model: it exerts a strong influence on the equilibrium species composition, on the rate of community change and on the time a community requires to reach equilibrium. Simulations with varying transition probabilities mimicked a changing climate, producing four main results:
1. Unless the duration of climate states is very long or very short, forest composition is in a continual state of disequilibrium.
2. Species vary in their response times to changing climate.
3. The mean abundance of each species under a varying climate scenario is different from that expected from the mean climate state. 4. The rare, long-lived species was favored by climatic fluctuations at the expense of more common shorter lived species. Differential mortality rates provide an equilibrium-based mechanism for coexistence, and temporally fluctuating recruitment probabilities a non-equilibrium mechanism. Composition could be maintained by differential longevity among species and climatic fluctuations allowing periodic recruitment of the less common species.

Keywords: Climate change; Community disequilibrium; Gap forest; Temporal variability; Transition matrix.

Nomenclature: Hitchcock & Cronquist (1973).

Introduction

Environmental patchiness has long been known to have profound theoretical and practical implications for ecological communities (e.g. Wiens 1976; Kolasa & Pickett 1991). The spatial and temporal heterogeneity in regeneration opportunities induced by gaps in the forest canopy is critical to the dynamics of many forest communities (e.g. Sernander 1936; Watt 1947; Runkle 1981, 1982, 1985; Naka 1982; Nakashizuka 1983; Brokaw 1985a,b; Veblen 1985, 1986; Denslow 1987; Lertzman & Krebs 1991; Lertzman 1992; Liu & Hytteborn 1991). Two contrasting roles have been demonstrated for gaps as mediators of community dynamics. Because the gap environment often meets the requirements of species which could not otherwise establish, gaps can promote coexistence by maintaining shade intolerant species in the forest community (e.g. Connell 1978; Denslow 1987; Whitmore 1989; Liu & Hytteborn 1991). Alternatively, they may be the site of tree-by-tree successional replacement (e.g. Horn 1971, 1975; Glitzenstein et al. 1986; Lertzman 1992). The sum of the individual transitions of space from the trees whose mortality creates gaps (gap-makers) to those who replace them (gap-fillers) is an estimate of whether the species composition of the forest is changing. Thus, the net result of the gap creation and filling processes can be used to determine the equilibrium status of the forest community.

Research to date has largely focused on gaps as a source of spatial variability in the recruitment opportunities in forests (e.g. Runkle 1981, 1982, 1985; Brokaw 1985a,b; Liu & Hytteborn 1991). The hypothesis in such cases is that spatial variability within and among the gaps present at any given time is sufficient to maintain the current species composition of the forest canopy. The hypothesis that temporal variability in recruitment patterns in gaps may be a process leading to coexistence has received little attention in gap-regenerating forests relative to the examination of spatial variability. Given the known variability in climate over time scales relevant to tree population dynamics (e.g. Davis 1986), assessing the potential roles of temporal variability in driving recruitment probabilities seems an important, if difficult, problem to address before coming to firm conclusions regarding the net role of gap-phase processes in a forest community. In fact, forests with persistent, multiparous, long-lived individuals are excellent candidates for Chesson and Warner's 'storage effect' (Chesson & Warner 1981; Chesson 1986; Chesson & Case 1986). The storage effect promotes coexistence of competing species under fluctuating environmental conditions where reproductive potential can be 'stored' through unfavourable periods (through mechanisms such as seed and bud banks, persistent saplings, or very long-lived adults).

One common approach to assessing the equilibrium status of a community is to project the consequences of different patterns of recruitment probabilities through the use of transition matrix models (Horn 1971, 1975; Runkle 1981; Acevedo 1981; McAuliffe 1988). Each element in such a matrix represents the probability that a canopy tree of species *i* will be replaced by a recruit of species *j*. Most applications of such models assume that transitions are a first order Markov process (Kemeny & Snell 1960; Cox & Miller 1965), i.e. the factors determining the transition probabilities are unchanging in time (the matrix is stationary), and the state at time (t+1) depends only on the state at time (t) and not on any past states. The Markovian criterion is said to pertain in systems where 'history' is not important (van Hulst 1979a,b). It is perhaps more correct to say that the sequence of events leading to the current state are important only in terms of how they are reflected in the current state. A common use of such models is to assess the equilibrium status of a community by comparing the predicted equilibrium composition with the current canopy composition (Horn 1971, 1975; Runkle 1981; Veblen 1985; White et al. 1985; Taylor & Zisheng 1988). Given the Markovian assumptions, the equilibrium composition is determined by the transition probabilities alone, irrespective of the initial state.

The conditions which determine species-specific transition probabilities, such as climate, do change over time scales relevant to the population and community dynamics of long lived organisms such as trees (Davis 1986; Ritchie 1986; Kullman 1987; Steijlen & Zackrisson 1987; Huntley 1990; Bradshaw & Zackrisson 1990; Bradshaw 1993). For such systems, Markov projections are more appropriately treated as estimates of the current trajectory of community change than as predictors of future equilibrium states. For systems that are unlikely to reach equilibrium, the predicted equilibria are useful primarily as indices of the consequences of a particular set of transition probabilities or the environment that determined them.

In its basic form, a Markov model only specifies the fate of open space once it has been created. It does not incorporate patterns in the creation of open space, such as differential longevity among species. The latter can be an important factor moderating the results of the transition probabilities in some communities, and the effects of longevity need to be added to Markov models of communities containing species with diverse lifespans (Horn 1975; Acevedo 1981; White et al. 1985; Veblen 1986; McAuliffe 1988).

Lertzman (1992) examined patterns among the transitions between gap-makers and gap-fillers in a subalpine old growth forest at Cypress Provincial Park in SW British Columbia, Canada. A matrix of species-specific transitions was constructed based on the identities of those individuals whose mortality created gaps (gap-makers) and those which were recruiting to fill gaps (gap-fillers). The transitions were strongly weighted in favor of one species, *Abies amabilis* (Pacific silver fir), at the expense of the others. I examined the hypothesis that spatial variability within and among gaps would lead to coexistence, but was not able to find any aspect of variability in the gap environment that was acting strongly to compensate for the firs' dominance among transitions. In particular, it was expected that variation in the size of gaps would be associated with differences in species dominance among gap-fillers, as has been found elsewhere (e.g. Denslow 1987; Brokaw 1985a,b; Whitmore 1989). However, while the number of gap-fillers increased with opening size, the relative proportions of each species among those gap-fillers did not. Thus the current transition probabilities from gap-makers to gap-fillers indicated that species composition was not in equilibrium and over time would lead to a shift in community composition in favor of *A. amabilis*.

