Title

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Journal

Journal of Theoretical Biology, 205

Author

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Publication Date

2000

Peer reviewed

J. theor. Biol. (2000) **205,** 515–526
doi:10.1006/jtbi.2000.2055, available online at http://www.idealibrary.com on IDEAL®

Community Dynamics: What Happens When We Rerun the Tape?

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(*Received on* 7 *September* 1999, *Accepted in revised form on* 22 *March* 2000)

The role of historical events, such as disturbances, in producing alternative developmental outcomes in forest structure has long been debated. Diversity in the assemblages of coexisting species is one measure of alternative outcomes of succession. The intermediate disturbance hypothesis proposes that a moderate disturbance level produces the highest levels of species diversity. Here, we use an agent-based model of forest development under a gradient of lightning strike frequency to analyse long-term dynamics of species coexistence in a multi-species forest. The configurations of species that result from disturbance dynamics reflect the interactions between life-history characteristics of the species and disturbance characteristics. Model results suggest that low levels of disturbance lead to highly ordered landscapes which exclude fire and are captured by late successional species. High levels of disturbance lead to oscillation between domination by early successional species and large disturbances. At intermediate levels of disturbance, the forest displays the broadest array of developmental pathways, highest entropy as measured by Shannon's index of diversity, and critical slowing near steady states. Long transients at intermediate regimes may reflect the working out of closely balanced constraints of competition between species with varying strategic adaptations to disturbance. Intermediate disturbance levels also result in the greatest number of alternative diversity configurations as outcomes of succession, reflecting an unpredictable and nonequilibrium forest dynamic.

Introduction

The study of diversity and community dynamics in natural systems has been hampered in the past by what Ricklefs has called "the eclipse of history" (1987). Can the structure of ecological communities be explained solely by deterministic processes, without reference to historical events, such as disturbances? If the role of autogenic processes such as competitive interactions is stressed in explanations of species coexistence, a unique and equilibrium species assemblage is often the outcome. In classical ecological theory, such interactions were considered the controlling mechanisms in population dynamics, generating predictable successional outcomes, such as Clements' monoclimax forest (Clements, 1916; Hutchinson, 1958).

But if historical events, such as natural disturbances, play a significant role in successional development, then alternative developmental trajectories and multiple successional outcomes are possible, even likely (Sutherland, 1974; May, 1986; Ricklefs, 1987). Several decades of empirical studies in forest ecosystems have documented the near ubiquity of disturbance events in natural

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0022–5193/00/160515 + 12 $35.00/0

ecosystems, and fire, windthrow and climate events are now widely recognized as forces patterning forest structure (White, 1979; Sousa, 1980; Veblen, 1975) and generating species diversity (Connell, 1978; Pickett & White, 1985). Yet, the effect of disturbance regimes on species coexistence in multispecies systems is still poorly understood.

A general model of disturbance and diversity is lacking in part because the temporal scale of forests has frustrated investigation. The long lifespans of forest canopy species has made simulation a compelling tool for the study of forest development (e.g. Botkin *et al*., 1972; Shugart & West, 1977; Pacala & Tilman, 1994; Bolker *et al*., 1995; Moloney & Levin, 1996). Successional dynamics have been explored through assembly of simulated communities from a regional pool of species (e.g. Huston & Smith, 1987; Law & Morton, 1993, 1996). This work suggests that in systems dominated by biotic interactions, different successional outcomes can arise from a similar pool of species by varying the initial species' densities or by varying the order of species introduction (e.g. Post & Pimm, 1983; Robinson & Dickerson, 1987; Drake, 1991).

Such studies, however, do not explicitly consider system dependencies on disturbance regime or spatial structure. Computational experiments which have incorporated the influence of disturbance have stressed the interaction of disturbance and species' life-history traits (Baker *et al*., 1991; Clark, 1991; Moloney *et al*., 1992; Moloney & Levin, 1996; Deutschman *et al*., 1997). A few case studies offer empirical evidence for alternating successional outcomes in forests, whether due to allogenic (Fox, 1977; McCune & Allen, 1985; Halpern, 1989) or autogenic processes (Watt, 1947). The question of whether alternative sets of coexisting species tend to result from successional dynamics of communities under similar disturbance regimes has not been examined.

In this paper, we use a forest model to investigate the structure of successional pathways and the resulting species assembly states to which multispecies systems tend under varying levels of disturbance. We ask how forests, composed of species with diverse successional adaptations to fire, will be assembled across a spectrum of disturbance frequency. We make no assumptions about the stability of the outcome, but prefer to treat such alternative configurations, as Holling (1973) does, as attractors. We use Sutherland's (1974) more narrow definition of "steady state", as the persistence of a set of coexisting species with relatively similar abundances for some period of time.

We inspect model behavior for variance in diversity structure, compositional states, and multiple pathways of development. We characterize the richness and entropy of these successional outcomes, viewed as the diversity of configurations, or diversity architectures. Do forests initialized with similar species parameters develop toward predictable architectures under the same disturbance regime, or will multiple developmental pathways or multiple compositional structures result?