The analysis in Lertzman (1992) did not incorporate differential mortality among canopy species or temporal variability in transition probabilities. In this paper, two hypotheses are examined: (1) differential longevity among species is sufficient to maintain the current species composition in the forest canopy, and (2) temporal fluctuations in climate, as expressed in recruitment probabilities, can lead to non-equilibrium coexistence of these species.

Material, Methods and Models

Study system

Details about the Cypress Park forest, tree species autecology, and the methods with which the data discussed here were collected can be found in Lertzman (1989), Lertzman & Krebs (1991) and Lertzman (1992). The empirically determined transition matrix is based on the detailed descriptions of 112 gap-maker/gap-filler transitions in 60 gaps located in four stands at Cypress Provincial Park.

Four species of trees occupy the canopy at Cypress Park: *Abies amabilis*, *Tsuga heterophylla* (Western hemlock), *T. mertensiana* (Mountain hemlock), and *Chamaecyparis nootkatensis* (Alaska Yellow-cedar). The stands studied are above the local elevational limit for *Pseudotsuga menziesii* (Douglas-fir). *T. mertensiana* and *C. nootkatensis* are sub-alpine species and the focal stands are near their lower elevational limits. *T. heterophylla* is a low elevation species which reaches its upper distributional limit in these stands. The focal stands at Cypress Park represent roughly the center of the local elevational distribution for *A. amabilis*.

All four species are relatively long-lived and are broadly represented among age and size classes at Cypress Park. However, there are significant differences in longevity among the species with *A. amabilis* being the shortest lived and *C. nootkatensis* the longest. The maximum recorded age at stump height for *A. amabilis* is 697 yr at Cypress Park and for the *Tsugas* 944 yr (Lertzman 1989; Lertzman mscr.). Several nearby large *C. nootkatensis* have been aged at > 1100 yr (R. Stoltmann, L. Josza, pers. comm.). The stands at Cypress Park have apparently been without a major fire for much longer than the age of these old trees; they are frequently found on the uncharred stumps of trees of similar size.

General data on gap-fillers and definitions

Some applications of Markov models have been criticized on the basis of how the transition probabilities were estimated. For instance, basing transition probabilities on comparisons of overstory species composition with understory species composition assumes an equality in growth rates and survival of the understory trees that can result in substantial error (White et al. 1985). Better estimates of species-specific transitions are obtained by comparing the species of gap-makers with the species of those individuals destined to replace them in the gaps (White et al. 1985). The transitions discussed here are based on comparisons of the species of gap-maker with the species of its definitive gap-filler(s). Definitive gap-fillers are those trees which, by virtue of their height, growth rate and location, are deemed most likely to successfully occupy the open space in a gap (Lertzman 1992). In most cases there were one to three such individuals which could easily identified as dominant among the gap-fillers associated with a particular gap-maker. See Lertzman (1992) for a detailed description of the derivation of the transition probabilities from these identifications.

The modified Markov model

To build Markov models, it is assumed that the probability with which each species replaces each other species is equal to the relative frequency of each gap-maker-gap-filler transition. A demographic component is added to the models to investigate the effects of differential longevity among species on the time-course of change to equilibrium, and on the equilibrium predicted by the models. Differential longevity is expressed as variation in species-specific mortality rates. The model simulates a population of 1000 individuals. At each 10-yr time step, species-specific mortality rates are applied to the community: a fixed proportion of the individuals of each species is 'killed'. These gap-makers are then replaced according to the probabilities in the transition matrix. The simulated population is not age- or size-structured, so mortality rates are not age- or size-specific. Trees whose mortality can create a gap in which young trees recruit must be at least canopy co-dominants, so only mortality of these is simulated.

Other modeling approaches could be used to examine the problems addressed here, notably the forest succession models classed as 'gap models' (e.g. Shugart 1984; Smith et al. 1994). The use of Markov models was chosen primarily because they allowed isolation of the specific factors to be examined; differential mortality rates among species and temporal variability in recruitment probabilities. Tree mortality rates would be more difficult to address directly in the gap models. Further, the gap models have not been parameterized for the Cypress Park forest type and previous empirical work there provided direct estimates of the base transition matrices (Lertzman 1992). However, future modeling efforts would profit from considering the gap type models because of their more explicit process orientation.

Calculating differential mortality rates

There are no published mortality rates for old growth of the type found at Cypress Park, and few for any similar systems. Estimates of mortality rates were generated in two ways: based on measured mortality rates in a related system in Oregon and based on the ages of canopy trees at Cypress Park. Using these estimates, two scenarios were developed with equal mortality rates among species (one high and one low), and two scenarios with differential mortality rates among species.

The mortality rates in the scenario Differential Mortality 1 (Table 1) were based on the data from an old growth *Pseudotsuga menziesii* forest in Oregon (Franklin & DeBell 1988), combined with the distribution of species among gap-makers at Cypress Park (Table 2). To generate mortality rates for the Cypress Park system based on the Franklin & DeBell (1988) data, I made several assumptions. First, in their stand, mortality rate generally decreases with tree size, and *Abies amabilis* and *Tsuga heterophylla* are represented in smaller size classes than they are at Cypress. So, rather than their species-specific mortality rates, the overall mean mortality rate for individuals of all species > 37 cm DBH (0.57 %/yr) was used as an estimate of annual mortality for the stand as a whole. Assuming a steady state distribution of gap-makers among species at Cypress Park, species-specific mortality rates were calculated by as-

Table 1. Annual mortality rates for each species in each model. Differential Mortality 1 uses data from Franklin & DeBell (1988) combined with each species' proportions among gap-makers at Cypress Provincial Park to determine species-specific mortality rates. Equal Mortality Rate Model 1 uses the maximum of the mortality rates from Differential Mortality 1 for all species, and Equal Mortality Rate Model 2, the mean. Differential Mortality 2 uses mortality rates based on the ages of canopy trees at Cypress Park as explained in the text. See text for further explanation of each model. The inverse of these rates is an estimate of canopy turnover by species.

Model	Species			
	Abies amabilis	*Tsuga heterophylla*	*Tsuga mertensiana*	*Chamaecyparis nootkatensis*
Equal MR 1	0.00842	0.00842	0.00842	0.00842
Equal MR 2	0.00447	0.00447	0.00447	0.00447
Diff. MR 1	0.00842	0.00389	0.00388	0.00170
Diff. MR 2	0.00184	0.00125	0.00125	0.00091

suming that total stand mortality would be allocated among species in the proportions in which species occur among gap-makers at Cypress (Table 2). For instance, based on Franklin & DeBell (1988), of 1000 total trees, 57 die each decade (0.57 % annual mortality rate). *A. amabilis* represents a proportion of 0.638 of the gap-makers at Cypress (Table 2); so 0.638×57=36.37 of the gap-makers during that decade would be allocated to *A. amabilis*.

In one of the stands (STRACHAN2), where *T. mertensiana* was most common in the canopy, there was a higher frequency of unidentifiable gap-makers (Lertzman & Krebs 1991), causing *T. mertensiana* to be under-represented among gap-makers. To correct for this in the proportions of gap-makers applied to the Franklin & DeBell (1988) rate above, all hemlocks from Table 5 in Lertzman & Krebs (1991) were lumped (*T. heterophylla*, *T. mertensiana* and generic 'HEM's). Given equal mortality rates between the hemlock species, it was assumed that total hemlock mortality was distributed among gap-makers in proportions equal to each species canopy. Because *C. nootkatensis* decays more slowly than *T. mertensiana*, and is therefore recognizable for a longer period in the decay process, no correction to its representation among gap-makers was applied. Table 1 presents the mortality rates obtained through this process.

The two equal mortality rate scenarios were based on the mortality rates calculated for Differential Mortality 1. Equal Mortality Rates 1 applied the mean mortality rate from this scenario to all species, and Equal Mortality Rates 2, the maximum mortality rate (Table 1).

The mortality rates for Differential Mortality 2 were based on the ages of trees found at Cypress Park (Lertzman 1989). For *A. amabilis* and the two hemlock species, the mean age of trees greater than the median age was used as an estimate of longevity, and its inverse as an estimate of the mortality rate of large, gap-forming trees. For *C. nootkatensis*, 1/1100 yr was used as the mortality rate. This generated mortality rates substantially lower than those in Differential Mortality Model 1, but with less overall differential between species.

I do not assume that these estimated mortality rates accurately represent the true rates at Cypress Park; the data with which to assess actual mortality rates do not exist. Rather, it is suggested that these estimates are reasonable guesses based on partial information, and that they are adequate to assess the qualitative effects of changes in the overall rate of mortality and how mortality is distributed among species on patterns of relative abundance over time.

To characterize each model, the equilibrium was defined as the proportion of each species after 5000 yr. In all cases, the changes in the abundances of each species during the last 1000 yr of simulation was far less than 1 %. Equilibrium species abundances could be obtained analytically (Kemeny & Snell 1960; Cox & Miller 1965), but using the simulations facilitated examination of changes over time when the forest is far from equilibrium, which would have been more difficult analytically (Coale 1972). An estimate of the community disequilibrium is obtained by calculating, at each time step, the sum over all species of the difference between their current abundance and their equilibrium abundance. Examination of change in this value over time allows an assessment of the rate of change in the community during its approach to equilibrium, and of the time it

Table 2. Proportions of each species among primary and secondary gap-makers combined, canopy trees, and definitive gap-fillers. Data are modified from Fig. 1 of Lertzman (1992), Table 5 of Lertzman & Krebs (1994) and Lertzman (1989).

	Abies amabilis	*Tsuga heterophylla*	*Tsuga mertensiana*	*Chamaecyparis nootkatensis*	*N*
Gap-makers	0.638	0.242	0.102	0.019	147
Canopy	0.432	0.355	0.150	0.063	602
Definitive gap-fillers	0.670	0.195	0.090	0.045	221

takes to reach equilibrium conditions. This refers to the percentage species' abundance in the community as a whole. If otherwise, i.e. referring to percentage change in a species' abundance, this will be indicated (see also Fig. 1).

Though the equilibrium species composition is independent of initial conditions for a given transition matrix, the time to reach equilibrium will vary greatly with the initial distance from equilibrium. By using the current composition of the Cypress Park forest as initial conditions for all simulations (Table 2), it was possible to assess the implications of each model for change at Cypress Park and compare the equilibria and time-course of change between models.

Simulations with non-stationary transition matrix: Changing environmental conditions

Climate has not been stable over time scales relevant to the population and community dynamics of long-lived trees, and we cannot assume *a priori* that tree communities are in equilibrium with climate today (Davis 1981, 1986; Kullman 1987; Ritchie 1986; Colinvaux 1987; Steijlen & Zackrisson 1987). To examine the potential role of a changing environment in the dynamics of the Cypress Park community, the assumption of stationary transition probabilities was relaxed. This was done by constructing two alternate transition matrices, one for an arbitrary warmer climate, and one for a colder climate (Table 3). Both were based on the empirically determined matrix used in the above simulations. The goal was to make changes in the matrix that would reflect fluctuations in climate of approximately the magnitude of the change from the medieval optimum to the little ice age, or the little ice age to the early 20th century warming (Lamb 1982; Kullman 1986, 1987; Ritchie 1986; Steijlen & Zackrisson 1987). For instance, the warming trend earlier this century resulted in the invasion by trees of sub-alpine meadows such as occur 100-

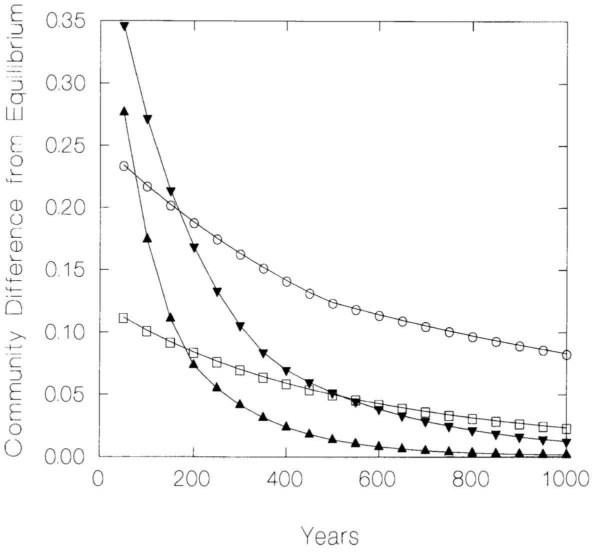

Fig. 1. Total community difference from equilibrium composition: models with empirical transition matrix. Data points represent the summed deviations of each species from its equilibrium value. Units are the proportion of the total community. Open squares = Differential Mortality 1; open circles = Differential Mortality 2; filled point-up triangles = Equal Mortality 1; filled point-down triangles = Equal Mortality 2.