We are specifically interested in characterizing the successional outcomes in the context of the intermediate disturbance hypothesis, which proposes that moderate disturbance levels produce the highest species diversity (Loucks, 1970; Connell, 1978; Petraitis *et al*., 1989). Disturbances, mediated through species-specific competitive strategies, allow the coexistence of the most species at global, or landscape, scales. Maximum structure and diversity of behaviors are traits also displayed by some adaptive systems at intermediate regimes (Nicolis & Prigogine, 1989; Crutchfield & Young, 1990; Langton, 1990). Complexity studies suggest that certain aspects of biological systems tend to be poised at the transition between highly ordered and disordered states. There, the balance of regularity and randomness introduces variation while retaining memory, and structure is at a maximum (Kauffman, 1993; Solé & Manrubia, 1995). We ask, do intermediate levels of disturbance generate maximum diversity?

To identify the range of successional responses to varied disturbance frequency regimes, we tracked individual successional pathways. As Gould (1989) suggested, we "ran the tape" of community development many times in order to observe the distribution of successional trajectories under each disturbance regime. Iterative studies of this kind are possible in the natural world in "fast" communities such as intertidal systems (e.g. Paine & Levin, 1981) but not those

in which the mean lifespan of individuals is of the order of centuries. The modelling goal was to find the 'texture' of system dynamics (Judson, 1994), and to explain long-term compositional structure.

The model we employ, Arborscapes, like many forest models, is based on the mechanism of species' life-history traits interacting with disturbance events (e.g. Acevedo *et al*., 1996; Tanner *et al*., 1996; Deutschman *et al*., 1997). Life-history traits reflect adaptations to environmental constraints, with a tradeoff between maximal competitive ability and adaptation to disturbance stresses (Petraitis *et al*., 1989). The model also shares with individual-based models the attributes that each tree is tracked individually, and that agent interactions with neighbors are crucial to landscape dynamics (Huston *et al*., 1988). Unlike mean-field modelling approaches, individual-based models do not mask diversity structures arising from local behaviors (Huston *et al*., 1988). The object-oriented structure of the model is decentralized, with global, or emergent, behaviors resulting from local interaction rather than general mechanisms that impose system-wide constraints (Bascompte & Solé, 1995; Turner & O'Neill, 1995). Such models are apt vehicles for exploring ecological systems, since organisms themselves possess the properties that govern interactions (Judson, 1994).

Methods

MODEL DESCRIPTION

Arborscapes was developed to explore the role of disturbance in generating community structure and species diversity in multi-species forests (Savage & Askenazi, 1998). Individual trees interact through regenerational response to competition for light, but the success of a species in the landscape is mediated by strategic adaptations to prevailing conditions of disturbance. Species success is measured by the capture of the landscape cells. The community of species in Arborscapes was suggested by the fire-adapted, mixed-conifer montane forests of California (Savage, 1997). While the model can be parameterized with the traits of actual species to predict real system outcomes, that was not the intent here. Maynard Smith (1974) suggests that ecological systems can be approached either by a detailed mathematical description of specific systems, or by a general and abstract description that aims to capture the essential properties of the system. The goal here was the analysis of a hypothetical community in order to explore the ranges of, and constraints on, successional behaviors of forest systems. A more complete model description is provided in Savage & Askenazi (1998).

GENERAL MODEL STRUCTURE

Landscape dynamics in the Arborscapes model depend on competitive interactions of individual trees for light coupled with regenerational response to an exogenous disturbance. The simulated landscape is a mosaic of continually shifting patches of regenerating trees following in the wake of disturbance. Seeds are dispersed onto the forest floor and germinate, and trees grow, reproduce and die from old age or fire mortality. The landscape is a two-dimensional cell grid (100×100 cells or 10 000 cells), in which each cell may be simultaneously occupied by an adult tree and an understory successor seedling or sapling.

Species possess suites of traits from early to late successional adaptations, including (1) longevity, including varying age at reproductive maturity, (2) seeding periodicity, (3) fecundity, (4) seed dispersal abilities, (5) rate of seed mortality in the soil, (6) canopy density, and (7) shade tolerance. In addition, trees have age-dependent thresholds for mortality from fire and age-dependent fuel loads, both species-specific traits. Disturbance propagates according to rules governing species response to disturbance, and landscape patterns depend on the interaction of disturbance with local forest structure and recovery of populations.

Connections across the landscape occur through (1) dispersal of seeds and (2) adaptations to fire. Reproductively mature trees cast seeds into neighboring cells. Fires burn from cell to cell, within the constraints of the rules of contagion, propagating disturbance. The boundaries of the landscape do not form a torus. If boundaries were contiguous, every fire that touched a boundary would then become a new fire in the landscape, artificially increasing the number of disturbances. The model schedule proceeds on an

annual step basis, and the background environment is homogenous. Species-specific traits are deterministic, but the model includes three sources of randomness: (1) demographic initialization, (2) germination lottery, and (3) lightning strike frequency. Asynchronous updating of the state of each cell is employed to avoid conflicts in the model dynamics.