Table 3. Transitions between species of gap-makers and gap-fillers for three alternative climate states.

	Gap-fillers			
	Abies amabilis	*Tsuga heterophylla*	*Tsuga mertensiana*	*Chamaecyparis nootkatensis*
Gap-makers				
'Warmer climate' matrix				
Abies amabilis	0.504	0.496	0	0
Tsuga heterophylla	0.600	0.400	0	0
T. mertensiana	0.680	0.260	0.060	0
Chamaecyparis nootkatensis	0.680	0.260	0.060	0
Empirical matrix: Current conditions				
Abies amabilis	0.605	0.312	0.083	0
Tsuga heterophylla	0.766	0.213	0.021	0
T. mertensiana	0.692	0	0.231	0.077
Chamaecyparis nootkatensis	0.500	0	0.250	0.250
'Colder climate' matrix				
Abies amabilis	0.504	0.212	0.183	0.101
Tsuga heterophylla	0.670	0.110	0.120	0.100
T. mertensiana	0.492	0	0.331	0.177
Chamaecyparis nootkatensis	0.300	0	0.350	0.350

Table 4. Equilibrium species compositions for several versions of the Markov model. See Table 1 for explanation of the models. For the first six models, values are the proportion represented by each species after 5000 yr of model time. The 'Warm matrix' and 'Cold matrix' results represent the equilibrium obtained for Differential Mortality 1 using the two 'alternative climate' transition matrices shown in Table 3. The values for Cyclic and Random climates are the overall mean proportions of each species for simulations with all durations of climate states, i.e. 50, 100, 200, 300 yr; see Figs. 3, 4 and 5. The mean proportions varied negligibly among simulations with different durations of climate states. For the random climate simulations, the data represent samples drawn every 200 years from 100 replicates of 5000 year model runs.

Model	Species			
	Abies amabilis	*Tsuga heterophylla*	*Tsuga mertensiana*	*Chamaecyparis nootkatensis*
Current canopy	0.432	0.355	0.150	0.063
Equal MR 1	0.653	0.259	0.080	0.008
Equal MR 2	0.653	0.259	0.080	0.008
Diff. MR 1	0.457	0.392	0.122	0.029
Diff. MR 2	0.558	0.324	0.102	0.016
'Cold' matrix	0.239	0.124	0.253	0.385
'Warm' matrix	0.359	0.642	< 0.001	< 0.001
Cyclic climate	0.385	0.382	0.126	0.107
Random climate	0.373	0.382	0.125	0.121

200 m in elevation above these stands (Brink 1959; Franklin et al. 1971).

The rules used to generate these alternate climate matrices were that changes in a given cell should be (1) in the range of 10 - 20 %, and (2) based on patterns observed in the empirical matrix - such as a low frequency of transitions between the high elevation species and the low elevation species, and a higher frequency of transitions involving *A. amabilis* and all other species; see Lertzman (1992) for discussion of these patterns. In a few cases changes were greater than 20 %, such as the proportion of *T. mertensiana* and *C. nootkatensis* gapmakers replaced by *T. heterophylla* in the intermediate matrix compared with the warm climate matrix.

The warm climate matrix favors the low elevation species, *T. heterophylla*, at the expense of the others, especially *T. mertensiana* and *C. nootkatensis*. The cold climate matrix favors the high elevation species, *T. mertensiana* and *C. nootkatensis*, at the expense of the others, especially *T. heterophylla*. *A. amabilis* is most favored under the intermediate empirically derived conditions, but never does badly.

As with the estimates of mortality rates, these alternate climate matrices are not intended to reflect specific real climates, but rather are 'best guesses' of what transitions might look like under changed climatic conditions in either direction. Because these species have coexisted in varying proportions in this stand under a variety of climates over the last five millennia (Lertzman & Brubaker unpubl. data), the conditions reflected in these alternative matrices should have existed at some time in the history of the stands.

In order to create smoother transitions from one climate state to another, two additional matrices were created with values halfway between the empirical matrix and those at either climatic extreme. In simulating changing environmental conditions, there were thus five possible climate states: colder, cold, empirical matrix, warm, warmer.

Two components of a changing climate were examined: the pattern in which climate states occur, and the duration of each state. Two patterns of change were used in climate states; one in which states followed each other in a sinusoidal sequence (e.g. one period would be: neutral, warm, warmer, warm, neutral, cold, colder, cold), and one in which the climate states were randomly chosen. For each pattern, cases were simulated where the duration of climate states was 50 yr, 100 yr, 200 yr, and 300 yr. These give periods for a cycle from neutral → warm → neutral → cold of 200 to 1200 yr. Changing climate simulations were run with both Equal Mortality 2 mortality rates and Differential Mortality 1 mortality rates. To generate summary statistics for the random climate simulations, 100 replicates of each scenario were run - with samples taken every 200 yr from 5000-yr time series.

Results

Equilibria and time to equilibrium with and without differential mortality

With equal mortality rates, the forest experiences substantial change from its initial conditions, reaching an equilibrium where *Abies amabilis* is substantially more common than it is now and the other species are less common (Equal MR 1 and 2; Table 4, Fig. 1). Thus, as expected, based solely on the replacements currently occurring in gaps, we would conclude the forest is far from equilibrium and undergoing substantial change towards dominance by *A. amabilis*. Reducing the overall mortality rate, but holding it proportional among species does not change the outcome of succession, but can delay reaching equilibrium (compare equilibrium compositions for Equal MR 1 and Equal MR 2 in Table 4, and rates of change in Fig. 1).

Even with equal mortality rates, species vary in the length of time they take to reach their equilibrium proportion, depending on the magnitude of change required. For instance, under Equal MR 2, *A. amabilis* increases 22 % from initial conditions, and takes 310 years to approach within 5 % of the equilibrium. *Tsuga heterophylla* decreases with 9 %, and takes 90 yr to approach within 5 % of its equilibrium value. Time to reach equilibrium defined for the community as a whole appears to be very different from what one might estimate based on examination of individual species. Each species' contribution to overall community disequilibrium will depend on its abundance within the community, its rate of change, and how far it is from its own steady state value.

However, mortality rates do differ among species, and the results of Equal MR 1 and 2 are mainly useful as baselines against which to judge the effects of differential mortality. Incorporating differential mortality into the models has two main effects: changing the equilibrium species composition and extending the time taken to reach equilibrium. In both the models with differential mortality among species, the equilibrium species composition is substantially moderated relative to that for the equal mortality models. Each species is intermediate in abundance between its current representation in the canopy and that predicted by the equal mortality rate models. Thus the dominance of *A. amabilis* among definitive gap-fillers is partially compensated for by its shorter lifespan (compare Differential mortality 1 and 2 with Current canopy, Equal MR 1 and Equal MR 2; Table 4). In fact, the initial conditions for all species (= current canopy composition) are within 5 % of their equilibrium values predicted by Differential Mortality Model 1.

Differential Mortality models 1 and 2 predict different equilibrium compositions from each other because of the difference in the ratio of mortality rates between species. For instance, the ratio of the mortality rates of *A. amabilis* and *C. nootkatensis* for Differential Mortality 1 is 4.95, whereas for Differential Mortality 2 it is 2.02. Because there is less overall differential in mortality rates in Differential Mortality 2, its equilibrium composition is intermediate between that of Differential Mortality 1 and the Equal Mortality Rate models. The lower rate of total stand mortality in Differential Mortality 2, combined with the larger initial difference from its equilibrium composition, means that under this model the approach to equilibrium is quite slow and prolonged: after 1,000 years the community is still almost 10 % from its equilibrium composition (Fig. 1).

Species also take different lengths of time to reach equilibrium under the Differential Mortality models. Species with faster turnover of individuals, such as *A. amabilis*, more quickly approach to within a few percent of their equilibrium proportion, whereas the species with the slowest turnover (*C. nootkatensis*) takes substantially longer. Though close to the equilibrium species composition initially, the forest at Cypress today may still be hundreds of years to millennia from reaching a state of no change. Under Differential Mortality 1, with higher overall mortality, species vary from 330 to 1,050 years to reach within 1 % of the equilibrium value. Under Differential Mortality 2, with lower overall mortality, species vary from 1665 to 3095 yr. The rate of change over the last few percent is so slow that it would certainly be undetectable in field data. During this time, the turnover of individuals of the longest lived species may be rate-limiting for the equilibration of the community as a whole.

Without knowledge of the actual mortality rates at Cypress Park it is not possible to choose one set of mortality rates over the other to assess definitively the equilibrium status of the forest in this area. It is clear though, that the initial assessment that the forest is far from equilibrium is unlikely to be correct. Using reasonable assumptions about differential mortality, it is possible for the current regime of gap-phase replacement to maintain the current canopy composition.

The remaining simulations with varying climate states use Differential Mortality 1 mortality rates because (1) they are in better accord with the little data that do exist, and (2) the sample of gap-maker species composition at Cypress Park is better than the sample of the age distributions.

Equilibria produced by warm climate and cold climate matrices

The cold matrix and warm matrix results in Table 4 show the equilibrium species composition for Differential Mortality 1 using the two alternative climate matrices (Table 3). The equilibrium compositions reflect the intent of the matrices: the cold matrix produces a forest dominated by *C. nootkatensis*, *T. mertensiana* and *A. amabilis*, and the warm matrix produces a forest dominated by *T. heterophylla* and *A. amabilis* with the two high elevation species virtually excluded. In general, times to equilibrium with the alternative matrices are longer than with the empirical matrix, reflecting the difference between the current species composition and the equilibria for either alternative matrix (Fig. 2).

The forest produced by the cold matrix resembles the current species composition at higher elevations in the *T. mertensiana* zone, where the forest grades into sub-alpine parkland, except that *T. heterophylla* is normally excluded in such areas altogether. Although *C. nootkatensis* is the most common species at equilibrium under the cold matrix, it takes an exceptionally long time for *C. nootkatensis* to reach this abundance. Over most of the first 1000 yr there is a more equitable split between *A. amabilis*, *T. mertensiana* and *C. nootkatensis*.

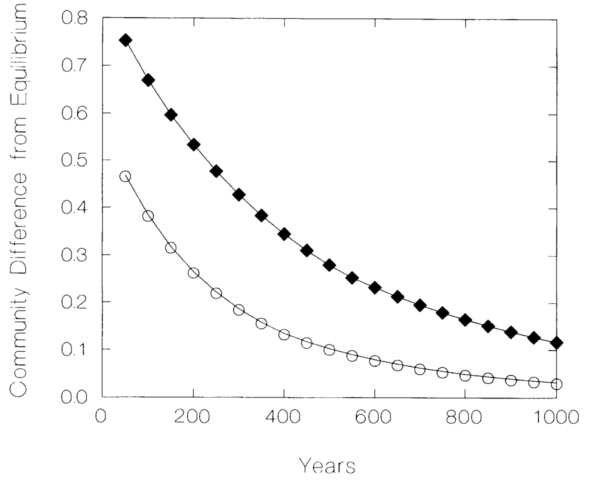

Fig. 2. Total community difference from equilibrium composition: cold climate and warm climate transition matrices. Units are the proportion of the total community. Both simulations used Differential Mortality 1 mortality rates. Data points represent the summed deviations of each species from its equilibrium value. Filled diamonds = Cold Climate transition matrix. Open circles = Warm Climate transition matrix.