DEMOGRAPHIC SUBMODEL

The life-history attributes (sensu Noble & Slatyer, 1980) used to parameterize species in Arborscapes reflect the grammar of many forest models where light is assumed to be the principal mechanism controlling regenerational success (e.g. Botkin *et al*., 1972; Pacala *et al*., 1993; Moloney & Levin, 1996). Tree species have often been categorized, both empirically (e.g., Whitmore, 1989) and for modeling purposes (e.g. Shugart, 1984; Shugart & Urban, 1989; Acevedo *et al*., 1996) based on regeneration success relative to light availability. Bolker *et al*. (1995) present data that suggest that the role of other factors, such as nutrient availability, are overwhelmed by that of light, and Huston & Smith (1987) have shown that modeled competitive interactions based on life-history traits related to light produce realistic outcomes.

Tree species possess suites of traits spanning a spectrum from early to late successional adaptations to light. Species are named 1–8, where species 1 displays the most late seral adaptations and species 8, the most early seral adaptations. Whereas growth rates are commonly modelled by differential equations (e.g. Coffin & Urban, 1993; Moloney & Levin, 1996), in Arborscapes growth is modeled by the assignment of discrete life stages (seedling, sapling, young adult, mature adult, and senescent), and within each stage attributes are constant.

Germination is governed by rules that depend on species adaptations to disturbance and the light environment and probabilistic events, such as timing and location of fires and germination success. Each cell accumulates dispersed seeds from nearby adult trees. Germination occurs by weighted lottery relative to the number of seeds of each species in the cell. Remaining seeds are susceptible to mortality each year at a species-specific rate. A seed can germinate in a vacant cell or under an adult tree, but saplings become adults on sites occupied by overstory trees only if their species-specific shade tolerance permits. Having captured a site, a young tree will succeed to later life stages until it dies of old age or is burned. Burned sites are recolonized, but preferentially by seeds of early successional species, which mature more rapidly, are more fecund, and have seeds that disperse farther.

Life history attributes are:

(1) *Longevity*. Each individual spends a species-specified time span in its life stages. (Life-history values are available in the source code at the web address below.) Growth is achieved by graduation from each of five life stages: seedling, sapling, young adult, mature adult, and senescent adult, with the length of each stage varying by species longevity. Trees reach reproductive maturity and produce seeds at the mature adult stage, and die at the end of the senescent stage.

(2) *Seeding periodicity*. Trees often do not seed prolifically in every year, but with species-specific periodicity. Seeding periodicity is expressed as an integer that describes the interval of years between seed production events.

(3) *Fecundity*. Species vary by the abundance of seeds produced, and is expressed as an integer that describes the number of seeds that fall into each cell to which seeds can disperse.

(4) *Seed dispersal ability*. Seeds are dispersed on the ground near the parent depending on species dispersal capacity, expressed as a seeding radius of number of cells distant from the tree. Each cell in the seeding radius receives the same number of seeds.

(5) *Rate of seed mortality*. Seeds in the soil bank suffer mortality as a species-specific proportion of seeds within a cell that die during each time step.

(6) *Canopy density*. Canopy density describes light penetration through a tree's canopy into the understory and governs overstory capture. It is designated by an integer representing sparse, intermediate, or dense cover.

(7) *Shade tolerance*. Shade tolerance determines a species' potential to achieve the overstory, and is designated by an integer reflecting

categorization as tolerant, intermediate, or intolerant.

(8) *Heat given off by burning trees.* Heat radiated by a burning tree varies by values specific to its age and specific to its species. Heat output depends on the amount of fuel provided by various life stages of a tree and can be sensed by eight neighbors.

(9) *Heat required to ignite.* Fire spreads only when heat is propagated from tree to tree. A tree burns if the sum of total heat of burning neighbors exceeds its designated ignition threshold, which depends on values specific to its life stage, and specific to its species.

DISTURBANCE SUBMODEL

Simulated fires in Arborscapes vary in frequency and in intensity. Disturbance frequencies are expressed by the number of lightning strikes occurring in the landscape per year, and can be set for a complete run, or varied during a run. In any year, actual lightning strike frequency (LSF*i*) is a uniformly distributed random number between 0 and *i*. Lightning strike frequency at LSF4, for example, is a randomly chosen number between 0 and 4 in each year. Fire intensity is produced by the sum of heat values from burning neighboring trees. Each burning tree emits a designated heat value specific to its species and life stage.

Disturbance results from a combination of exogenous and endogenous features. Lightning strikes in the landscape are exogenous, but fires result from the interplay of species age structure and neighborhood patch structure. Mortality from fire is dependent on the susceptibility of a tree due to its assigned species susceptibility and life stage, and also on heat intensity generated by burning neighboring trees. Fire is contagious when the heat level radiated by a lightning-ignited tree exceeds the burn threshold of neighboring trees.