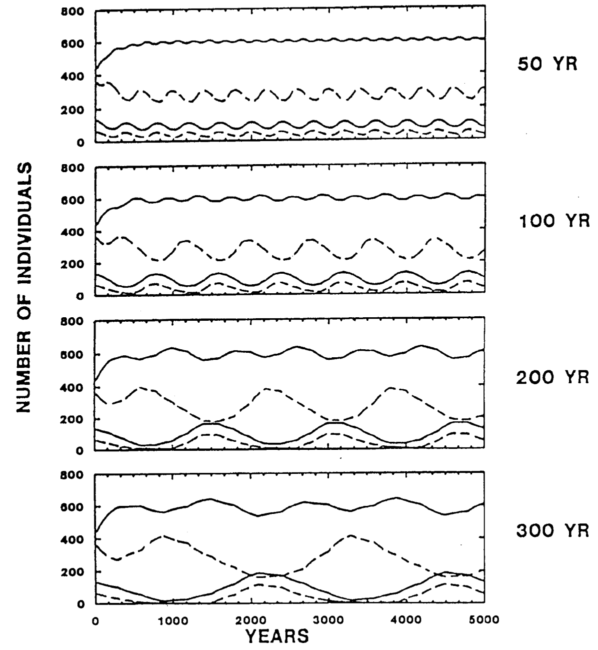

Fig. 3. Forest change with equal mortality rates and cyclic climate. In each case, the total individuals in the community is 1000, so that the vertical axis value divided by 10 = percent composition. Different graphs represent different durations of climate states; 50, 100, 200 and 300 yr. Upper solid line is *A. amabilis*; Upper broken line is *T. heterophylla*; Lower solid line is *T. mertensiana*; Lower broken line is *C. nootkatensis*.

During much of this time it resembles fairly closely the current species composition in one of the stands where the empirical data were gathered (STRACHAN2; Lertzman 1989).

The effects of changing climate and climate-differential mortality interactions.

Fig. 3 shows the results of simulations with equal mortality rates under a regularly varying climate. The species' fluctuations are always either in phase or 180° out of phase with each other. When the duration of each climate state is long enough (> 100 yr), *C. nootkatensis* is eliminated from the stand during warm periods. Though species fluctuate in abundance, only with the longest periods is there a reversal in ordinal rank of species abundance, and *A. amabilis* is always the most abundant.

In these simulations and those that follow, *A. amabilis* has two periods for every one of the other species. This is because the climate only passes through the optimum for the other species once per period, whereas, since the optimum for *A. amabilis* is in intermediate states, the climate passes through its optimum on both the ascending and descending phases. With equal mortality rates, the height of the two peaks for *A. amabilis* are the same.

With differential mortality under a regularly varying climate, there are some important differences which become increasingly clear as the duration of climate states increases (Fig. 4). First, the species are not in phase; lags develop which are proportional to the differential in mortality rate among species. This is most clearly seen for *C. nootkatensis* and *T. mertensiana* where the lagged response of *C. nootkatensis* can cause a reversal in relative abundance twice per period. Second, *A. amabilis* and *T. heterophylla* also show reversals of relative dominance. Third, the two peaks of *A. amabilis* abundance per climatic period are unequal in height: silver fir does better when it is growing cooler after a warm period than when it is growing warmer after a cool period. This is because the *T. heterophylla* population tracks the worsening climate (from its perspective) faster than does *C. nootkatensis*, creating more gaps for the firs to fill during the transient periods when it is most competitive. Finally, *C. nootkatensis* is not eliminated from the community under any of the scenarios examined. Its longevity allows it to persist through unfavorable periods of 900 yr duration (warm → warmer → warm; 300 yr each), even though for the middle 300 yr it does not successfully fill any gaps (Table 3).

Under random climate sequences, the dynamics were similar, except that the fluctuations were erratic rather than regular. Little can be concluded from one realiza-

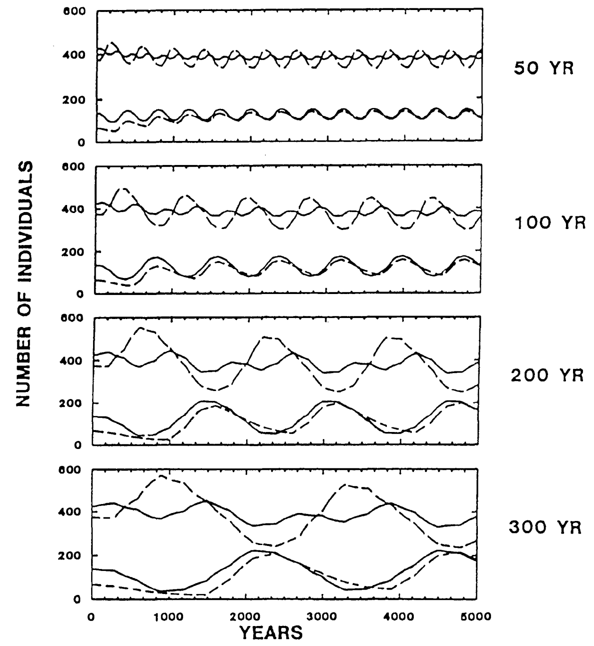

Fig. 4. Forest change with differential mortality rates among species and cyclic climate. Axes, climate states and species are as in Fig. 3: upper solid line is *A. amabilis*; upper broken line is *T. heterophylla*; lower solid line is *T. mertensiana*; lower broken line is *C. nootkatensis*.

tion of a random process, so the discussion of random climate simulations is based on the results of a large number of such runs.

For all model runs incorporating a changing environment, the system state observed in any given window in time is transient. These transient dynamics can be summarized by the mean abundance of each species over time and the variability about the mean. The mean abundances of each species are very similar under random and cyclic climate sequences, though the *A. amabilis* does slightly less well, and *C. nootkatensis* slightly better under random climates (Table 4). Within a given pattern of climatic fluctuation, mean abundances varied negligibly between simulations with different durations of climate states.

For both the cyclic and random climates, the realized mean species abundances differ from what is expected from the mean climate state. The intermediate empirical transition matrix is the average climate for all scenarios, but relative to the equilibrium composition for this matrix (Table 4), varying climates result in a decrease in the abundance of silver fir (0.457 to 0.385, cyclic climate mean; Table 4) and an increase in the abundance of *C. nootkatensis* (0.029 to 0.107, cyclic climate mean; Table 4). While this represents only a 16 % change in the fir population, it represents a 279 % increase in *C. nootkatensis* abundance (expressed in terms of their own abundances). These differences can be attributed to a combination of the system tracking a constantly changing climate, differential mortality among species, and the interaction between the two.

The component of this difference due to the system tracking a changing climate alone can be seen in the simulations with changing climate and equal mortality rates. The reduction in *A. amabilis* and increase in *C. nootkatensis* is seen to a lesser extent here. The mean abundances for the 100-yr duration simulation with equal mortality are: *A. amabilis*: 0.592; *T. heterophylla*: 0.275; *T. mertensiana*: 0.093; *C. nootkatensis*: 0.040. These are intermediate between the results from the equal mortality rate simulations without changing climate and the simulations with differential mortality and changing climate (Table 4).

Variability in species abundance over time increases with increasing duration of climate states under both random and cyclic climate sequences (Fig. 5): when the system has more time to reach an equilibrium to one climate, it is farther from the equilibrium for another and the magnitude of the oscillations increases. Several patterns among species are apparent in Fig. 5. Though *T. heterophylla* consistently has the highest variability (represented by the standard deviation of its abundance), *C. nootkatensis* has the largest coefficients of variation because it has the smallest mean population size. At low numbers of individuals, the absolute magnitude of fluctuations in population size may be less important than the proportion they represent of the mean population size (see discussion of *C. nootkatensis* below). Note that the biggest difference in summary statistics between cyclic climate simulations and random climate simulations is the increase in the coefficients of variation for the two least common species - *T. mertensiana* and *C. nootkatensis* - under random climates.

Discussion and Conclusion

These simulations support the hypotheses that differential longevity among species and temporal fluctuations in recruitment probabilities can each separately mitigate the apparent future dominance of *Abies amabilis* projected in Lertzman (1992). Differential longevity alone can act as an equilibrium based mechanism for coexistence, but, given the time scale involved, is unlikely to act in isolation from the non-equilibrium-based processes of temporal variability. Consideration of these factors should be a necessary aspect of assessing the equilibrium status of a gap-phase regenerating forest (White et al. 1985; Veblen 1986). Further, differential

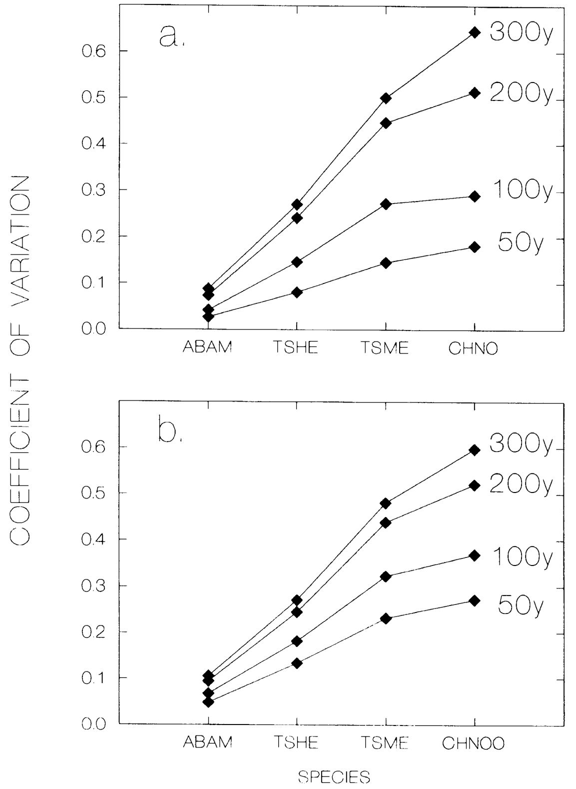

Fig. 5. Change in coefficient of variation (CV) by species as the duration of each climate state increases; data based on those shown in Figs. 3 and 4. Means corresponding to CV values are shown in Table 4. **a.** Climate Cyclic. **b.** Climate Random.

longevity interacts with a fluctuating climate in ways which increase the average abundance of rare, long-lived species at the expense of more common, shorter-lived species. Coexistence in this system may be promoted by both equilibrium and non-equilibrium mechanisms that are not reflected in the current tree-by-tree replacements which determine the empirical gap-maker-gap-filler transition matrix.

Both hypotheses based on spatial variability and on temporal variability focus on the provision of variable regeneration opportunities as a mechanism of coexistence. This consideration of differential mortality rates supports the notion that, for some species, consideration of life history attributes influencing senescence and the ability for established individuals to persist is at least as important early life history phenomena. The 'senescence niche' of long-lived organisms deserves the degree of attention that has been paid to the regeneration niche (e.g. Grubb 1977).

These results can be seen as a special case of lottery model of Chesson &Warner (1981) where environmental fluctuation promotes coexistence through recruitment fluctuations (Chesson & Warner 1981; Warner & Chesson 1985; Chesson 1986). The changes in the transition matrices explicitly represent variation in recruitment probabilities with a changing environment. Species are long-lived, with overlapping generations, and *Chamaecyparis nootkatensis*, especially, benefits from the 'storage effect'. In particular, the persistence of *C. nootkatensis* in the community during the 300 yr duration fluctuations of Fig. 4, when it is excluded in those of Fig. 3, is an example of the 'storage' by long-lived individuals allowing coexistence. It is important to note that both differential longevity and temporal variability are required for this mechanism to operate.

Long-term dynamics of the Cypress Park system: Assessing change in the field

Without estimates of the actual mortality rates at Cypress Park, it is difficult to assess with certainty how close the forest is to equilibrium. If the real mortality rates are similar to those in Differential Mortality 1, then the forest is near its equilibrium composition, and the replacement processes occurring today are more-or-less maintaining the current canopy composition. However, the modest change in species proportions necessary to reach equilibrium under Differential Mortality 2 will take a very long time. As well, the simulations suggest that conditions similar to those present today could result from a sequence of changing climates, during which the forest was never in equilibrium. What can be concluded, is that transition probabilities alone are inadequate to assess the compositional stability of the forest. Even without changing climate, processes affecting canopy tenure at long time scales can interact with patterns of recruitment to create different dynamics than would be inferred from short term transitions alone (see White et al. 1985).

Recognizing the significance of climatic variation increases the problem of inferring long-term trends from short-term data. The patterns of fluctuation in species abundances shown in Fig. 4 are readily explained, given knowledge of the model structure and the simple climatic forcing function. However, if one had only field data similar to Fig. 4, explaining the patterns of change would be enormously more difficult, especially if they were only from an arbitrarily chosen period of 10-20 yr. For instance, we might sample a period when *Tsuga mertensiana* had begun to show a response to a favorable climate, but *C. nootkatensis* had not. Similarly, the longer periods of the other species compared to *A. amabilis* are an obvious consequence of the transition matrices and the pattern of climatic fluctuation. But without much more detailed knowledge of species interactions and the history of climate and vegetation than is usual, would one be likely to tease out the causal pattern from an empirical time series? Realistically complex patterns of climate fluctuations make an affirmative answer to this question even less likely.