Mortality from fire depends in part on the landscape structure created by past fires and is thus not a fixed probability. If, by chance, time passes with no lightning strikes in a neighborhood, shade tolerance species tend to dominate, and fires will become less contagious. On the other hand, if lightning strikes repeated in a locality, the site tends to be dominated by early successional species, which burn hotter and recover more quickly after fire. Stochastic patterns of disturbance in time and space, then, instantiate patchy patterns of susceptibility to disturbance in the landscape. Disturbance is thus recursive, that is, dependent on landscape structure, which is in turn dependent on prior disturbance history. In this, Arborscapes differs from models where location, size, and frequency of disturbance events are random (e.g. Moloney *et al*., 1992). Some recent gap models have also adopted recursive disturbance architectures (e.g. Mladenoff *et al*., 1996).

SWARM PLATFORM

Arborscapes was implemented on Swarm, a publicly available software platform with standardized libraries of objects and schedules, and architectural features such as inheritance, message passing, encapsulation, and hierarchical structure (Minar *et al*., 1996). Swarm employs an object-oriented language which provides objects which contain attributes and communicate by message passing. In inheritance, object subclasses are defined which "inherit" attributes and methods of the original class by augmentation to specialize them. Swarm also provides (1) probes for the inspection of values stored in attributes of objects, (2) measurement tools that collect statistical data on runs, (3) event scheduling that minimizes system-specific dependencies, and (4) nested hierarchies, which cluster objects and activities that mimic the hierarchical scales of ecological systems. These features reduce system-specific idiosyncrasies of ecological models developed from scratch and strengthens the potential for collaboration on computational experiments.

SIMULATION EXPERIMENTS

We simulated the dynamics of a multi-species forest through time at six levels of disturbance, from LSF2 to LSF7. At each disturbance level, 100 simulation experiments were conducted. Disturbance frequency varied across disturbance levels, but was held constant during all runs at a given disturbance level. Ignition of fires from lightning strikes, as well as size and shape of fires, depended on neighborhood age and species structure.

Forest development at each disturbance level was iterated for 50 000 steps, or years, an ecologically unrealistic period, but one which allowed the inspection of asymptotic behavior. In the simulation experiments, transient behavior lasted of the order of 1000–1500 time steps before settling down to long-term behavior, a ecologically reasonable span of time for succession of long-lived tree species. We were specifically interested in the timing and shape of transient behavior early in forest development.

Each model run was begun from similar initial conditions: 1250 individuals of each of eight species (one-eighth of 10 000 cells) were randomly distributed in the (100×100)-cell homogenous landscape. If we assume that each tree occupies a 10×10 m cell, landscape size may be estimated at 100 ha. Eight component species represent a spectrum of strategies from early to late successional adaptations to light resource and fire disturbance.

We calculated two values for each of 100 runs at each of six disturbance levels: species abundances, and Shannon's index of diversity, or entropy. The analysis of species performance, measured by abundance, was based on data points taken at 100 step intervals over each 50 000 step run. Abundances of each species in the landscape were plotted separately for every run and displayed together on a single graph for each disturbance level, giving one graph with 100 trajectories of species abundance over time for each species at each disturbance level. By running the model 100 times at each LSF parameter, we constructed an "ensemble" of forest instantiations. For species abundance, we recorded the trajectory of each instantiation of forest development rather than the "average" behavior. Shannon's index of diversity and richness were averaged over all 100 runs for each disturbance level, in order to produce a diversity value at each disturbance level for purposes of comparison. Diversity across instantiations cannot be averaged.

We also tracked fire frequency and fire size (f), that is, the number of cells the fire burned. We concatenated all the fire data for each fire parameter and binned the data for fire size $f < 500$, $500 < f < 1000$ cells, etc. Fires of only one or two cell size were excluded from the analysis.

We define the trajectory of a run as the trajectory of species abundances in the landscape through time. The full trajectory is a curve in the eight-dimensional space of species abundances. A trajectory consists of a transient leading to limiting behaviors, and we define these limiting behaviors as attractors. If species abundances stabilize, we define the attractor as a fixed point. If the attractor is a repetitive pattern, we term this a limit cycle. The ensemble of trajectories constructs an attractor basin portrait of the dynamical system. We do not define the set of behaviors of the system *a priori*, but use emergent dynamics of the simulation to classify dynamical regimes.

We observed statistical regularities in species abundances across ensembles of runs, but did not average run behaviors in order to detect variance in run trajectories. As a result, the model gives a narrative history appropriate to history-dependent systems. We used bulk metrics of species abundance, fire frequency, and fire size distribution to classify different dynamical behaviors, based on correlations between measures of entropy and disturbance frequency. As landscapes developed through time, species abundances displayed adaptive configurations with respect to disturbance parameter gradient. Characteristic species abundance trajectories occurred at each disturbance level and clustered in differentiated patterns. Sources of variation in the direction of trajectories come from randomness in lightning strikes and randomness in demographic structure.