Beyond any complexities in the pattern of change, the slow rates of change exhibited in the model output suggest that assessing the stability of forest communities with time series of the lengths usually available may be very difficult. Forest composition may appear constant over the life of a researcher and yet be in a state of substantial, but slow, change.

To summarize the implications of these results for the Cypress Park forest, the numerical dominance of *A. amabilis* among smaller canopy trees, suppressed, saplings, and gap-fillers will not necessarily lead to an equilibrium where that species is more abundant than it is today. Similarly, despite its poor representation among the younger age classes, *C. nootkatensis* will not necessarily decrease in abundance, and cannot be expected to be excluded from the stands. The forest is probably close to the equilibrium species composition for the current empirical transition probabilities, but cannot be assumed to be stable in that composition. Though the stand itself is old enough that species composition might have been able to come to equilibrium, the current species composition could as easily be a transient state that is a consequence of a sequence of climatic fluctuations, rather than the slow approach to equilibrium under constant conditions. Indeed, this latter case seems more likely in the light of actual climate history.

Factors not included in the models

The models presented here are simple, incorporating only the biology implicit in the transition matrices and differential mortality rates among species. In reality, a variety of other biological and physical processes will be important. While differential longevity is represented through species-specific mortality rates, age-structure and as such is absent from the model, as is the time required for filling a gap (which may be substantial; Lertzman & Krebs 1991). Both of these could increase the possibility of lags between tree populations and climate. Though the survival of adult trees is less sensitive to climatic fluctuations than recruitment (Ritchie 1986), at some level of climatic fluctuation, the mortality rates of canopy trees will be affected. This will increase the ability of tree populations to track fluctuations in climate, but will likely act in a highly non-linear way (such as catastrophic mortality after some threshold is reached).

The models presented here apply so long as the disturbance regime is one of small gaps forming in a matrix of largely intact forest. However, fire frequency will also be affected by changing climate (Green 1982; Cwynar 1987; Clark 1988; Johnson & Larsen 1991). Fires can act to overcome the inertia caused by persistent individuals established under past climatic conditions. When adults are removed, the new forest may reflect current climate much more accurately than did the old one (Ritchie 1986; Steijlen & Zackrisson 1987; Kullman 1986, 1987; Payette & Gagnon 1985; Payette et al. 1985).

Other factors than fires will also alter the disturbance regime in ways that will drastically alter the transition probabilities. Periodic insect or pathogen outbreaks could alter competitive asymmetries or the distribution of gap sizes. These models do not account for changes in disturbance regime other than simple fluctuations in climate. They could not, for instance, predict the community response to the removal of a species by pathogens, such as occurred for *Tsuga canadensis* (eastern hemlock) in the mid-Holocene over much of eastern North America (Allison et al. 1986).

Finally, there is no frequency dependence in the transition probabilities in these models (Acevedo 1981). At low densities, populations may not be self-maintaining, and recolonization after local extinctions may be limited by seed sources. If strong frequency dependence had been included in the models, *C. nootkatensis* might not have been able to recover from some of its low periods in the simulations with equal mortality rates and changing climate (Fig. 3). True local extinctions were not possible in these models, as they are in the real world.

Applicability of results to other systems

Differential longevity among competing tree species is an important factor promoting coexistence in a variety of forests (Acevedo 1981; White et al. 1985; Veblen 1986; Aplet et al. 1988). There are, however, some notable differences between the system modeled here and many other forests. Coniferous trees of western North America are longer-lived than most, and those at Cypress Park are among the longer-lived of the species in this region (Fowells 1965; Franklin 1988). Time scales of gap creation and filling are proportionately slower than in many other forests (Lertzman & Krebs 1991; Spies et al. 1990). The overall differences in longevity among species are probably less unusual than the long lifespans themselves: early successional gap colonists in eastern hardwood and tropical forests can be substantially shorter lived than their shade tolerant associates (Fowells 1965; White et al. 1985; Hubbell & Foster 1986; Whitmore 1989). Though the time scales over which the patterns described here are expressed may vary in other systems, the kind of roles played by differential mortality rates and climatic variability should be similar.

Thus many old-growth, gap-regenerating forests are not likely to be in compositional equilibrium, given a realistic assessment of changing climate. Further, these results support the idea that this non-equilibrium status can make a substantial contribution to species coexistence over the long-term. In fact, few old-growth forests have been found to be compositionally stable (Stephens & Waggoner 1980; Harcombe & Marks 1983; Lang & Knight 1983; Whitney 1984; Glitzenstein et al. 1986; Steijlen & Zackrisson 1987; Foster 1988; Franklin & DeBell 1988). It seems likely that detailed reconstructions of stand histories combined with palaeoecological and palaeoclimatic data will be required to arrive at any general conclusions about long term forest dynamics (Davis 1981, 1986; Clark 1986a,b; Delcourt & Delcourt 1987; Bradshaw & Miller 1988; Foster & Zebryk 1993; Payette et al. 1989). Indeed, the differences in the timing and magnitude of the response to changing climate among species at Cypress Park suggest demographic mechanisms for trends in the palaeoecological record such as the highly individualistic pattern of Holocene repopulation of eastern North America (e.g. Davis 1981, 1986). Similarly, the lagged response of *C. nootkatensis* to environmental change here is consistent with its relatively late and prolonged re-establishment through most of its current range following deglaciation (Hebda & Matthewes 1984).

The long time taken by the forest to equilibrate to the 'warm climate' transition matrix from current conditions (500 years to reach within 10 %, summed over the whole community; Fig. 2) has interesting implications for the consequences of current trends in global climate. If current estimates of anthropogenic climate change over the next 100 years are at all accurate, then we can anticipate changes in the climatic variables driving change in stands such as at Cypress Park that are greater than any in their recent history (Houghton et al. 1990). Fig. 2 represents a conservative estimate of the degree and duration of disequilibrium to be expected both because it is likely an underestimate of the magnitude of change which will occur and because it illustrates only the changes following a simple shift to a stable warm climate matrix. If climate states exhibit increasing variability as well as a changing mean, the duration of disequilibrium may increase. We should be more concerned with the transient dynamics that forests will exhibit over the next several hundred years than with any putative equilibrium species distributions that those dynamics might point to in some distant future. If, as is likely, the frequency of larger scale disturbances, such as fires, changes in response to changing climate as well (e.g. Clark 1988; Johnson & Larsen 1991), the mix of vegetation response types and rates distributed over the landscape will be complex indeed.

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