Although the analysis of spatial pattern will undoubtedly yield insights into system function, there was no specific tracking of the location of the disturbance or species patch mosaic. Fire size parameters, on the other hand, clearly reflect colonization patterns, with early successional species colonizing large patches and late successional species adapted to regeneration in small gaps.

Results

Species abundance trajectories at all levels of disturbance were uniformly characterized by uniformly timed transients which led to a variety of long-term behaviors. Following the approach of Law and Morton (1993), we qualitatively

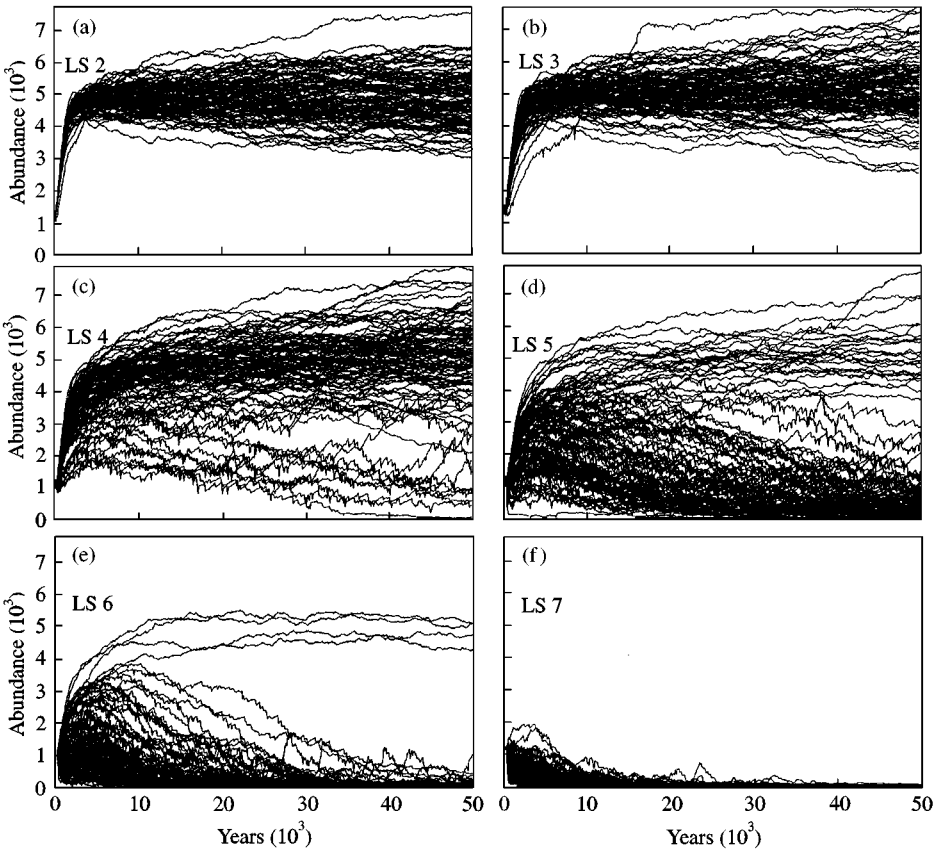

FIG. 1. Simulation outcomes for 100 runs of species 1 abundances at six levels of lightning strike frequency. LSF_ is the number of lightning strikes/year chosen randomly and uniformly from [0 <_]. As a late successional species, species 1 tends to capture the landscape at low disturbance levels (a,b), but rapidly dies out at high disturbance levels (f). Variance is highest at intermediate levels of disturbance (c–e), where run histories display a fuzzy bifurcation.

recognize three classes of long-term behavior, convergence onto a fixed point, stochastic oscillation, and "fuzzy bifurcation".

At low fire frequency (LSF 2,3), late succession species quickly capture the landscape and exclude disturbance, tending toward a fixed-point attractor. Variance in trajectory shape across the 100 runs is low for late successional species, species 1 for example [Fig. 1(a) and (b)]. (Curve wiggle is produced by population depressions due to periodic fires.) Either species 1 or 2 succeed in dominating the landscape, or more rarely, share dominance in large patches. In virtually all runs, the remaining six species become extinct at the transient at low fire frequency.

Parametric plots of abundances of species 1 and 2, across the disturbance gradient, illustrate attractor basin structure of the model (Fig. 2). Different proportions of the two species are assembled, that is, a wider diversity of histories is seen as disturbance increases to an intermediate level. At low lightning strike frequency, we see coherent trajectories leading to a well-defined attractor [Fig. 2(a) and (b)]. As lightning strike frequency is turned up, fewer trajectories end up on the original attractor [Fig. 2(c)–(e)], until at the highest level, all trajectories end up at extinction [Fig. 2(f)]. At the intermediate regime, many trajectories follow long unique transients without arriving at either attractor, and the number of pathways is at a maximum [Fig. 2(c) and (d)].

At high fire frequency (LSF6,7), variance in trajectory form is high. The steady state of the system is an oscillation between an entirely burned landscape and co-domination by either one or both of the two most early successional species (Fig. 3), an oscillation resembling a limit-cycle attractor. Both low and high disturbance

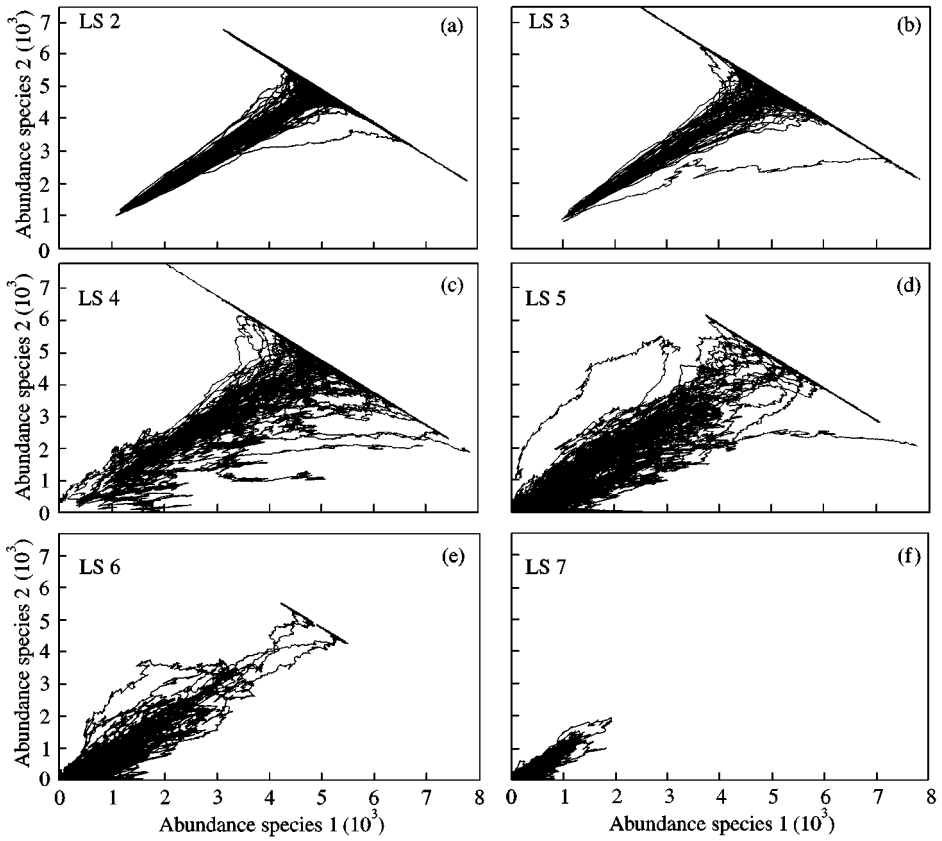

FIG. 2. Simulation outcomes of 100 runs plotted parametrically for species 1 and 2 at six levels of lightning strike frequency (LSF2-7). Initial abundances are (1250, 1250). The diagonal line in the upper right of LSF2-6 depicts an attractor of the dynamics, in which the two species codominate, excluding all other species. As LSF increases, trajectory variance initially rises, and by LSF4 (c), not all trajectories impinge on the attractor. At intermediate disturbance levels (c–e), multiple trajectories shapes and endpoints are seen. At LSF7 (f), species 1 and 2 are excluded by fire-adapted species, and all trajectories converge on an extinction attractor.

level behaviors, then, clearly display limiting behavior.

Intermediate disturbance frequency regimes (LSF 4,5) display more complex behavior, that is, more structural possibilities, than low and high disturbance levels. In many runs, instead of one or two species dominating the landscape, more species coexist for longer, and in some instances also participate in the end-of-run composition. Even in runs where only two species co-dominate, a variety of species pairs occur. In no runs where three or more species coexist is a state reached where species abundances remain stable over time. As fire frequency increases, trajectory variance increases, resulting in a "fuzzy" bifurcation of the ensemble of trajectories [Fig. 1(c)–(e)]. At the end of 50 000 steps in the intermediate range of disturbance levels, some runs had reached attractors similar to those co-dominated by two species, but other runs were characterized by very long transients and the continued participation of three or more species.

Some successional pathways do not impinge on any identifiable attractor within the simulation time. There may be additional attractors, but the convergence is so slow that they are not observed at long-time-scales. These sets of species do not display permanence, in the sense that not all final compositional architectures include all species initially present in the species pool (Law & Morton, 1993).

A transient characteristic of all species trajectories and all disturbance levels occurred at around 1000–1500 years. Transients to limiting behavior were fastest at the extremes of the disturbance gradient, while at the intermediate

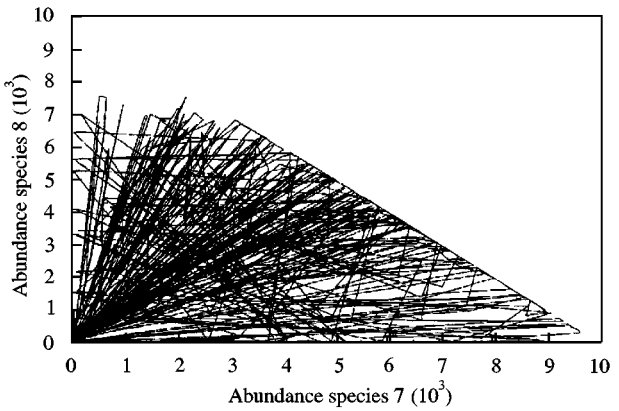

FIG. 3. Simulation outcome of one run plotted parametrically for species 7 and 8 at LSF7. Asymptotic temporal behavior is codominated by the two early successional species most adapted to high disturbance levels. The system develops alternating dynamical behavior, oscillating in radial trajectories between fully populated and burned landscapes.

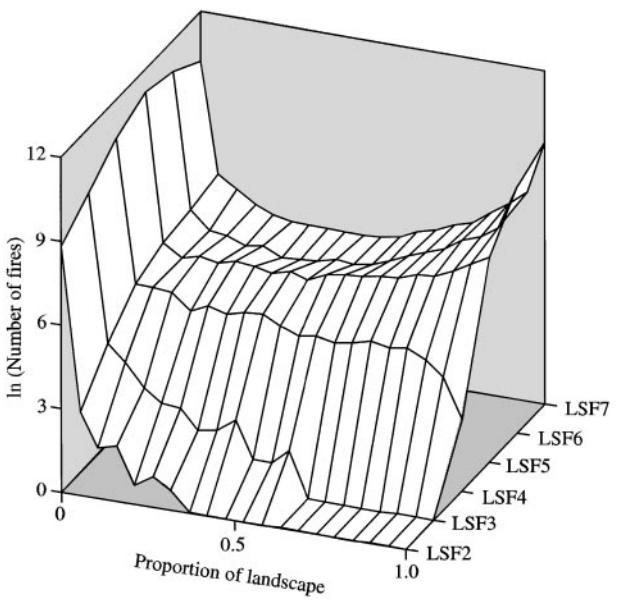

FIG. 4. Area burned at each of six levels of disturbance, expressed as a proportion of the total landscape. Vertical axis is the natural log of the total number of fires in all runs at a disturbance level. As LSF increases, fires become more abundant and their characteristic size increases, until at the highest disturbance level landscape-scale fires dominate.

range, species abundance shift more slowly. At low and high levels of disturbance, species abundances continue the trend set early on. At the intermediate range, transient behavior persists longer, and in some cases continued to the end of the run [Fig. 1(b)–(d)]. Long transients at intermediate regimes reflect the working out of closely balanced constraints of competition between species with varying strategic adaptations to disturbance. In no instance did we observe a system travel through one attractor to another.

Despite the relatively smooth gradient of species traits, there is a surprising discontinuity in species performance as the disturbance parameter is turned up. Species 2, a late successional species, dominates many low-level disturbance landscapes but also occasionally performs well at intermediate levels of disturbance. Species 4 also does well in some intermediate disturbance level runs, occasionally persisting in the final assembly of some runs. Adjacent to both these species in adaptive traits, species 3 becomes quickly extinct at all disturbance levels.

Disturbance characteristics also vary with frequency, and fire size distributions are not stationary over time (Fig. 4). At low frequency, fires are initially numerous and small, and soon excluded by fire-resistant species, leaving a frozen, unchanging landscape. At high frequency, fires become larger over time until the system is dominated by landscape-scale fires in all runs. At intermediate frequency, fires of all sizes occur throughout the runs, giving the greatest variance of fire size. These patterns of fire size and abundance are created by differential species colonization.

Both entropy (Fig. 5) and species richness were maximal at intermediate disturbance levels, though not for the full length of the runs. For low levels of disturbance (LSF2–4), both entropy and richness asymptote to a constant value. Above LSF4, no constant value is reached, but rather the population is characterized by a slow decrease in entropy, with the slowest rate for LSF5, and LSF6 and LSF7 decaying faster. The results thus support the intermediate disturbance hypothesis, but with caveats. For the period after the initial fluctuations die out, intermediately disturbed systems have the highest diversity. If the runs are extended for enormous amounts of time, diversity drops very gradually until it is very close to the diversity of low disturbance ecosystems. It is unlikely that external conditions would remain stable for times of this magnitude.

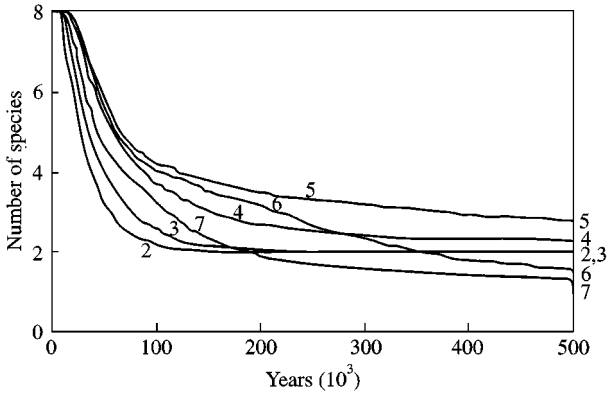

FIG. 5. Mean species diversity of the forest for each LSF level as a function of time, calculated by $H' = -\Sigma p_i \ln p_i$ (equivalent to Shannon's index of diversity). Intermediate LSF values give highest diversity. Low values reach a constant value quickly. High values consistently trend lower, and together with intermediate values are characterized by long transients.

Discussion

History is clearly important in modelled forest development. If we replay the tape of forest development many times, in certain regimes we observe diverging outcomes resulting in multiple architectures of species diversity. Multiple architectures of diversity reflect different species composition and abundances across instantiations. At low levels of disturbance, the simulated forest resembles a deterministic Clementsian climax forest. At high levels of disturbance, the fluctuating assemblage of early successional species resembles a forest that regularly experiences high levels of disturbance, for example, from hurricane damage or fires (e.g. Whitmore, 1989). At low and high levels of disturbance, forest instantiations are not sensitive to probabilistic events, and bifurcations are not seen. Between the extremes of disturbance, we see the interplay of probability and determinism. Here, forest instantiations are highly sensitive to probabilistic events and diverse trajectories occur. At intermediate disturbance levels, the dependence of trajectories on early interactions is reminiscent of Gleason's (1926) emphasis on the role of chance in species assembly.

Here, we extend the notion of diversity to include ensemble diversity, meaning that an ensemble of forest ecosystems at the same level of disturbance will display diversity across instantiations. Two forms of diversity are maximized at the intermediate distance level: run diversity, with varying numbers of participating species, and ensemble diversity, with similar numbers of species, but varying component species.

Chance and necessity, or stochastic and deterministic behavior, are very closely balanced at the intermediate regime. Because of this balance, the dynamical pressure pushing the system towards either a chaotic or stable state is small, and the arrival at a "steady state" is so delayed that it may never happen at all. Over such long timescales, changes in parameters such as climate and geology are likely to redefine the system. This model suggests that at any time-scale there is little use for the notion of equilibrium.

Do species composition attractors characterize the dynamics of this model? In the low and high extremes of fire disturbance, clearly yes. In the intermediate regime, there are at least two attractors and the time to arrival onto these is longer. Still, at all levels of disturbance, the species assembly is only roughly predictable, since the attractors are sets of abundances. Fuzzy bifurcation reflects the potential for alternative stable states under the influence of small random events, both spatial and temporal, that occur early on. Since the definition of attractor excludes the possibility of passing through one attractor to another, this means that once captured by an attractor, the assembly cannot go backward.

The development of ecological systems can be illuminated by analogy to thermodynamic systems (Morowitz, 1968; Nicolis & Prigogine, 1989). This forest model displays strong similarities to phase transition phenomena observed in such systems. For example, we can consider lightning strike frequency to be analogous to temperature. At very low temperatures, the system is robust against perturbations and has a unvarying ground state. Every instantiation rapidly converges to this ground state and development patterns are simple and deterministic. At very high temperatures, behavior is reminiscent of a gaseous phase in which randomness dominates the dynamics and structural memory does not exist. In a sense the two extremes of disturbance are both static, but in different ways, deterministically at low levels and statistically at high levels of disturbance.

The intermediate regime is most complex in thermodynamic systems as well. The lengthening of transient times as characterized by the slow decay of entropy for LSF4 and LSF5 is reminiscent of phase transition behavior, namely the phenomena of critical slowing (Jones & March, 1973). Near a phase transition transient times become elongated, possible outcomes are no longer unique, and sensitivity to initial conditions becomes important. In addition, the spectrum of fire sizes obeys a power law at intermediate fire disturbance regimes, another signature of phase transition like behavior. This suggests that there may be a threshold phenomenon in forest successional development.

The structure of a modeled forest ecosystem has been shown to be very closely coupled to the level of fire disturbance. If this disturbance level is changed, either naturally or anthropogenically, the impacts may be far-reaching. Merely restoring the original level of disturbance will not necessarily result in the restoration of the concomitant forest structure. As Knowlton (1992) suggests, once the straw has broken the camel's back, merely taking the straw off will not allow the camel to get up. Relatively small perturbations may result in large differences in trajectory, particularly at intermediate disturbance regimes. In theory this aspect of sensitivity to initial conditions might be exploited by human intervention, but in practice, it may be impossible to track the state of the system sufficiently. We may find ourselves managing for surprise, when natural, and especially anthropogenic events, lead to unexpected or even novel forest states.

Code: The full, free source code of Arborscapes 1.0 is available at: ftp://ftp.swarm.org/pub/swarm/src/users-contrib/anarchy/arborgames-2.1.tar.g2

This work was supported in part by funding from a National Science Foundation Career Advancement Award Grant No. 9510318 to the first author, and by the Santa Fe Institute. We thank Robert Bell, Keith Hadley, Chris Langton, and Glen Ropella for advice and assistance.

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